

1 **Title**

2 Microclimate shapes intraspecific trait patterns in sub-Arctic plants

3

4 **Abstract**

5 1. Within-species trait variation is a substantial part of plant functional diversity. However,
6 this intraspecific trait variation (ITV) is rarely investigated in relation to the key characteristic
7 of the Arctic and alpine ecosystems: fine-scale microclimatic heterogeneity. Here, we
8 quantified the influence of microclimate (namely, soil moisture, snow, and local
9 temperatures) on plant functional traits, specifically on intraspecific trait variation.

10

11 2. We focused on six wide-spread northern vascular plant species, and measured four traits,
12 namely plant height, leaf area, leaf dry matter content (LDMC), and specific leaf area (SLA).
13 We related intraspecific trait variation with field and remotely sensed microclimate data
14 collected for 150 study plots within six distinct study grids. The grids were located within a
15 76-metre altitudinal belt in three contrasting environments: the tundra, tundra-forest ecotone,
16 and mountain birch forest in Kilpisjärvi, northwestern Finland.

17

18 3. We compared the range of the observations in this local trait dataset (n = 5493) to
19 observations in global trait databases (n = 10383). We found that the information in the local
20 dataset covers a relatively large portion of the global databases. The proportion varied from
21 trait and species to another, and the largest portion was 74% for variation in leaf area of
22 *Vaccinium uliginosum*, and the lowest 19% for LDMC of *Betula nana*.

23

24 4. We found that intraspecific variation in height was mostly related to local temperatures,
25 and leaf area showed less clear patterns along any of the microclimatic gradients. Whereas,
26 SLA and LDMC were more related to soil moisture and snow conditions. However, species
27 also showed contrasting relationships with the microclimate drivers.

28

29 5. We conclude that microclimate profoundly shapes the within-species variation in northern
30 plants and that even a very compact geographic area can contain a large amount of ITV. The
31 influence of the microclimatic conditions varies from functional trait and species to another,
32 which highlights the adaptive but complex capability of tundra plants to cope with the mosaic
33 of microclimatic conditions.

34

35 **Abstract in Finnish**

36 1. Lajin sisäinen vaihtelu kattaa huomattavan osa kasvillisuuden toiminnallisesta
37 monimuotoisuudesta. Tästä huolimatta lajin sisäistä vaihtelua tutkitaan harvoin suhteessa
38 arktisten ja alpiinisten ekosysteemien keskeiseen piirteeseen eli paikallisilmastoon. Tässä
39 tutkimuksessa selvitimme mikä on paikallisilmaston (maaperän kosteus-, lumi- ja lämpöolot)
40 vaikutus kasvien toiminnallisiin ominaisuuksiin, etenkin lajin sisäiseen vaihteluun.

41

42 2. Tutkimuskohteenamme olivat kuusi yleistä pohjoisten ekosysteemien putkilokasvia, joista
43 mittasimme neljä toiminnallista ominaisuutta: kasvin korkeus, lehtipinta-ala, lehden kuiva-
44 ainepitoisuus ja massakohtainen lehtipinta-ala. Tutkimme lajin sisäistä vaihtelua suhteessa
45 pienilmastoon, jota mittasimme maastossa ja kaukokartoittamalla 150 tutkimusruutua
46 kuudessa tutkimusruudukossa. Ruudukoiden välillä oli 76 metrin korkeusero ja ne sijaitsivat
47 kolmessa erilaisessa ympäristössä: paljakalla, metsänrajalla ja tunturikoivikossa
48 Kilpisjärvellä, luoteis-Suomessa.

49

50 3. Vertasimme paikallisen kasviaineistomme (n = 5493) vaihteluväliä maailmanlaajuisen
51 tietokannan (n = 10383) vaihteluväliin. Havaitimme, että aineistomme pitää sisällään
52 huomattavan osan siitä vaihtelusta, jonka maailmanlaajuiset tietokannat kattavat. Aineistojen
53 päällekkäisyys vaihteli toiminnallisesta ominaisuudesta ja lajista toiseen, ja suurin
54 päällekkäinen osuus koski juolukan lehtipinta-alaa (74 %) ja matalin osuus puolestaan
55 vaivaiskoivun lehden kuiva-ainepitoisuutta (19 %).

56

57 4. Havaitimme, että kasvin korkeuden lajin sisäisellä vaihtelulla oli ennen kaikkea yhteys
58 paikallisiin lämpöoloihin ja lehtipinta-alalla ei ollut selvää yhteyttä yhteenkään
59 pienilmastomuuttajaan. Kun taas lehden kuiva-ainepitoisuudella ja massakohtaisella
60 lehtipinta-alalla oli yhteys maaperän kosteuteen ja lumioloihin. Havaitimme, että lajeilla
61 saattoi usein olla päinvastaisia yhteyksiä eri pienilmastomuuttajiin.

62

63 5. Päättelimme, että maaperän kosteus, lumi ja paikalliset lämpötilat muokkaavat suuresti
64 lajin sisäistä vaihtelua pohjoisilla kasveilla. Pienilmaston vaikutus vaihtelee toiminnallisesta
65 ominaisuudesta ja lajista toiseen, mikä korostaa näiden lajien kykyä mukautua vallitseviin
66 ympäristöoloihin. Paljakalla ja tunturikoivikossa kasvien saatavilla oleva vesi,
67 talvehtimisolosuhteet, kasvukauden pituus ja lämpöolot maan alla ja päällä vaihtelevat hyvinkin
68 paikallisesti, ja lajit ovat sopeutuneet tähän paikallisilmastojen tilkkutäkkiin.

69

70 **Key words**

71 Leaf area, leaf dry matter content, plant functional trait, plant height, soil moisture, snow,
72 specific leaf area, temperature

73

74 **Introduction**

75 In the high-latitude ecosystems, a mosaic of contrasting habitats is created by soil moisture,
76 snow, and temperature conditions that often vary greatly over short spatial distances (Dobbert
77 et al., 2021; le Roux et al., 2013; Litaor et al., 2008; Stewart et al., 2018). This environmental
78 heterogeneity is translated into fine-scale variation in functional community composition
79 (Carlson et al., 2015; Kemppinen et al., 2021a; Thomson et al., 2021). This may also be
80 reflected on how individual species cope with local conditions, and thus, it can be observed in
81 functional traits of plant individuals (Andrew et al., 2022; Henn et al., 2018). Functional traits
82 are chiefly related to size and resource acquisitiveness, and they inform about the abilities of
83 a plant to survive, grow, and reproduce in a given environment (Díaz et al., 2016; Funk et al.,
84 2017). Broad-scale investigations show that plant functional traits show consistent trends
85 along climate gradients (Bjorkman et al., 2018a; Bruelheide et al., 2018) but little is known
86 about the very local within-species variation, its magnitude and drivers (Weemstra et al.,
87 2021).

88

89 In the northern ecosystems, the focus on plant functional trait variation is often at the
90 community level (Choler, 2005; Kemppinen et al., 2021a; Niittynen et al., 2020). However,
91 trait variation within-species (intraspecific trait variation, hereafter, ITV) calls for more
92 investigation as it forms a large portion of the overall plant functional trait variation, and is
93 particularly relevant in local-scale studies (Siefert et al., 2015; Thomas et al., 2020). ITV is
94 an important component of functional diversity especially in harsh environments, such as the
95 tundra (Niu et al., 2020), as ITV is an essential form of adaptation for responding to changing
96 environmental conditions (Norberg et al., 2001). The relative importance of ITV is also
97 higher in ecosystems with low species richness (Siefert et al., 2015; Thomas et al., 2020). In
98 the tundra, ITV has been investigated in relation to increasing warming (Baruah et al., 2017;
99 Bjorkman et al., 2018a) and along elevational and snow melt gradients (Cruz-Maldonado et
100 al., 2021; Henn et al., 2018; Kudo, 1996; Kudo et al., 1999; Rixen et al., 2022; Weemstra et
101 al., 2021). However, from a tundra plant's perspective, especially soil moisture and snow are

102 highly relevant microclimatic factors to consider when investigating plant trait variation
103 (Dobbert et al., 2021; Happonen et al., 2019; Taseski et al., 2021).

104

105 Microclimate refers to the local manifestation of atmospheric conditions, which are regulated
106 for instance, by the accumulation of water and snow, the local input of solar radiation, and air
107 flow (De Frenne et al., 2021). Community-level functional traits are strongly related to fine-
108 scale soil moisture patterns in the tundra (Kemppinen et al., 2021a). Snowpack controls the
109 survival of plants for most of the year by regulating conditions at the soil surface, and thus,
110 snow depth can also be one the most influential factors for functional composition (Happonen
111 et al., 2019). The temperatures are rapidly rising in the Arctic (Post et al., 2019), which has
112 profound consequences on plant functional traits (Bjorkman et al., 2018a). In general, tundra
113 plants grow taller in warmer conditions (Hudson et al., 2011; Moles et al., 2009), however,
114 changes in their resource acquisitiveness depends also on available water resources
115 (Bjorkman et al., 2018a). To fully understand the effects of climate change on cold climate
116 ecosystems, it is important to quantify also the local variability and plasticity of plant
117 functional traits to account for the potential for individual and population level adaptations
118 (Andrew et al., 2022; Dudley et al., 2019).

119

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

128

129 **Materials and methods**

130 *Study area*

131 The study area was located in Kilpisjärvi, Finland (N69.06, E20.81, 521-597 m above sea
132 level). The mean annual air temperature is -1.9°C and annual precipitation sum is 487 mm as
133 measured by the nearby meteorological station of Enontekiö Kilpisjärvi kyläkeskus (Pirinen
134 et al. 2012). The topography is relatively heterogeneous across the area. The soils are a
135 mixture of organic and mineral soils. The main vegetation type is dwarf shrub heat dominated

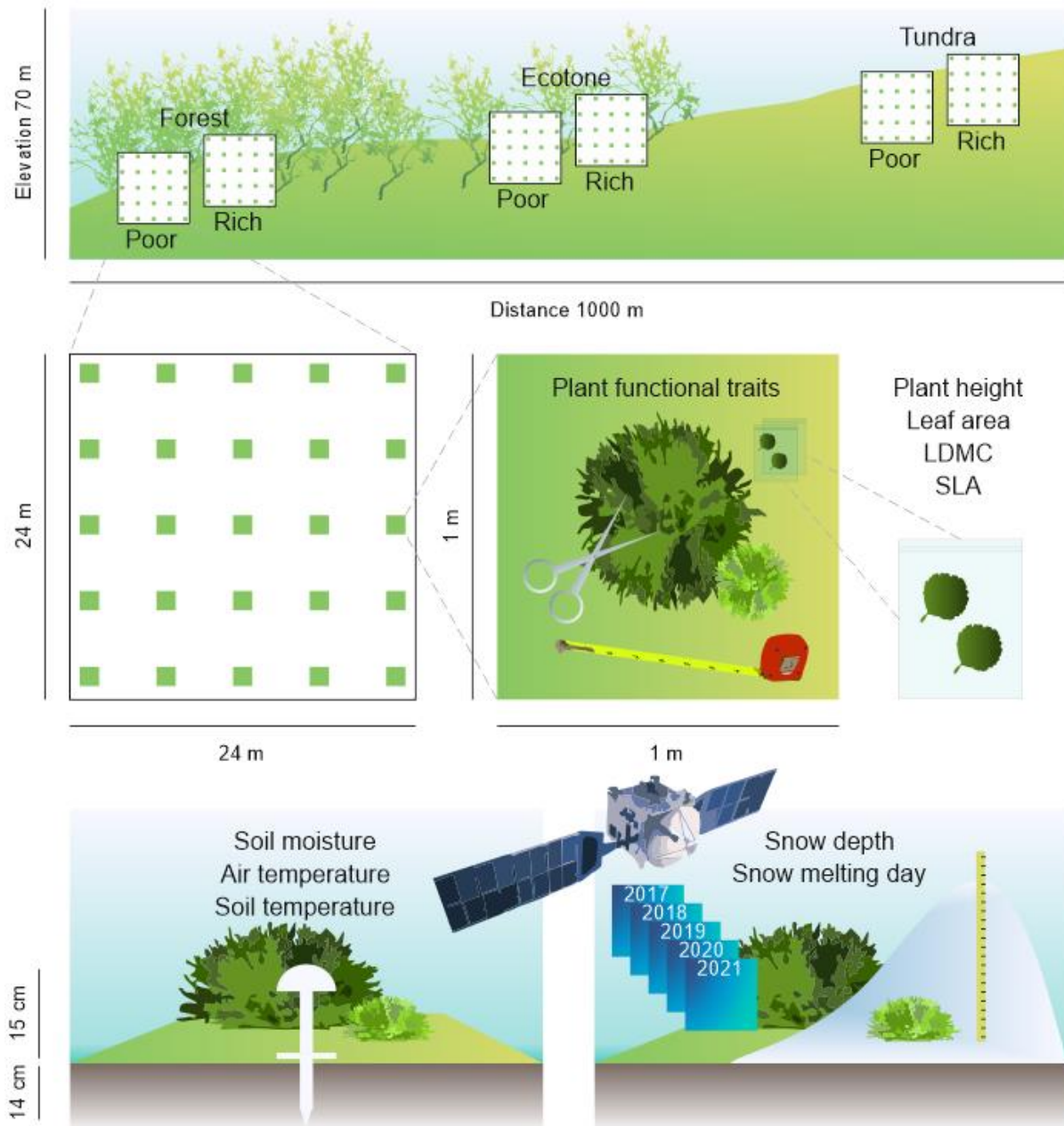
136 by *Empetrum nigrum* subsp. *hermaphroditum*, *Betula nana* subsp. *nana*, and *Vaccinium* spp.
137 (Kemppinen et al., 2021b). *Betula pubescens* subsp. *czerepanovii* forms relatively sparse
138 forests in valleys. Herb-rich meadows are present in moist and nutrient-rich habitats but are
139 restricted mainly to topographic depressions and slopes fed by meltwater from late melting
140 snow patches. The study area is chiefly grazed by *Cricetidae* sp. and semi-domesticated
141 *Rangifer tarandus tarandus*.

142

143 *Study design*

144 The study design (Figure 1) consisted of 150 study plots (1 m x 1 m) within six study grids
145 (24 m x 24 m). Each grid holds 25 plots located at 6 m intervals. The study design follows a
146 paired design where two of the grids were located in the tundra, two in the tundra-forest
147 ecotone (hereafter, ecotone), and two in the mountain birch forest. We had two criteria for the
148 locations. Firstly, in each pair, one grid covered lush vegetation (likely indicating abundant
149 soil moisture and nutrients; hereafter, rich) and one covered more barren vegetation (limited
150 resources; hereafter, poor). Secondly, all grids were on mesotopographical gradients (i.e.,
151 gradient from a small depression to a small ridge) where microclimatic conditions (and thus,
152 plant traits) likely vary greatly over short distances. In the forest and ecotone, the pairs were
153 located ~50 m apart. In the tundra, the grids were ~600 m from each other due to the absence
154 of suitable topographic gradients and vegetation types closer to each other. The maximum
155 elevational difference across the six grids was 76 m, and the maximum distance was 1000 m.
156 We recorded the locations of each plot using a GPS receiver with centimetre accuracy (Emlid
157 Reach RS2, Emlid Ltd.).

158



159

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

165

166 *Plant data*

167 We selected six vascular plant species for trait measurements, namely *Bistorta vivipara*,
 168 *Solidago virgaurea*, *Betula nana*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, and
 169 *Vaccinium vitis-idaea*. The species are common in the area (Kemppinen et al., 2021b) and

170 also wide-spread across the boreal and sub-Arctic zones. See a detailed description of the six
171 study species in Supplementary Text.

172

173 We collected data on plant height (cm), leaf area (cm²), leaf dry matter content (dry
174 weight/fresh weight; g/g; hereafter, LDMC), and specific leaf area (leaf area/dry weight;
175 cm²/g; hereafter, SLA). When any of the six study species were present at the plots, we
176 measured and sampled them as close as possible to the centre of the plot while also ensuring
177 that the sampled plants were considered as separate individuals.

178

179 We collected the leaf samples on 20.7.2021 and processed them within the following 48h
180 before drying them. Firstly, we selected up to four plant individuals per species per plot and
181 measured their heights from the soil surface to the highest photosynthetic part (i.e., excluding
182 flowering part and stem) using rulers (mm precision). Secondly, we collected two leaf
183 samples from the dwarf shrub species, and one from the forb species per individual. We
184 sampled only mature leaves without marks of any kind of damage. For the forb species, we
185 sampled rosette leaves because stem leaves are typically much smaller and stems are not
186 present in sterile individuals. We kept the samples moist in zip-lock bags with dampened
187 paper towels. In the laboratory, we kept the samples in the zip-lock bags at 4°C between
188 measurements. Thirdly, we weighed the leaves by using a Mettler AE 100 scale (0.0001 g
189 precision) to measure their fresh weight. Fourthly, we scanned the leaves using a Canon
190 CanoScan LiDE 20 scanner (600 dpi resolution) to measure their area. We calculated leaf
191 area from the scans by using the ImageJ software via R with functions from the *LeafArea* R
192 package (Katabuchi, 2015). Finally, we dried the leaves in 70°C for 48 h using VWR
193 VENTI-Line ovens, and then reweighed the dry leaves. The level of observations were plant
194 individual for plant height, individual leaf for leaf area, and plot-level means for LDMC and
195 SLA. This resulted in a total of 5816 observations for the studied six species and four traits.

196

197 To compare the trait values and ranges in locally collected data to the ITV of the species
198 across the species' whole distributions, we gathered trait data from global trait databases,
199 namely TRY plant database (Kattge et al., 2020), Botanical Information and Ecological
200 Network (Enquist et al., 2016) (Maitner 2020) and Tundra Trait Team database (Bjorkman et
201 al. 2018b). A full list of original data sources used in the study are provided in the Data
202 sources section. The same trait observations were clearly present in multiple datasets and
203 thus, we divided the data into sub-datasets based on the reported original data provider and

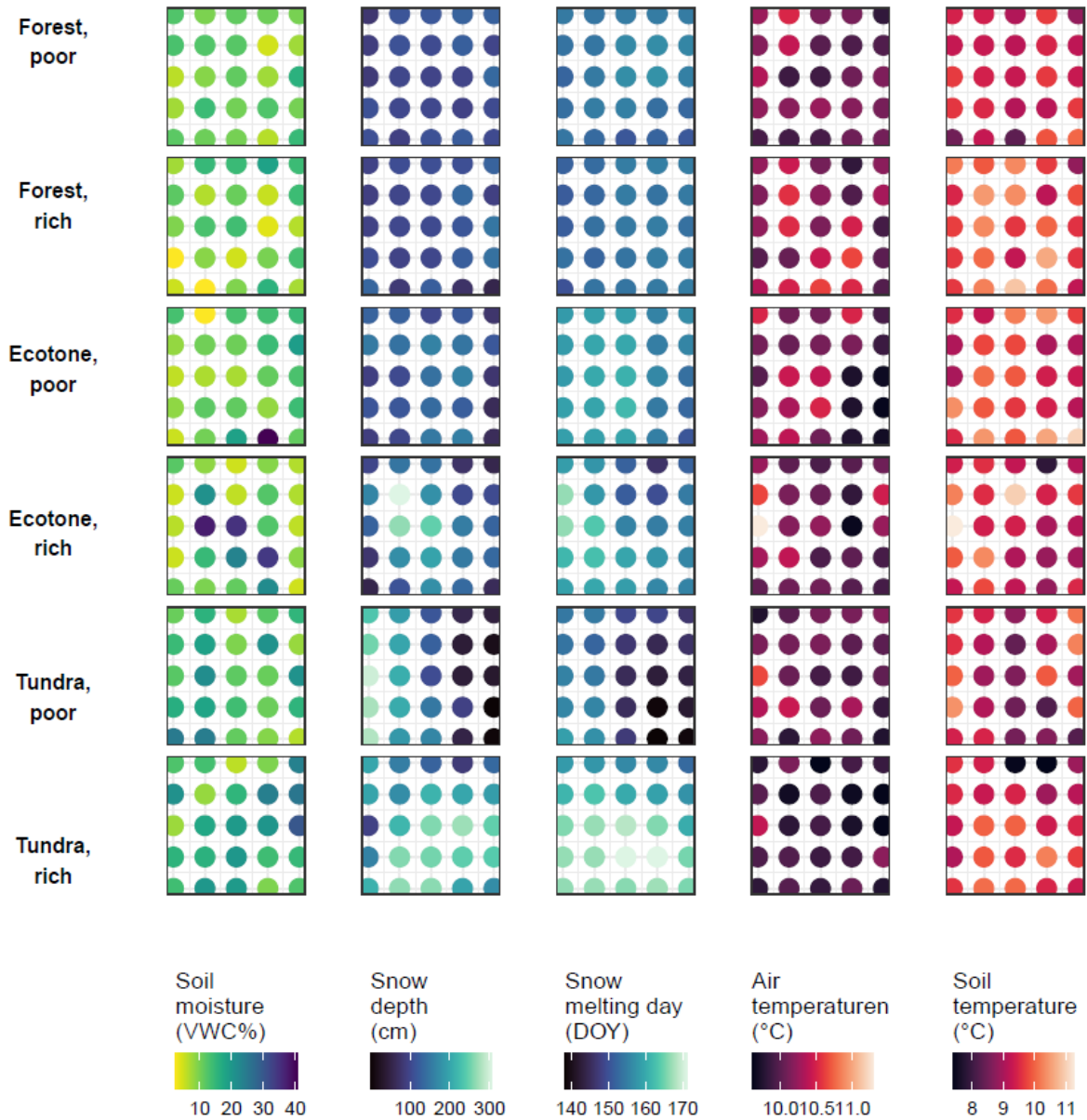
204 cross-tabulated all sub-dataset pairs to calculate how many identical observations they shared.
205 If the percentage of exact duplicates was over 20%, we merged the subdatasets and removed
206 the duplicates. This resulted in a total of 10977 observations for the studied six species and
207 four traits. However, histograms of the traits values indicated presence of suspicious outliers
208 that are likely errors in the heterogeneous data sources. Therefore, we excluded trait values
209 falling outside the 95% percentiles (separately for trait*species) both in the data extracted
210 from databases and in our local data before comparing the ranges of these data. This filtering
211 was conducted only for these global~local comparisons, and the local data used in the rest of
212 the analyses was not filtered.

213

214 *Environmental data*

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

218



219

220 Figure 2. Fine-scale variation in soil moisture, snow conditions, and local temperatures. The
 221 points represent the study plots ($n = 150$) and the panels study grids ($n = 6$). VWC =
 222 volumetric water content. DOY = day of year.

223

224 We measured soil moisture, air temperature, and soil temperature 16.7.-31.8.2021 from the
 225 centre of each plot. We used TMS-4 dataloggers (TOMST Ltd., Prague, Czech Republic),
 226 which measure soil moisture to a depth of c. 14 cm, as well as soil temperature at - 6 cm
 227 depth, and air temperature at 15 cm above soil surface (Wild et al., 2019). The loggers
 228 measured with a 15-minute interval and recorded 2,028,150 measurements. The loggers
 229 produce raw time-domain transmission data on soil moisture, which we calibrated into
 230 volumetric water content (VWC%) using a calibration function adopted from (Kopecký et al.,

231 2021). We plotted all soil moisture and temperature time series and inspected them visually
232 (Supplementary Figure 1-3). One logger fell down during the measurement period and for
233 this logger we imputed the moisture and temperature time-series by using a Random forest -
234 based method from the *missForest* R package (Stekhoven & Bühlmann, 2012). Finally, we
235 calculated mean soil moisture, air temperature, and soil temperature for each logger for the
236 whole study period. These mean values were used as predictors in the analyses.

237

238 We measured snow depth on 3.4.2022 (c. maximum snow depth time) from the centre of each
239 plot. We used an aluminium probe to measure, and a high-accuracy GPS device to navigate
240 to the plots.

241

242 We calculated the snow melting day by utilising information from PlanetScope satellite
243 images (3 m x 3 m resolution) from years 2017-2021. See a detailed description of this
244 method in Supplementary Text.

245

246 *Statistical Analyses*

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

253

254 We log-transformed all response variables (traits) and rescaled and centred all predictor
255 variables. We used the default priors (i.e., noninformative priors for all slope parameters) of
256 *brms* in the models. Four Markov chain Monte Carlo (MCMC) chains were used in all
257 models with a minimum of 8000 iterations and a burn-in of 4000 iterations. We checked the
258 convergence of the MCMC chains by visually evaluating MCMC trace plots, histograms of
259 the sampled parameters, autocorrelation plots, and by comparing the distributions of the raw
260 values of the response and the posterior predictions. We also checked Effective sample size
261 and Rhat statistics for all model parameters that help determine if the MCMC chains have
262 mixed well (Gelman & Rubin, 1992). Additionally, we calculated the k-pareto statistic for all
263 observations with approximate Leave one out (LOO) cross validation that tells if there are
264 especially problematic observations.

265

266 The level of observations were plant individual for plant height, individual leaf for leaf area,
267 and plot-level means for LDMC and SLA. Due to these differences the model structures were
268 slightly different for different traits.

269

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

272

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

275

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

280

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

283

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

290

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

293

294 LDMC and SLA models for *B. vivipara* were different from above, however, because the
295 species was recorded only on 13 plots. Due to the low number of observations we simplified
296 the model to avoid severe overfitting. We included only three predictors which we expected
297 to be ecologically the most relevant ones and did not account for the structure of the study

298 design. Thus, the *B. vivipara* models for LDMC and SLA should be interpreted with extra
299 care. We stated this clearly in the results.

300

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

302

303 The log-transformed response variables had approximately normal distributions and thus, we
304 first fitted Gaussian models. However, posterior predictive checks revealed that some of the
305 models were not able to replicate the data distribution well. Additionally, we calculated the
306 approximate LOO cross-validation, which showed that in many cases models predicted
307 poorly multiple observations (k-pareto values > 0.7). Thus, we ran all models also with
308 Student-t and skewed normal distributions. We decided the best model by calculating LOO-
309 based model weight and selected the model with the highest weight score (i.e., lowest LOO
310 SE). Parameter estimates were interpreted as being “significant” when the 95% credible
311 interval of the posterior distribution did not cross zero. We calculated Bayesian R² values for
312 the models both with and without the effects of the random factors (Gelman et al., 2019).

313

314 *Data availability*

315 Data and code are available here in an anonymized repository:

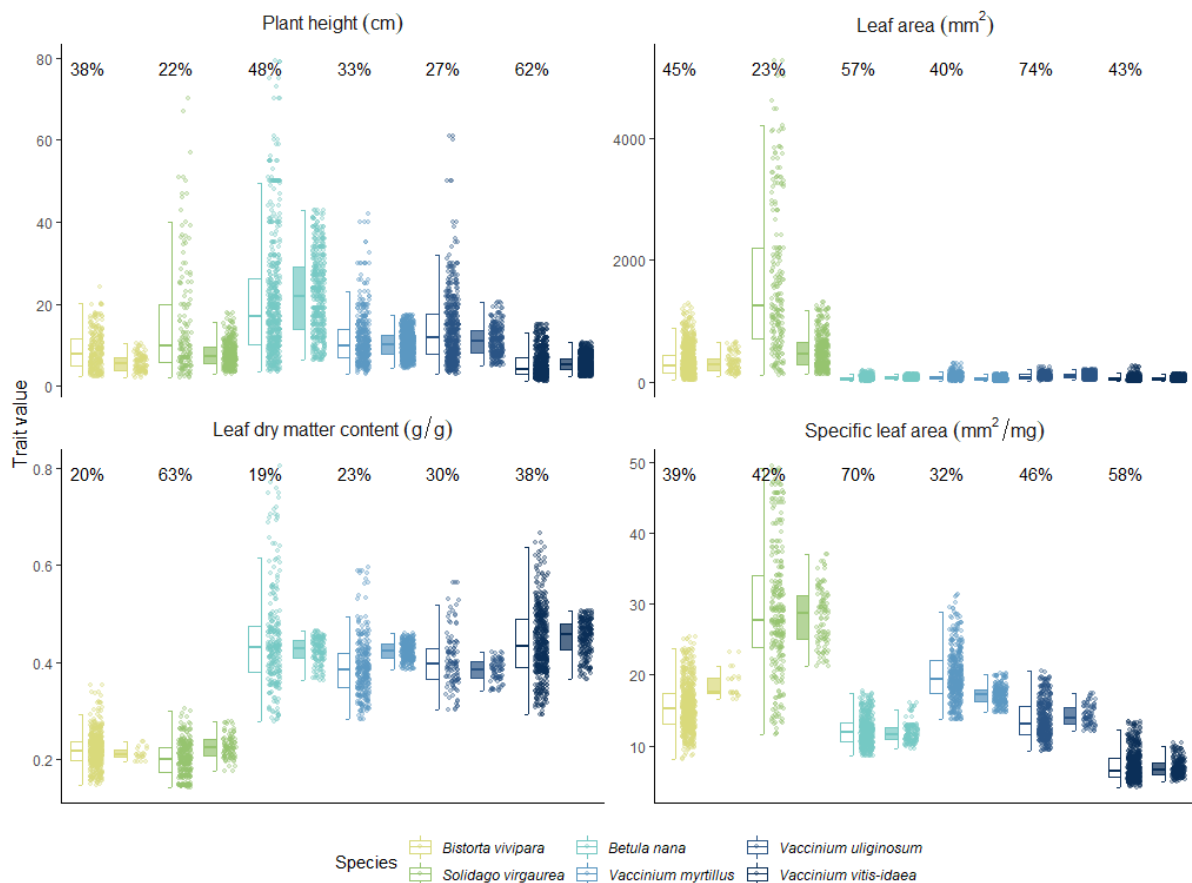
316 https://anonymous.4open.science/r/ITV_grids-105D/README.md

317 A stable version of the repository will be archived with DOI in Zenodo upon acceptance for
318 publication.

319

320 **Results**

321 This study is based on 5493 intraspecific trait observations of six common northern species
322 and their four functional traits. Data from global databases for the corresponding species and
323 their traits consists of 10,383 observations. These species have large distributional extents
324 both in geographic and climatic terms. Yet, this local dataset consists of a relatively large
325 portion of the global ITV (Figure 3). In this comparison, the largest portion was 74% for
326 variation in leaf area of *V. uliginosum*, and the lowest 19% for LDMC of *B. nana* (Figure 3).
327 When averaged over the species, the highest variation in local dataset compared to global
328 variation was in SLA (47.7%) followed by leaf area (47.0%), plant height (38.3%) and
329 LDMC (32.2%). When averaged over traits, *V. vitis-idaea* holds the highest amount of
330 relative variation in the local dataset (50.2%) followed by *B. nana* (48.5%), *V. uliginosum*
331 (44.2%), *S. virgaurea* (37.5%), *B. vivipara* (35.5%) and *V. myrtillus* (32.0%).



333

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

339

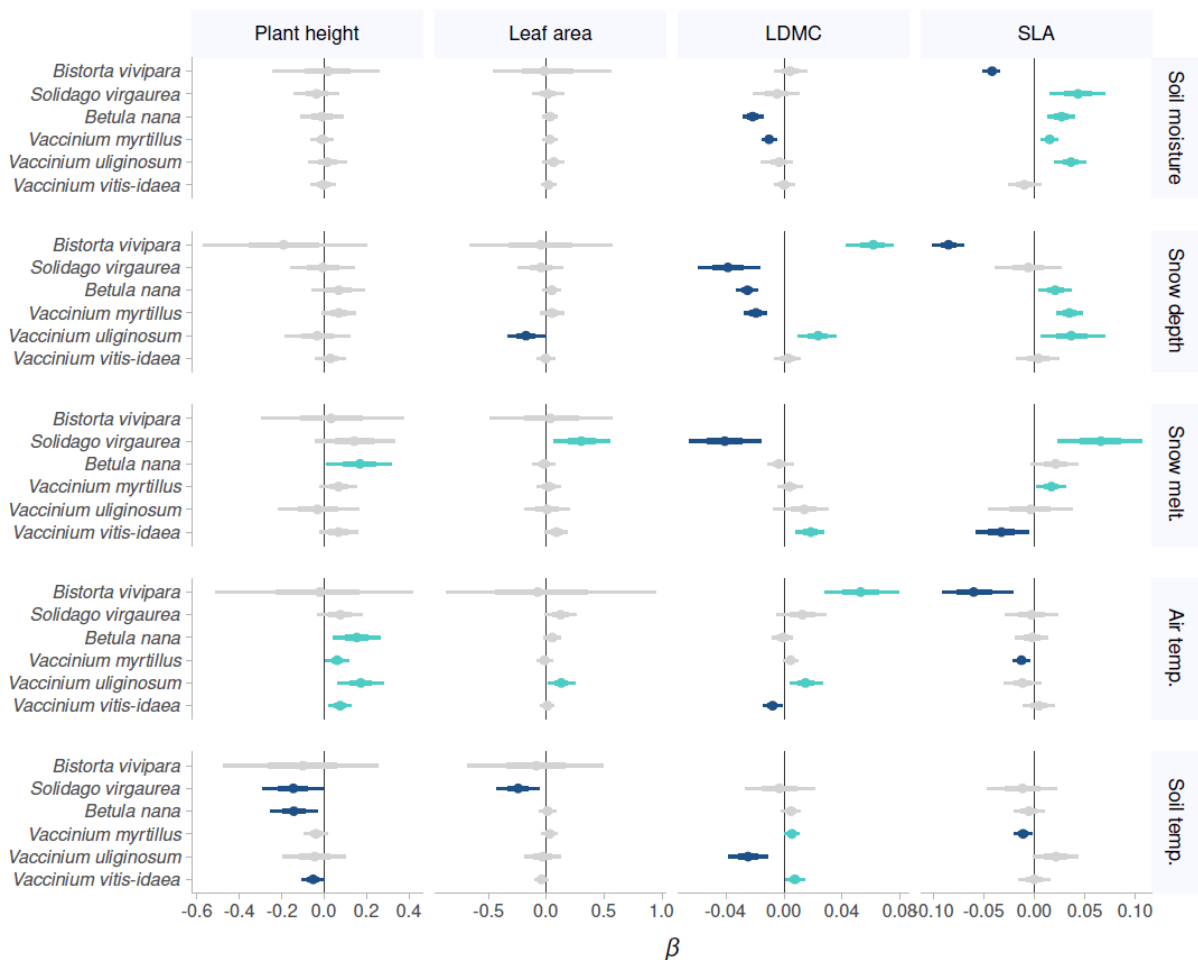
340 The ranges in plant height were largest within the deciduous dwarf shrub species, particularly
 341 *B. nana*, and smallest within *B. vivipara* and *V. vitis-idaea* (Figure 3). Regarding leaf area,
 342 large ranges were found within the two forb species, and small ranges within the dwarf shrub
 343 species (Figure 3). The range in LDMC was largest within *V. vitis-idaea* and smallest within
 344 *B. vivipara* (Figure 3). Regarding SLA, *S. virgaurea* had a distinctly larger range compared to
 345 the rest of the species (Figure 3). See detailed trait distributions aggregated by study grid in
 346 Supplementary Figures 4 and 5.

347

348 High spatial and temporal variation in microclimate was found (Figure 2; Supplementary

349 Figures 1-3). Plant height ITV of the species was chiefly related to the temperature variables,

350 especially air temperature (Figure 4; Supplementary Figure 6). Plant height and air
 351 temperature had positive associations, whereas soil temperature had negative relationships.
 352 Soil moisture and snow depth showed no significant relationships with plant height.
 353 Regarding leaf area ITV, the models had very few significant predictors: soil moisture
 354 showed no significant relationships and rest of the predictors each were a significant
 355 predictor to one of the six species (Figure 4). SLA and LDMC, instead, were more related to
 356 soil moisture and snow than to the temperature variables. For example, soil moisture was a
 357 significant predictor for SLA for five out of six species, and similarly snow depth for LDMC
 358 for five out of six species. Higher soil moisture was generally linked with higher SLA, but
 359 with *B. vivipara* soil moisture had the opposite effect. Bivariate trait-microclimate
 360 relationships for each species can be found in Supplementary Figures 7-11.
 361



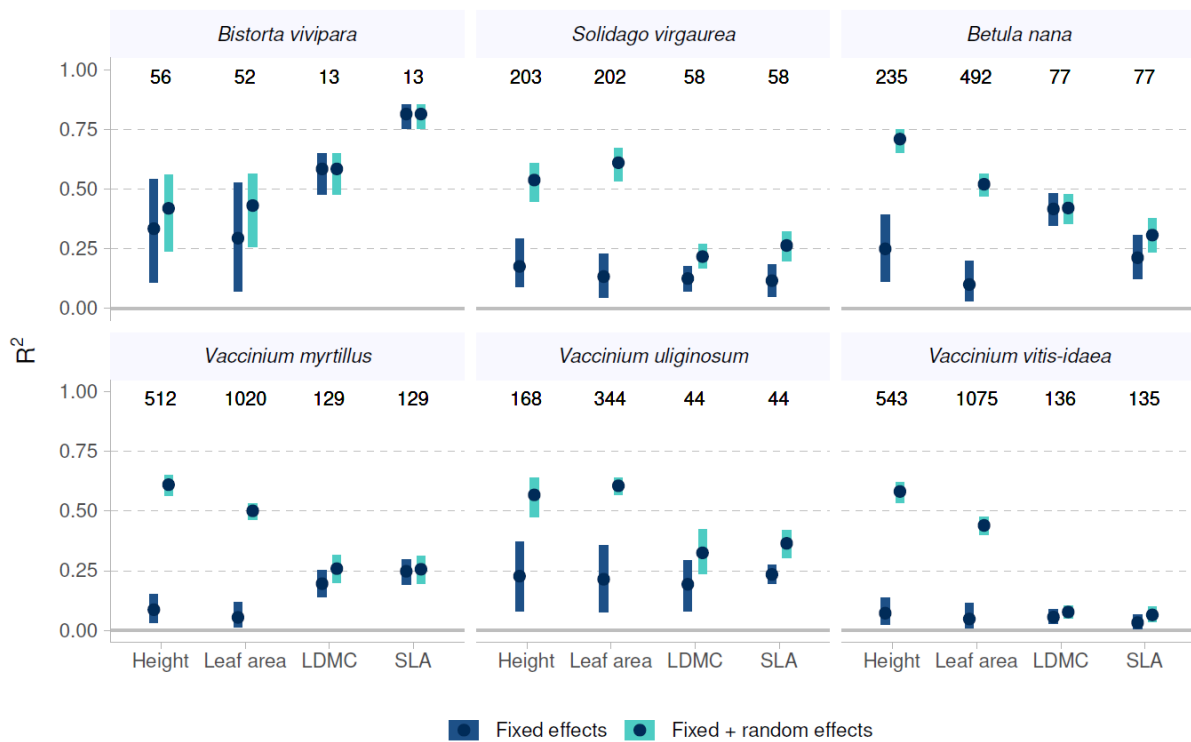
362
 363 Figure 4. Slope (β) estimates for the predictors in hierarchical Bayesian linear models.
 364 Models were fitted separately for each species and trait. The points represent the posterior
 365 medians for the slope parameters, thickened lines the 66% credible intervals, and the thin
 366 lines the 95% credible intervals. The coloured slope estimates were interpreted as

367 “significant”, as their 95% credible intervals did not cross zero. LDMC = leaf dry matter
 368 content. SLA = specific leaf area.

369

370 The best performing models were the models for *B. vivipara* (R^2 averaged over traits = 0.51)
 371 (Figure 5; Supplementary Table 1; Supplementary Table 2), however, it must be noted that its
 372 sample size for all traits were low compared to the other species, and this affected the model
 373 performance when models are likely overfitting. For the rest, the highest average R^2 was for
 374 *B. nana* (0.25), *V. uliginosum* (0.22), *V. myrtillus* (0.15), *S. virgaurea* (0.14) and *V. vitis-*
 375 *idaea* (0.05) (Figure 5). When averaged over species, SLA models had the highest R^2 (0.28),
 376 followed by LDMC (0.26), plant height (0.19) and leaf area (0.14). If the likely overfitting *B.*
 377 *vivipara* models were excluded, the average R^2 values were slightly lower and the order of
 378 SLA and LDMC was flipped but leaf area models remained with lowest average R^2 value.
 379 Apart from the *B. vivipara* models, the highest individual R^2 (0.42) was for *Betula nana*
 380 LDMC model (Figure 5).

381



382

383 Figure 5. Model performance. Bayesian R^2 metrics with and without the effect of random
 384 factors. Plant height and leaf area models included nested study plots within study grids as
 385 random factors, whereas the LDMC and SLA models had only study grids as a random
 386 factor. The numbers represent the count of observations in a given model. LDMC and SLA
 387 models for *Bistorta vivipara* included only three instead of five predictors and no random

388 factors due to low number of observations. LDMC = leaf dry matter content. SLA = specific
389 leaf area.

390

391 **Discussion**

392 We found that the local trait variation at our study area constitutes a relatively high portion of
393 the global trait variation for the six species, when we compared our local trait dataset to
394 measurements from global trait databases. Specifically, we compared six widespread and
395 common tundra/boreal species and their four functional traits. Our local dataset consisted of
396 over 5000 trait observations, while the global trait databases consisted of over 10000
397 observations collected around the globe. The range in the traits from our dataset corresponded
398 to 19-74% of the variation seen in the global databases. This comparison provides
399 generalisability for our results, as these are high proportions considering our small study (< 1
400 km² with 76 m elevational difference). Tundra environments are known for high local-scale
401 environmental heterogeneity (Graae et al., 2018; le Roux et al., 2013). Here, we were able to
402 capture a wide range of this local microclimatic variability. For example, the snow depth
403 gradient from one centimetre to three metres depth is close to the maximum variability within
404 the whole region (Kemppinen et al., 2021b). In this light, it is not surprising to find such a
405 high amount of local trait variability even within the relatively small spatial extent.

406

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

418

419 Leaf area had only few relationships with the microclimatic predictors, and the models
420 explained less variation than models for other traits. This suggests that there are less strong
421 mechanisms in plant adaptation to surrounding microclimates that would manifest through

422 leaf size, at least at this scale. Furthermore, Siefert et al. (2015) found that ITV is low in leaf
423 area compared to e.g., in plant height. Midolo et al (2019) also did not find clear ITV patterns
424 in leaf area along elevations globally in their meta-analyses. However, Bjorkman et al.
425 (2018a) found a significant positive relationship between leaf area ITV of tundra plants and
426 coarse-scale summer temperatures across the Arctic, yet they did not find any indication of an
427 increase in leaf area with warming over time. This indicates that even if there was adaptation
428 through leaf size across populations over large extents, Arctic species may lack local
429 plasticity in leaf area that could have readily responded to recent warming, or be visible along
430 local microclimate gradients (see also (Kudo, 1996; Kudo et al., 1999)). However, in our
431 results, leaf area showed rather large local variation compared to global. Therefore, a more
432 plausible explanation to the lack of relationships could be that leaf area has also more within-
433 individual variability causing noise in the models (e.g., leaves at different positions along the
434 stems) and it may be more responsive to factors that we could not test in our models (e.g.,
435 local light conditions affected by shadowing neighbour species).

436

437 LDMC and SLA were related to soil moisture. LDMC of *B. nana* and *V. myrtillus* had
438 negative associations with soil moisture. Whereas for SLA, all species had positive
439 associations with soil moisture, except for *B. vivipara* (negative relationship) and *V. vitis-*
440 *idaea* (no relationship). Interestingly, we found that the size-structural traits were not
441 explained by the fine-scale variation in soil moisture at all. It should be noted that our
442 moisture gradient falls a bit short in the wettest extreme, and thus, we can only speculate if
443 plants growing on actual wetland sites would change the results. However, most of the
444 studied species do not generally occur in tundra wetlands and thus, our moisture gradient
445 likely covers the moisture niches of the species well within this ecosystem. The relationships
446 were in general similar as found in Happonen et al. (2019) and Kempainen et al. (2021) at the
447 community level. However, to best of our knowledge, ITV patterns have not been related to
448 soil moisture gradients in tundra, but its importance has been highlighted in studies in other
449 ecosystems (Harzé et al., 2016; Roybal & Butterfield, 2019; Westerband et al., 2021) and
450 also for root traits (Taseski et al., 2021).

451

452 LDMC and SLA were also related to snow conditions. Particularly, snow depth (measured at
453 the peak snow season) explained LDMC of all species, except for *V. vitis-idaea*. LDMC of *B.*
454 *vivipara* and *V. uliginosum* were positively associated with snow depth, whereas the rest of
455 the species were negatively associated. For SLA, all deciduous dwarf shrub species were

456 positively related to snow depth, and *B. vivipara* negatively. Noteworthy, both LDMC and
457 SLA of *V. uliginosum* had positive associations with snow depth, although typically these
458 traits are negatively correlated and thus, have the opposite directions in the responses to
459 environment (Díaz et al., 2016; Thomas et al., 2020). Regarding snow melting day, the
460 species and their traits had less significant relationships. However, the leaf economic traits of
461 *S. virgaurea* and *V. vitis-idaea* had significant relationships with snow melting day. Overall,
462 the findings are in line with the previous studies although many have considered community
463 level traits not ITV (Choler, 2005; Happonen et al., 2019; Kudo, 1996; Kudo et al., 1999;
464 Onipchenko et al., 2020).

465

466 The highest proportion of variation in traits explained by the microclimate was found for *B.*
467 *nana* and *V. uliginosum* models, in addition to the likely overfitting *B. vivipara* models. Both
468 species are deciduous dwarf shrubs with wide environmental niches in the tundra which may
469 explain why the trait-microclimate relationships were strongest for them. *V. myrtillus* is also a
470 deciduous dwarf shrub but our study site is rather close to its cold range margin, and this may
471 partly explain why it showed less defined trait variability compared to the other deciduous
472 shrubs. *B. vivipara* occurred only in a small number of our study plots, which is unfortunate,
473 because based on our limited data on its trait trends along the microclimate gradients (see
474 bivariate plots in Supplementary Figures 7-11), it seems that the species is very responsive to
475 microclimatic differences (also documented in (Opedal et al., 2015)). The models for *S.*
476 *virgaurea* also explained a consistently low proportion of variation, which may be due to
477 large variation in the species' ecomorphs (or differences between sterile and reproductive
478 shoots) and perhaps because the species is intensively grazed by *R. tarandus tarandus*.
479 Lastly, out of all six species, *V. vitis-idaea* had clearly the lowest model performance and
480 very few strong relationships with the microclimatic predictors. *V. vitis-idaea* also showed
481 rather little trait variation. This indicates that the strategy of this evergreen species is
482 conservative and shows less plasticity compared to the deciduous species.

483

484 We found that in many cases species differ in their response directions along the
485 microclimate gradients, as has been shown also along other environmental gradients
486 (Bjorkman et al., 2018a; Kichenin et al., 2013; Onipchenko et al., 2020; Roybal &
487 Butterfield, 2019). The species might have unimodal trait-environment responses when the
488 whole distribution of the species is covered, and thus, the response is different in certain parts
489 of the gradients (Albert et al., 2010). However, unimodal responses have been rarely reported

490 and the ITV patterns have been mostly linear (Bjorkman et al., 2018a; Kichenin et al., 2013).
491 Another explanation is related to biotic interactions that affect species differently and that
492 biotic effects may even shift from competitive to facilitative along environmental gradients
493 (Adams et al., 2022; Callaway et al., 2002).

494

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

504

505 The models were able to explain approximately one fifth of the variation in the traits, which
506 leaves a high amount of variation unexplained. Likely a large part of the unexplained
507 variation is random variation related to for instance, the plant individual's status, and
508 potential sampling and measurement errors. However, we cannot exclude that we may have
509 lacked some important environmental factors in the models (Mod et al., 2016), for instance,
510 the fine-scale variation of soil nutrients (Chapin et al., 1996). However, we did control for the
511 overall fertility of the sites with the paired study design, in which half of the study grids were
512 located with more nutrient-rich habitats and half in the more nutrient-poor habitats. When the
513 effect of the study grid (as a random factor) was included in the R^2 calculations the variation
514 explained increased by 0.06 (0.08 when *B. vivipara* models excluded) in the LDMC and SLA
515 models, in which the random factor consisted of only the grid. This means that there was not
516 much variation that could have been explained by the plants' growing locations, namely, the
517 tundra, ecotone, or forest grids, or the poor or rich grids.

518

519 This study design enabled us to control for many potential sources for error. For example, all
520 plants were measured and their leaves sampled within a couple of hours under equivalent
521 weather conditions. In addition, the leaf measurements were carried out within two days
522 before drying the samples. The plants were sampled in late July, thus, phenological
523 differences caused by the differences were likely largely levelled off. However, we were not

524 exclusively able to control for plant individuals' age (Büntgen et al., 2018), although we
525 avoided juvenile individuals. Presumably, more individuals and leaves would have decreased
526 the noise in the data, and consequently, increased the deviation explained by the models.
527 However, as noise in data is by definition random, it should not affect the strongest
528 relationships we found between the trait values and microclimate. Therefore, we are
529 confident that potential error sources should not compromise our main findings and
530 conclusions. Also, we want to highlight the size of the dataset, which for these species' and
531 traits is approximately half of the number of observations found in global trait databases
532 (Figure 3).

533

534 **Conclusions**

535 We conclude that microclimate profoundly shapes ITV patterns in northern plants. Our local-
536 scale findings are largely in line with results from studies that consider larger environmental
537 gradients which suggest that the climatic processes filtering individual adaptations or driving
538 plant plasticity are similar from spatial scale to another. However, the influence of the
539 microclimate varies from trait and species to another. Afterall, water availability, snow
540 conditions, and local summer temperatures above and below ground can vary over short
541 distances in sub-Arctic ecosystems, and local plant populations show capacity to shape their
542 functional traits in relation to this mosaic of microclimatic conditions.

543

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