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1 **Intraspecific trait variation in alpine plants relates to their**
2 **elevational distribution**

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47

48 **Abstract**

49

50 Climate warming is shifting the distributions of mountain plant species to higher elevations.
51 Cold-adapted plant species are under increasing pressure from novel competitors that are
52 encroaching from lower elevations. Plant capacity to adjust to these pressures may be
53 measurable as variation in trait values within a species. In particular, the strength and patterns
54 of intraspecific trait variation along abiotic and biotic gradients can inform us whether and
55 how species can adjust their anatomy and morphology to persist in a changing environment.
56 Here, we tested whether species specialized to high elevations or with narrow elevational
57 ranges show more conservative (i.e. less variable) trait responses across their elevational
58 distribution, or in response to neighbours, than species from lower elevations or with wider
59 elevational ranges. We did so by studying intraspecific trait variation of 66 species along 40
60 elevational gradients in four countries in both hemispheres. As an indication of potential
61 neighbour interactions that could drive trait variation, we also analysed plant species' height
62 ratio, its height relative to its nearest neighbour.

63 Variation in alpine plant trait values over elevation differed depending on a species' median
64 elevation and the breadth of its elevational range, with species with lower median elevations
65 and larger elevational range sizes showing greater trait variation, i.e. a steeper slope in trait
66 values, over their elevational distributions. These effects were evidenced by significant
67 interactions between species' elevation and their elevational preference or range for several
68 traits: vegetative height, generative height, specific leaf area and patch area. The height ratio
69 of focal alpine species and their neighbours decreased in the lower part of their distribution
70 because neighbours became relatively taller at lower elevations. In contrast, species with
71 lower elevational optima maintained a similar height ratio with neighbours throughout their
72 range.

73 *Synthesis.* We provide evidence that species from lower elevations and those with larger
74 range sizes show greater intraspecific trait variation, which may indicate a greater ability to
75 respond to environmental changes. Also, larger trait variation of species from lower
76 elevations may indicate stronger competitive ability of upslope shifting species, posing one
77 further threat to species from higher ranges.

78

79 Keywords: climate change, cold-adapted plants, elevation gradient, elevation range,
80 neighbour interactions, plant traits, species distribution

81

82

83 **Introduction**

84

85 There is a pressing need to identify how species and communities will respond to
86 environmental change, but the inherent complexity of natural ecosystems impedes progress.
87 One way to address this complexity is to view ecosystems from a functional trait perspective
88 (McGill et al. 2006). Functional traits are measurable features of an individual that have the
89 potential to impact its survival, growth and fitness (see STable 1 for traits and important
90 functional indications). While most studies have focused on differences in mean trait values
91 among species (e.g. Pellissier et al. 2010, MacLean and Beissinger 2017), there is increasing
92 evidence that there is much intraspecific trait variation as a result of environmental factors,
93 which in the context of global environmental change have the potential to determine outcomes
94 for individual species, competitive interactions among species and community-level responses
95 (Kichenin et al. 2013, Siefert et al. 2015, Bjorkman et al. 2018, Henn et al. 2018, Midolo et al.
96 2019, Giejsztowt et al. 2020).

97 Some plant-specific functional traits, especially size-related ones (e.g. height or leaf
98 size), are powerful indicators of plant performance, vary among species, and are useful for
99 inferring functional changes (e.g. biomass or competitive ability) in communities across
100 ecological scales (Lavorel and Garnier 2002, Cornelissen et al. 2007, Pearson et al. 2013,
101 Freschet et al. 2021). In particular, these traits may show species-specific patterns of variation
102 over environmental gradients. In tundra plants, for example, intraspecific temperature-trait
103 relationships for size-related traits varied significantly between different species over spatial
104 and temporal gradients (Bjorkman et al. 2018). While plant species that are able to grow taller
105 in warmer conditions (e.g. through relatively high phenotypic trait plasticity/variability) may
106 have an advantage under climate change over those that remain small in height irrespective of

107 growing conditions (relatively low trait plasticity/variability), the link between trait variation
108 and competitive outcomes remains untested for most traits (but see Bret-Harte et al. 2001).
109 Also, trait variation may not always be adaptive with regard to environmental circumstances.
110 The large variation in the shape of trait-environment relationships reported for vegetative,
111 economic and reproductive traits for cold-biome species (Bjorkman et al. 2018, Kielyk 2018,
112 Midolo et al. 2019) suggest that these responses depend on the traits studied (for belowground
113 traits see Weemstra et al. 2020b). In addition, the response to any single environmental change
114 can vary, so that members of a community may utilise a diversity of plastic responses (Freschet
115 et al. 2018, Weemstra et al. 2020a). Clearly, systematic, empirical data describing the pattern
116 of intraspecific trait variation over environmental gradients will enhance our understanding of
117 the range of species' responses to shifting environments (Albert et al. 2010, Violle et al. 2012,
118 Siefert et al. 2015). Fortunately, trait values for species have become more common in global
119 trait data repositories (e.g., TRY; Kattge et al. 2020). However, systematic data on intraspecific
120 variation in trait values along entire species ranges are not commonly available across multiple
121 species within ecosystems (Midolo et al. 2019), and this situation limits our understanding of
122 species' responses to environmental change in a community context.

123

124 Intraspecific plant trait variation over environmental gradients is a function of both
125 biotic and abiotic drivers. Generally, the relative importance of biotic drivers decreases towards
126 higher elevations due to cold temperatures according to the stress gradient hypothesis (Bertness
127 and Callaway 1994). There has been a strong research focus on changes to the leading edge of
128 species' geographic distributions (e.g. on mountain summits), where plants are colonising new
129 habitats to track a warming climate (Walther et al. 2005, Pauli et al. 2012, Winkler et al. 2016,
130 Steinbauer et al. 2018, Crepez et al. 2020). However, it is the trailing edge where alpine species
131 can be expected to disappear (Thuiller et al. 2008, Alexander et al. 2015, Wiens 2016, Freeman

132 et al. 2018, Rumpf et al. 2019). Indeed, increasing competition from novel lowland species is
133 considered the most important factor driving local extinctions at the trailing edge of species
134 distributions (Pauli et al. 2007, Engler et al. 2011, Alexander et al. 2015). Although studies are
135 few, there is evidence that the trailing edges of alpine species ranges shift upslope as much or
136 even more than their leading edges do (Rumpf et al. 2019). Hence, if plant intraspecific trait
137 variation can provide insight into the susceptibility of different plant species with respect to
138 their range, much improved predictions can be gained from a better understanding of within-
139 community trait variation over species' entire elevational ranges.

140

141 Alpine plant species differ in their habitat preferences, which is in part expressed by
142 their disparate spatial distributions. Within a complete alpine flora, species may for instance
143 demonstrate different elevational distributions and related temperature ranges, which can be
144 quantified as the median elevation of all observations for that species (Fig. 1; see methods for
145 quality of median as a proxy for a species range). These different habitat preferences along
146 elevational gradients may be reflected in interspecific differences of particular traits (Sundqvist
147 et al. 2013). For example, we may expect different trait values for species that occupy
148 environmentally harsher habitats, such as barren high-alpine scree slopes, compared with those
149 that occupy more benign habitats, such as low-alpine meadows. Species from high alpine and
150 other cold regions often have more conservative life history strategies compared to species
151 from lower elevations; they are slow-growing and small-sized (Körner 2003) with relatively
152 small and tough leaves resulting in low specific leaf area (SLA) and high leaf dry matter content
153 (LDMC; Perez-Harguindeguy et al. 2013, Bjorkman et al. 2018, Thomas et al. 2020). The
154 conservative strategies of high-alpine species may not only be expressed by absolute trait
155 values, but also by relatively low trait variation across their elevational range, that is, low
156 intraspecific trait variation. Conversely, plants that occupy lower elevations of the alpine zone

157 may express larger trait variation across their elevational range because they are likely to be
158 confronted with numerous and more competitive neighbouring species of varying sizes and
159 trait properties. We therefore expect plant species that prefer higher alpine environments to
160 show less trait variation over equivalent elevational increment than species that inhabit lower
161 alpine zones. However, to the best of our knowledge, no study has investigated the generality
162 of this relationship.

163

164 Plant species are specialised to their preferred habitats to different degrees. In the
165 context of alpine species, this degree of specialisation may be expressed as the width of the
166 elevational distribution of each species relative to others within its landscape (Fig. 1). The
167 degree of elevational range specialisation may influence a species' success *vis a vis* global
168 environmental change, e.g., declines of small-ranged plant species across contrasting habitats
169 across Europe (Staude et al. 2021). In aquatic systems, intraspecific trait variation alters the
170 outcome of competition among species (Floder et al. 2021). We do, however, not yet know if
171 specialist species that inhabit a narrow ecological range, and thus a relatively homogenous
172 biotic and abiotic environment, express little trait variation over that range. We hypothesize
173 that generalist species express more trait variation than specialist species over similar vertical
174 elevational increments, however, empirical evidence in the literature that addresses these
175 hypotheses is lacking.

176

177 Here, we studied how aboveground plant functional traits of 66 species vary along
178 environmental gradients that span their entire elevational distributions (upper and lower limits
179 of the alpine zone) on mountain ranges in Switzerland, China, Australia and New Zealand as
180 they represent major mountain regions of the globe. We chose traits that respond to both abiotic
181 and biotic drivers (e.g., plant height, leaf traits) and that could be measured efficiently and in a

182 standardised way in remote field settings. We aimed to identify general patterns of intraspecific
183 trait variation among the alpine species from these diverse environments to reveal whether
184 plants show species-specific patterns of trait variation, and whether the characteristics of the
185 species' geographic distributions (i.e., elevational preference and elevational range) relate to
186 elevation. We defined "preference" as the realized niche where species occurred. Specifically,
187 we asked:

188 1) What are the patterns of species' traits along elevational gradients throughout their
189 entire elevational range? We predicted that traits related to leaf and plant size and reproductive
190 output (i.e., vegetative height, generative height, plant area, flower count and specific leaf area)
191 would decrease in value with elevation, while traits associated with tissue or individual
192 longevity (i.e., leaf dry matter content, horizontal plant size) would increase in value with
193 elevation;

194 2) Is the range of trait values expressed by a plant species related to its elevational
195 preference or range extent? We predicted that, for a given elevational increment (as
196 standardized by mountain range, see methods), species with preferences for higher elevations
197 would express less trait variation than species with preferences for lower elevations. Over
198 similar elevational increments, we also expected that specialist species with narrow elevational
199 ranges would express less trait variation compared to generalist species with broad elevational
200 ranges;

201 3) How do neighbouring plants affect the size of the target species over their elevational
202 distribution? We predicted that plants with a preference for higher elevations would be less
203 capable of increasing their size relative to their neighbours near the lower edge of their
204 distributions, than plants with a preference for lower elevations.

205

206

207

208 **Methods**

209

210 *Selection of research sites and species*

211 In each of the four countries Australia (AU), Switzerland (CH), China (CN) and New
212 Zealand (NZ), we chose multiple transects extending from the nival or alpine zone downwards
213 to the subalpine zone. The low elevation limit of each transect was determined by the minimum
214 elevation of our target species, which was usually at or slightly below treeline. This ensured
215 that the elevational ranges over which we sampled target species were not truncated at their
216 lower end. In Australia and Switzerland, all transects were placed within single mountain
217 ranges (i.e. Australian and European Alps), while transects occurred in numerous mountain
218 ranges in New Zealand and China (see Supporting information SFig. 1, STables 2 and 3, SFig.
219 11).

220

221 Within each country, we selected native plant species (dwarf shrubs, herbs and/or
222 graminoids) that were common enough to be found both at multiple locations along an
223 individual transect and along multiple transects. Further, we selected species known to occupy
224 different elevational range sizes and elevational preferences. This iterative selection process
225 resulted in 11 species from 11 transects each in AU and NZ (one species in common), with
226 each species sampled at an average of five transects. In CH, seven species at 11 transects were
227 selected, with the majority of species recorded in every transect. In CN, 7 transects and a total
228 of 43 species were selected. A total of 71 species were sampled across four countries. As the
229 distance between transects was large in China, only seven of these species were sampled in
230 more than one transect (see Table S2 for all study species by country and transect).

231

232 *Trait and field measurements*

233 Along each transect, we established ~100 m² field sites in regular vertical elevational
234 increments; in AU, where gradients were relatively short (often c. 500 m), field sites were
235 located every 50 m. In CN and NZ sites occurred at 100 m increments, and in CH at every 150
236 m increase in elevation. At each of the sites, we recorded GPS coordinates, elevation, aspect,
237 and slope. We photographed the field site and all target species. We estimated the abundances
238 of the target species in five classes (1 = 1 individual, 2 = 2-3 ind., 3 = 4-10 ind., 4 = 11-50 ind.,
239 5 = >50 ind.). For each target species, we then measured seven traits at each collection site
240 based on their ecological relevance for our research questions and feasibility of measurement
241 in the field (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). As an indication of plant
242 stature, we measured vegetative and generative height, where vegetative height was distance
243 from soil to highest vegetative leaf and generative height was distance to the highest point on
244 the reproductive shoot. As a measure of reproductive investment, we noted the presence of
245 flowers on the randomly chosen individuals (see below). As a measure of individual and genet
246 basal area, we measured individual plant and patch diameters, in two dimensions (along the
247 largest diameter and perpendicular to it). In clonal plant species, plant diameter was equivalent
248 to an individual rosette, whereas patch diameter referred to the whole genet and could represent
249 the size of a tuft, tussock or cushion. For genera with more singular growth forms (e.g., some
250 *Gentiana* species) plant and patch diameter were the same. The two diameter measurements
251 were made at right angles, allowing estimates of patch and plant areas to be calculated as an
252 ellipse (i.e., area = 0.5 a 0.5 b Π). All traits were measured on ten randomly selected individuals
253 per site. Flower count data was considered in a binary fashion on a per individual basis (because
254 for some species individuals only produce one flower when flowering) so that the presence or
255 absence of flower(s) was a nominal value between 0 and 10 for each species at each site. We

256 then collected at least three leaves (up to 30 for small and light leaves) from each of the first
257 three individuals selected from each species for determination of leaf dry matter content
258 (LDMC) and specific leaf area (SLA). For calculations of LDMC and SLA, fresh leaves were
259 scanned on a flatbed scanner to determine leaf area. Leaves were then weighed on a balance to
260 a precision of +/- 0.001g, prior to being air dried and reweighed with a balance to a precision
261 of +/- 0.0001g. LDMC was calculated by dividing dry leaf mass by fresh leaf mass. SLA was
262 calculated by dividing leaf area by dry leaf mass. Additionally, within an area of 10 cm
263 diameter around the target individual, we determined the tallest neighbouring species and
264 measured its vegetative and generative height, and estimated the percent cover of the target
265 species, other vegetation, rock, and bare soil. To examine the height of target plants in relation
266 to neighbouring plants, we calculated the ratio of target to neighbour height as the ratio of the
267 scaled target plant vegetative height (see scaling below) to the unscaled vegetative height of its
268 nearest neighbour. We did not scale the neighbours' height as the neighbours represent
269 different plant species, which were not systematically sampled. Hence, scaling by the mean of
270 the respective neighbour plant was not possible as it was for the target plant species.

271

272

273 *Data analysis*

274 All analyses were conducted in the statistical programming environment R version R-4.1.2 (R
275 Development Core Team 2021). For each analysis we included only the plant species that were
276 recorded at a minimum of ten locations. This resulted in five species being excluded from the
277 data set and 66 species being included in at least one analysis because not all traits were
278 recorded for each species at each site. We considered the response of species' vegetative height,
279 generative height, SLA, LDMC, patch area, plant area, presence of flowers and target to
280 neighbour height ratio for all species over their standardized elevational range (equation 1).

281 Elevational range was standardized to enable comparisons among plant species from mountain
 282 regions in very different climatic zones (Fig SF1). The elevation of each observation was
 283 standardized across the entire dataset by applying equation 1. We checked that results were not
 284 driven by individual mountain regions by including them in a separate analysis as a fixed factor.
 285 Mountain region did not explain any response variable significantly (always $p > 0.1$, in most
 286 cases $p > 0.7$, see STable 6), which justified standardising elevation across mountain regions.

287

$$288 \text{ Standardized elevation } (obs)_{ij} = 1 + \left[\frac{Elev (obs)_{ij} - Elev (max)_{ij}}{Elev (max)_{ij} - Elev (min)_{ij}} \right] \quad eqn. 1$$

289

290 Therefore, the elevation of an observation ($Elev(obs)$) for species i was relative to the maximum
 291 and minimum elevation ($Elev(max)$ and $Elev(min)$, respectively) of all observations of that
 292 species in mountain region j .

293

294 Likewise, vegetative height, generative height, SLA, LDMC, patch area, and plant area values
 295 were scaled for each species within each mountain region to enable comparisons among plant
 296 species of different sizes. Traits were scaled by applying equation 2.

297

$$298 \text{ Scaled trait value } (obs)_{ij} = \left[\frac{tra \text{ value } (obs)_{ij}}{trait \text{ value } (mean)_{ij}} \right] \quad eqn. 2$$

299

300 where ‘trait value (mean)_{ij}’ is the mean of all observed trait values of plant species = i , in
 301 mountain region = j . Therefore, the changes in trait values for different species were
 302 comparable to each other across mountain regions.

303

304 We characterised two aspects of species' elevational distributions, which may reflect species'
305 relative habitat specialisation or generalism for alpine environments: elevational preference
306 (EP) and species range (SR; Fig. 1). A species' EP reflects its standardized median elevation
307 relative to all species within its mountain region. EP varies between 0 and 1 with values
308 approaching 0 for species whose median elevation approaches the tree line, and 1 for species
309 whose median elevation approaches the nival zone. We calculated the elevational preference
310 of each species by equation 3.

311

$$312 \quad \text{Elevational preference (obs)}_{ij} = 1 + \left[\frac{\text{Elev (median)}_{ij} - \text{Elev(max)}_j}{\text{Elev(max)}_j - \text{Elev (min)}_j} \right] \quad \text{eqn. 3}$$

313

314 Therefore, the elevation preference of species i was relative to the maximum and minimum
315 elevation of all species in mountain region j . Overall data, species' median elevations were a
316 good proxy for the elevation at which they achieve maximum abundance into account ($r^2=0.87$,
317 see SFig 2.)

318

319 Finally, we estimated each plant species' range (SR), which reflects its standardized elevational
320 distribution relative to all species within its mountain region. SR varies between 0 and 1 with
321 values approaching 0 for species whose elevation range approaches 1 m, and 1 for species
322 whose elevational range approaches the entire alpine zone. We estimated SR for each species
323 by equation 4.

324

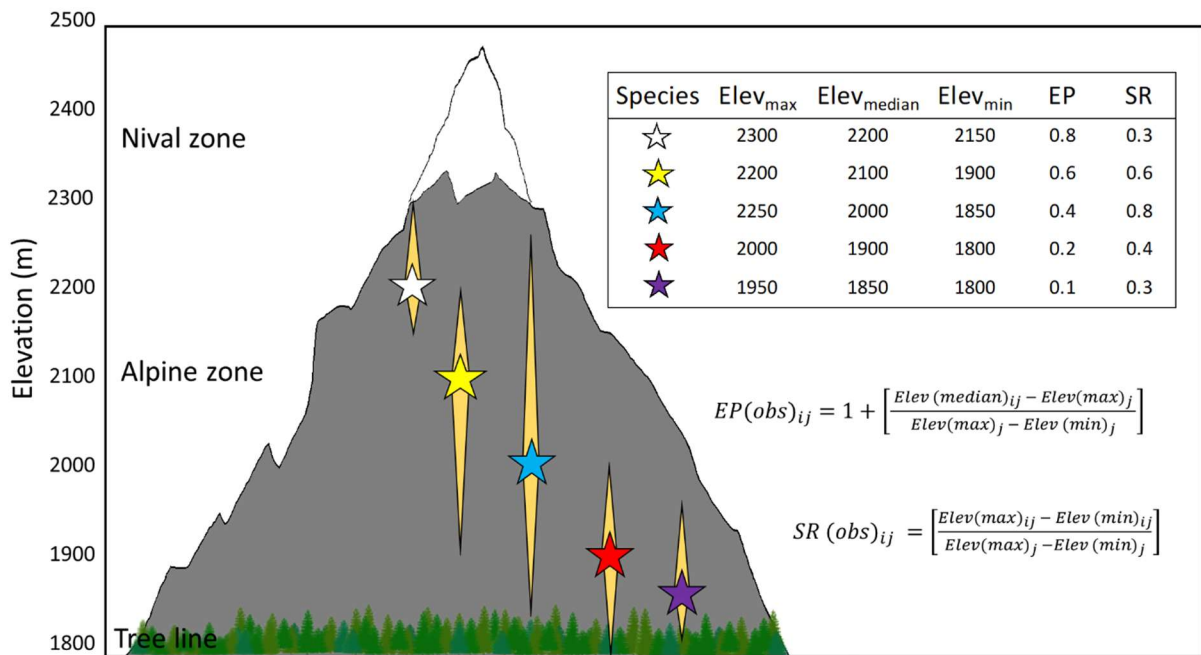
$$325 \quad \text{Species range (obs)}_{ij} = \left[\frac{\text{Elev(max)}_{ij} - \text{Elev (min)}_{ij}}{\text{Elev(max)}_j - \text{Elev (min)}_j} \right] \quad \text{eqn. 4}$$

326

327 Therefore, the species range of species i was relative to the maximum and minimum elevation
 328 of all species in mountain region j .

329

330



331

332 **Fig. 1.** Schematic representation of the quantification of species' elevational preferences (EP)
 333 and range (SR) in this study. In this exemplary mountain range j , the alpine zone spans 500m
 334 of elevation from the nival zone (at 2300m) to the tree line (at 1800m). The median elevations
 335 ($Elev_{median}$) of five alpine plant species are represented by the vertical position of the respective
 336 stars. The range of each species is represented by its corresponding pale-orange diamond, with
 337 the vertical points extending to its maximum elevation ($Elev_{max}$) and minimum elevation
 338 ($Elev_{min}$). Species' elevational preference and species range were uncorrelated (see below).

339

340

341

342

343 *Mixed-effects models and data visualisation*

344

345 To consider the patterns of plant trait variation over standardised elevation, we applied mixed-
346 effects models using the *lmer* function from the *lme4* package (Bates et al. 2015). To meet the
347 assumption of normally distributed residuals, vegetative height, generative height, and SLA
348 were transformed by $\log(x + 1)$, while patch and plant areas and the target-neighbour ratios
349 were log-transformed. LDMC did not need to be transformed in order to meet model
350 assumptions. Degrees of freedom were calculated via Satterthwaite's degrees of freedom
351 method with the R package *lmerTest*.

352

353 To examine the shape and generality of species trait-environment relationships over their entire
354 elevational distributions, we constructed two mixed-effects models for each of vegetative
355 height, generative height, SLA, LDMC, plant area, patch area and the presence of flowers (for
356 the latter *glmer()* was used with family=binomial, also in models below). The first model
357 included standardised elevation as a linear fixed effect while the second model included
358 standardised elevation as quadratic fixed effect. Comparison of these two models allowed us
359 to determine whether species traits values had a linear or non-linear relationship with elevation.

360 All mixed-effects models included the count of days since January 1st or July 1st (for northern
361 and southern hemisphere, respectively) to account for potential measurement bias due to
362 seasonality, and transect and species as crossed random intercept terms to account for potential
363 non-independence of the data. Model optimisation was carried out using the default *lmer*
364 optimisation method and Akaike Information Criteria (AIC) were calculated for the two models
365 by maximizing the log-likelihood (i.e., REML set to false). The best model was selected based
366 on the delta AIC and then recalculated by maximizing the restricted log-likelihood (REML).

367 Model selection was done using AIC with the following ranked criteria: 1. models within 8

368 AIC of each other were considered comparable, 2. priority was given to models with significant
369 interactions between fixed effects (applies to models below), 3. priority was given to linear
370 rather than polynomial representations of fixed effects (see STables 4-5). The generality of the
371 effect of standardised elevation on values for each trait was assessed by the significance of the
372 p-value in the best model. We consider models within delta AIC of <8 as comparable in order
373 to appropriately account for model uncertainties (Burnham and Anderson 2002, Richards
374 2008). Furthermore, we aim at testing specific hypotheses about interactions of our response
375 variables, which is the reason for priority #2 to include interactions if the model AICs are in a
376 comparable range.

377

378 Next, we considered how species' elevational preferences may affect their trait values over
379 their entire elevational distributions. We computed seven mixed-effects models for each of the
380 response variables vegetative height, generative height, SLA, LDMC, plant area, patch area
381 and the presence of flowers. These seven models (M1-M7) covered the various possible
382 combinations of elevational preference (EP) and standardized elevation (SE), on trait values
383 (Y) as follows: M1: $Y \sim SE$, M2: $Y \sim SE^2$, M3: $Y \sim EP$, M4: $Y \sim SE + EP$, M5: $Y \sim SE^2 + EP$, M6:
384 $Y \sim SE \times EP$, M7: $Y \sim SE^2 \times EP$. The mixed-effects model structure and model selection were
385 carried out as described above, except in one case where the models for generative height as a
386 function of EP failed to converge. For this model, the Nelder-Mead method was used for
387 optimisation. Species' elevational preference and species range showed no linear or non-linear
388 relationship and were uncorrelated (Pearson's $r = -0.0298$, $p = 0.803$, as computed with the
389 *cor.test* function). We therefore applied the same modelling approach to examine the effect of
390 a species range on its trait values over its standardised elevation by replacing elevational
391 preference (EP) with species range (SR) in all seven models.

392 To explore whether patterns of trait variation were consistent among species with similar
393 elevational distributions but different geographic origins, we plotted all species' EP against SR
394 and considered the response of each species' vegetative height to standardized elevation.

395 To test how the height of our target species changed in relation to those of their neighbours (of
396 different species) over their standardised elevation, we computed a similar mixed-effects model
397 for the ratio of the scaled height of target species to their neighbour's unscaled heights as
398 response variable. As the neighbouring plants belonged to different species, the ratio was due
399 to different species composition (see discussion below). We calculated marginal r-squared
400 values using the *r.squaredGLMM* function from the *MuMIn* package (Barton 2019).

401

402

403 **Results**

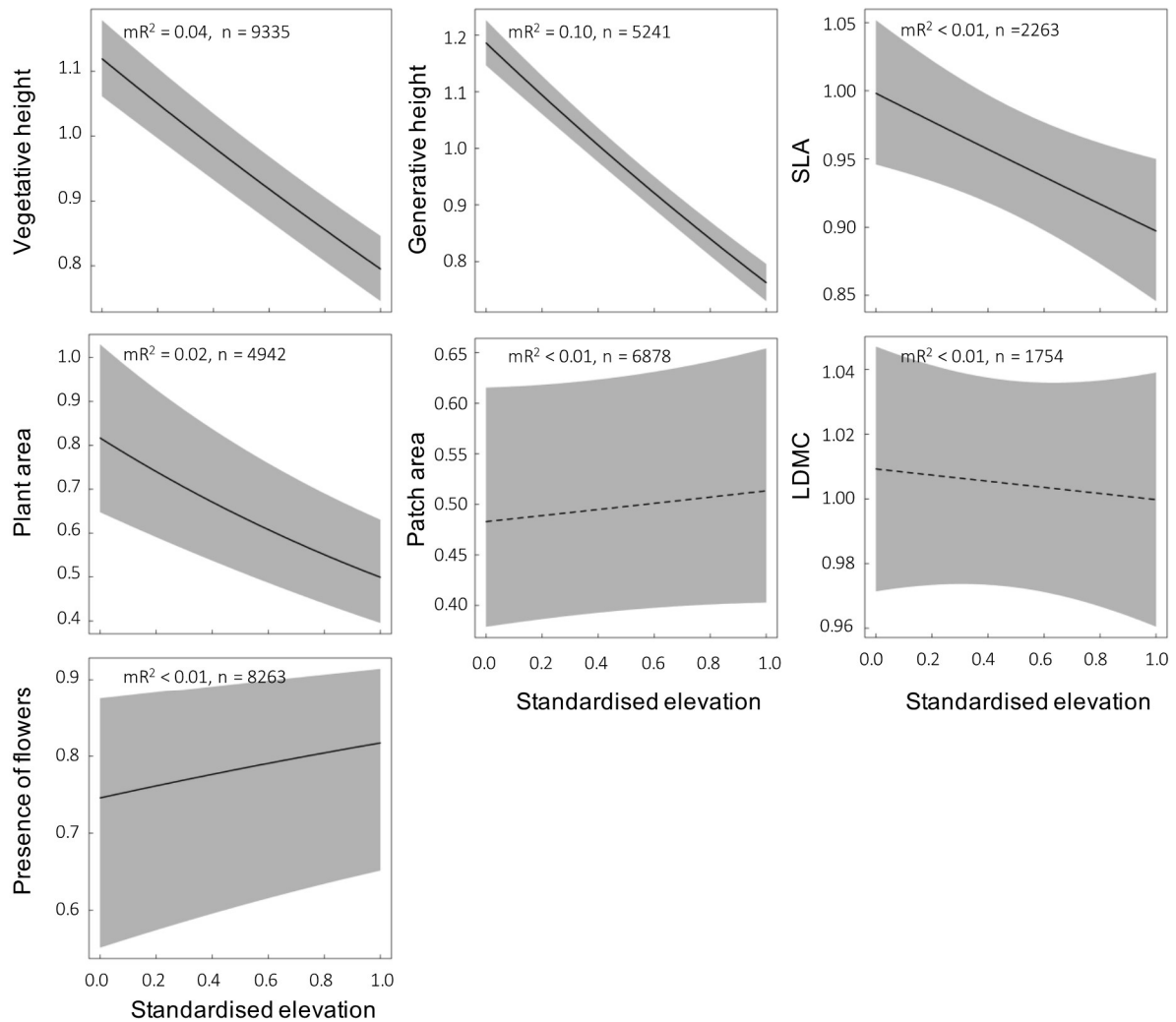
404

405 *Patterns of alpine plant traits along elevational gradients*

406

407 Across all species, plants were shorter and had tougher leaves at higher elevation (i.e.,
408 vegetative and generative height, SLA and plant area all decreased significantly with
409 increasing elevation; Fig. 2) compared to low-alpine situations. In contrast, despite large
410 variation across all species, the number of flowering individuals increased significantly with
411 increasing elevation. However, neither LDMC nor patch area showed a significant overall
412 pattern with elevation due to high variability in the responses of individual species (see trends
413 for individual species in the Supporting Information SFigs 4-10).

414



415

416 **Fig. 2.** Intraspecific changes in trait values across all alpine species from all 40 alpine
 417 elevational gradients, as represented by scaled plant trait values: vegetative height, generative
 418 height, specific leaf area (SLA), plant area, patch area, leaf dry matter content (LDMC), and
 419 the presence of flowers or inflorescences along species' entire elevational distributions
 420 (standardised value). The line of best fit for each linear model (solid lines represent
 421 significant relations) and the upper and lower limits of the 95% confidence interval are
 422 illustrated for each trait. Marginal R^2 values and the sample size (n), are reported for each
 423 model. Trait values are scaled relative to the mean value for each species in each mountain
 424 region (see methods) and therefore do not reflect the actual trait values (i.e., no units on y
 425 axes). The elevation of each observation was standardised relative to the maximum and

426 minimum elevation of all observations of that species in its mountain region. Trait data are
427 for alpine plant species from Australia, China, New Zealand and Switzerland. All depicted
428 effects were back-transformed to show the real trait-elevation relationships despite the
429 scaling of trait values.

430

431

432

433 *Effects of elevation on trait values for species with different elevational preferences (EP) and*
434 *ranges (SR)*

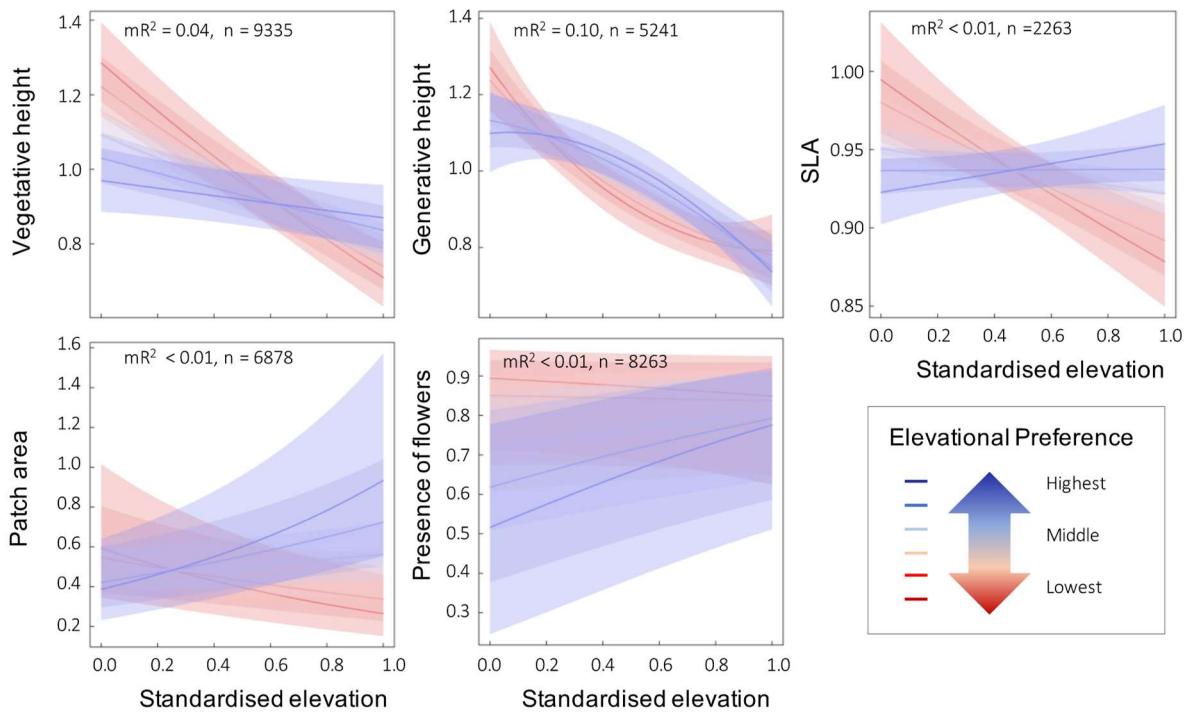
435

436 The relationship between plant traits and elevation differed significantly among species
437 depending on their elevational preference (EP) and species range (SR). These relationships
438 were evidenced by significant interactions between standardised elevation and EP as well as
439 for standardized elevation and SR for several traits: vegetative height, generative height, SLA
440 and patch area. For vegetative height and SLA, species with a preference for higher
441 elevations retained similar trait values throughout their elevational ranges, whereas plants
442 with preferences for relatively low elevations displayed greater change in trait values over
443 elevational gradients (Fig 3). For example, plants with higher EP maintained similar
444 vegetative heights (and SLA) throughout their elevational range, so that they remained small
445 near their lower range. By contrast, plants with lower EP were tall near their elevational
446 minima but declined sharply in height toward their elevational maxima. Patch areas of
447 species with lower EP became smaller towards their elevational maxima, but the opposite
448 was true for species with higher EP, these achieved the greatest patch sizes near their
449 elevational maxima. Patch area was uncorrelated with abundance. In contrast, the presence of

450 flowers increased with elevation for species with higher EP but changed little over elevation
451 for species with lower EP.

452

453



454

455 **Fig. 3.** Relationship between species trait values and elevation across 66 alpine species from
456 all 40 alpine elevational gradients, as influenced by species elevational preference (EP).

457 Results are shown only for models that revealed a significant effect of elevational preference

458 on the trait values over standardised elevation. For each model EP was analysed as a

459 continuous variable but, for simplicity, it is illustrated here as the line of best fit for six

460 elevational bands, along with upper and lower limits of the 95% confidence interval as

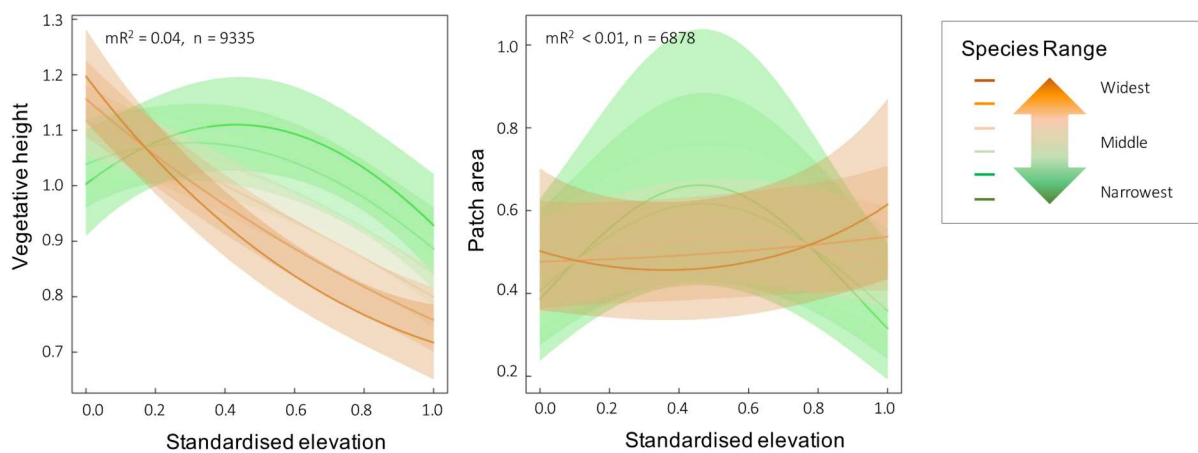
461 shades. See further details in caption of figure 2 and statistics in STables 4-5.

462

463

464 The response of plant traits to elevation also differed significantly among species depending
 465 on their elevational range size (SR) for two traits. This was evidenced by significant
 466 interactions between standardized elevation and SR, for vegetative height, and patch area
 467 (Fig. 4). Species with narrow elevation ranges showed a bell-shaped curve in trait values
 468 (vegetation height and patch area) along elevation. In contrast, species with wide SR were
 469 tallest near their elevational minima but declined in height toward their elevational maxima.
 470 Likewise, species with narrow SR achieved optimal patch areas mid-way along their
 471 elevational distributions, but species with wide SR displayed no such trend. We found no
 472 significant interactions among standardized elevation and SR for the other plant traits
 473 measured.

474



475

476 **Fig. 4.** Relationship between species trait values and standardized elevation across 72 alpine
 477 species from all 40 alpine elevational gradients, as influenced by species' elevational range
 478 size (SR). Results are shown only for models that revealed a significant effect of species
 479 range on the trait values over standardised elevation. For each model, EP was analysed as a
 480 continuous variable but, for simplicity, it is illustrated here as the line of best fit for six
 481 elevational bands, along with upper and lower limits of the 95% confidence interval. See
 482 further details in caption of figure 2.

483

484

485 *Intraspecific height variation among alpine plants*

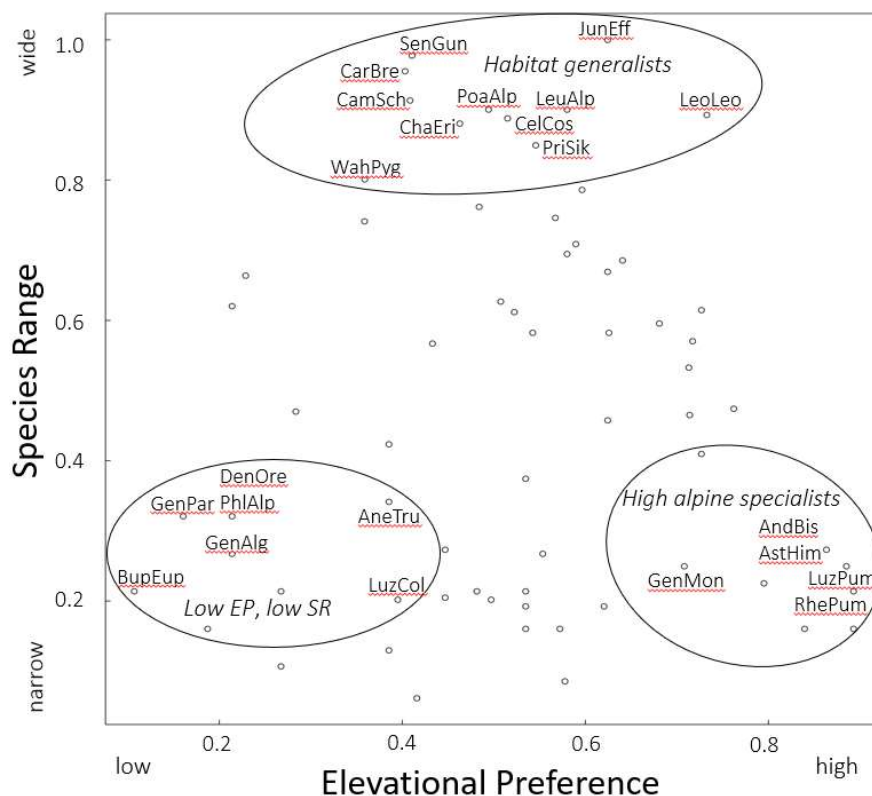
486

487 To identify plant species with similar elevational distributions, we plotted species
488 ranges against their elevational preferences for the 66 plant species (Fig. 5). This procedure
489 illustrates which species, or groups of species, drive the statistical patterns reported above. The
490 plot revealed that species with the greatest elevational ranges had intermediate elevational
491 preferences (i.e., those with $SR > 0.8$, $EP 0.2-0.8$) and accordingly, we consider these species to
492 be alpine habitat generalists. While species with small range sizes spanned the entire range of
493 elevational preferences, very few species that occupied broad elevational ranges showed
494 preference for very high or low relative elevations, which is intuitively pleasing as it is
495 improbable for species to reach extremely high or low EP if they have a very wide SR unless
496 they are very abundant. Although this result is plausible, it is by no means a foregone
497 conclusion as EP used in our study represents the median of species distribution and not the
498 mean or midpoint. However, also evident was a small group of species that had narrow
499 elevational ranges at the two extremes of elevational preference (i.e., $SR < 0.3$, $EP < 0.3$ or > 0.7).
500 We considered intraspecific trait values over elevation for species that exhibit these three
501 unique distributional patterns. We found that the overall strongly negative response of
502 vegetative height over elevation (i.e., Fig 2), was exemplified at the level of individual species
503 by nearly all of the habitat generalists (Table 1). In contrast, we found non-significant or
504 idiosyncratic responses of vegetative height to elevation in species that occupied narrow
505 elevational ranges at the highest relative elevations, the high-alpine specialists. While the small
506 number of species with this pattern of elevational distribution means that this observation must
507 be interpreted cautiously, it may suggest that high alpine specialists express less trait variation

508 over elevation than other alpine species. Finally, plant species with high fidelity to low alpine
 509 environments (i.e. both low EP and SR) expressed similar patterns of vegetative height over
 510 elevation as the alpine generalist species (i.e., mostly significantly negative relationships; Table
 511 1).

512

513



514

515 **Fig. 5.** Alpine plant species as characterised by their elevational preference (EP) and range
 516 (SR) for 66 alpine species from 4 countries. Species' 6-letter codes appear where $n > 20$
 517 observations for the species (see Table 1 for full names). At the level of individual species,
 518 patterns of intraspecific variation in vegetative height over standardised elevation are distinct
 519 for habitat generalists (i.e., those with $SR > 0.8$, $EP 0.2-0.8$) and high-alpine specialist species
 520 (i.e., those with $SR < 0.3$, $EP > 0.7$).

521

522 **Table 1.** Alpine plant species as from Figure 5 for n >20 observations (see Fig. 5) and for the
523 groups of habitat generalists (i.e., those with SR>0.8, EP 0.2-0.8), high-alpine specialist
524 species (i.e., those with SR<0.3, EP>0.7) and species low EP and low SR. For the shapes of
525 vegetation height over elevation of individual species see also Fig. S4.

Ꝁ	Species· CodeꝀ	Species·nameꝀ	CountryꝀ	Shape·veg·height· over·stand·elev.Ꝁ
HabitatꝀ	Ꝁ	Ꝁ	Ꝁ	Ꝁ
GeneralistsꝀ	CarBreꝀ	<i>Carex-breviculmisꝀ</i>	AUꝀ	n.s.Ꝁ
Ꝁ	CelCosꝀ	<i>Celmisia-costinianaꝀ</i>	AUꝀ	-Ꝁ
Ꝁ	SenGunꝀ	<i>Senecio-gunniiꝀ</i>	AUꝀ	-Ꝁ
Ꝁ	CamSchꝀ	<i>Campanula-scheuchzeriꝀ</i>	CHꝀ	-Ꝁ
Ꝁ	LeuAlpꝀ	<i>Leucanthemopsis-alpinaꝀ</i>	CHꝀ	-Ꝁ
Ꝁ	PoaAlpꝀ	<i>Poa-alpinaꝀ</i>	CHꝀ	-Ꝁ
Ꝁ	JunEffꝀ	<i>Juncus-effususꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	LeoLeoꝀ	<i>Leontopodium-leontopodioidesꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	PriSikꝀ	<i>Primula-sikkimensisꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	WahPhyꝀ	<i>Wahlenbergia-pygmaeaꝀ</i>	NZꝀ	U-shapedꝀ
High·AlpineꝀ	Ꝁ	Ꝁ	Ꝁ	Ꝁ
SpecialistsꝀ	AndBisꝀ	<i>Androsace-bisulcaꝀ</i>	CNꝀ	parabolicꝀ
Ꝁ	AstHimꝀ	<i>Aster-himalaicusꝀ</i>	CNꝀ	n.s.Ꝁ
Ꝁ	RhePumꝀ	<i>Rheum-pumilumꝀ</i>	CNꝀ	n.s.Ꝁ
Ꝁ	GenMonꝀ	<i>Gentianella-montanaꝀ</i>	NZꝀ	n.s.Ꝁ
Ꝁ	LuzPumꝀ	<i>Luzula-pumilaꝀ</i>	NZꝀ	-Ꝁ
Low·EP,Ꝁ	Ꝁ	Ꝁ	Ꝁ	Ꝁ
Low·SRꝀ	AneTruꝀ	<i>Anemone-trullifoliaꝀ</i>	CNꝀ	+Ꝁ
Ꝁ	BupEupꝀ	<i>Bupleurum-euphorbioidesꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	DenOreꝀ	<i>Dendranthema-oreastrumꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	GenAlgꝀ	<i>Gentiana-algidaꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	GenParꝀ	<i>Gentiana-parvulaꝀ</i>	CNꝀ	n.s.Ꝁ
Ꝁ	PhlAlpꝀ	<i>Phleum-alpinumꝀ</i>	CNꝀ	-Ꝁ
Ꝁ	LuzColꝀ	<i>Luzula-colensoiꝀ</i>	NZꝀ	n.s.Ꝁ

526

527

528

529 *Height of target plants relative to neighbouring species over elevation*

530

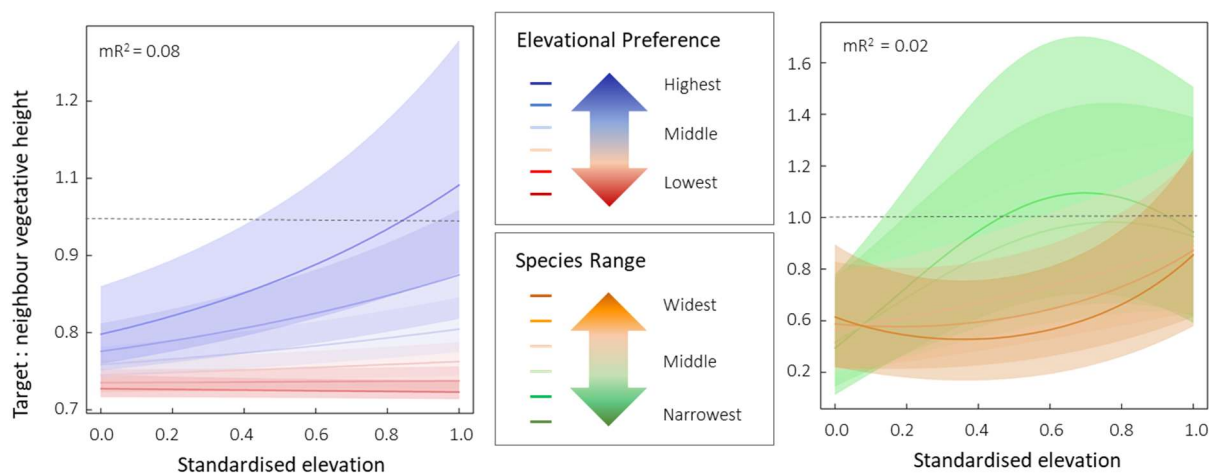
531 In general, target species were smaller than their tallest neighbour (i.e., target-neighbour

532 vegetative height <1) over much of their elevational distribution, but the ratio of target-

533 neighbour vegetative height over elevation varied significantly depending on the EP and SR

534 of the target plant species (Fig 6, SFig. 10). Species with higher EP became tall relative to
535 their neighbours near their elevational maxima. In contrast, species with lower EP remained
536 smaller than their neighbours throughout their elevation distribution. Plants with narrow and
537 wide SR had contrary optimum curves: plants with a narrow SR decreased sharply in height
538 relative to their neighbours towards their elevational minima, while no such pattern was
539 detected for species with wider SR.

540



541

542 **Fig. 6.** Relationships between the ratio of scaled target plant height to unscaled height of
543 neighbouring plants and standardised elevation across 72 alpine species from all 40 alpine
544 elevational gradients, as influenced by species' elevational preference (EP) and range (SR).
545 In both models EP and SR were analysed as continuous variables but, for simplicity, are
546 illustrated here as the line of best fit for six elevational bands or ranges, respectively, along
547 with upper and lower limits of the 95% confidence interval.

548

549

550 Discussion

551

552 Despite the occurrence of species specific trends (see also, Kichenin et al. 2013,
553 Bjorkman et al. 2018, Weemstra et al. 2020a), we detected general intraspecific trends in a
554 range of plant traits over elevation; with vegetative and generative heights, SLA, and patch
555 area declining with elevation, and the number of flowering individuals increasing with
556 elevation. Most importantly, these relationships depended upon the species' elevational
557 preference (i.e. median elevation) and width of elevational range. In particular, the strong
558 decline in vegetative and generative height, SLA and patch area over elevation were mainly
559 driven by plant species with lower elevational preference, suggesting that higher alpine
560 species might have a reduced potential to express trait variation in response to environmental
561 gradients such as those that occur with elevation. We provided preliminary evidence that
562 patterns of intraspecific trait variation of alpine generalist species, which prefer mid
563 elevations and occupy wide elevational ranges, differ from high alpine specialist species,
564 which occupy a narrow range of high alpine environments. Additionally, we demonstrate that
565 species with higher elevational preference became taller relative to their neighbours near their
566 elevational maxima, whereas species with lower elevational preference remained smaller than
567 their neighbours throughout their elevational range. Taken together, our results indicate that
568 species with lower elevational preference and wider range of occurrence show greater trait
569 variation, which may indicate a greater potential to respond flexibly to environmental
570 changes and their potentially increasing interspecific competition from upslope shifting
571 species (Alexander et al. 2015, Rumpf et al. 2018, Steinbauer et al. 2018). The velocity of
572 responses to warming, however, would depend on whether trait variation is due to plasticity
573 (relatively fast) or to genetic differentiation among populations (relatively slow). While we
574 cannot distinguish the two in this study, it will be important to disentangle plasticity and
575 genetic differentiation in future research.

576

577 **Overall trait distributions along elevation**

578

579 Our finding that alpine plant species show general patterns of intraspecific trait variation
580 along elevational gradients broadly agrees with previous large-scale studies and meta-
581 analyses (Bjorkman et al. 2018, Midolo et al. 2019). We found that vegetative and generative
582 species heights, SLA, and patch area declined, while the number of flowering individuals
583 increased with elevation. The negative relationships between plant height and size with
584 elevation has long been recognised (Bonnier 1890, Körner 2003) and attributed to both
585 intraspecific population adaptation (Halbritter et al. 2018) and plastic changes (Read et al.
586 2014). For example, common garden experiments find that individuals originating from high
587 elevations are generally shorter and have less biomass than their lower elevation counterparts,
588 suggesting intraspecific adaptation of plant size to elevation (Halbritter et al. 2018).

589 Likewise, the negative relationship between SLA and elevation also met our expectations
590 reflecting the tendency of species growing at lower temperatures to grow a higher number of
591 small cells per unit area across more cell layers, and therefore an increased proportion of cell
592 wall material per unit leaf volume (Atkin et al. 2006, Poorter et al. 2009). The negative
593 relationship between SLA and elevation likely reflects the increasing divergence of daytime
594 to night time leaf-to-air temperature differences with increasing elevation (Wright et al.
595 2017). While the climatic factors that drive variation in SLA are also likely to affect LDMC,
596 we found high interspecific variability and no overall trend in LDMC values with elevation.
597 This ratio of dry to fresh leaf weight is likely to be strongly affected by plant available water,
598 which is more responsive to regional gradients, such as continentality, than to elevation
599 (Marshall and Zhang 1994, Körner 2007). We saturated leaves before LDMC measurements
600 to control for water availability as recommended (Perez-Harguindeguy et al. 2013), but
601 nevertheless LDMC did not show consistent patterns in our study. Likewise, we found high

602 variability and no overall trend in patch size over elevation, with both significant positive and
603 negative relationships for species of the same growth form and mountain range (e.g., the
604 forbs *Leucanthemopsis alpina* and *Campanula scheuchzeri* from the Swiss Alps; see
605 Supplementary Information). Despite high interspecific variation, the number of flowering
606 individuals increased with elevation, and there was no evidence for an optimum curve as may
607 have been expected based on previous work (Kieltyk 2018). This pattern could be a stress-
608 response (Malkinson and Tielbörger 2010), or may indicate a trade-off between vegetative
609 and generative traits for alpine species: although individuals at high elevation tend to be
610 shorter and have smaller leaves, the probability of flowering, which is ultimately an
611 important fitness trait, is greater at higher elevations than at lower elevations, where species
612 may experience more benign biotic growing conditions, but are also likely to experience
613 more negative biotic interactions (Callaway et al. 2002). Such negative interactions may in
614 particular be exerted through shading, which often a cause for suppressed flowering.
615 Although numerous traits show trends in elevation, most marginal R^2 values are low,
616 indicating that elevation only explains a small fraction of variation in the data. This is not
617 surprising as alpine habitats are usually heterogenous at a very fine scale, and, for instance,
618 temperature differences can differ by several degrees within a few meters in complex terrain
619 (Scherrer and Körner 2011). Furthermore, elevation is merely a proxy for other factors that
620 change along a mountain slope (Körner 2007). Only air pressure changes universally along
621 elevation, but many other factors, such as moisture, may not be related to elevation or show
622 non-linear relationships. Nevertheless, our gradients studied do not show strong moisture
623 gradients, and elevation can be assumed to be a reasonable (even if not perfect) proxy for
624 temperature. Therefore, despite much unexplained variation in our data set we believe that
625 our analyses can indicate important ecological processes along elevation. Interestingly,
626 mountain region did not affect trait patterns significantly when added to the statistical model

627 as a fixed effect. Despite considerable climatic and geographical differences between the
628 studied mountain regions, the results shown in our study apparently apply across larger
629 scales.

630

631 **Trait variation for species with different elevational preferences or ranges**

632

633 We showed that patterns of trait variation over elevation depended upon the elevational
634 preferences and ranges of alpine plant species. In particular, the decline in vegetative and
635 generative heights, SLA and patch area over elevation was mainly driven by plant species
636 with lower elevation preferences. Likewise, the slight overall increase in the probability of
637 flowering with elevation was driven by species with higher elevational preference.

638 Collectively, these results suggest that alpine specialist species may be subjected to trade-offs
639 in vegetative and generative traits differently than alpine species with lower elevational
640 preference. While these observations must be interpreted cautiously given the high residual
641 variance left unexplained in our probability of flowering model (i.e., low marginal R^2 values),
642 this significant effect is consistent with the stress gradient hypothesis (Bertness and Callaway
643 1994, Maestre et al. 2009). Alpine plant species that specialise in high elevation habitats are
644 likely to experience more abiotic stress but less interspecific competition relative to species
645 that prefer lower elevations. This may enable them to increase resource allocation to
646 flowering, while maintaining overall conservative growth strategies by remaining short and
647 small. In contrast, species that prefer lower alpine environments are likely to experience more
648 variable interspecific competition from a higher diversity of neighbours. The variability of
649 interspecific competition experienced by alpine plants with lower elevational preference is
650 likely to select for the maintenance of vegetative trait flexibility, as demonstrated by the
651 strong decline in vegetative and generative heights, SLA and patch area over elevation for

652 these species. However, our data revealed no significant negative relationship between the
653 presence of flowers and elevation for species with lower elevational preference. Thus, our
654 data may suggest that a maintenance of vegetative trait flexibility may come at the expense of
655 flexibility of flowering for alpine plant species with lower elevational preference. However,
656 given the low statistical explanatory power of some of our models, trade-offs between
657 vegetative and reproductive traits deserve further investigation.

658

659 More generally, our data suggest that high alpine specialists have relatively little
660 potential to express variability in vegetative traits in response to elevation. Species that
661 preferred higher elevations showed little variation in trait values over elevation as well as
662 some evidence of weaker performance at lower elevations (e.g., smaller patches, lower
663 probability of flowering). By contrast, species that preferred lower elevations grew taller and
664 larger and had relatively larger leaves, near their elevational minima. Similarly, species with
665 wide elevational ranges were tallest near their elevational minima. Therefore, our trait data
666 provide evidence that lower-alpine plant species might have more capability to respond to
667 climate warming than high-alpine plant species. Hence, our findings support and extend
668 previous demographic studies which show that lower-alpine plant species are able to respond
669 positively to recent environmental change by increasing their abundances and colonizing
670 upslope relative to more static higher-alpine species (Rumpf et al. 2018). Consequently, the
671 relatively low trait and demographic flexibility of high alpine plants may concur with the
672 general decline of high-alpine specialists (Pauli et al. 2007) and the thermophilisation of
673 alpine plant species composition in recent decades, which has been demonstrated in Europe
674 (Lamprecht et al. 2018). In terms of upward species shifts (Chen et al. 2011, Freeman et al.
675 2018, Rumpf et al. 2019), our study indicates that high-alpine plants, with their relatively

676 constrained trait variation, may be increasingly disadvantaged when interacting with more
677 flexible low-alpine species and those with wider elevational ranges.

678 While we interpret the more pronounced clines of lower-elevation and wider-ranged species
679 much in the light of interspecific competition, numerous other factors also change along
680 elevation (see also discussion above). To a small extent, other factors and their variations
681 might also influence the observed trait patterns, such as growing season length, nutrient
682 availability, and abundance of pollinators. Also, statistical effects might drive some of our
683 results. It is possible that trait variation increases with the mean (but see scaling in methods),
684 which could result in less pronounced trait variation in high-alpine or in narrow-range species
685 and less statistical power to detect changes in elevation. It is therefore important for future
686 research to consider other ecological factors, such as moisture or snow cover. Nevertheless,
687 we believe that it is ecologically relevant to understand trait changes and variation along
688 altitudinal ecological gradients because they have the potential to indicate species
689 responsiveness to changing environmental conditions.

690

691 **Intraspecific height variation among alpine plants**

692

693 Visualising plant species as a function of their range and elevational preferences allowed us
694 to distinguish two alpine plant groups, with distinct patterns of intraspecific trait variation in
695 response to elevation. Namely, the alpine habitat generalists were those species that
696 demonstrated high variation in vegetative height over elevation, being tallest near their
697 elevational minima and rapidly declining in height near their elevational maxima. In contrast,
698 the high alpine specialist species, which occupied narrow elevational ranges at the highest
699 relative elevations, showed no consistent response of vegetative height to elevation, again
700 supporting the view that these species express a conservative range of trait values with

701 elevation. Finally, it was interesting to observe that plant species with both low elevational
702 preference and range of occurrence, which may be the subset of species that are likely to
703 experience the greatest interspecific competition as sub-alpine species advance into alpine
704 zones, were generally similar to the habitat generalist species in expressing mostly
705 significantly negative relationships between vegetative height and standardised elevation.
706 Such differentiations in trait variation between different species groups may help us in the
707 long term to understand the future of alpine plants (Guisan and Theurillat 2001). While our
708 analysis of traits at the species-level is limited by a small sample size, this finding may
709 suggest that the low-alpine flora retains significant vegetative height flexibility, which may
710 serve these species well in rapidly changing climates (Loveys et al. 2003). We suggest that
711 verification of this pattern through the analysis of intraspecific trait variation of many more
712 alpine species, different evolutionary lineages and growth forms, and from more geographic
713 regions, is a high priority for future research.

714

715

716 **Height of plants relative to neighbouring species**

717

718 Plant traits respond to both abiotic and biotic drivers, therefore we wished to learn how the
719 vegetative heights of our target species changed in relation to their nearest neighbours
720 standardising for elevation, and whether these patterns would differ among species according
721 to their elevational preferences and range. We found that species with higher elevational
722 preference were smaller than their neighbours (belonging to different species) near their
723 elevational minima and became taller relative to their neighbours near their elevational
724 maxima, where few other species were likely to be present. This agrees with our finding that
725 species with higher elevational preference showed relatively little height variation over

726 elevation and maintained conservative height values while their neighbours became taller at
727 lower elevations (see SFig. 3). In contrast, we found that target species with lower elevational
728 preferences maintained a more constant height ratio with their neighbours throughout their
729 elevational distributions, indicating that they were able to increase their vegetative heights
730 apace with their neighbours near their elevational minima. These findings may in part be
731 explained by net facilitative plant-plant interactions in harsh high alpine conditions and net
732 competitive interactions at lower elevations (Callaway et al. 2002). Due to the net facilitative
733 species interactions at high elevation, growing tall might be less necessary (and effective) as
734 a means of competition with neighbours. However, to compete at lower elevations the ability
735 to grow taller is probably a relevant survival mechanism.. The ratio of target plant to
736 neighbour plant height over elevation varied for species with different range sizes. Species
737 with narrower ranges were tallest relative to their neighbours in the upper half of their
738 elevational distributions but declined in relative height near their elevational minima.
739 Conversely, species with wider range of occurrence showed constant or increasing heights
740 relative to their neighbours as they approached their elevational maxima. These findings
741 provide additional evidence that plant species with wider range of occurrence and a
742 preference for lower elevation express considerable variation in height over elevation, which
743 permits them to grow taller in less stressful environments, and potentially enhances their
744 competitive outcomes with neighbours. Equally, our data suggest that species that prefer high
745 alpine environments or have narrow range of occurrence, achieve peak heights relative to
746 their neighbours only in the upper reaches of their elevational distributions, but are unable to
747 maintain their relative stature at lower elevations, where competition from neighbours is
748 likely to be the greatest (Alexander et al. 2015). As neighbours in our study belong to
749 different species (whichever species grew in the vicinity of our target plant), the comparison

750 to neighbours holds for the species composition at a given site/elevation and does not
751 represent direct interactions between specific species.

752

753 **Conclusions**

754

755 We showed that alpine plant species exhibit general intraspecific trends in traits over
756 elevation, and that these relationships depend upon the elevational preferences and ranges of
757 the species. More precisely, species that were more generalist in their elevational
758 distributions expressed higher trait variation over standardised elevation, than those with a
759 preference for higher elevations and narrower elevational ranges. In particular, this higher
760 variability of height allowed these species to grow taller in favourable habitats, apace with
761 their neighbours, suggesting that these species might be more capable of responding to recent
762 and future abiotic and biotic changes in alpine zones. The trait-environment relationships of
763 alpine plant species were broadly generalizable among plant species from around the world
764 suggests that plant species' elevational preferences and range sizes may be useful proxies for
765 inferring functional trait responses to environmental gradients globally.

766

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775 Sumner, Zoe Oldfield, Micheal Dimuantes and Anne Bjorkman.

776

777 **Conflict of Interest statement**

778 None of the authors have a conflict of interest.

779

780

781

782 **Author Contributions statement**

783 CR and SW and conceived the ideas and designed methodology; CR, SW, SBR and JRD
784 analysed the data and wrote the manuscript with substantial input from JG, JM, JWM, AN
785 and SV. Data were collected by CR, SW, KD, GTF, JG, CK, JL, JWM, AN, HP, BP, EQ,
786 SBR, XS, SV, WW, XW, HY, SZ and JRD, and all authors contributed to the drafts and gave
787 final approval for publication. Authorship order was determined as follows: (1) core authors;
788 (2) major contributors to data, analysis and writing (alphabetical); (3) authors contributing
789 data and to an advanced version of the manuscript (alphabetical).

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791 **Data archiving statement**

792 We will deposit our data on the WSL Data Archive ENVIDAT (<https://www.envidat.ch>). We
793 will store files in open archival formats, e.g. Word files converted to PDF and Excel files
794 converted to CSV. For R code, we will include information on the software used and its
795 version number.

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798 **References**

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- 800 Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A
801 multi-trait approach reveals the structure and the relative importance of intra- vs.
802 interspecific variability in plant traits. *Functional Ecology* **24**:1192-1201.
- 803 Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species'
804 responses to climate change. *Nature* **525**:515-+.
- 805 Atkin, O. K., B. R. Loveys, L. J. Atkinson, and T. L. Pons. 2006. Phenotypic plasticity and
806 growth temperature: understanding interspecific variability. *Journal of Experimental*
807 *Botany* **57**:267-281.
- 808 Barton, K. 2019. MuMIn: Multi-Model Inference. R package version xx. [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
809 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn).
- 810 Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects
811 Models Using lme4. *Journal of Statistical Software* **67**:1-48.
- 812 Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in*
813 *Ecology & Evolution* **9**:191-193.
- 814 Bjorkman, A. D., I. H. Myers-Smith, S. C. Elmendorf, S. Normand, N. Ruger, P. S. A. Beck,
815 A. Blach-Overgaard, D. Blok, J. H. C. Cornelissen, B. C. Forbes, D. Georges, S. J.
816 Goetz, K. C. Guay, G. H. R. Henry, J. HilleRisLambers, R. D. Hollister, D. N.
817 Karger, J. Kattge, P. Manning, J. S. Prevey, C. Rixen, G. Schaepman-Strub, H. J. D.
818 Thomas, M. Vellend, M. Wilmsking, S. Wipf, M. Carbognani, L. Hermanutz, E.
819 Levesque, U. Molau, A. Petraglia, N. A. Soudzilovskaia, M. J. Spasojevic, M.
820 Tomaselli, T. Vowles, J. M. Alatalo, H. D. Alexander, A. Anadon-Rosell, S. Angers-
821 Blondin, M. te Beest, L. Berner, R. G. Bjork, A. Buchwal, A. Buras, K. Christie, E. J.
822 Cooper, S. Dullinger, B. Elberling, A. Eskelinen, E. R. Frei, O. Grau, P. Grogan, M.
823 Hallinger, K. A. Harper, M. Heijmans, J. Hudson, K. Hulber, M. Iturrate-Garcia, C.
824 M. Iversen, F. Jaroszynska, J. F. Johnstone, R. H. Jorgensen, E. Kaarlejarvi, R. Klady,
825 S. Kuleza, A. Kulonen, L. J. Lamarque, T. Lantz, C. J. Little, J. D. M. Speed, A.
826 Michelsen, A. Milbau, J. Nabe-Nielsen, S. S. Nielsen, J. M. Ninot, S. F. Oberbauer, J.
827 Olofsson, V. G. Onipchenko, S. B. Rumpf, P. Semenchuk, R. Shetti, L. S. Collier, L.
828 E. Street, K. N. Suding, K. D. Tape, A. Trant, U. A. Treier, J. P. Tremblay, M.
829 Tremblay, S. Venn, S. Weijers, T. Zamin, N. Boulanger-Lapointe, W. A. Gould, D. S.
830 Hik, A. Hofgaard, I. S. Jonsdottir, J. Jorgenson, J. Klein, B. Magnusson, C. Tweedie,
831 P. A. Wookey, M. Bahn, B. Blonder, P. M. van Bodegom, B. Bond-Lamberty, G.
832 Campetella, B. E. L. Cerabolini, F. S. Chapin, W. K. Cornwell, J. Craine, M. Dainese,
833 F. T. de Vries, S. Diaz, B. J. Enquist, W. Green, R. Milla, U. Niinemets, Y. Onoda, J.
834 C. Ordóñez, W. A. Ozinga, J. Penuelas, H. Poorter, P. Poschlod, P. B. Reich, B.
835 Sande, B. Schamp, S. Sheremetev, and E. Weiher. 2018. Plant functional trait change
836 across a warming tundra biome. *Nature* **562**:57-+.
- 837 Bonnier, G. 1890. Cultures expérimentales dans les Alpes et les Pyrénées. *Revue Générale de*
838 *Botanique* **2**:513-546.
- 839 Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R.
840 F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity
841 allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology*
842 **82**:18-32.
- 843 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A
844 practical information-theoretic approach. Springer, New York.

- 845 Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini,
846 F. L. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J.
847 Cook. 2002. Positive interactions among alpine plants increase with stress. *Nature*
848 **417**:844-848.
- 849 Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts
850 of species associated with high levels of climate warming. *Science* **333**:1024-1026.
- 851 Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B.
852 Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H.
853 Poorter. 2003. A handbook of protocols for standardised and easy measurement of
854 plant functional traits worldwide. *Australian Journal of Botany* **51**:335-380.
- 855 Cornelissen, J. H. C., P. M. van Bodegom, R. Aerts, T. V. Callaghan, R. S. P. van Logtestijn,
856 J. Alatalo, F. S. Chapin, R. Gerdol, J. Gudmundsson, D. Gwynn-Jones, A. E. Hartley,
857 D. S. Hik, A. Hofgaard, I. S. Jonsdottir, S. Karlsson, J. A. Klein, J. Laundre, B.
858 Magnusson, A. Michelsen, U. Molau, V. G. Onipchenko, H. M. Quested, S. M.
859 Sandvik, I. K. Schmidt, G. R. Shaver, B. Solheim, N. A. Soudzilovskaia, A.
860 Stenstrom, A. Tolvanen, O. Totland, N. Wada, J. M. Welker, X. Q. Zhao, and M. O.
861 L. Team. 2007. Global negative vegetation feedback to climate warming responses of
862 leaf litter decomposition rates in cold biomes. *Ecology Letters* **10**:619-627.
- 863 Crepaz, H., G. Niedrist, J. Wessely, M. Rossi, and S. Dullinger. 2020. Resident vegetation
864 modifies climate-driven elevational shift of a mountain sedge. *Alpine Botany*.
- 865 Engler, R., C. F. Randin, W. Thuiller, S. Dullinger, N. E. Zimmermann, M. B. Araujo, P. B.
866 Pearman, G. Le Lay, C. Piedallu, C. H. Albert, P. Choler, G. Coldea, X. De Lamo, T.
867 Dirnbock, J. C. Gegout, D. Gomez-Garcia, J. A. Grytnes, E. Heegaard, F. Hoistad, D.
868 Nogues-Bravo, S. Normand, M. Puscas, M. T. Sebastia, A. Stanisci, J. P. Theurillat,
869 M. R. Trivedi, P. Vittoz, and A. Guisan. 2011. 21st century climate change threatens
870 mountain flora unequally across Europe. *Global Change Biology* **17**:2330-2341.
- 871 Floder, S., J. Yong, T. Klauschies, U. Gaedke, T. Poprnick, T. Brinkhoff, and S. Moorthi.
872 2021. Intraspecific trait variation alters the outcome of competition in freshwater
873 ciliates. *Ecology and Evolution* **11**:10225-10243.
- 874 Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding,
875 shifting and shrinking: The impact of global warming on species' elevational
876 distributions. *Global Ecology and Biogeography* **27**:1268-1276.
- 877 Freschet, G. T., C. Roumet, L. H. Comas, M. Weemstra, A. G. Bengough, B. Rewald, R. D.
878 Bardgett, G. B. De Deyn, D. Johnson, J. Klimesova, M. Lukac, M. L. McCormack, I.
879 C. Meier, L. Pages, H. Poorter, I. Prieto, N. Wurzbürger, M. Zadworny, A.
880 Bagniewska-Zadworna, E. B. Blancaflor, I. Brunner, A. Gessler, S. E. Hobbie, C. M.
881 Iversen, L. Mommer, C. Picon-Cochard, J. A. Postma, L. Rose, P. Ryser, M. Scherer-
882 Lorenzen, N. A. Soudzilovskaia, T. Sun, O. J. Valverde-Barrantes, A. Weigelt, L. M.
883 York, and A. Stokes. 2021. Root traits as drivers of plant and ecosystem functioning:
884 current understanding, pitfalls and future research needs. *New Phytologist* **232**:1123-
885 1158.
- 886 Freschet, G. T., C. Violle, M. Y. Bourget, M. Scherer-Lorenzen, and F. Fort. 2018.
887 Allocation, morphology, physiology, architecture: the multiple facets of plant above-
888 and below-ground responses to resource stress. *New Phytologist* **219**:1338-1352.
- 889 Giejsztowt, J., A. T. Classen, and J. R. Deslippe. 2020. Climate change and invasion may
890 synergistically affect native plant reproduction. *Ecology* **101**.
- 891 Guisan, A., and J.-P. Theurillat. 2001. Assessing alpine plant vulnerability to climate change:
892 a modeling perspective. *Integrated Assessment* **1**:307-320.
- 893 Halbritter, A. H., S. Fior, I. Keller, R. Billeter, P. J. Edwards, R. Holderegger, S. Karrenberg,
894 A. R. Pluess, A. Widmer, and J. M. Alexander. 2018. Trait differentiation and

895 adaptation of plants along elevation gradients. *Journal of Evolutionary Biology*
896 **31**:784-800.

897 Henn, J. J., V. Buzzard, B. J. Enquist, A. H. Halbritter, K. Klanderuds, B. S. Maitner, S. T.
898 Michaletz, C. Potschs, L. Seltzer, R. J. Telford, Y. Yang, L. Zhang, and V. Vandvik.
899 2018. Intraspecific Trait Variation and Phenotypic Plasticity Mediate Alpine Plant
900 Species Response to Climate Change. *Frontiers in Plant Science* **9**.

901 Kattge, J., G. Bonisch, S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D.
902 A. Werner, T. Aakala, M. Abedi, A. T. R. Acosta, G. C. Adamidis, K. Adamson, M.
903 Aiba, C. H. Albert, J. M. Alcantara, C. C. Alcazar, I. Aleixo, H. Ali, B. Amiaud, C.
904 Ammer, M. M. Amoroso, M. Anand, C. Anderson, N. Anten, J. Antos, D. M. G.
905 Apgaua, T. L. Ashman, D. H. Asmara, G. P. Asner, M. Aspinwall, O. Atkin, I. Aubin,
906 L. Bastrup-Spohr, K. Bahalkeh, M. Bahn, T. Baker, W. J. Baker, J. P. Bakker, D.
907 Baldocchi, J. Baltzer, A. Banerjee, A. Baranger, J. Barlow, D. R. Barneche, Z.
908 Baruch, D. Bastianelli, J. Battles, W. Bauerle, M. Bauters, E. Bazzato, M. Beckmann,
909 H. Beeckman, C. Beierkuhnlein, R. Bekker, G. Belfry, M. Belluau, M. Beloiu, R.
910 Benavides, L. Benomar, M. L. Berdugo-Lattke, E. Berenguer, R. Bergamin, J.
911 Bergmann, M. B. Carlucci, L. Berner, M. Bernhardt-Romermann, C. Bigler, A. D.
912 Bjorkman, C. Blackman, C. Blanco, B. Blonder, D. Blumenthal, K. T. Bocanegra-
913 Gonzalez, P. Boeckx, S. Bohlman, K. Bohning-Gaese, L. Boisvert-Marsh, W. Bond,
914 B. Bond-Lamberty, A. Boom, C. C. F. Boonman, K. Bordin, E. H. Boughton, V.
915 Boukili, D. Bowman, S. Bravo, M. R. Brendel, M. R. Broadley, K. A. Brown, H.
916 Bruelheide, F. Brunnich, H. H. Bruun, D. Bruy, S. W. Buchanan, S. F. Bucher, N.
917 Buchmann, R. Buitenwerf, D. E. Bunker, J. Burger, S. Burrascano, D. Burslem, B. J.
918 Butterfield, C. Byun, M. Marques, M. C. Scalon, M. Caccianiga, M. Cadotte, M.
919 Cailleret, J. Camac, J. J. Camarero, C. Company, G. Campetella, J. A. Campos, L.
920 Cano-Arboleda, R. Canullo, M. Carbognani, F. Carvalho, F. Casanoves, B.
921 Castagneyrol, J. A. Catford, J. Cavender-Bares, B. E. L. Cerabolini, M. Cervellini, E.
922 Chacon-Madrigal, K. Chapin, F. S. Chapin, S. Chelli, S. C. Chen, A. P. Chen, P.
923 Cherubini, F. Chianucci, B. Choat, K. S. Chung, M. Chytry, D. Ciccarelli, L. Coll, C.
924 G. Collins, L. Conti, D. Coomes, J. H. C. Cornelissen, W. K. Cornwell, P. Corona, M.
925 Coyea, J. Craine, D. Craven, J. Cromsigt, A. Cseceserits, K. Cufar, M. Cuntz, A. C. da
926 Silva, K. M. Dahlin, M. Dainese, I. Dalke, M. Dalle Fratte, T. D. L. Anh, J.
927 Danihelka, M. Dannoura, S. Dawson, A. J. de Beer, A. De Frutos, J. R. De Long, B.
928 Dechant, S. Delagrangue, N. Delpierre, G. Derroire, A. S. Dias, M. H. Diaz-Toribio, P.
929 G. Dimitrakopoulos, M. Dobrowolski, D. Doktor, P. Drevojan, N. Dong, J.
930 Dransfield, S. Dressler, L. Duarte, E. Ducouret, S. Dullinger, W. Durka, R. Duursma,
931 O. Dymova, A. E-Vojtko, R. L. Eckstein, H. Ejtehadi, J. Elser, T. Emilio, K.
932 Engemann, M. B. Erfanian, A. Erfmeier, A. Esquivel-Muelbert, G. Esser, M. Estiarte,
933 T. F. Domingues, W. F. Fagan, J. Fagundez, D. S. Falster, Y. Fan, J. Y. Fang, E.
934 Farris, F. Fazlioglu, Y. H. Feng, F. Fernandez-Mendez, C. Ferrara, J. Ferreira, A.
935 Fidelis, B. Finegan, J. Firn, T. J. Flowers, D. F. B. Flynn, V. Fontana, E. Forey, C.
936 Forgiarini, L. Francois, M. Frangipani, D. Frank, C. Frenette-Dussault, G. T. Freschet,
937 E. L. Fry, N. M. Fyllas, G. G. Mazzochini, S. Gachet, R. Gallagher, G. Ganade, F.
938 Ganga, P. Garcia-Palacios, V. Gargaglione, E. Garnier, J. L. Garrido, A. L. de Gasper,
939 G. Gea-Izquierdo, D. Gibson, A. N. Gillison, A. Giroldo, M. C. Glasenhardt, S.
940 Gleason, M. Gliesch, E. Goldberg, B. Goldel, E. Gonzalez-Akre, J. L. Gonzalez-
941 Andujar, A. Gonzalez-Melo, A. Gonzalez-Robles, B. J. Graae, E. Granda, S. Graves,
942 W. A. Green, T. Gregor, N. Gross, G. R. Guerin, A. Gunther, A. G. Gutierrez, L.
943 Haddock, A. Haines, J. Hall, A. Hambuckers, W. X. Han, S. P. Harrison, W.
944 Hattingh, J. E. Hawes, T. H. He, P. C. He, J. M. Heberling, A. Helm, S. Hempel, J.

945 Hentschel, B. Herauld, A. M. Heres, K. Herz, M. Heuertz, T. Hickler, P. Hietz, P.
 946 Higuchi, A. L. Hipp, A. Hirons, M. Hock, J. A. Hogan, K. Holl, O. Honnay, D.
 947 Hornstein, E. Q. Hou, N. Hough-Snee, K. A. Hovstad, T. Ichie, B. Igie, E. Illa, M.
 948 Isaac, M. Ishihara, L. Ivanov, L. Ivanova, C. M. Iversen, J. Izquierdo, R. B. Jackson,
 949 B. Jackson, H. Jactel, A. M. Jagodzinski, U. Jandt, S. Jansen, T. Jenkins, A. Jentsch,
 950 J. R. P. Jespersen, G. F. Jiang, J. L. Johansen, D. Johnson, E. J. Jokela, C. A. Joly, G.
 951 J. Jordan, G. S. Joseph, D. Junaedi, R. R. Junker, E. Justes, R. Kabzems, J. Kane, Z.
 952 Kaplan, T. Kattenborn, L. Kavelenova, E. Kearsley, A. Kempel, T. Kenzo, A.
 953 Kerkhoff, M. I. Khalil, N. L. Kinlock, W. D. Kissling, K. Kitajima, T. Kitzberger, R.
 954 Kjoller, T. Klein, M. Kleyer, J. Klimesova, J. Klipel, B. Kloeppe, S. Klotz, J. M. H.
 955 Knops, T. Kohyama, F. Koike, J. Kollmann, B. Komac, K. Komatsu, C. Konig, N. J.
 956 B. Kraft, K. Kramer, H. Kreft, I. Kuhn, D. Kumarathunge, J. Kuppler, H. Kurokawa,
 957 Y. Kurosawa, S. Kuyah, J. P. Laclau, B. Lafleur, E. Lallai, E. Lamb, A. Lamprecht,
 958 D. J. Larkin, D. Laughlin, Y. Le Bagousse-Pinguet, G. le Maire, P. C. le Roux, E. le
 959 Roux, T. Lee, F. Lens, S. L. Lewis, B. Lhotsky, Y. Z. Li, X. E. Li, J. W. Lichstein, M.
 960 Liebergesell, J. Y. Lim, Y. S. Lin, J. C. Linares, C. J. Liu, D. J. Liu, U. Liu, S.
 961 Livingstone, J. Llusia, M. Lohbeck, A. Lopez-Garcia, G. Lopez-Gonzalez, Z.
 962 Lososova, F. Louault, B. A. Lukacs, P. Lukes, Y. J. Luo, M. Lussu, S. Y. Ma, C. M.
 963 R. Pereira, M. Mack, V. Maire, A. Makela, H. Makinen, A. C. M. Malhado, A.
 964 Mallik, P. Manning, S. Manzoni, Z. Marchetti, L. Marchino, V. Marcilio-Silva, E.
 965 Marcon, M. Marignani, L. Markesteijn, A. Martin, C. Martinez-Garza, J. Martinez-
 966 Vilalta, T. Maskova, K. Mason, N. Mason, T. J. Massad, J. Masse, I. Mayrose, J.
 967 McCarthy, M. L. McCormack, K. McCulloh, I. R. McFadden, B. J. McGill, M. Y.
 968 McPartland, J. S. Medeiros, B. Medlyn, P. Meerts, Z. Mehrabi, P. Meir, F. P. L. Melo,
 969 M. Mencuccini, C. Meredieu, J. Messier, I. Meszaros, J. Metsaranta, S. T. Michaletz,
 970 C. Michelaki, S. Migalina, R. Milla, J. E. D. Miller, V. Minden, R. Ming, K. Mokany,
 971 A. T. Moles, V. A. Molnar, J. Molofsky, M. Molz, R. A. Montgomery, A. Monty, L.
 972 Moravcova, A. Moreno-Martinez, M. Moretti, A. S. Mori, S. Mori, D. Morris, J.
 973 Morrison, L. Mucina, S. Mueller, C. D. Muir, S. C. Muller, F. Munoz, I. H. Myers-
 974 Smith, R. W. Myster, M. Nagano, S. Naidu, A. Narayanan, B. Natesan, L. Negoita, A.
 975 S. Nelson, E. L. Neuschulz, J. Ni, G. Niedrist, J. Nieto, U. Niinemets, R. Nolan, H.
 976 Nottebrock, Y. Nouvellon, A. Novakovskiy, K. O. Nystuen, A. O'Grady, K. O'Hara,
 977 A. O'Reilly-Nugent, S. Oakley, W. Oberhuber, T. Ohtsuka, R. Oliveira, K. Ollerer, M.
 978 E. Olson, V. Onipchenko, Y. Onoda, R. E. Onstein, J. C. Ordonez, N. Osada, I.
 979 Ostonen, G. Ottaviani, S. Otto, G. E. Overbeck, W. A. Ozinga, A. T. Pahl, C. E. T.
 980 Paine, R. J. Pakeman, A. C. Papageorgiou, E. Parfionova, M. Partel, M. Patacca, S.
 981 Paula, J. Paule, H. Pauli, J. G. Pausas, B. Peco, J. Penuelas, A. Perea, P. L. Peri, A. C.
 982 Petisco-Souza, A. Petraglia, A. M. Petritan, O. L. Phillips, S. Pierce, V. D. Pillar, J.
 983 Pisek, A. Pomogaybin, H. Poorter, A. Portsmouth, P. Poschlod, C. Potvin, D. Pounds,
 984 A. S. Powell, S. A. Power, A. Prinzing, G. Puglielli, P. Pysek, V. Raevel, A. Rammig,
 985 J. Ransijn, C. A. Ray, P. B. Reich, M. Reichstein, D. E. B. Reid, M. Rejou-Mechain,
 986 V. R. de Dios, S. Ribeiro, S. Richardson, K. Riibak, M. C. Rillig, F. Riviera, E. M. R.
 987 Robert, S. Roberts, B. Robroek, A. Roddy, A. V. Rodrigues, A. Rogers, E. Rollinson,
 988 V. Rolo, C. Romermann, D. Ronzhina, C. Roscher, J. A. Rosell, M. F. Rosenfield, C.
 989 Rossi, D. B. Roy, S. Royer-Tardif, N. Ruger, R. Ruiz-Peinado, S. B. Rumpf, G. M.
 990 Rusch, M. Ryo, L. Sack, A. Saldana, B. Salgado-Negret, R. Salguero-Gomez, I.
 991 Santa-Regina, A. C. Santacruz-Garcia, J. Santos, J. Sardans, B. Schamp, M. Scherer-
 992 Lorenzen, M. Schleuning, B. Schmid, M. Schmidt, S. Schmitt, J. V. Schneider, S. D.
 993 Schowanek, J. Schrader, F. Schrodt, B. Schuldt, F. Schurr, G. S. Garvizu, M.
 994 Semchenko, C. Seymour, J. C. Sfair, J. M. Sharpe, C. S. Sheppard, S. Sheremetiev, S.

- 995 Shiodera, B. Shipley, T. A. Shovon, A. Siebenkas, C. Sierra, V. Silva, M. Silva, T.
996 Sitzia, H. Sjöman, M. Slot, N. G. Smith, D. Sodhi, P. Soltis, D. Soltis, B. Somers, G.
997 Sonnier, M. V. Sorensen, E. E. Sosinski, N. A. Soudzilovskaia, A. F. Souza, M.
998 Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K. Steinbauer, J. G. Stephan, F.
999 Sterck, D. B. Stojanovic, T. Strydom, M. L. Suarez, J. C. Svenning, I. Svitkova, M.
1000 Svitok, M. Svoboda, E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U. Tappeiner,
1001 R. Tarifa, S. Tauougourdeau, C. Tavsanoğlu, M. te Beest, L. Tedersoo, N. Thiffault, D.
1002 Thom, E. Thomas, K. Thompson, P. E. Thornton, W. Thuiller, L. Tichy, D. Tissue,
1003 M. G. Tjoelker, D. Y. P. Tng, J. Tobias, P. Torok, T. Tarin, J. M. Torres-Ruiz, B.
1004 Tothmeresz, M. Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk, J. L. Tsakalos, I.
1005 Tsiripidis, N. Tysklind, T. Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi, F.
1006 Valladares, J. Vamosi, P. M. van Bodegom, M. van Breugel, E. Van Cleemput, M.
1007 van de Weg, S. van der Merwe, F. van der Plas, M. T. van der Sande, M. van
1008 Kleunen, K. Van Meerbeek, M. Vanderwel, K. A. Vanselow, A. Varhammar, L.
1009 Varone, M. Y. Valderrama, K. Vassilev, M. Vellend, E. J. Veneklaas, H. Verbeeck,
1010 K. Verheyen, A. Vibrans, I. Vieira, J. Villacis, C. Violle, P. Vivek, K. Wagner, M.
1011 Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang, F. Wang, W.
1012 Q. Wang, H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. P. Wei, P. Weigelt, E.
1013 Weiher, A. W. Wells, C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White,
1014 M. Whitten, M. Williams, D. E. Winkler, K. Winter, C. Womack, I. J. Wright, S. J.
1015 Wright, J. Wright, B. X. Pinho, F. Ximenes, T. Yamada, K. Yamaji, R. Yanai, N.
1016 Yankov, B. Yguel, K. J. Zanini, A. E. Zanne, D. Zeleny, Y. P. Zhao, J. M. Zheng, J.
1017 Zheng, K. Ziemska, C. R. Zirbel, G. Zizka, I. C. Zo-Bi, G. Zotz, C. Wirth, and N.
1018 Nutrient. 2020. TRY plant trait database - enhanced coverage and open access. *Global*
1019 *Change Biology* **26**:119-188.
- 1020 Kichenin, E., D. A. Wardle, D. A. Peltzer, C. W. Morse, and G. T. Freschet. 2013.
1021 Contrasting effects of plant inter- and intraspecific variation on community-level trait
1022 measures along an environmental gradient. *Functional Ecology* **27**:1254-1261.
- 1023 Kieltyk, P. 2018. Variation of vegetative and floral traits in the alpine plant *Solidago minuta*:
1024 evidence for local optimum along an elevational gradient. *Alpine Botany* **128**:47-57.
- 1025 Körner, C. 2003. *Alpine plant life*. 2nd edition. Springer Verlag, Berlin.
- 1026 Körner, C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*
1027 **22**:569-574.
- 1028 Lamprecht, A., P. R. Semenchuk, K. Steinbauer, M. Winkler, and H. Pauli. 2018. Climate
1029 change leads to accelerated transformation of high-elevation vegetation in the central
1030 Alps. *New Phytologist* **220**:447-459.
- 1031 Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and
1032 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*
1033 **16**:545-556.
- 1034 Loveys, B. R., L. J. Atkinson, D. J. Sherlock, R. L. Roberts, A. H. Fitter, and O. K. Atkin.
1035 2003. Thermal acclimation of leaf and root respiration: an investigation comparing
1036 inherently fast- and slow-growing plant species. *Global Change Biology* **9**:895-910.
- 1037 MacLean, S. A., and S. R. Beissinger. 2017. Species' traits as predictors of range shifts under
1038 contemporary climate change: A review and meta-analysis. *Global Change Biology*
1039 **23**:4094-4105.
- 1040 Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-
1041 gradient hypothesis for competition and facilitation in plant communities. *Journal of*
1042 *Ecology* **97**:199-205.
- 1043 Malkinson, D., and K. Tielbörger. 2010. What does the stress-gradient hypothesis predict?
1044 Resolving the discrepancies. *Oikos* **119**:1546-1552.

- 1045 Marshall, J. D., and J. W. Zhang. 1994. Carbon-isotope discrimination and water-use
1046 efficiency in native plants of the North-Central Rockies. *Ecology* **75**:1887-1895.
- 1047 McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community
1048 ecology from functional traits. *Trends in Ecology & Evolution* **21**:178-185.
- 1049 Midolo, G., P. De Frenne, N. Holz, and C. Wellstein. 2019. Global patterns of intraspecific
1050 leaf trait responses to elevation. *Global Change Biology* **25**:2485-2498.
- 1051 Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G.
1052 Coldea, J. Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G.
1053 Kazakis, J. Kollar, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L.
1054 Nagy, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, A. O. Syverhuset, J. P. Theurillat,
1055 M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent
1056 Plant Diversity Changes on Europe's Mountain Summits. *Science* **336**:353-355.
- 1057 Pauli, H., M. Gottfried, K. Reiter, C. Klettner, and G. Grabherr. 2007. Signals of range
1058 expansions and contractions of vascular plants in the high Alps: observations (1994-
1059 2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. *Global Change
1060 Biology* **13**:147-156.
- 1061 Pearson, R. G., S. J. Phillips, M. M. Lorant, P. S. A. Beck, T. Damoulas, S. J. Knight, and S.
1062 J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate
1063 change. *Nature Climate Change* **3**:673-677.
- 1064 Pellissier, L., B. Fournier, A. Guisan, and P. Vittoz. 2010. Plant traits co-vary with altitude in
1065 grasslands and forests in the European Alps. *Plant Ecology* **211**:351-365.
- 1066 Perez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S.
1067 Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas,
1068 P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N.
1069 Buchmann, G. Funes, F. Quetier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter
1070 Steege, M. G. A. van der Heijden, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti,
1071 G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for
1072 standardised measurement of plant functional traits worldwide. *Australian Journal of
1073 Botany* **61**:167-234.
- 1074 Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and
1075 consequences of variation in leaf mass per area (LMA): a meta-analysis. *New
1076 Phytologist* **182**:565-588.
- 1077 R Development Core Team. 2021. R Foundation for Statistical Computing. *in* R. D. C. Team,
1078 editor., Vienna, Austria.
- 1079 Read, Q. D., L. C. Moorhead, N. G. Swenson, J. K. Bailey, and N. J. Sanders. 2014.
1080 Convergent effects of elevation on functional leaf traits within and among species.
1081 *Functional Ecology* **28**:37-45.
- 1082 Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of
1083 Applied Ecology* **45**:218-227.
- 1084 Rumpf, S. B., K. Hulber, G. Klonner, D. Moser, M. Schutz, J. Wessely, W. Willner, N. E.
1085 Zimmermann, and S. Dullinger. 2018. Range dynamics of mountain plants decrease
1086 with elevation. *Proceedings of the National Academy of Sciences of the United States
1087 of America* **115**:1848-1853.
- 1088 Rumpf, S. B., K. Hulber, N. E. Zimmermann, and S. Dullinger. 2019. Elevational rear edges
1089 shifted at least as much as leading edges over the last century. *Global Ecology and
1090 Biogeography* **28**:533-543.
- 1091 Scherrer, D., and C. Körner. 2011. Topographically controlled thermal-habitat differentiation
1092 buffers alpine plant diversity against climate warming. *Journal of Biogeography*
1093 **38**:406-416.

- 1094 Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen,
1095 C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. D. Dantas, F. de Bello, L. D. S.
1096 Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B.
1097 Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B.
1098 Kraft, A. Lagerstrom, Y. Le Bagousse-Pinguet, Y. Z. Li, N. Mason, J. Messier, T.
1099 Nakashizuka, J. McC Overton, D. A. Peltzer, I. M. Perez-Ramos, V. D. Pillar, H. C.
1100 Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schob, B. Shipley, M. Sundqvist,
1101 M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the
1102 relative extent of intraspecific trait variation in plant communities. *Ecology Letters*
1103 **18**:1406-1419.
- 1104 Staudé, I. R., H. M. Pereira, G. N. Daskalova, M. Bernhardt-Römermann, M. Diekmann, P.
1105 H., and al. 2021. Directional temporal turnover toward plant species with larger
1106 ranges across habitats. *Ecology Letters* **00**:000-000.
- 1107 Steinbauer, M. J., J. A. Grytnes, G. Jurasinski, A. Kulonen, J. Lenoir, H. Pauli, C. Rixen, M.
1108 Winkler, M. Bardy-Durchhalter, E. Barni, A. D. Bjorkman, F. T. Breiner, S. Burg, P.
1109 Czortek, M. A. Dawes, A. Delimat, S. Dullinger, B. Erschbamer, V. A. Felde, O.
1110 Fernandez-Arberas, K. F. Fossheim, D. Gomez-Garcia, D. Georges, E. T. Grindrud,
1111 S. Haider, S. V. Haugum, H. Henriksen, M. J. Herreros, B. Jaroszewicz, F.
1112 Jaroszynska, R. Kanka, J. Kapfer, K. Klanderud, I. Kuhn, A. Lamprecht, M.
1113 Matteodo, U. M. di Cella, S. Normand, A. Odland, S. L. Olsen, S. Palacio, M. Petey,
1114 V. Piscova, B. Sedlakova, K. Steinbauer, V. Stockli, J. C. Svenning, G. Teppa, J. P.
1115 Theurillat, P. Vittoz, S. J. Woodin, N. E. Zimmermann, and S. Wipf. 2018.
1116 Accelerated increase in plant species richness on mountain summits is linked to
1117 warming. *Nature* **556**:231-234.
- 1118 Sundqvist, M. K., N. J. Sanders, and D. A. Wardle. 2013. Community and Ecosystem
1119 Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global
1120 Change. Pages 261-280 *in* D. J. Futuyma, editor. *Annual Review of Ecology,*
1121 *Evolution, and Systematics*, Vol 44.
- 1122 Thomas, H. J. D., A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, J. Kattge, S. Diaz,
1123 M. Vellend, D. Blok, J. H. C. Cornelissen, B. C. Forbes, G. H. R. Henry, R. D.
1124 Hollister, S. Normand, J. S. Prevey, C. Rixen, G. Schaepman-Strub, M. Wilmking, S.
1125 Wipf, W. K. Cornwell, P. S. A. Beck, D. Georges, S. J. Goetz, K. C. Guay, N. Ruger,
1126 N. A. Soudzilovskaia, M. J. Spasojevic, J. M. Alatalo, H. D. Alexander, A. Anadon-
1127 Rosell, S. Angers-Blondin, M. te Beest, L. T. Berner, R. G. Bjork, A. Buchwal, A.
1128 Buras, M. Carbognani, K. S. Christie, L. S. Collier, E. J. Cooper, B. Elberling, A.
1129 Eskelinen, E. R. Frei, O. Grau, P. Grogan, M. Hallinger, M. Heijmans, L. Hermanutz,
1130 J. M. G. Hudson, J. F. Johnstone, K. Hulber, M. Iturrate-Garcia, C. M. Iversen, F.
1131 Jaroszynska, E. Kaarlejarvi, A. Kulonen, L. J. Lamarque, T. C. Lantz, E. Levesque, C.
1132 J. Little, A. Michelsen, A. Milbau, J. Nabe-Nielsen, S. S. Nielsen, J. M. Ninot, S. F.
1133 Oberbauer, J. Olofsson, V. G. Onipchenko, A. Petraglia, S. B. Rumpf, R. Shetti, J. D.
1134 M. Speed, K. N. Suding, K. D. Tape, M. Tomaselli, A. J. Trant, U. A. Treier, M.
1135 Tremblay, S. E. Venn, T. Vowles, S. Weijers, P. A. Wookey, T. J. Zamin, M. Bahn,
1136 B. Blonder, P. M. van Bodegom, B. Bond-Lamberty, G. Campetella, B. E. L.
1137 Cerabolini, F. S. Chapin, J. M. Craine, M. Dainese, W. A. Green, S. Jansen, M.
1138 Kleyer, P. Manning, U. Niinemets, Y. Onoda, W. A. Ozinga, J. Penuelas, P. Poschlod,
1139 P. B. Reich, B. Sandel, B. S. Schamp, S. N. Sheremetiev, and F. T. de Vries. 2020.
1140 Global plant trait relationships extend to the climatic extremes of the tundra biome.
1141 *Nature Communications* **11**.
- 1142 Thuiller, W., C. Albert, M. B. Araujo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F.
1143 Midgely, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008.

1144 Predicting global change impacts on plant species' distributions: Future challenges.
 1145 Perspectives in Plant Ecology Evolution and Systematics **9**:137-152.
 1146 Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J.
 1147 Messier. 2012. The return of the variance: intraspecific variability in community
 1148 ecology. Trends in Ecology & Evolution **27**:244-252.
 1149 Walther, G. R., S. Beissner, and C. A. Burga. 2005. Trends in the upward shift of alpine
 1150 plants. Journal of Vegetation Science **16**:541-548.
 1151 Weemstra, M., N. Kiorapostolou, J. van Ruijven, L. Mommer, J. de Vries, and F. Sterck.
 1152 2020a. The role of fine-root mass, specific root length and life span in tree
 1153 performance: A whole-tree exploration. Functional Ecology **34**:575-585.
 1154 Weemstra, M., K. G. Peay, S. J. Davies, M. Mohamad, A. Itoh, S. Tan, and S. E. Russo.
 1155 2020b. Lithological constraints on resource economies shape the mycorrhizal
 1156 composition of a Bornean rain forest. New Phytologist **228**:253-268.
 1157 Wiens, J. J. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant
 1158 and Animal Species. PLoS Biology **14**.
 1159 Winkler, M., A. Lamprecht, K. Steinbauer, K. Hülber, J.-P. Theurillat, F. Breiner, P. Choler,
 1160 S. Ertl, A. Gutiérrez Girón, G. Rossi, P. Vittoz, M. Akhalkatsi, C. Bay, J.-L. Benito
 1161 Alonso, T. Bergström, M. L. Carranza, E. Corcket, J. Dick, B. Erschbamer, R.
 1162 Fernández Calzado, A. M. Fosaa, R. G. Gavilán, D. Ghosn, K. Gigauri, D. Huber, R.
 1163 Kanka, G. Kazakis, M. Klipp, J. Kollar, T. Kudernatsch, P. Larsson, M. Mallaun, O.
 1164 Michelsen, P. Moiseev, D. Moiseev, U. Molau, J. Molero Mesa, U. Morra di Cella, L.
 1165 Nagy, M. Petey, M. Puşcaş, C. Rixen, A. Stanisci, M. Suen, A. O. Syverhuset, M.
 1166 Tomaselli, P. Unterluggauer, T. Ursu, L. Villar, M. Gottfried, and H. Pauli. 2016. The
 1167 rich sides of mountain summits – a pan-European view on aspect preferences of
 1168 alpine plants. Journal of Biogeography **43**:2261-2273.
 1169 Wright, I. J., N. Dong, V. Maire, I. C. Prentice, M. Westoby, S. Diaz, R. V. Gallagher, B. F.
 1170 Jacobs, R. Kooyman, E. A. Law, M. R. Leishman, U. Niinemets, P. B. Reich, L. Sack,
 1171 R. Villar, H. Wang, and P. Wilf. 2017. Global climatic drivers of leaf size. Science
 1172 **357**:917-921.
 1173