

1 Consistent trait-environment relationships within and across 2 tundra plant communities

3 **Introductory paragraph**

4 A fundamental assumption in trait-based ecology is that relationships between traits and
5 environmental conditions are globally consistent. We use field-quantified microclimate and soil
6 data to explore if trait-environment relationships are generalisable across plant communities and
7 spatial scales. We collected data from 6720 plots and 217 species across four distinct tundra
8 regions from both hemispheres. We combine this data with over 76000 database trait records to
9 relate local plant community trait composition to broad gradients of key environmental drivers:
10 soil moisture, soil temperature, soil pH, and potential solar radiation. Results revealed strong,
11 consistent trait-environment relationships across Arctic and Antarctic regions. This indicates that
12 the detected relationships are transferable between tundra plant communities also when fine-
13 scale environmental heterogeneity is accounted for, and that variation in local conditions heavily
14 influences both structural and leaf economic traits. Our results strengthen the biological and
15 mechanistic basis for climate change impact predictions of vulnerable high-latitude ecosystems.

16

17 **Introduction**

18 A fundamental assumption in trait-based ecology is that trait characteristics of communities
19 show consistent relationships with environmental gradients^{1,2,3}. To test this assumption, we ask:
20 “*Are trait-environment relationships consistent within and across tundra plant communities?*”
21 This important question has rightly received much attention in recent studies⁴, yet this is the first
22 test based on a harmonised study design and extensive field-quantified data considering the fine-

23 scale nature of environmental variation in the tundra ^{5,6}. Plant communities exist on local
24 gradients of temperature, moisture, and soil chemistry that may correspond in length to the broad
25 gradients among regions, and therefore fine-scale environmental drivers should be carefully
26 considered when studying plant-environment relationships. ^{2,7,8}. Moreover, if these relationships
27 hold along local gradients, they can provide even better insights into urgent questions about the
28 effects of climate change and help develop a more mechanistic understanding and realistic
29 predictive ecology across spatio-temporal scales ^{9,10,11}.

30
31 In the past decades, plant functional trait compositions have significantly changed ⁴, as tundra
32 ecosystems have experienced rapid climate change ^{12,13,14}. Plant traits can be rough proxies for
33 ecosystem functioning and respond to the biogeochemical and biophysical properties of
34 ecosystems ^{15,16,17,18}. Above-ground traits vary primarily on two axes ^{17,18,7,19}. One axis
35 differentiates plant species and communities according to size-structural traits affecting, for
36 instance snow trapping ²⁰, shading ²¹, albedo ²², and carbon cycling ²³. The other axis describes
37 variation in leaf economics and resource-use strategy, which influences photosynthetic
38 efficiency, biogeochemical cycles, and forage quality ^{24,25}. In tundra, size traits, such as plant
39 height, are positively correlated with warming ⁴. This is important, because plants are closely
40 connected to the carbon cycle and half of the global below-ground carbon stock is located in
41 tundra soils ^{10,26}. Recent shifts in tundra vegetation are linked back to climate change, therefore
42 the investigation of trait-environment relationships in the tundra is relevant beyond the scope of
43 the high-latitudes or theoretical ecology ^{4,27,28}.

44

45 As temperatures, precipitation, and environmental conditions overall are changing in both Arctic
46 and Antarctic tundra^{29,30,31,32,33}, an open question is, how will these changes influence ecosystem
47 functioning? In tundra, geographic distributions of species are largely determined by variation in
48 snow cover^{34,20,35}, resource availability^{36,37,38}, and the length of the growing season³⁹⁻⁴¹. These
49 abiotic conditions can vary dramatically at fine spatial scales^{5,8}, driving variation in diversity
50 and composition of plant communities over short distances^{42,43,44}. Thus, we test the strength of
51 trait-environment relationships with predictors at two spatial scales: 1) fine-scale field
52 measurements representing microclimate and local soil chemistry (1 m²), and 2) coarse-scale
53 climate and soil data representing macroclimate and coarse-scale soil chemistry (1 km²). We
54 hypothesise that the former outperforms the latter, as coarse-scale data depicts local
55 heterogeneity poorly^{6,45}, and thus, the fine-scale field-quantified environmental factors are
56 expected to provide stronger evidence for the existence of universal trait-environment
57 relationships.

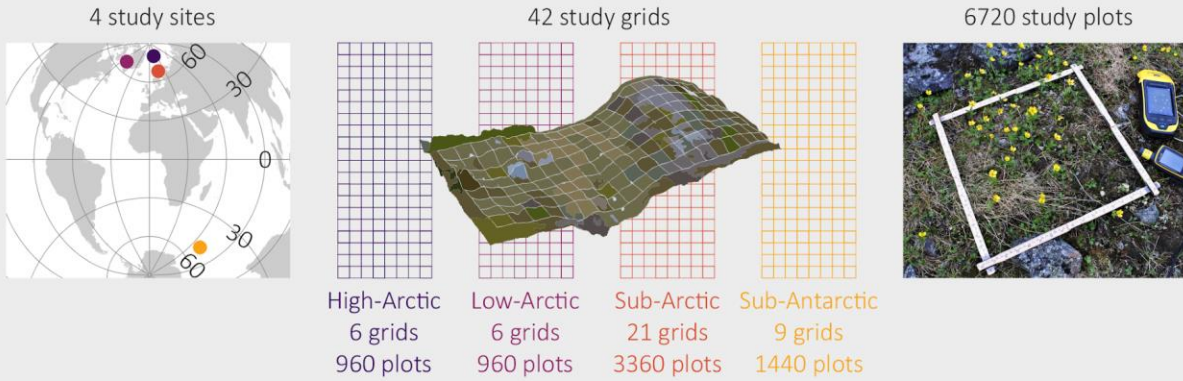
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59 **Results**

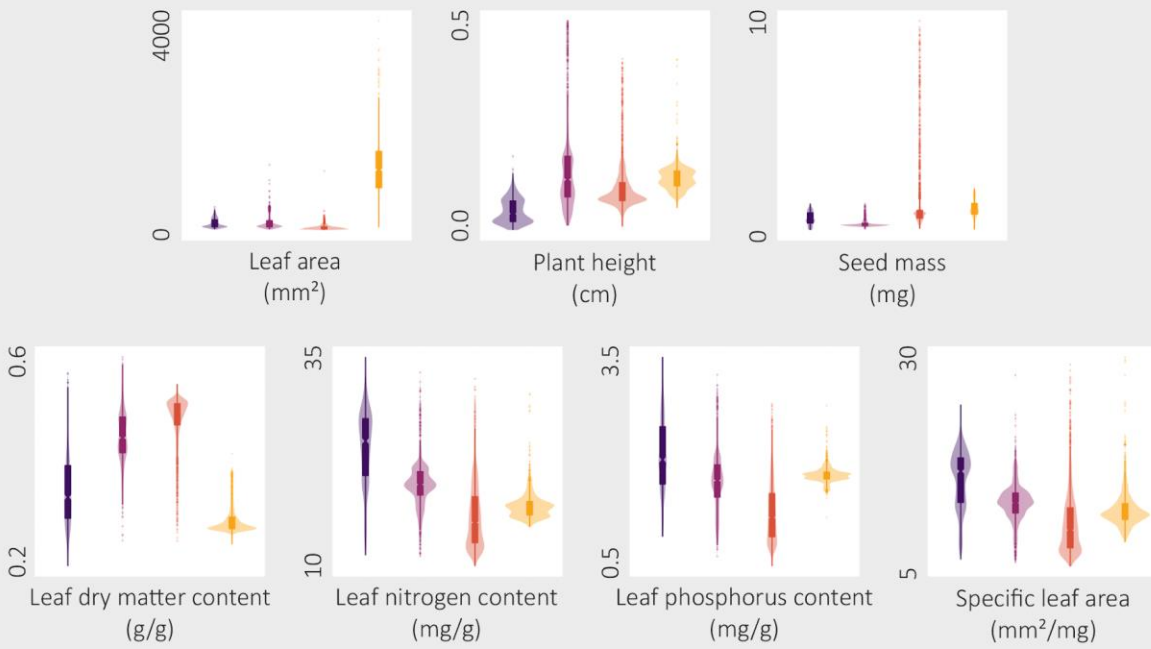
60 We collected detailed data on vascular plant community compositions and local abiotic
61 conditions across four geographically and climatically distinct tundra sites in the high-Arctic
62 Svalbard, low-Arctic western Greenland, sub-Arctic northern Fennoscandia, and sub-Antarctic
63 Marion Island (for study design and data details, see Methods and Figure 1). In each of the 6720
64 vegetation plots (1 m²) within 42 sampling grids (8 m x 20 m, 160 plots each), we analyse the
65 community weighted means (CWM) of key plant functional traits related to vegetation structure
66 (namely, leaf area, plant height, and seed mass) and the leaf economic spectrum (leaf dry matter
67 content, leaf nitrogen content, leaf phosphorus content, and specific leaf area). We collected *in*

68 *situ* species composition data across wide gradients of microclimatic conditions and soil
69 chemistry, and we combine this with over 76000 trait records from global databases provided by
70 the Tundra Trait Team, TRY Plant Trait Database, and the Botanical Information and Ecological
71 Network^{46,47,48}.

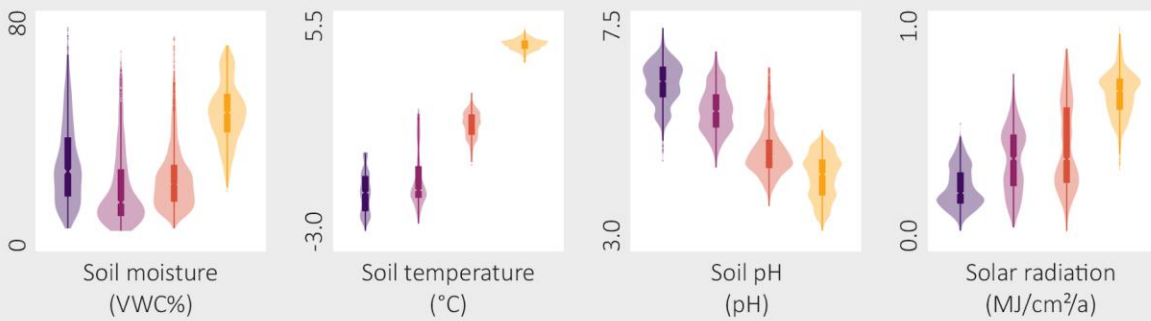
Hierarchical study design



Community weighted means of plant functional traits



Environmental data from the field



73 Figure 1. Data and study design. We collected data from four tundra sites. Each of the sites had
74 multiple sampling grids, which were situated in topographically complex landscapes to maximise
75 environmental variation within a restricted spatial extent (8 m x 20 m). Each grid consists of 160
76 plots (1 m x 1 m). From each plot, we collected *in situ* data on plant species composition and
77 field-quantified key environmental drivers, and extracted species trait records from databases
78 from which we calculated the community weighted means of key plant functional traits. Data
79 (non-transformed) on the variables are presented as violin plots overlaid with box plots. In the
80 box plots, the notches and hinges represent the 25th, 50th, and 75th percentiles, with whiskers
81 representing 95% confidence intervals, and with outliers shown as points. In the violin plot, the
82 thickness of the violin polygon corresponds to the local density of the observations.

83

84 We collected data on field-quantified environmental drivers, namely, soil moisture, annual mean
85 soil temperature, soil pH, and potential solar radiation. This revealed pronounced fine-scale
86 variation as well as larger environmental gradients within and across the four study sites. For
87 example, soil pH ranged from 4.7 to 7.4 within the high-Arctic site located in Svalbard and its
88 overall range across all the sites was from 3.3 to 7.4 (Figure 1). The ranges of the environmental
89 variables generally overlapped among the sites, except for soil temperature (Figure 1).

90

91 We used the environmental variables as predictors in hierarchical generalized additive models
92 (HGAM), a powerful tool for modelling variability among sites ⁴⁹. HGAM allows the use of
93 flexible response shapes, and thus, enables inferring if the trait composition at different sites
94 follows a “global” trait-environment relationship; that is a relationship transferable within the
95 four study sites ⁴⁹. We use HGAMs to study whether the functional relationships between plant

96 traits and the environmental drivers are consistent across the four study sites, as we are interested
97 to determine if trait-environment relationships are “global” (generalisable among the sites) rather
98 than “local” (restricted by unique responses of local species pools).

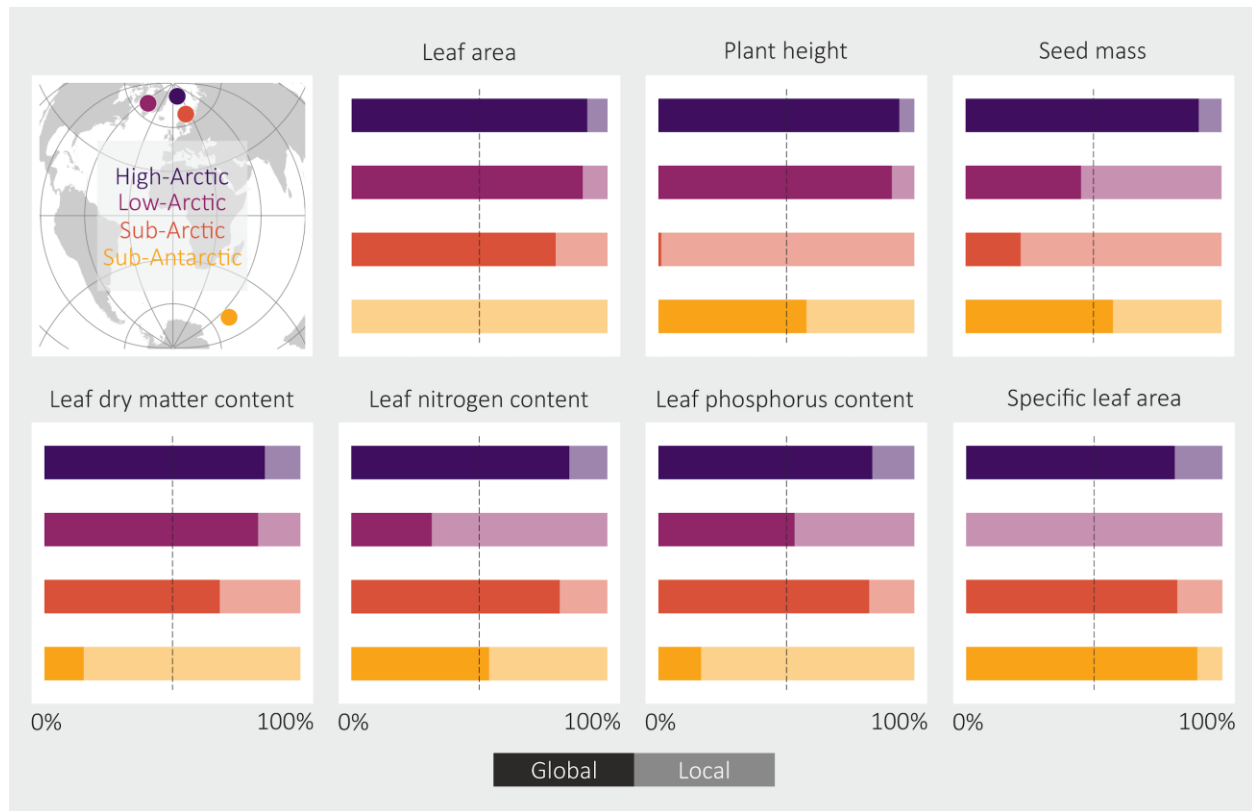
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100 First, we calculated the amount of variation, which we measured as range and standard deviation,
101 in the CWM traits and environmental variables within the 42 study grids and compared these to
102 the total variation in the entire dataset (Appendix 1). We found that soil moisture shows
103 especially great within-grid variability: on average a grid has approximately 50% of the variation
104 of the entire dataset. Of the four environmental variables, soil temperature displays the least
105 within-grid variability. Regarding the CWM traits, plant height and specific leaf area varied most
106 over short distances, while leaf area and leaf dry matter content had the least pronounced within-
107 grid variability of the seven CWM traits.

108

109 We found consistent trait-environment patterns across the four sites (Figure 2). In 20 out of 28
110 trait-site comparisons, environmentally explained trait composition was more strongly
111 determined by global trait-environment relationships than by local deviations from the global
112 pattern. The global trait-environment relationship is determined with the data from all four sites,
113 whereas the local deviation is determined only by site-specific data. In other words, in models of
114 trait composition, including smoothers describing the global trait-environment relationships
115 increased model r^2 more than further adding smoothers accounting for local deviations from the
116 global trend (Table 1). The trait-environment relationships are thus not dependent on
117 geographical location, which means that community-level plant traits respond to environmental
118 variation consistently across the tundra sites, forming a general and transferable pattern. We also

119 compared our fine-scale *in situ* environmental data with coarse-scale climate and soil data, and
 120 we found the first to outperform the latter for all seven plant functional traits (see Methods and
 121 Appendix 2 for details).



122
 123 Figure 2. Environmentally explained variation in plant functional trait composition. Each colour
 124 represents a different site. The darker shading within each horizontal bar represents the
 125 percentage of the total explained variation that is accounted for by global trait-environment
 126 relationships and the lighter shading represents the variation accounted for by local trait-
 127 environment relationships. In over half of the sites, variation in two size related traits (leaf area,
 128 plant height) and variation in all leaf economic traits are most strongly explained by global rather
 129 than local trait-environmental relationships. See Methods and Table 1 for details.

130 Table 1. The r^2 values for the models divided between the random effect, the global trait-
 131 environment relationship, and the local trait-environment relationship. The higher the value, the
 132 greater proportion explained by the factor.

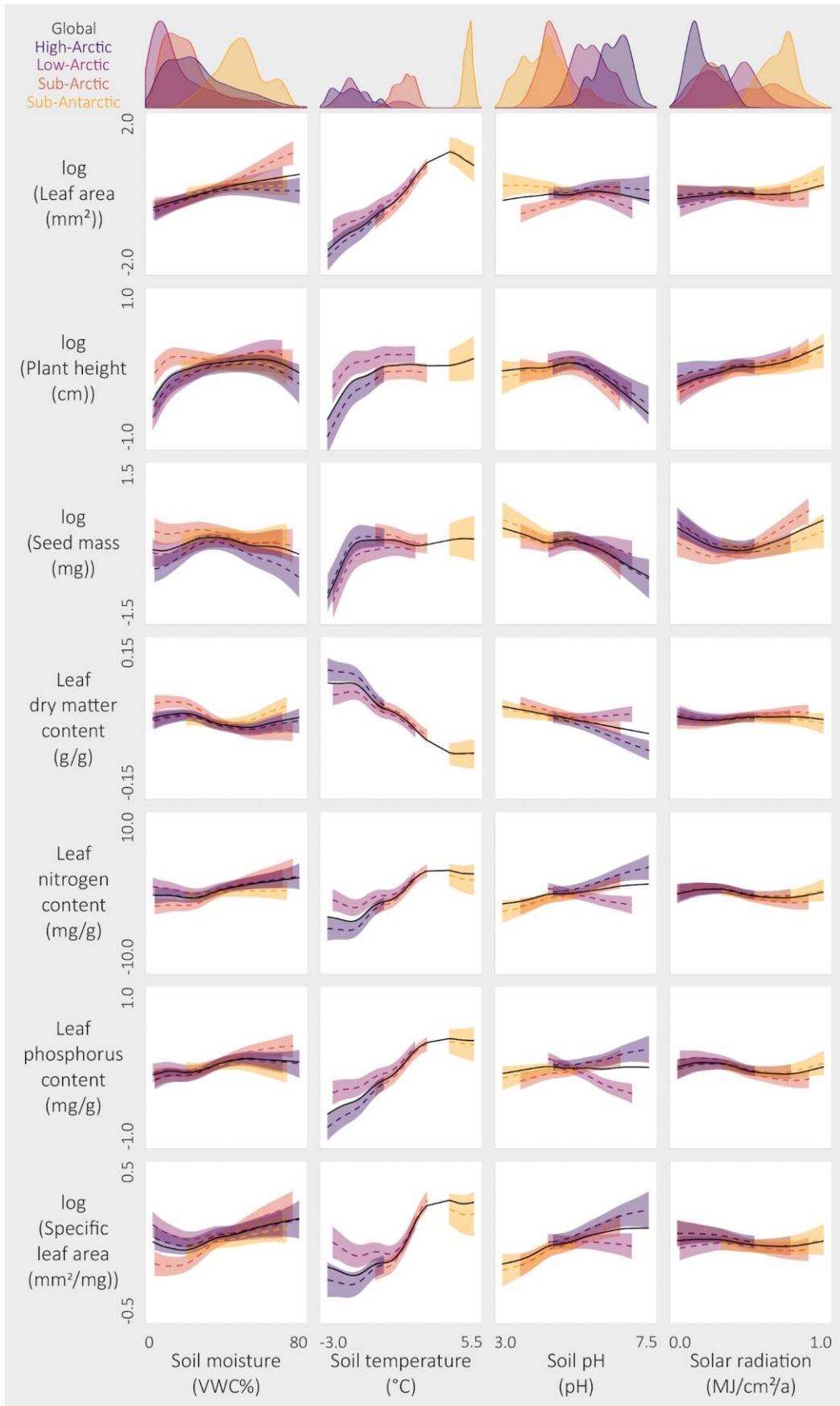
Plant trait	Site	Random effect	Global relationship	Local relationship
Leaf area	High-Arctic	0.22	0.35	0.03
	Low-Arctic	0.11	0.37	0.04
	Sub-Arctic	0.27	0.21	0.05
	Sub-Antarctic	0.30	-0.01	0.06
Plant height	High-Arctic	0.19	0.38	0.02
	Low-Arctic	0.02	0.28	0.03
	Sub-Arctic	0.18	0.00	0.08
	Sub-Antarctic	0.32	0.03	0.02
Seed mass	High-Arctic	0.12	0.35	0.03
	Low-Arctic	0.05	0.14	0.17
	Sub-Arctic	0.22	0.03	0.10
	Sub-Antarctic	0.17	0.05	0.04
Leaf dry matter content	High-Arctic	0.42	0.18	0.03
	Low-Arctic	0.20	0.24	0.05
	Sub-Arctic	0.19	0.20	0.09
	Sub-Antarctic	0.35	0.03	0.18
Leaf nitrogen content	High-Arctic	0.21	0.24	0.04
	Low-Arctic	0.15	0.06	0.13
	Sub-Arctic	0.24	0.21	0.05
	Sub-Antarctic	0.00	0.12	0.10
Leaf phosphorus content	High-Arctic	0.34	0.24	0.05
	Low-Arctic	0.19	0.16	0.14
	Sub-Arctic	0.25	0.19	0.04
	Sub-Antarctic	0.02	0.04	0.21
Specific leaf area	High-Arctic	0.45	0.14	0.03
	Low-Arctic	0.15	-0.03	0.10
	Sub-Arctic	0.30	0.23	0.05
	Sub-Antarctic	0.01	0.10	0.01

133

134

135 In addition, we carried out a principal component analysis (PCA) to investigate the key
 136 dimensions in both the environmental and trait space, as well as the correlation between the two
 137 spaces (Appendix 3, Appendix 4). All variables were scaled to unit variance. The primary axis in
 138 the trait space (55.22% of the total variance) was related to the leaf economic spectrum (leaf dry

139 matter content, leaf nitrogen content, leaf phosphorus content, and specific leaf area) and
140 correlated (0.40) with the secondary axis of the environmental space (20.97%) related to soil
141 moisture. The secondary axis in the trait space (22.46%) was related to structural traits (leaf area,
142 plant height, and seed mass) and correlated (0.67) with the first axis of the environmental space
143 (58.87%) related to soil temperature, soil pH, and radiation.
144



146 Figure 3. Plant functional trait-environment relationships. The black line represents the spline for
147 the global trait-environment relationship (that is, the trend based on all data from all four sites).
148 The coloured lines represent the sum of the global spline and the spline depicting the local
149 deviation from the global trait-environment relationships. The shaded areas represent two
150 standard deviations for each spline, taking into account the uncertainty in both the global and the
151 local smoothers. The analysis was based on a hierarchical generalized additive model, using
152 global and group-level (that is, one for each of the four sites) smoothers (for details, see
153 Methods). Density plots in the top row represent the distribution of the environmental variables
154 at each site.

155

156 The responses of plant functional traits to environmental drivers were chiefly globally consistent
157 (Figure 3, Figure 2). The traits responded strongly to soil temperature, with particularly large
158 changes at the 0°C mean annual temperature threshold. For example, at higher soil temperatures,
159 plants on average grow taller and have larger leaves with higher nitrogen and phosphorus
160 contents. In addition, we assessed the relative importance of the environmental drivers
161 explaining community composition (Appendix 5). The results concurred with the response
162 curves (Figure 3), showing chiefly that trait composition responds most strongly to soil
163 temperature, both within and across sites.

164

165 **Discussion**

166 **Consistent trait-environment relationships**

167 We found consistent relationships between plant functional traits and local environmental
168 conditions across tundra plant communities. Our findings show strong, field-quantified fine-scale

169 evidence for one of the core claims in trait-based ecology: trait-environment relationships are
170 generalisable across geographical locations and taxonomic composition. In 20 out of 28
171 comparisons, the trait-environment relationship was most strongly explained by global trait-
172 environment relationships (Figure 2, Figure 3). Importantly, considering the fine-scale
173 environmental gradients and communities in the analyses did not generate random noise but
174 made the relationships even stronger compared to the coarse-scale investigations (Appendix 2).
175 These patterns hold across unique species pools and other site-specific characteristics.

176
177 The trait-environment relationships differ in magnitude and transferability (Figure 2, Figure 3,
178 Table 1). All traits were strongly and consistently related to soil temperature. The relationships to
179 soil moisture and potential solar radiation were consistent but weaker. In some sites, the
180 relationship between traits and soil pH was the opposite compared to other sites. However, even
181 if some sites showed minor local deviations from the global trait-environment relationship, they
182 manifested in only one environmental variable - site -combination per trait, and do not change
183 the general pattern: trait-environment relationships are generalisable within and across the four
184 tundra plant communities and the seven traits.

185
186 The magnitude of local variation in trait composition and environmental conditions is itself an
187 important determinant of the transferability of trait-environment relationships, as shorter local
188 gradients lead to higher uncertainty in the direction and magnitude of the relationships. In our
189 results, local trait-environment relationships were reversed when local gradients were short
190 compared to the full range of environmental variation, for example soil pH in the low-Arctic site
191 and soil temperature in the sub-Antarctic site (Figure 3). Thus, our results emphasise the

192 importance of covering as broad local gradients as possible when investigating fine-scale
193 vegetation patterns ⁵⁰.

194

195 Our results are based on a hierarchical statistical analysis of strictly quantitative and
196 harmoniously collected data across four tundra sites located on both hemispheres. Our *in situ*
197 investigations concur with the results reported in previous literature, as we found support for
198 trait-environment relationships based on gridded climate datasets suggesting strong biome-wide
199 links between temperature and plant height, leaf dry matter content, and specific leaf area ⁴
200 (Figure 3, Appendix 5). Similar results to the generalised relationships found in our study have
201 also been reported beyond the tundra for temperature and soil moisture in central Europe ⁵¹. Our
202 results together with existing literature provide robust evidence for globally generalisable trait-
203 environment relationships beyond a single study ^{1,2,51,4}.

204

205 **Fine-scale variability and large gradients**

206 We found strong fine-scale variation and large gradients of soil moisture at all four sites (Figure
207 1, Appendix 1). In rugged tundra landscapes, topographic variation can create contrasting
208 moisture conditions within a few meters distance ^{8,44,52}. Across the sites, we derived moisture
209 data from the top-soil layer (0 - 10 cm). The moisture conditions ranged from extremely dry soils
210 found on small hilltops and ridges to water-logged conditions in depressions (15 - 70 volumetric
211 water content %; Figure 1). Our results indicate that most plant traits are positively correlated
212 with soil moisture (Figure 3). These results provide quantitative evidence to support research that
213 have shown that soil moisture regime influences the strength and direction of trait-temperature
214 relationships in the tundra ⁴. Overall, soil moisture is a vital resource for tundra plants ⁵³. It

215 distributes nutrients and influences geomorphological disturbance ^{54,55,56}, and in turn, controls the
216 overall establishment of vegetation and contributes to providing refugia together with other
217 microclimatic factors in a warming climate ^{57,58,59}.

218

219 We found that temperature was a strong driver of trait variation at a fine spatial scale (Figure 3;
220 Appendix 5), in line with previous studies that have found a positive relationship between plant
221 height and temperature at a coarse spatial scale ⁴. We derived the mean annual temperature from
222 miniature loggers (buried at 5 to 10 cm depth). Thus, it is evident that the temperatures also
223 reflect the pivotal winter conditions, to which the plants are exposed, as our study sites chiefly
224 experience long winters, short growing-seasons, and seasonal snow coverage ⁵⁰. These
225 conditions are changing dramatically in the high-latitudes ^{29,30}. This change is significant for both
226 plant functional composition and species composition, as they are strongly affected by snow in
227 the tundra ^{60,35,61,4}. Nevertheless, climate change will not result in consistently warmer conditions
228 across the high-latitudes ²⁹, as, for instance, parts of Antarctica are also cooling ⁶².

229

230 We found higher mean annual soil temperatures at the sub-Antarctic site located on Marion
231 Island compared to the Arctic sites, where temperatures drop below 0°C. This may explain why
232 the traits did not respond as strongly to soil temperature at the sub-Antarctic site compared to the
233 Arctic sites and why leaf area had a negative response to temperature at the sub-Antarctic site
234 (Figure 3). These results may be due to the strong oceanicity (and, as a result, very buffered
235 thermal regime) of the site compared to the Arctic sites ⁶³. Marion island is also part of a small
236 and extremely remote sub-Antarctic island group with especially low vascular plant species
237 richness ⁶⁴. Thus, the species pool at the sub-Antarctic site may be strongly filtered by

238 environmental factors other than the prevailing abiotic conditions, for instance long-distance
239 dispersal, and thus, different responses to temperature compared to the Arctic sites are not
240 surprising.

241
242 We observed that higher soil pH corresponded with decreased average seed size and faster leaf
243 economic traits (higher specific leaf area, leaf nitrogen content, and leaf phosphorus content, and
244 lower leaf dry matter content). Higher soil pH increases nutrient mineralisation rates and is
245 related to local soil nutrient availability^{65,66}. Consequently, our results suggest that higher soil
246 nutrient availability leads to plant communities that invest in fast acquisition of resources, and
247 produce smaller seeds. Both observations agree with theory. Resource conservation is a losing
248 strategy in conditions of high resource availability⁶⁷. Furthermore, the benefit of equipping
249 seeds with large stores of nutrients and energy decreases when soil resource availability is high
250 but productivity is not high enough to trigger exclusion by shading⁶⁸, as is probably the case in
251 these tundra landscapes. However, the leaf economic traits in the relatively alkaline soils in the
252 low-Arctic site in Greenland did not respond to soil pH in concordance with the other tundra
253 sites (Figure 1, Figure 3). This mismatch is probably not due to trait responses to nutrient
254 availability being idiosyncratic, but the fact that pH is an incomplete proxy for nutrient
255 availability, whose usefulness might depend on soil acidity⁶⁹ or soil-specific factors that affect
256 pH independently of nutrient mineralisation rates.

257
258 Potential solar radiation is relatively important for plant community composition and species
259 richness in the tundra^{50,53} However, we found that trait compositions were not strongly related to
260 solar radiation, nonetheless the size-structural traits, plant height and leaf area, had a positive

261 relationship with solar radiation after accounting for the other environmental factors (Figure 3).
262 Thus, we expect communities composed of larger plants under conditions of more potential
263 incoming solar energy. Other studies have found actual incoming radiation to affect leaf
264 economic traits as well ^{70,71}, but these studies were mainly conducted in forests where the chief
265 control of exposure to sunlight is the density of the tree canopy. Our study suggests that the leaf-
266 economic trait composition of tundra plant communities is less directly affected by varying solar
267 conditions. This may be perhaps because locally measured temperatures already partly reflect
268 incoming energy, and because radiative conditions in treeless biomes are more homogeneous
269 compared to environmental factors that vary at finer scales, such as soil temperature or soil
270 moisture ^{72,44,73}.

271
272 Our fine-scale field investigations revealed large local gradients in both traits and key
273 environmental drivers, namely microclimatic conditions and soil chemistry, in four distinct
274 tundra systems (Figure 1, Appendix 1; for biome-wide traits, see ⁴). It is notable that in tundra
275 environments CWM traits may vary on a 20 m distance (that is the extent of an individual study
276 grid; see Figure 1 for details) nearly as much as they vary across four contrasting Arctic and
277 Antarctic sites (Appendix 1). Environmental conditions also varied considerably over short
278 distances. However, it should be noted that due to evident limitations of the trait data, we cannot
279 consider the effects of intraspecific trait variation (ITV) along the microclimatic gradients, and
280 thus, we cannot explicitly evaluate how this may impact our results. Nevertheless, biome-wide
281 explorations have demonstrated that ITV varies largely in the same direction as the trait variation
282 caused by species turnover along the environmental gradients ⁴. Therefore, it is reasonable to

283 assume that accounting for the ITV in our analysis should at least not weaken the trait-
284 environment relationships found here.

285

286 **Microclimate and macroclimate**

287 We found that fine-scale *in situ* data outperformed coarse-scale climate and soil data in
288 modelling the trait-environment relationships (Appendix 2). This suggests that fine-scale
289 environmental drivers, such as microclimate, are important for understanding and predicting the
290 current and future microhabitat conditions affecting community composition and functioning
291 ^{72,74}. However, the interactions between vegetation, microclimate, and macroclimate are complex
292 ⁷⁵. This is because microclimate is a result of various horizontal (such as vegetation structure,
293 and snow and soil characteristics) and vertical processes (e.g. effects of local topography on
294 incoming radiation and air flow) ⁴⁵. One consequence of these processes is that microclimate
295 may buffer against unfavourable changes in the macroclimate ⁵⁹ via for instance, soil moisture,
296 which reduces the variability in local temperatures ^{76,77}. This may potentially be one mechanism
297 through which soil moisture can influence the strength and direction of plant trait-temperature
298 relationships ⁴. Equally, vegetation is affected by both microclimate and macroclimate, but it also
299 affects both, especially microclimate by, for instance, shading and transpiration ^{21,77}.
300 Consequently, the local manifestation of climate change and the response of plants are
301 challenging to predict ^{76,6}.

302

303 We measured environmental drivers at a biologically-meaningful scale, which captures the local
304 heterogeneity in the microhabitats that plants experience ⁴⁴. However, this variation created by
305 topography may be undetected (or averaged over) when using coarse-scale data ⁷⁶. Coarse-scale

306 studies investigating variation in plant traits at the community-level typically only explain a
307 relatively small proportion of the variation in functional composition ^{7,4}. This is most probably
308 due to low-resolution environmental data, which ignore the fine-scale nature of the
309 environmental drivers ^{5,6,76,72}. For example, precipitation is typically weakly related to traits as it
310 poorly captures the actual plant-available water ^{7,78,79}. Even though microclimate and
311 macroclimate are interrelated, local heterogeneity in environmental conditions can be more
312 important for plant distributions and functional composition than coarse-scale macroclimatic
313 factors ^{6,60,73}. Therefore, as more trait data is made available globally through trait databases,
314 more field-quantified microclimate data are urgently needed to document trait-environment
315 relationships, and to determine their generality, across other biomes ^{80,45}. New frameworks and
316 techniques for recording and producing estimates of soil moisture and temperature data are
317 available ^{81,82,83,84}, as well as new methods for modelling past, current, and future conditions
318 ^{85,74,86}. Therefore, when exploring fine-scale trait ecology, we encourage considering the use of
319 microclimate predictors at an ecologically relevant scale.

320

321 **The future of the tundra and beyond**

322 Experimental and observational studies have shown that tundra plant communities and functional
323 composition are responding to the changes in climate (see ^{87,88}). For example, biome-wide long-
324 term monitoring has shown an increase in plant height in reaction to warming temperatures in the
325 tundra over a 30-year period, but no concurrent rapid changes in community-level leaf economic
326 traits ⁴. Therefore, together with previous literature, our results suggest that it is very likely that
327 as temperatures rise at high-latitudes plants will grow taller. It is also possible (especially over

328 longer periods) that warming will lead to an increase in leaf size ⁴, and if sufficient moisture is
329 available, to higher leaf nutrient levels.

330

331 Temperature, precipitation, snow, permafrost, and the overall hydrological conditions in tundra
332 are changing ^{89,90}, and consequently, the availability of soil moisture will also likely change ³⁰. In
333 the Arctic, snowfall in general is expected to decrease, while rainfall is increasing ³¹, which is
334 partly explained by regional warming ⁹¹. In contrast, nonetheless, in parts of the Arctic, a net
335 water deficit has, for instance, caused ponds and lakes to dry over the past decades ^{92,93,94}. As a
336 result, many tundra ecosystems have shown strong negative responses to regional drying, such as
337 large changes in moss vitality and community composition and declines in bird species richness
338 ^{12,95}. We expect that both temporal and spatial variation in plant-available water will significantly
339 influence vascular plant communities as well, and water will be an even more important resource
340 and disturbance in the warmer future of the tundra ecosystems ^{53,56}.

341

342 Our results highlight clear correlations between microclimatic conditions and key plant traits. In
343 turn, this may have reciprocal effects on, for instance, local moisture conditions, as plants
344 transpire water ⁹⁶, intercept precipitation ⁹⁷, and increase the hydraulic redistribution in soils ⁹⁸.

345 The expected changes in tundra ecosystems' functions and processes may thus influence
346 microclimatic conditions ^{21,96,99}, and in turn, also have dramatic impacts on nutrient and carbon
347 cycling ^{100,101}. For instance, shrub expansion is expected to feedback onto climate change
348 through changes in ecosystem functions and processes ^{10,23}. However, there is currently no
349 consensus on, for instance, how the expansion of woody plants may affect the tundra carbon

350 cycle ^{23,102,103}. Nevertheless, there is great potential for the use of plant functional traits to
351 examine changes in the above- and below-ground ecosystem functioning of the tundra.

352

353 **Conclusions**

354 To conclude, we find strong, consistent trait-environment relationships across four sites located
355 in the high-Arctic, low-Arctic, sub-Arctic, and sub-Antarctic tundra. We used a harmonised
356 study design consisting of field-quantified data, which often is lacking from coarse-scale studies.
357 Our results show that these trait-environment patterns are universal across four distinct tundra
358 ecosystems, as local variation within the sites was overridden by strong, global trait-environment
359 relationships. This knowledge is significant for improving the biological basis for climate change
360 impact predictions for vulnerable high-latitude ecosystems.

361

362 **Material and methods**

363 **Study design**

364 All plant species data and abiotic data have been collected following a peer-reviewed,
365 harmonised field protocol ^{44,53}. We surveyed 42 study grids: six grids in the high-Arctic, six in
366 the low-Arctic, 21 in the sub-Arctic, and nine in the sub-Antarctic. Each grid contained 160
367 study plots of 1 m² and covered a range of environmental conditions (see for instance ⁷⁷). In total,
368 we collected the plant species composition and abiotic data from 6720 plots (see Figure 1 for
369 details on the data).

370

371 We chose the locations of the sites based on their topographic and vegetation gradients (Figure
372 1). We situated the study grids within each site to maximise variation in mesotopography ^{5,8}, as

373 well as vegetation cover and composition. Despite their floristic dissimilarities, these regions
374 have several shared characteristics, with, specifically, the sub-Antarctic and sub-Arctic tundra
375 exhibiting a similar range of vegetation types⁶³. All sampled landscapes are dominated by
376 alternation of minor topographic terrain features, such as hilltops, ridges, and small depressions.
377 In addition, there are several substrate types ranging from rock outcrops, boulders, glacial till,
378 and fluvial deposits to peat deposits.

379

380 **Study sites**

381 High-Arctic site

382 The high-Arctic study site is located in Svalbard, on the slopes of Adventdalen and Endalen
383 valleys (78.20 N, 15.73 E). We collected the abiotic and biotic data in the 2018 growing-season.
384 On average, the annual temperature is -5.9 °C and precipitation 196 mm (1971–2000), as
385 measured at the Svalbard Airport observation site (78.25 N, 15.50 E; 28 m a.s.l.), which is
386 located 7.7 km from the study site¹⁰⁴. The site is dominated by *Dryas octopetala*, *Salix polaris*,
387 and *Cassiope tetragona*, and to a lesser extent by *Bistorta vivipara*, *Festuca rubra*, and *Poa*
388 *pratensis*. The elevation of the study grids ranged from 30 to 110 m a.s.l..

389

390 Low-Arctic site

391 The low-Arctic study site is located in western Greenland, on the highland of Ammalortup
392 Nunaa (66.95 N, -50.72 W). We collected the abiotic and biotic data in the 2018 growing-season.
393 On average, the mean annual temperature is -4.9 °C and annual precipitation 252 mm (1977-
394 2013) as measured at the Kangerlussuaq Airport (67.02 N, -50.70 W; 50 m a.s.l.), which is
395 located 7.0 km from the study site¹⁰⁵. The site was dominated by *Vaccinium uliginosum*, *Betula*

396 *nana*, and *Salix glauca*, and to a lesser extent by *Cassiope tetragona*, *Salix herbacea*, and
397 *Rhododendron tomentosum*. The elevation of the study grids ranged from 520 to 560 m a.s.l.

398

399 Sub-Arctic site

400 The sub-Arctic study site is located in northwestern Fennoscandia, on Mount Saana (69.05 N,
401 20.81 E). We collected the biotic data over three consecutive growing-seasons (2011 – 2013),
402 and abiotic data in the 2013 growing-season. On average, the mean annual temperature is -3.1 °C
403 and annual precipitation 518 mm (1991–2018), temperature measured at the nearby Saana
404 meteorological station (69.04 N, 20.85 E; 1002 m a.s.l.) and precipitation at Kyläkeskus
405 meteorological station (69.04 N, 20.80 E; 480 m a.s.l.), which are located ca. 1.5 km and 1.0 km
406 from the study site ^{106,107}. The site was dominated by *Empetrum hermaphroditum*, *Betula nana*,
407 and *Juniperus communis*, and to a lesser extent by *Vaccinium vitis-idaea*, *Vaccinium uliginosum*,
408 and *Vaccinium myrtillus*. The elevation of the study grids ranged from 595 to 810 m a.s.l.. All
409 the grids were situated above the treeline (comprised of *Betula pubescens* ssp. *czerepanovii*).

410

411 Sub-Antarctic site

412 The sub-Antarctic study site is located on Marion Island in the southern Indian Ocean (-46.90 S,
413 37.73 E). The data were collected over one year, from autumn 2016 to autumn 2017. The mean
414 annual maximum temperature is 8.7 °C, with a mean annual minimum temperature of 3.2 °C,
415 and mean annual precipitation of 1800 mm (2008 - 2018, measured at the nearest weather
416 station, approximately 1 km away). The island has a hyper-oceanic climate, characterised by low
417 temperatures, low variations in temperature and high humidity ⁶⁴. Gale force winds blow on
418 more than 100 days of the year and most days experience precipitation and near-complete cloud

419 cover⁶⁴. The main vegetation types at the site are fernbrake (dominated by the fern *Blechnum*
420 *penna-marina*), mire (dominated by the grass *Agrostis magellanica*) and fellfield (dominated by
421 the cushion plant *Azorella selago*; for details see¹⁰⁸). The elevation of the study grids ranged
422 from 40 to 104 m a.s.l.

423

424 **Vegetation data**

425 We identified all vascular plant species and estimated their cover percentage in the 6720 plots
426 (see full species list in Appendix 6). We extracted trait observations for seven plant functional
427 traits (namely, plant height, specific leaf area, seed mass, leaf dry mass content, leaf area, leaf
428 nitrogen content, and leaf phosphorus content) for each species from three databases: the Tundra
429 Trait Team database (TTT⁴⁶), TRY Plant Trait Database (TRY⁴⁸), the Botanical Information
430 and Ecological Network (BIEN⁴⁷) and from published articles and theses' (see Appendix 7 for a
431 full citation list of the trait data). We searched the databases for the full species list (including
432 their synonyms), which we recorded at our study sites. Additionally, for genus-level trait values,
433 we extracted trait observations from TRY for all species occurring in TTT database and in
434 Fennoscandian countries according to the occurrence records of the Global Biodiversity
435 Information Facility (GBIF; <https://www.gbif.org/>). From BIEN, we searched data by using all
436 genera found in our vegetation plot dataset. The nomenclature of all datasets was standardised to
437 match to the GBIF backbone nomenclature.

438

439 TRY trait observations correspond to TRY trait ID numbers 3106 (plant height), 3115, 3116, and
440 3117 (specific leaf area), 26 (seed mass), 47 (leaf dry matter content), 3108, 3109, 3110, 3111,

441 3112, 3113, and 3114 (leaf area; for species with compound leaves only 3108, 3110, 3112, and
442 3114), 14 (leaf nitrogen content), and 15 (leaf phosphorus content).

443

444 We cleaned the combined trait data chiefly following the data cleaning procedures *sensu*⁴. For
445 each observation, we determined its error risk by calculating how many standard deviations (SD)
446 it differs from the mean of the given species and trait (the focal observation excluded in the SD
447 and mean calculations). If there were less than four trait observations we included all data, if less
448 than 10 observations we included only observations with error risk less than 2.25, and otherwise
449 we used an error risk threshold of three.

450

451 In addition, we plotted the histograms of trait observations for each species and trait and based
452 on expert knowledge we manually excluded trait values that were considered impossible in the
453 context of tundra vegetation, for instance 10 m for the height of *Juniperus communis* or
454 otherwise suspicious values. If a species missed data for a trait, we used genus-level
455 observations. Here, we selected only georeferenced observations within the tundra climatic zone
456 (class "ET" in ¹⁰⁹) and then averaged the trait values over the species within the genus. After
457 filtering, we had 76475 trait observations at the species level for the species recorded in the study
458 plots and an additional 38322 observations (partially overlapping with the former), which we
459 used to calculate the genus-level traits, if no species-level data were available.

460

461 We used hierarchical sampling and bootstrapping to construct community weighted mean
462 (CWM) values for the vegetation plots to account for the varying relevance of the trait
463 observation for tundra vegetation and the intraspecific variation present in the trait observation

464 data (we used a slightly modified version of the code available at
465 <https://github.com/richardjtelford/traitstrap>). For each trait observation, we checked whether it
466 had location information, and for georeferenced observations, we extracted information about its
467 climate using a fine-scale climate classification ¹⁰⁹.

468

469 First, we used five nested hierarchies to classify the relevance of the trait observations: three
470 nested Köppen-Geiger climate classifications (I-III), the status of georeferencing (IV), and the
471 global level, in which all trait records were included (V). Then each trait observation got a
472 weight based on the abundance of the species in a plot, which is the finest hierarchy level at
473 which the trait observation matches to the plot data. This means that for example a georeferenced
474 trait observation recorded within the tundra climate class (matching all hierarchy levels with our
475 plot data) got five times a higher weight (because of the I-V hierarchy levels) compared to a non-
476 georeferenced global-level observation. Based on these weights, we took a random sample of
477 100 trait observations and calculated the CWM values for each plot. We repeated this sampling
478 100 times for each plot to see how much the intraspecific variation in the trait data affects the
479 CWMs. We selected CWMs to the statistical analyses only if trait data (species or genus level)
480 were available for the species that comprise at least 90% of the total cover in the plot.

481

482 Depending on the trait, species-level trait data covered on average 96.9% (seed mass) to 99.5%
483 (plant height) of the recorded species weighted by their cover in the study plots. When genus-
484 level trait data was included the corresponding numbers were 99.1% and 99.9%. The average
485 number of trait observations per species weighted by their abundance in the plots varied between
486 32.9 (seed mass) and 667.0 (plant height) depending on trait. See Appendix 8 for a

487 comprehensive summary and basic statistics of the coverage of the trait data and CWM
488 bootstrapping estimates by study site and by functional trait.

489
490 In the analyses, we use CWM and log-transformed the following traits: plant height, specific leaf
491 area, seed mass, and leaf area. We had 61 vascular plant species from the high-Arctic, 75 from
492 the low-Arctic, 134 from the sub-Arctic, and 18 from the sub-Antarctic (see full species list in
493 Appendix 6). In total we had 217 species, of which 88 species were found in more than one of
494 the sites. If traits were available, ferns were included in the analyses, except for the seed mass
495 analysis.

496 497 **Environmental data**

498 Soil moisture

499 In tundra, plants distribute a large part of their biomass below ground surface, as their roots are
500 relatively shallow^{110,111}. The rooting depth of plants is limited due to permafrost and a rather
501 shallow A-horizon¹¹², consequently, plant-available water is found in the top-soil layer^{53,55}. We
502 used a hand-held time-domain reflectometry sensor to measure soil moisture (as volumetric
503 water content (VWC%)) up to a depth of 10 cm in the low-Arctic site and 7.5 cm in the rest of
504 the sites (FieldScout TDR 300; Spectrum Technologies, Plainfield, IL, USA). Soil moisture was
505 measured once in the high-Arctic and low-Arctic sites (August 8th and July 9th 2018), on three
506 occasions in the sub-Arctic site (June 12th to 13th; July 23rd to 24th; August 9th 2013), and on
507 five occasions in the sub-Antarctic site (June 22nd, July 27th, October 3rd 2016; January 26th
508 and April 15th 2017). On each sampling occasion, three measurements were taken from each
509 plot, accounting for possible within-plot moisture variation. Consequently, the mean of the three

510 points was used for calculating the soil moisture level of each plot. In sites where we measured
511 soil moisture on several occasions, we took the mean of the measurements to represent the
512 overall soil moisture level of a given plot ^{44,52}. To ensure comparability of measurements, each
513 set of measurements was taken on a day where there had been no precipitation for at least the
514 preceding 24 hours ⁸².

515

516 Soil temperature

517 We measured soil temperature using miniature temperature loggers (Thermochron iButton
518 DS1921G and DS1922L; temperature range between -40 and 85°C, resolution of 0.5°C, and
519 accuracy of 0.5°C). We installed the loggers 5 to 10 cm below the ground surface. The loggers
520 collected data for one year with 2-4 hour intervals (except at the sub-Antarctic site where the
521 year fell short by two weeks). High-quality data were obtained from 69 loggers from the high-
522 Arctic site in 2018-2019, 72 from the low-Arctic in 2018-2019, 322 from the sub-Arctic in 2013-
523 2014, and 52 from the sub-Antarctic in 2016-2017. The study grids had a maximum of 18
524 loggers per grid and a minimum of three. We calculated mean annual soil temperature for each
525 logger plot and estimated values for the remaining plots using bilinear interpolation. We forced
526 the values to stay between the minimum and maximum of the true measured mean annual soil
527 temperatures within a given grid.

528

529 Soil pH

530 We collected soil samples for the pH analysis from a subset of plots at the sites. In the high-
531 Arctic and low-Arctic sites, we collected 12 samples from each grid (in total 72 per site). In the
532 sub-Arctic, we collected 18 samples from each grid (in total 378). In the sub-Antarctic, we

533 collected between 16 and 39 samples per grid (in total 180). We estimated the pH values for the
534 remaining plots using bilinear interpolation. We forced the values between the minimum and
535 maximum of the laboratory measured soil pH within a given grid.

536

537 In the three Arctic sites, soil pH was determined from air-dried soil samples using distilled water
538 as a solution liquid following the International Organization for Standardization 10390:1994 (E)
539 protocol. The only difference in the protocol regarding the three Arctic sites was that the high-
540 Arctic and low-Arctic samples were oven-dried, whereas the sub-Arctic samples were freeze
541 dried. For the sub-Antarctic site, soil pH was determined from air-dried soil samples, measured
542 in calcium chloride solution (0.01 M). Calcium chloride in the solution increases dissolution of
543 H⁺ from soil particles to the measurement solution and measured pH values can be lower
544 compared to the pH values measured from soil-water solution ¹¹³. This may affect the
545 comparability of pH values between sub-Antarctic and Arctic sites, thus, we chose to analyse the
546 data using hierarchical generalized additive models, which enabled us to account for possible
547 minor differences between the sites.

548

549 Potential solar radiation

550 Incident radiation was calculated as the maximum potential solar radiation per plot (i.e. assuming
551 clear sky conditions) using field-quantified slope and aspect values of each plot for the Northern
552 Hemisphere ¹¹⁴ and for the Southern Hemisphere ¹¹⁵.

553

554 Coarse-scale variables

555 Data on annual mean air temperature (2 m above the soil surface) and annual precipitation at a
556 resolution of circa 1000 meters were downloaded from the Chelsa Climate database ¹¹⁶. Potential
557 solar radiation was calculated using the ASTER Global Digital Elevation Model downloaded
558 from NASA's Land Processes Distributed Active Archive Center ¹¹⁷. Data on soil pH in H₂O
559 solution at the resolution of 250 m were downloaded from the SoilGrids database ¹¹⁸. The
560 Spearman's correlation between the field-quantified and coarse-scale environmental variables
561 were as follows: temperature 0.83, moisture 0.52, soil pH 0.48, and radiation 0.83. See Appendix
562 2 for comparison between results derived from the fine-scale and coarse-scale data.

563

564 **Statistical analysis**

565 The environmental drivers showed weak collinearity (Spearman's correlations -0.31 to 0.42;
566 Appendix 9), thus, we included them all as predictors. All trait-environment relationships were
567 significant ($p \leq 0.05$), except for three global relationships: leaf dry matter content and radiation
568 ($p = 0.90$), leaf phosphorus and soil pH ($p = 0.14$), and specific leaf area and radiation ($p = 0.12$).

569

570 We analysed the data using hierarchical generalized additive models (Hierarchical GAMs or
571 HGAMs ⁴⁹). The generalized additive model (GAM) is a flexible technique for modelling
572 outcomes as nonlinear functions of predictor variables. HGAMs are a conceptual extension of
573 GAMs, in a similar way that linear mixed models are an extension of linear models. HGAMs can
574 be used to study whether the functional relationship between response and predictor has the same
575 form for all levels of a grouping variable (in this study across the four sites). The relative
576 importance of the global relationship vs. site-specific deviations from the relationship for
577 explaining the response variable can then be assessed. We chose HGAMs as our modelling

578 approach because our data set is nested into four distinct study sites. We modelled the fine-scale
579 and coarse-scale models using the same methodology.

580

581 We fitted the HGAMs with the package *mgcv* version 1.8-24¹¹⁹, using the following command:

582 `gam(response ~`

583 `s(soil moisture, k=20) + s(soil moisture, site, k=20, bs="fs")`

584 `+ s(soil temperature, k=20) + s(soil temperature, site, k=20, bs="fs")`

585 `+ s(soil pH, k=20) + s(soil pH, site, k=20, bs="fs")`

586 `+ s(radiation, k=20) + s(radiation, site, k=20, bs="fs")`

587 `+ s(site, grid, bs = "re"),`

588 `method="REML",`

589 `min.sp = c(rep(1,times=16),0))`

590 Our model structure was as follows: for each environmental driver, we used a thin plate spline to

591 represent the global trait-environment relationship. Site-specific deviations from the global

592 relationship were included as simple factor-smooth interactions, where the site-specific splines

593 had the same wiggleness as the global splines. Here, the wiggleness of a spline refers to how

594 quickly the function changes across its scale⁴⁹. Each spline was constructed of 20 basis

595 functions. We also included a random intercept for each site-grid combination (i.e., a random

596 effect for each unique grid). To avoid overfitting, we specified that the smoothing parameters of

597 the environmental response splines must have a minimum value of 1. This choice was based on

598 visual evaluation of preliminary models and their smoothness parameters. Higher values of the

599 smoothing parameter mean less wiggly splines. Separate models were fitted for all traits using

600 restricted maximum likelihood (REML) estimation. We used R version 3.5.1 for all analyses and
601 models ¹²⁰.

602

603 The fitted values of a GAM model are the sum of all splines (global, local, random intercept;
604 Table 1) and the model intercept. We quantified model fit as the squared correlation of observed
605 and fitted values (r^2). We assessed the relative importance of global and local trait-environment
606 relationships by first subtracting the site-specific splines from the fitted values and noting the
607 decrease in r^2 . We then continued to subtract the global splines and again noted the decrease in
608 r^2 . The sum of these decreases we interpret as the amount of variation explained by the
609 environment. We compared the relative magnitudes of these two values for each site-trait
610 combination to infer whether plant community functional trait composition is explained by
611 global or local trait-environment relationships (Figure 2).

612

613 We performed a principal component analysis (PCA) separately for the environmental and trait
614 data (Appendix 3). Here, we used the package *FactoMineR* to scale the data to unit variance and
615 derive the principal component scores for the first two components (PCA1 and PCA2) and the
616 variable contributions ^{121,122}. Then, we calculated the Spearman's correlation between the
617 components as follows: 1) environmental PCA1 and trait PCA1, 2) environmental PCA2 and
618 trait PCA2, 3) environmental PCA1 and trait PCA2, and 4) environmental PCA2 and trait PCA1
619 (Appendix 4).

620

621 We assessed the relative importance of each environmental variable using HGAM (Appendix 5).
622 Here, we compared the model (full model) with sets of reduced models. In the latter, we

623 excluded one variable at a time from the full model. This exclusion comprised both the global
624 and site-level terms of a given variable. Then, we compared the deviance explained of the full
625 model and the reduced models to quantify how well including a given variable improved the
626 prediction of the effect seen in the full model. In the reduced models, we used the same penalty
627 terms as in the full model, to ensure that the reduced model did not only increase the flexibility
628 of a term correlated with the excluded variable, which could have improved the fit of the model.

629

630 We repeated the HGAM analysis using coarse-scale climate and grid data instead of the fine-
631 scale *in situ* data using the following command:

```
632 gam(response ~  
633       s(soil moisture, k=10)  
634       + s(soil temperature, k=10)  
635       + s(soil pH, k=10)  
636       + s(radiation, k=10)  
637       + s(site, grid, bs = "re"),  
638       method="REML",  
639       min.sp = c(rep(1,times=4),0))
```

640

641 **Data availability**

642 We have provided the reviewers the data. The data will be deposited in a public repository upon
643 publication if the manuscript is accepted for publication.

644

645 **Code availability**

646 We have provided the reviewers the code. The code will be deposited in a public repository upon
647 publication if the manuscript is accepted for publication.

648 **Appendix 1**

649 Appendix 1. Within-grid variation versus variability in the whole dataset. We calculated the
650 amount of variation in each variable, which we measured as range and standard deviation of the
651 environmental predictors and CWM traits within each of the 42 study grids and compared the
652 variation to the whole data consisting all study sites. The values are averaged over all grids and
653 separately for each study site. For instance, we found that soil moisture shows especially great
654 within-grid variability, as on average a grid has approximately 50% of the variation of the entire
655 dataset. Whereas, soil temperature displays the least within-grid variability of the four
656 environmental variables.

	All sites	High-Arctic	Low-Arctic	Sub-Arctic	Sub-Antarctic
	Range				
Soil moisture	47.3	64.3	52.0	41.0	47.4
Soil temperature	17.3	25.3	26.4	16.1	8.9
Soil pH	31.3	32.4	41.0	29.3	28.8
Radiation	43.3	27.4	56.1	45.7	39.8
Leaf area	19.6	7.3	15.2	5.4	64.0
Plant height	44.9	23.9	75.9	47.5	32.2
Seed mass	35.6	11.4	7.6	59.2	15.2
Leaf dry matter content	37.1	60.7	48.4	34.4	20.4
Leaf nitrogen content	43.9	62.3	51.2	43.8	26.8
Leaf phosphorus content	45.7	65.8	56.8	46.8	22.3
Specific leaf area	50.5	51.8	57.8	49.4	47.2
	Standard deviation				
Soil moisture	48.7	72.7	59.6	38.4	49.7
Soil temperature	16.4	27.8	23.0	14.7	8.3
Soil pH	36.1	36.9	50.4	34.3	30.1
Radiation	36.7	23.2	49.3	37.2	36.1
Leaf area	27.0	13.0	20.1	6.6	88.6
Plant height	63.7	34.7	142.8	61.7	35.3
Seed mass	56.5	24.8	12.9	89.6	29.4
Leaf dry matter content	35.5	54.6	43.3	34.9	18.8
Leaf nitrogen content	58.5	81.6	57.9	63.9	30.9
Leaf phosphorus content	57.2	75.2	68.9	64.3	20.8
Specific leaf area	64.4	63.4	59.0	70.2	55.0

657

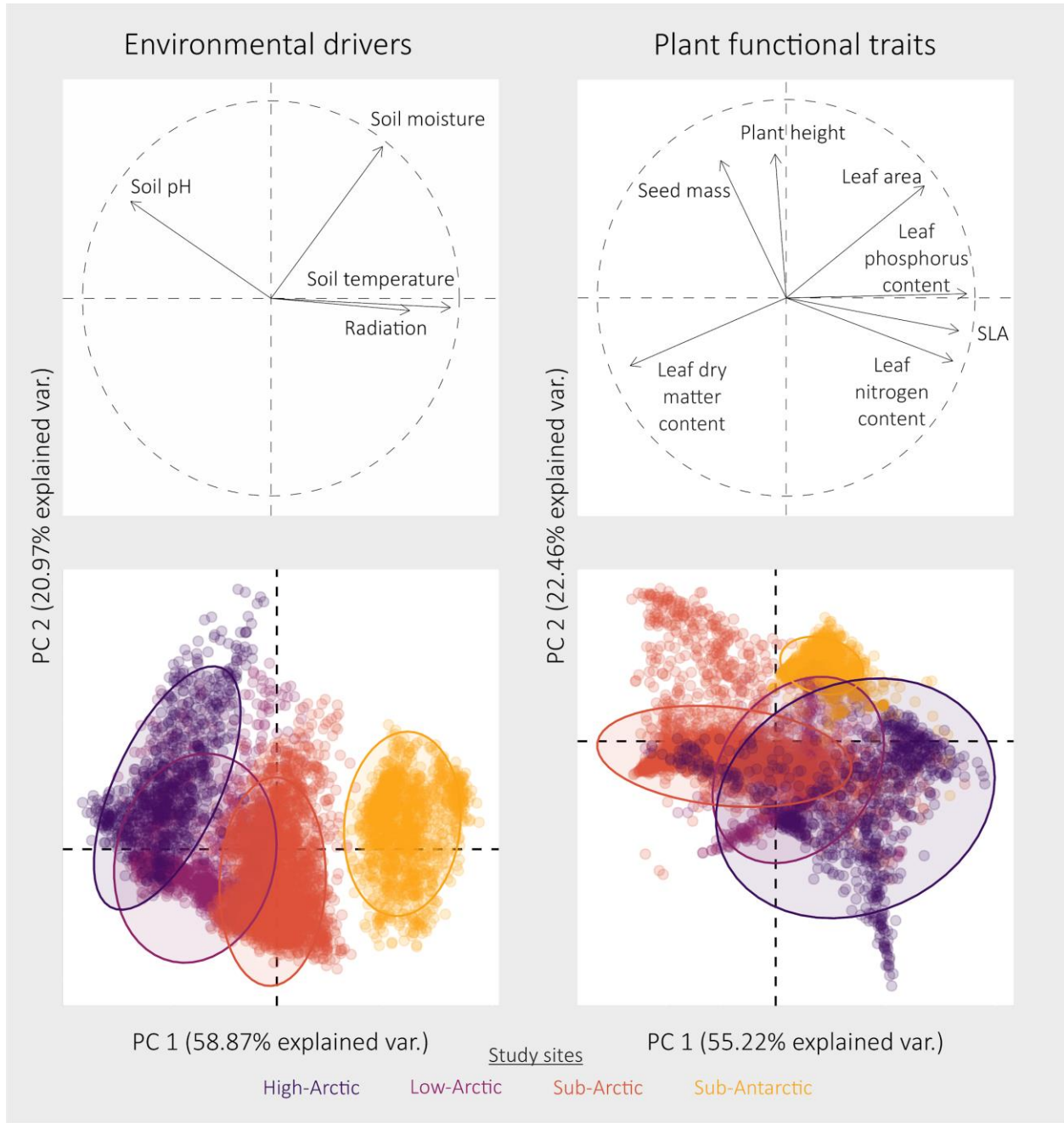
658 **Appendix 2**

659 Appendix 2. Comparison of the results based on the fine-scale and coarse-scale data. Results
 660 based on the fine-scale data outperformed the coarse-scale for all seven plant functional traits.
 661 The r^2 values for the models are divided between the random effect and the global trait-
 662 environment relationship, and for the fine-scale data also the local trait-environment relationship.
 663 The higher the value, the greater proportion explained by the factor.

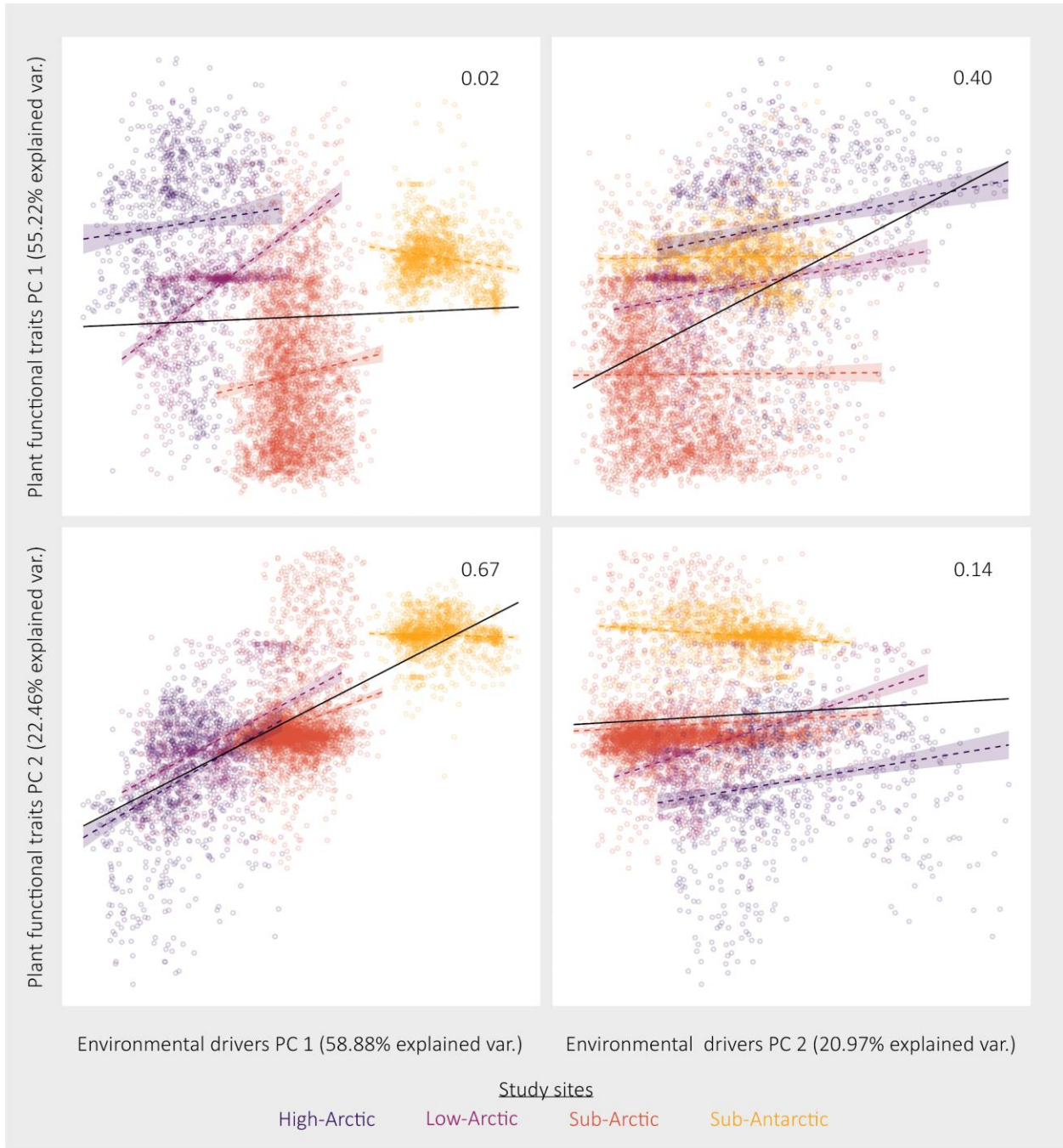
Plant trait	Deviance explained (%)		Site	Random effect		Global relationship		Local relationship
	Fine-scale	Coarse-scale		Fine-scale	Coarse-scale	Fine-scale	Coarse-scale	Fine-scale
Leaf area	87.7	86.5	High-Arctic	0.22	0.32	0.35	0.04	0.03
			Low-Arctic	0.11	0.33	0.37	0.03	0.04
			Sub-Arctic	0.27	0.21	0.21	0.15	0.05
			Sub-Antarctic	0.30	0.05	-0.01	0.06	0.06
Plant height	54.2	48.5	High-Arctic	0.19	0.17	0.38	0.19	0.02
			Low-Arctic	0.02	0.10	0.28	0.13	0.03
			Sub-Arctic	0.18	0.00	0.00	0.22	0.08
			Sub-Antarctic	0.32	0.43	0.03	0.01	0.02
Seed mass	55.6	48.9	High-Arctic	0.12	0.14	0.35	0.02	0.03
			Low-Arctic	0.05	0.17	0.14	0.01	0.17
			Sub-Arctic	0.22	0.12	0.03	0.18	0.10
			Sub-Antarctic	0.17	0.38	0.05	0.12	0.04
Leaf dry matter content	87.6	83.1	High-Arctic	0.42	0.46	0.18	0.03	0.03
			Low-Arctic	0.20	0.36	0.24	0.01	0.05
			Sub-Arctic	0.19	0.21	0.20	0.09	0.09
			Sub-Antarctic	0.35	0.28	0.03	0.11	0.18
Leaf nitrogen content	69.5	59.9	High-Arctic	0.21	0.28	0.24	0.02	0.04
			Low-Arctic	0.15	0.20	0.06	0.02	0.13
			Sub-Arctic	0.24	0.15	0.21	0.19	0.05
			Sub-Antarctic	0.00	0.00	0.12	0.25	0.10
Leaf phosphorus content	71.2	61.3	High-Arctic	0.34	0.41	0.24	0.01	0.05
			Low-Arctic	0.19	0.29	0.16	0.01	0.14
			Sub-Arctic	0.25	0.19	0.19	0.15	0.04
			Sub-Antarctic	0.02	0.09	0.04	0.03	0.21
Specific leaf area	65.0	57.0	High-Arctic	0.45	0.41	0.14	0.08	0.03
			Low-Arctic	0.15	0.15	-0.03	0.02	0.10
			Sub-Arctic	0.30	0.17	0.23	0.24	0.05
			Sub-Antarctic	0.01	0.07	0.10	0.37	0.01

664

665



668 Appendix 3. Principal component analysis of the environmental space and the plant functional trait
669 space. The upper panels present the data distributed according to the environmental space (left)
670 and the plant functional trait space (right). In the lower panels, the circles represent the 6720 study
671 plots and the ellipsoids the sites in relation to the environmental space (left) and the plant functional
672 trait space (right). The variation explained by each axis is shown in brackets. SLA = Specific leaf
673 area.
674



677 Appendix 4. Linear relationships between principal components of the environmental and trait
678 space. The strongest correlations are found between 1) the primary axis of the environmental
679 drivers (representing mainly the mean annual soil temperature, soil pH, and potential solar
680 radiation) and the secondary axis of the traits (plant height, leaf area, and seed mass), and
681 between 2) their secondary axis (soil moisture) and primary axis (specific leaf area, leaf dry
682 matter content, leaf nitrogen content, and leaf phosphorus content). The circles represent the
683 6720 study plots. The values in the upper corners of the panels show the Spearman's correlation
684 between the plotted principal component (PC) axes. The black line represents a linear trend
685 across all sites, and the coloured within each site and the band the confidence interval of 0.95%.
686 See Appendix 3 for details.

687 **Appendix 5**

688 Appendix 5. The relative importance of environmental drivers. We compared the full HGAM
 689 model with sets of reduced models. In the latter, we excluded one environmental variable at a
 690 time from the full model. This exclusion comprised both the global and site-level terms of a
 691 given environmental variable. In the reduced models, we used the same penalty terms as in the
 692 full model, to ensure that the reduced model did not only increase the flexibility of a term
 693 correlated with the excluded variable, which could have improved the fit of the model. Variable
 694 importance was assessed by repeating HGAM models after the exclusion of one environment
 695 variable at a time. The values reported here are the deviance explained values for the reduced
 696 models, with the lowest values for each trait indicating that a model performed worst after the
 697 exclusion of that specific predictor variable. In other words, the lower the value, the higher the
 698 relative importance of a given environmental variable. For example, soil temperature was
 699 relatively the most important variable for most of the traits, except for plant height, for which
 700 soil moisture was more important.

Plant trait	Soil moisture	Soil temperature	Soil pH	Solar radiation
Leaf area	0.87	0.86	0.87	0.88
Plant height	0.52	0.53	0.53	0.53
Seed mass	0.55	0.54	0.54	0.54
Leaf dry mass content	0.87	0.87	0.87	0.88
Leaf nitrogen content	0.68	0.66	0.68	0.69
Leaf phosphorus content	0.70	0.68	0.70	0.71
Specific leaf area	0.63	0.60	0.64	0.65

701

702 **Appendix 6**

703 Appendix 6. Species list shows the presence and absence of the species in the study plots of the
704 four study sites. The first row shows how many species were observed at each site. The last
705 column on the right shows in how many sites a given species was observed.

Species	High-Arctic	Low-Arctic	Sub-Arctic	Sub-Antarctic	Multiple sites	Species	High-Arctic	Low-Arctic	Sub-Arctic	Sub-Antarctic	Multiple sites
In total = 217 species	61	75	134	18	88						
<i>Aceno magellanica</i>	0	0	0	1	1	<i>Linnaea borealis</i>	0	0	1	0	1
<i>Achillea millefolium</i>	0	0	1	0	1	<i>Luzula arctica</i>	1	1	0	0	2
<i>Agrostis mertensii</i>	0	0	1	0	1	<i>Luzula arcuata</i>	0	0	1	0	1
<i>Agrostis stolonifera</i>	0	0	0	1	1	<i>Luzula confusa</i>	1	1	1	0	3
<i>Alchemilla sp.</i>	0	0	1	0	1	<i>Luzula multiflora</i>	0	1	1	0	2
<i>Alopecurus magellanicus</i>	1	0	0	0	1	<i>Luzula parviflora</i>	0	0	1	0	1
<i>Andromeda polifolia</i>	0	0	1	0	1	<i>Luzula spicata</i>	0	0	1	0	1
<i>Angelica archangelica</i>	0	0	1	0	1	<i>Luzula sudetica</i>	0	0	1	0	1
<i>Antennaria alpina</i>	0	1	1	0	2	<i>Luzula wahlenbergii</i>	0	0	1	0	1
<i>Antennaria canescens</i>	0	0	1	0	1	<i>Lycopodium clavatum</i>	0	0	1	0	1
<i>Antennaria dioica</i>	0	0	1	0	1	<i>Lysimachia europaea</i>	0	0	1	0	1
<i>Anthoxanthum monticola</i>	0	1	1	0	2	<i>Micranthes foliolosa</i>	1	0	1	0	2
<i>Anthoxanthum odoratum</i>	0	0	1	0	1	<i>Micranthes nivalis</i>	1	0	1	0	2
<i>Arctostaphylos uva-ursi</i>	0	0	1	0	1	<i>Micranthes tenuis</i>	1	0	0	0	1
<i>Arctous alpina</i>	0	0	1	0	1	<i>Mantia fontana</i>	0	0	0	1	1
<i>Artemisia borealis</i>	0	1	0	0	1	<i>Nardus stricta</i>	0	0	1	0	1
<i>Astragalus alpinus</i>	0	0	1	0	1	<i>Neottia cordata</i>	0	0	1	0	1
<i>Astragalus frigidus</i>	0	0	1	0	1	<i>Omalotheca norvegica</i>	0	0	1	0	1
<i>Astrablechnum penna r</i>	0	0	0	1	1	<i>Omalotheca supina</i>	0	0	1	0	1
<i>Austrolycopodium mage</i>	0	0	0	1	1	<i>Orthilia secunda</i>	0	0	1	0	1
<i>Avenella flexuosa</i>	0	0	1	0	1	<i>Oxyria digyna</i>	1	1	1	0	3
<i>Azorella selago</i>	0	0	0	1	1	<i>Papaver radiculatum</i>	1	0	0	0	1
<i>Bartsia alpina</i>	0	0	1	0	1	<i>Parnassia palustris</i>	0	0	1	0	1
<i>Betula nana</i>	0	1	1	0	2	<i>Pedicularis dasyantha</i>	0	1	0	0	1
<i>Betula pubescens</i>	0	0	1	0	1	<i>Pedicularis flammea</i>	0	1	0	0	1
<i>Bistorta vivipara</i>	1	1	1	0	3	<i>Pedicularis hirsuta</i>	1	0	0	0	1
<i>Botrychium lunaria</i>	0	0	1	0	1	<i>Pedicularis lapponica</i>	0	1	1	0	2
<i>Calamagrostis canadensis</i>	0	1	0	0	1	<i>Phlegmarium saururus</i>	0	0	0	1	1
<i>Calamagrostis lapponica</i>	0	0	1	0	1	<i>Phleum alpinum</i>	0	0	1	0	1
<i>Calamagrostis neglecta</i>	0	1	0	0	1	<i>Phyllocladus caerulea</i>	0	0	1	0	1
<i>Campanula rotundifolia</i>	0	1	1	0	2	<i>Pinguicula alpina</i>	0	0	1	0	1
<i>Cardamine bellidifolia</i>	1	1	1	0	3	<i>Pinguicula vulgaris</i>	0	0	1	0	1
<i>Carex aquatilis</i>	0	1	0	0	1	<i>Poa alpigena</i>	0	1	1	0	2
<i>Carex arctogena</i>	0	0	1	0	1	<i>Poa alpina</i>	1	1	1	0	3
<i>Carex atrata</i>	0	0	1	0	1	<i>Poa annua</i>	0	0	0	1	1
<i>Carex austrocompacta</i>	0	0	0	1	1	<i>Poa arctica</i>	1	1	1	0	3
<i>Carex bigelowii</i>	0	1	1	0	2	<i>Poa cookii</i>	0	0	0	1	1
<i>Carex canescens</i>	0	1	1	0	2	<i>Poa glauca</i>	1	1	0	0	2
<i>Carex capillaris</i>	0	0	1	0	1	<i>Poa nemoralis</i>	0	0	1	0	1
<i>Carex glacialis</i>	0	1	0	0	1	<i>Poa pratensis</i>	1	0	0	1	2
<i>Carex lachenalii</i>	1	0	0	0	2	<i>Polemonium boreale</i>	1	0	0	0	1
<i>Carex myosuroides</i>	0	1	0	0	1	<i>Polygopus magellanicus</i>	0	0	0	1	1
<i>Carex nardina</i>	0	1	0	0	1	<i>Potentilla crantzii</i>	0	0	1	0	1
<i>Carex norvegica</i>	0	0	1	0	1	<i>Potentilla hyperarctica</i>	1	0	0	0	1
<i>Carex panicea</i>	0	0	1	0	1	<i>Potentilla nivea</i>	0	1	0	0	1
<i>Carex parallela</i>	0	0	1	0	1	<i>Pyrola grandiflora</i>	0	1	0	0	1
<i>Carex raniflora</i>	0	1	0	0	1	<i>Pyrola minor</i>	0	0	1	0	1
<i>Carex rupestris</i>	1	1	1	0	3	<i>Pyrola rotundifolia</i>	0	0	1	0	1
<i>Carex saxatilis</i>	0	1	0	0	1	<i>Ranunculus acris</i>	0	0	1	0	1
<i>Carex supina</i>	0	1	0	0	1	<i>Ranunculus bitermatus</i>	0	0	0	1	1
<i>Carex vaginata</i>	0	0	1	0	1	<i>Ranunculus nivalis</i>	1	0	1	0	2
<i>Cassiope tetragona</i>	1	1	1	0	3	<i>Ranunculus pygmaeus</i>	1	1	0	0	2
<i>Cerastium sp.</i>	0	0	1	0	1	<i>Ranunculus sulphureus</i>	1	0	0	0	1
<i>Cerastium alpinum</i>	0	1	1	0	2	<i>Rhodiola rosea</i>	0	0	1	0	1
<i>Cerastium arcticum</i>	1	0	0	0	1	<i>Rhodiodendron lapponicum</i>	0	1	1	0	2
<i>Cerastium cerastoides</i>	0	1	0	0	1	<i>Rhodiodendron tomentosum</i>	0	1	0	0	1
<i>Cerastium fontanum</i>	0	0	0	1	1	<i>Rubus saxatilis</i>	0	0	1	0	1
<i>Cerastium regelii</i>	1	0	0	0	1	<i>Rumex acetosa</i>	0	0	1	0	1
<i>Cherleria biflora</i>	1	1	1	0	3	<i>Sabulina rubella</i>	1	1	0	0	2
<i>Cystopteris fragilis</i>	0	0	1	0	1	<i>Sagina nivalis</i>	1	0	0	0	1
<i>Dactylorhiza viridis</i>	0	0	1	0	1	<i>Sagina procumbens</i>	0	0	0	1	1
<i>Deschampsia alpina</i>	1	0	0	0	1	<i>Sagina saginoides</i>	0	0	1	0	1
<i>Deschampsia cespitosa</i>	0	0	1	0	1	<i>Salix arctophila</i>	0	1	0	0	1
<i>Diapensia lapponica</i>	0	1	1	0	2	<i>Salix glauca</i>	0	1	1	0	2
<i>Diphysastrum alpinum</i>	0	0	1	0	1	<i>Salix hastata</i>	0	0	1	0	1
<i>Draba sp.</i>	0	1	0	0	1	<i>Salix herbacea</i>	0	1	1	0	2
<i>Draba alpina</i>	1	0	0	0	1	<i>Salix lapponum</i>	0	0	1	0	1
<i>Draba arctica</i>	1	0	0	0	1	<i>Salix myrsinifolia</i>	0	0	1	0	1
<i>Draba fladinensis</i>	1	0	0	0	1	<i>Salix myrsinoides</i>	0	0	1	0	1
<i>Draba glabella</i>	1	1	1	0	3	<i>Salix phylicifolia</i>	0	0	1	0	1
<i>Draba lactea</i>	1	0	0	0	1	<i>Salix polaris</i>	1	0	1	0	2
<i>Draba micropetala</i>	1	0	0	0	1	<i>Salix reticulata</i>	0	0	1	0	1
<i>Draba nivalis</i>	1	1	1	0	3	<i>Saussurea alpina</i>	0	1	1	0	1
<i>Draba norvegica</i>	1	0	0	0	1	<i>Saxifraga cernua</i>	1	1	0	0	2
<i>Draba pauciflora</i>	1	0	0	0	1	<i>Saxifraga cespitosa</i>	1	0	1	0	2
<i>Draba subcapitata</i>	1	0	0	0	1	<i>Saxifraga hieracifolia</i>	1	0	0	0	1
<i>Dryas integrifolia</i>	0	1	0	0	1	<i>Saxifraga hirculus</i>	1	0	0	0	1
<i>Dryas octopetala</i>	1	0	1	0	2	<i>Saxifraga hyperborea</i>	1	0	0	0	1
<i>Empetrum nigrum</i>	0	1	1	0	2	<i>Saxifraga oppositifolia</i>	1	1	0	0	2
<i>Epilobium angustifolium</i>	0	0	1	0	1	<i>Saxifraga platysepalis</i>	1	0	0	0	1
<i>Epilobium latifolium</i>	0	1	0	0	1	<i>Saxifraga rivularis</i>	0	1	0	0	1
<i>Equisetum arvense</i>	1	1	0	0	2	<i>Saxifraga svalbardensis</i>	1	0	0	0	1
<i>Equisetum palustre</i>	0	0	1	0	1	<i>Saxifraga tricuspidata</i>	0	1	0	0	1
<i>Equisetum pratense</i>	0	0	1	0	1	<i>Scorzonoides autumnalis</i>	0	0	1	0	1
<i>Equisetum scirpoides</i>	1	0	1	0	2	<i>Selaginella selaginoides</i>	0	0	1	0	1
<i>Equisetum variegatum</i>	1	0	0	0	1	<i>Sibbaldia procumbens</i>	0	0	1	0	1
<i>Erigeron humilis</i>	0	1	0	0	1	<i>Silene acaulis</i>	1	1	1	0	3
<i>Erigeron uniflorus</i>	0	0	1	0	1	<i>Silene involucreta</i>	1	1	0	0	2
<i>Eriophorum angustifolium</i>	0	1	1	0	2	<i>Silene suecica</i>	0	0	1	0	1
<i>Euphrasia wettsteinii</i>	0	1	1	0	2	<i>Silene uralensis</i>	0	0	1	0	1
<i>Festuca brachyphylla</i>	0	1	0	0	1	<i>Solidago virgaurea</i>	0	0	1	0	1
<i>Festuca edlundiae</i>	1	0	0	0	1	<i>Spinulum annotinum</i>	0	0	1	0	1
<i>Festuca ovina</i>	0	0	1	0	1	<i>Stellaria humifusa</i>	0	1	0	0	1
<i>Festuca rubra</i>	1	1	0	0	2	<i>Stellaria longipes</i>	1	1	0	0	2
<i>Festuca viviparoides</i>	1	0	0	0	1	<i>Taraxacum sp.</i>	0	1	1	0	2
<i>Gentiana nivalis</i>	0	0	1	0	1	<i>Thalictrum alpinum</i>	0	1	1	0	2
<i>Geranium sylvaticum</i>	0	0	1	0	1	<i>Tofieldia coccinea</i>	0	1	0	0	1
<i>Grammitis poeppigiana</i>	0	0	0	1	1	<i>Tofieldia pusilla</i>	0	1	0	0	2
<i>Harrimanella hypnoides</i>	0	1	1	0	2	<i>Trichophorum cespitosum</i>	0	0	1	0	1
<i>Hieracium sp.</i>	0	0	1	0	1	<i>Trisetum spicatum</i>	1	1	1	0	3
<i>Huperzia selago</i>	0	0	1	0	1	<i>Vaccinium myrtillus</i>	0	0	1	0	1
<i>Hymenophyllum peltatum</i>	0	0	0	1	1	<i>Vaccinium uliginosum</i>	0	1	1	0	2
<i>Juncus biglumis</i>	1	1	1	0	3	<i>Vaccinium vitis-idaea</i>	0	1	1	0	2
<i>Juncus castaneus</i>	0	1	0	0	1	<i>Vahldeia atropurpurea</i>	0	0	1	0	1
<i>Juncus scheuchzerioides</i>	0	0	0	1	1	<i>Veronica alpina</i>	0	0	1	0	1
<i>Juncus trifidus</i>	0	1	1	0	2	<i>Veronica fruticans</i>	0	0	1	0	1
<i>Juniperus communis</i>	0	0	1	0	1	<i>Viola biflora</i>	0	0	1	0	1
<i>Kalmia procumbens</i>	0	0	1	0	1	<i>Woodсия alpina</i>	0	0	1	0	1
<i>Koenigia islandica</i>	1	0	0	0	1						

707 **Appendix 7**

708 Appendix 7. Full citation list of all sources regarding the plant functional traits data.

709 (Due to its large size, the list is attached as a separate PDF file for the convenience of the reader.)

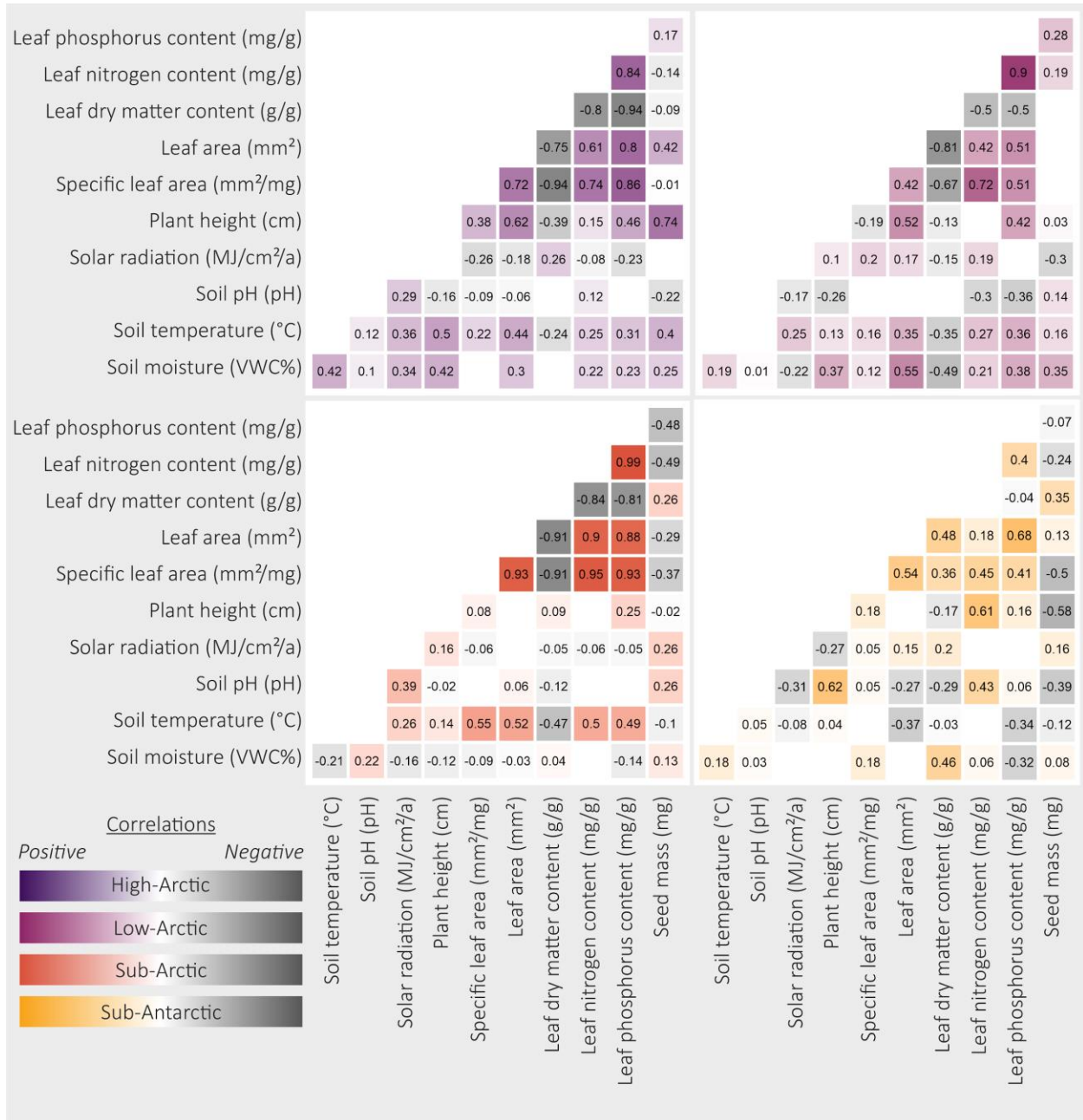
710 **Appendix 8**

711 Appendix 8. A comprehensive summary and basic statistics of the trait data. The table shows the
712 coverage of the trait data and CWM bootstrapping estimates separated by study site and
713 functional trait.

714

715 (Due to its large size, the table is attached as a separate excel file for the convenience of the
716 reader.)

717 **Appendix 9**



718

719 Appendix 9. Bivariate correlations. The correlation matrix shows the Spearman's correlations

720 between variables (n = 6720). Statistically significant ($P < 0.05$) correlations are shown as

721 squares, whereas non-significant correlations ($P \geq 0.05$) are blank.

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