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Intraspecific trait variation in alpine plants relates to their elevational distribution

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Abstract

Climate warming is shifting the distributions of mountain plant species to higher elevations. Cold-adapted plant species are under increasing pressure from novel competitors that are encroaching from lower elevations. Plant capacity to adjust to these pressures may be measurable as variation in trait values within a species. In particular, the strength and patterns of intraspecific trait variation along abiotic and biotic gradients can inform us whether and how species can adjust their anatomy and morphology to persist in a changing environment.

Here, we tested whether species specialized to high elevations or with narrow elevational ranges show more conservative (i.e. less variable) trait responses across their elevational distribution, or in response to neighbours, than species from lower elevations or with wider elevational ranges. We did so by studying intraspecific trait variation of 66 species along 40 elevational gradients in four countries in both hemispheres. As an indication of potential neighbour interactions that could drive trait variation, we also analysed plant species' height ratio, its height relative to its nearest neighbour.

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

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

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

Introduction

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

Some plant-specific functional traits, especially size-related ones (e.g. height or leaf size), are powerful indicators of plant performance, vary among species, and are useful for inferring functional changes (e.g. biomass or competitive ability) in communities across ecological scales (Lavorel and Garnier 2002, Cornelissen et al. 2007, Pearson et al. 2013, Freschet et al. 2021). In particular, these traits may show species-specific patterns of variation over environmental gradients. In tundra plants, for example, intraspecific temperature-trait relationships for size-related traits varied significantly between different species over spatial and temporal gradients (Bjorkman et al. 2018). While plant species that are able to grow taller in warmer conditions (e.g. through relatively high phenotypic trait plasticity/variability) may have an advantage under climate change over those that remain small in height irrespective of growing conditions (relatively low trait plasticity/variability), the link between trait variation and competitive outcomes remains untested for most traits (but see Bret-Harte et al. 2001). Also, trait variation may not always be adaptive with regard to environmental circumstances. The large variation in the shape of trait-environment relationships reported for vegetative, economic and reproductive traits for cold-biome species (Bjorkman et al. 2018, Kieltyk 2018, Midolo et al. 2019) suggest that these responses depend on the traits studied (for belowground traits see Weemstra et al. 2020b). In addition, the response to any single environmental change can vary, so that members of a community may utilise a diversity of plastic responses (Freschet et al. 2018, Weemstra et al. 2020a). Clearly, systematic, empirical data describing the pattern of intraspecific trait variation over environmental gradients will enhance our understanding of the range of species' responses to shifting environments (Albert et al. 2010, Violle et al. 2012, Siefert et al. 2015). Fortunately, trait values for species have become more common in global trait data repositories (e.g., TRY; Kattge et al. 2020). However, systematic data on intraspecific variation in trait values along entire species ranges are not commonly available across multiple species within ecosystems (Midolo et al. 2019), and this situation limits our understanding of species' responses to environmental change in a community context.

Intraspecific plant trait variation over environmental gradients is a function of both biotic and abiotic drivers. Generally, the relative importance of biotic drivers decreases towards higher elevations due to cold temperatures according to the stress gradient hypothesis (Bertness and Callaway 1994). There has been a strong research focus on changes to the leading edge of species' geographic distributions (e.g. on mountain summits), where plants are colonising new habitats to track a warming climate (Walther et al. 2005, Pauli et al. 2012, Winkler et al. 2016, Steinbauer et al. 2018, Crepaz et al. 2020). However, it is the trailing edge where alpine species can be expected to disappear (Thuiller et al. 2008, Alexander et al. 2015, Wiens 2016, Freeman et al. 2018, Rumpf et al. 2019). Indeed, increasing competition from novel lowland species is considered the most important factor driving local extinctions at the trailing edge of species distributions (Pauli et al. 2007, Engler et al. 2011, Alexander et al. 2015). Although studies are few, there is evidence that the trailing edges of alpine species ranges shift upslope as much or even more than their leading edges do (Rumpf et al. 2019). Hence, if plant intraspecific trait variation can provide insight into the susceptibility of different plant species with respect to their range, much improved predictions can be gained from a better understanding of within-community trait variation over species' entire elevational ranges.

Alpine plant species differ in their habitat preferences, which is in part expressed by their disparate spatial distributions. Within a complete alpine flora, species may for instance demonstrate different elevational distributions and related temperature ranges, which can be quantified as the median elevation of all observations for that species (Fig. 1; see methods for quality of median as a proxy for a species range). These different habitat preferences along elevational gradients may be reflected in interspecific differences of particular traits (Sundqvist et al. 2013). For example, we may expect different trait values for species that occupy environmentally harsher habitats, such as barren high-alpine scree slopes, compared with those that occupy more benign habitats, such as low-alpine meadows. Species from high alpine and other cold regions often have more conservative life history strategies compared to species from lower elevations; they are slow-growing and small-sized (Körner 2003) with relatively small and tough leaves resulting in low specific leaf area (SLA) and high leaf dry matter content (LDMC; Perez-Harguindeguy et al. 2013, Bjorkman et al. 2018, Thomas et al. 2020). The conservative strategies of high-alpine species may not only be expressed by absolute trait values, but also by relatively low trait variation across their elevational range, that is, low intraspecific trait variation. Conversely, plants that occupy lower elevations of the alpine zone may express larger trait variation across their elevational range because they are likely to be confronted with numerous and more competitive neighbouring species of varying sizes and trait properties. We therefore expect plant species that prefer higher alpine environments to show less trait variation over equivalent elevational increment than species that inhabit lower alpine zones. However, to the best of our knowledge, no study has investigated the generality of this relationship.

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

Here, we studied how aboveground plant functional traits of 66 species vary along environmental gradients that span their entire elevational distributions (upper and lower limits of the alpine zone) on mountain ranges in Switzerland, China, Australia and New Zealand as they represent major mountain regions of the globe. We chose traits that respond to both abiotic and biotic drivers (e.g., plant height, leaf traits) and that could be measured efficiently and in a standardised way in remote field settings. We aimed to identify general patterns of intraspecific trait variation among the alpine species from these diverse environments to reveal whether plants show species-specific patterns of trait variation, and whether the characteristics of the species' geographic distributions (i.e., elevational preference and elevational range) relate to elevation. We defined "preference" as the realized niche where species occurred. Specifically, we asked:

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

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

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

Methods

Selection of research sites and species

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

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

Trait and field measurements

Along each transect, we established ~100 m^2 field sites in regular vertical elevational increments; in AU, where gradients were relatively short (often c. 500 m), field sites were located every 50 m. In CN and NZ sites occurred at 100 m increments, and in CH at every 150 m increase in elevation. At each of the sites, we recorded GPS coordinates, elevation, aspect, and slope. We photographed the field site and all target species. We estimated the abundances of the target species in five classes (1 = 1 individual, 2 = 2-3 ind., 3 = 4-10 ind., 4 = 11-50 ind., 5 = >50 ind.). For each target species, we then measured seven traits at each collection site based on their ecological relevance for our research questions and feasibility of measurement in the field (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013). As an indication of plant stature, we measured vegetative and generative height, where vegetative height was distance from soil to highest vegetative leaf and generative height was distance to the highest point on the reproductive shoot. As a measure of reproductive investment, we noted the presence of flowers on the randomly chosen individuals (see below). As a measure of individual and genet basal area, we measured individual plant and patch diameters, in two dimensions (along the largest diameter and perpendicular to it). In clonal plant species, plant diameter was equivalent to an individual rosette, whereas patch diameter referred to the whole genet and could represent the size of a tuft, tussock or cushion. For genera with more singular growth forms (e.g., some *Gentiana* species) plant and patch diameter were the same. The two diameter measurements were made at right angles, allowing estimates of patch and plant areas to be calculated as an ellipse (i.e., area = 0.5 a 0.5 b Π). All traits were measured on ten randomly selected individuals per site. Flower count data was considered in a binary fashion on a per individual basis (because for some species individuals only produce one flower when flowering) so that the presence or absence of flower(s) was a nominal value between 0 and 10 for each species at each site. We then collected at least three leaves (up to 30 for small and light leaves) from each of the first three individuals selected from each species for determination of leaf dry matter content (LDMC) and specific leaf area (SLA). For calculations of LDMC and SLA, fresh leaves were scanned on a flatbed scanner to determine leaf area. Leaves were then weighed on a balance to a precision of +/- 0.001g, prior to being air dried and reweighed with a balance to a precision of +/- 0.0001g. LDMC was calculated by dividing dry leaf mass by fresh leaf mass. SLA was calculated by dividing leaf area by dry leaf mass. Additionally, within an area of 10 cm diameter around the target individual, we determined the tallest neighbouring species and measured its vegetative and generative height, and estimated the percent cover of the target species, other vegetation, rock, and bare soil. To examine the height of target plants in relation to neighbouring plants, we calculated the ratio of target to neighbour height as the ratio of the scaled target plant vegetative height (see scaling below) to the unscaled vegetative height of its nearest neighbour. We did not scale the neighbours' height as the neighbours represent different plant species, which were not systematically sampled. Hence, scaling by the mean of the respective neighbour plant was not possible as it was for the target plant species.

Data analysis

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

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

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

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

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

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

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

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

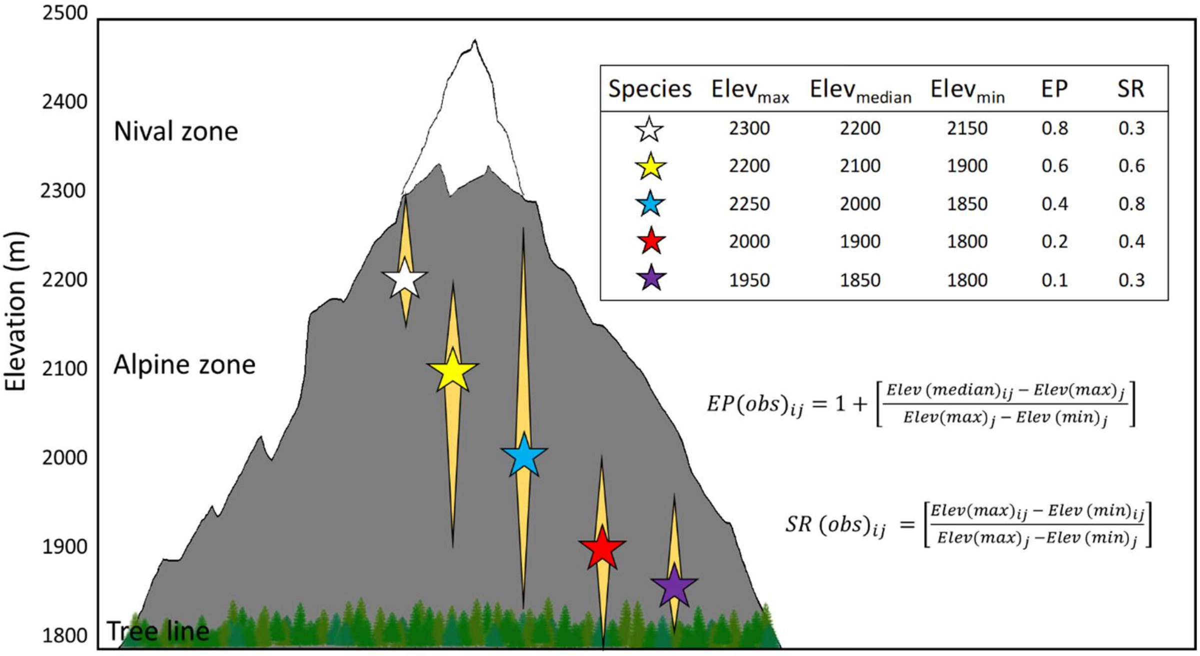
$$Elevational\ preference\ (obs)_{ij} = 1 + \left[\frac{Elev\ (median)_{ij} - Elev(max)_j}{Elev(max)_j - Elev\ (min)_j}\right] \qquad \textit{eqn. } 3$$

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

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

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

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



Species	$Elev_{max}$	$Elev_{median}$	$Elev_{min}$	EP	SR
☆	2300	2200	2150	0.8	0.3
★	2200	2100	1900	0.6	0.6
★	2250	2000	1850	0.4	0.8
★	2000	1900	1800	0.2	0.4
★	1950	1850	1800	0.1	0.3

$$EP(obs)_{ij} = 1 + \left[\frac{Elev\,(median)_{ij} - Elev(max)_j}{Elev(max)_j - Elev\,(min)_j}\right]$$

$$SR\,(obs)_{ij} = \left[\frac{Elev(max)_{ij} - Elev\,(min)_{ij}}{Elev(max)_j - Elev\,(min)_j}\right]$$

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

Mixed-effects models and data visualisation

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

To examine the shape and generality of species trait-environment relationships over their entire elevational distributions, we constructed two mixed-effects models for each of vegetative height, generative height, SLA, LDMC, plant area, patch area and the presence of flowers (for the latter *glmer()* was used with family=binomial, also in models below). The first model included standardised elevation as a linear fixed effect while the second model included standardised elevation as quadratic fixed effect. Comparison of these two models allowed us to determine whether species traits values had a linear or non-linear relationship with elevation. All mixed-effects models included the count of days since January 1st or July 1st (for northern and southern hemisphere, respectively) to account for potential measurement bias due to seasonality, and transect and species as crossed random intercept terms to account for potential non-independence of the data. Model optimisation was carried out using the default lmer optimisation method and Akaike Information Criteria (AIC) were calculated for the two models by maximizing the log-likelihood (i.e., REML set to false). The best model was selected based on the delta AIC and then recalculated by maximizing the restricted log-likelihood (REML). Model selection was done using AIC with the following ranked criteria: 1. models within 8

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

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

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

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

Results

Patterns of alpine plant traits along elevational gradients

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

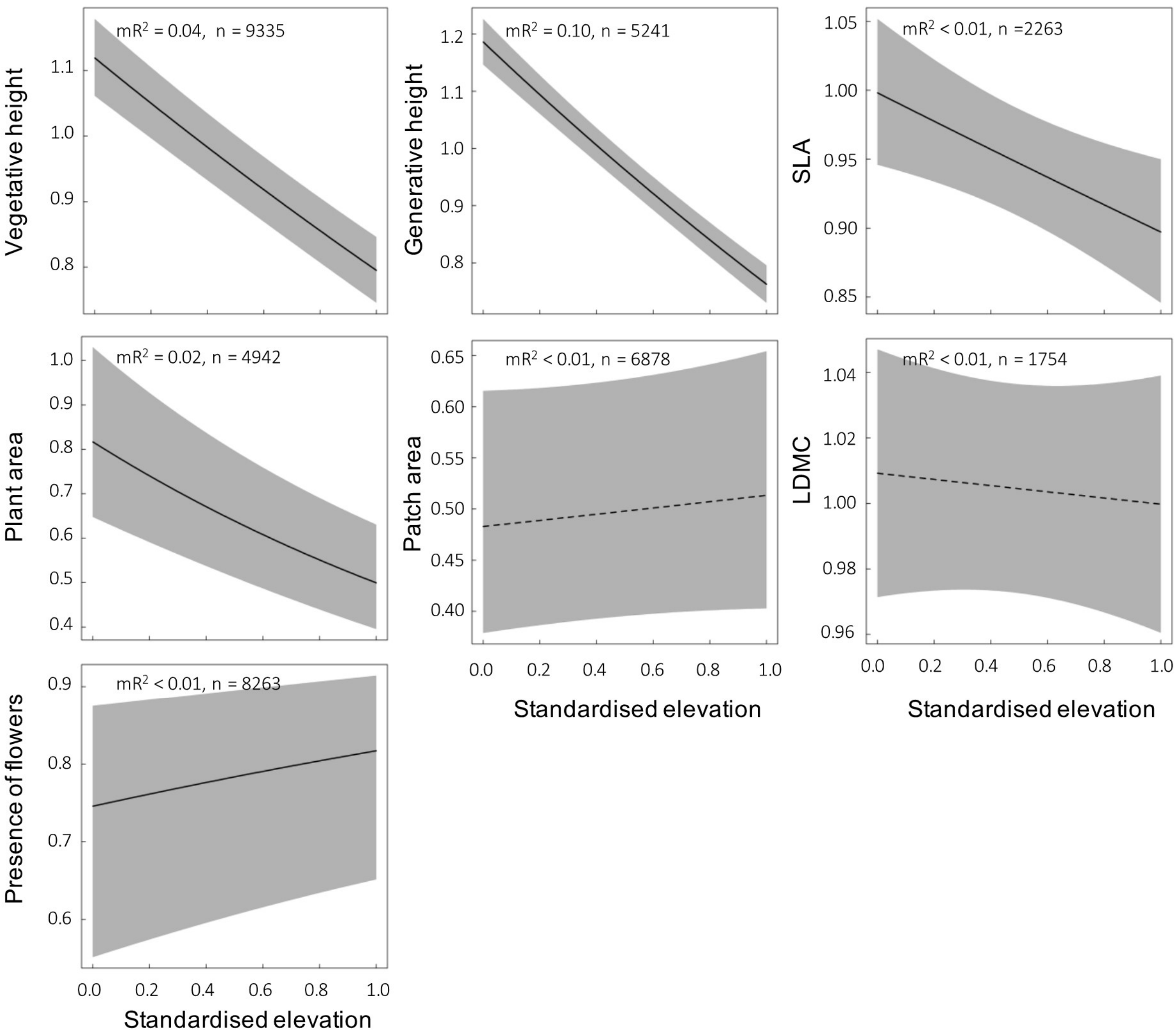


Fig. 2. Intraspecific changes in trait values across all alpine species from all 40 alpine elevational gradients, as represented by scaled plant trait values: vegetative height, generative height, specific leaf area (SLA), plant area, patch area, leaf dry matter content (LDMC), and the presence of flowers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

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

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

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

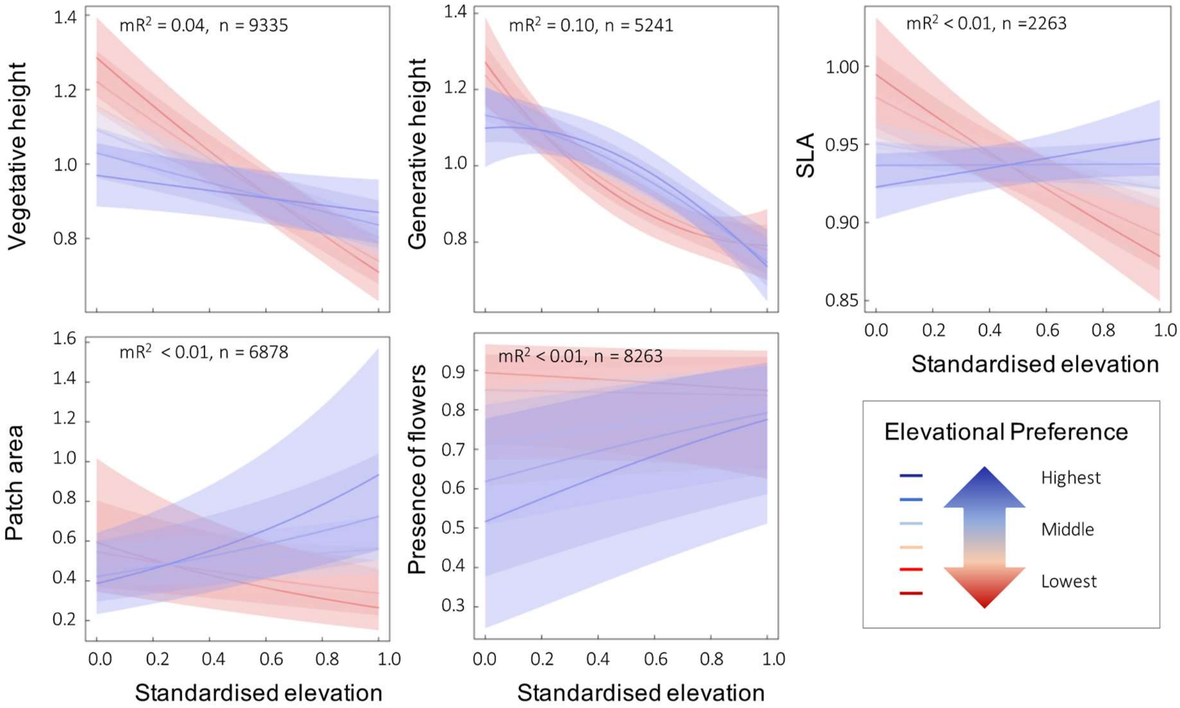


Fig. 3. Relationship between species trait values and elevation across 66 alpine species from all 40 alpine elevational gradients, as influenced by species elevational preference (EP). Results are shown only for models that revealed a significant effect of elevational preference on the trait values over standardised elevation. For each model EP was analysed as a continuous variable but, for simplicity, it is illustrated here as the line of best fit for six elevational bands, along with upper and lower limits of the 95% confidence interval as shades. See further details in caption of figure 2 and statistics in STables 4-5.

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

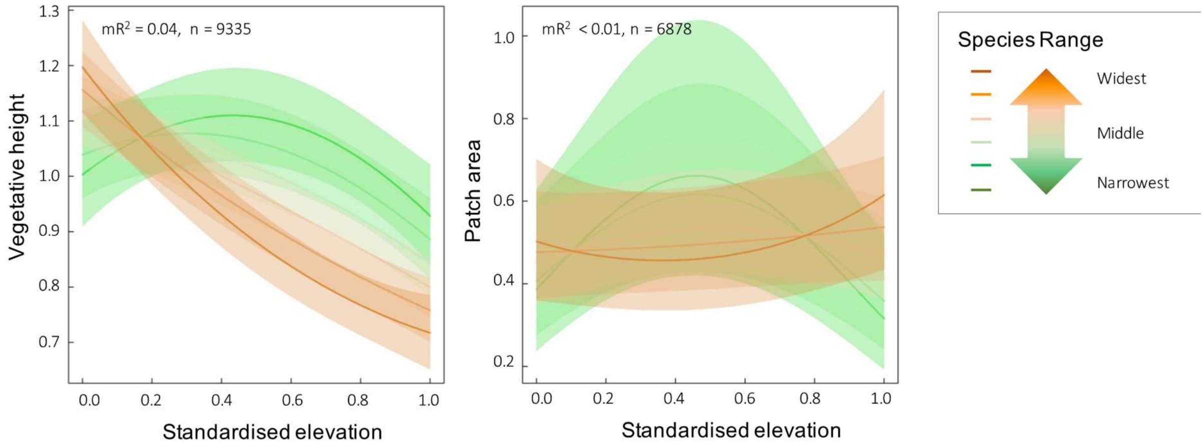


Fig. 4. Relationship between species trait values and standardized elevation across 72 alpine species from all 40 alpine elevational gradients, as influenced by species' elevational range size (SR). Results are shown only for models that revealed a significant effect of species range on the trait values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

Intraspecific height variation among alpine plants

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

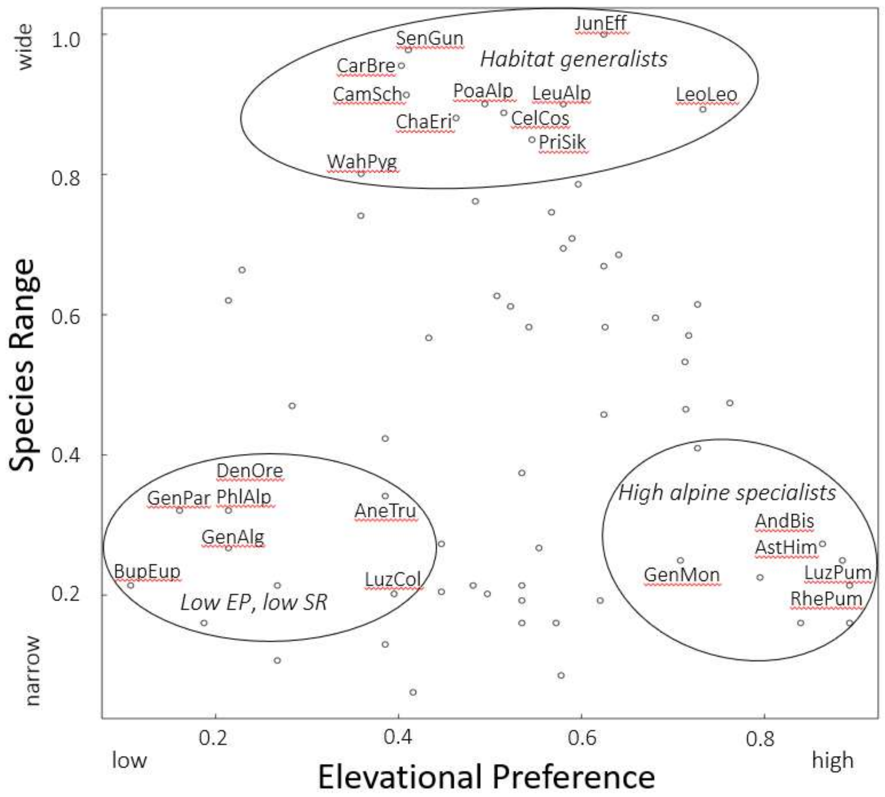


Fig. 5. Alpine plant species as characterised by their elevational preference (EP) and range (SR) for 66 alpine species from 4 countries. Species' 6-letter codes appear where n >20 observations for the species (see Table 1 for full names). At the level of individual species, patterns of intraspecific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

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

	Species Code	Species name	Country	Shape veg. height over stand. elev.
Habitat				
Generalists	CarBre	*Carex breviculmis*	AU	n.s.
	CelCos	*Celmisia costiniana*	AU	-
	SenGun	*Senecio gunnii*	AU	-
	CamSch	*Campanula scheuchzeri*	CH	-
	LeuAlp	*Leucanthemopsis alpina*	CH	-
	PoaAlp	*Poa alpina*	CH	-
	JunEff	*Juncus effusus*	CN	-
	LeoLeo	*Leontopodium leontopodioides*	CN	-
	PriSik	*Primula sikkimensis*	CN	-
	WahPhy	*Wahlenbergia pygmaea*	NZ	U-shaped
High Alpine				
Specialists	AndBis	*Androsace bisulca*	CN	parabolic
	AstHim	*Aster himalaicus*	CN	n.s.
	RhePum	*Rheum pumilum*	CN	n.s.
	GenMon	*Gentianella montana*	NZ	n.s.
	LuzPum	*Luzula pumila*	NZ	-
Low EP,				
Low SR	AneTru	*Anemone trullifolia*	CN	+
	BupEup	*Bupleurum euphorbioides*	CN	-
	DenOre	*Dendranthema oreastrum*	CN	-
	GenAlg	*Gentiana algida*	CN	-
	GenPar	*Gentiana parvula*	CN	n.s.
	PhlAlp	*Phleum alpinum*	CN	-
	LuzCol	*Luzula colensoi*	NZ	n.s.

Height of target plants relative to neighbouring species over elevation

In general, target species were smaller than their tallest neighbour (i.e., target-neighbour vegetative height <1) over much of their elevational distribution, but the ratio of target-neighbour vegetative height over elevation varied significantly depending on the EP and SR of the target plant species (Fig 6, SFig. 10). Species with higher EP became tall relative to their neighbours near their elevational maxima. In contrast, species with lower EP remained smaller than their neighbours throughout their elevation distribution. Plants with narrow and wide SR had contrary optimum curves: plants with a narrow SR decreased sharply in height relative to their neighbours towards their elevational minima, while no such pattern was detected for species with wider SR.

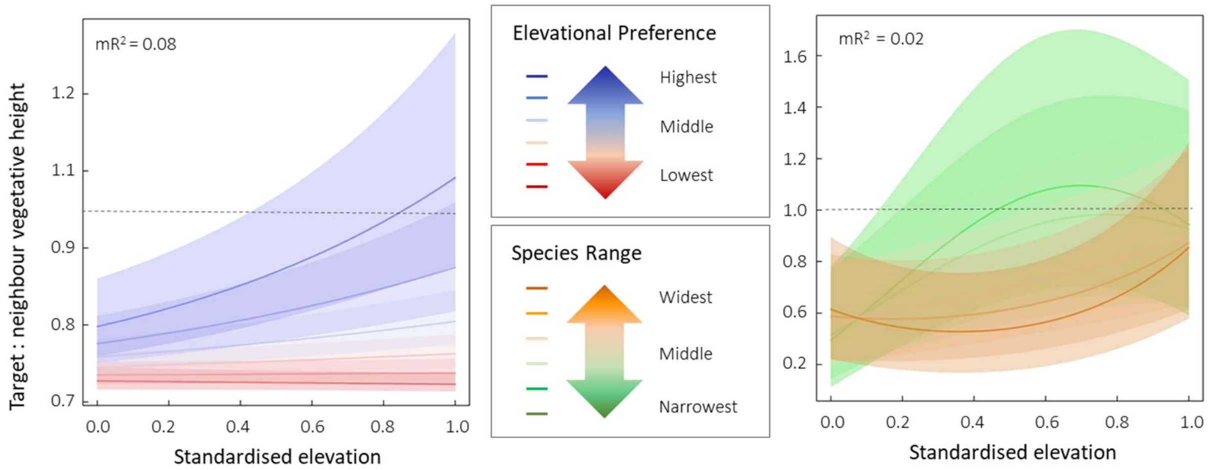


Fig. 6. Relationships between the ratio of scaled target plant height to unscaled height of neighbouring plants and standardised elevation across 72 alpine species from all 40 alpine elevational gradients, as influenced by species' elevational preference (EP) and range (SR). In both models EP and SR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

Discussion

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

Overall trait distributions along elevation

Our finding that alpine plant species show general patterns of intraspecific trait variation along elevational gradients broadly agrees with previous large-scale studies and meta-analyses (Bjorkman et al. 2018, Midolo et al. 2019). We found that vegetative and generative species heights, SLA, and patch area declined, while the number of flowering individuals increased with elevation. The negative relationships between plant height and size with elevation has long been recognised (Bonnier 1890, Körner 2003) and attributed to both intraspecific population adaptation (Halbritter et al. 2018) and plastic changes (Read et al. 2014). For example, common garden experiments find that individuals originating from high elevations are generally shorter and have less biomass than their lower elevation counterparts, suggesting intraspecific adaptation of plant size to elevation (Halbritter et al. 2018). Likewise, the negative relationship between SLA and elevation also met our expectations reflecting the tendency of species growing at lower temperatures to grow a higher number of small cells per unit area across more cell layers, and therefore an increased proportion of cell wall material per unit leaf volume (Atkin et al. 2006, Poorter et al. 2009). The negative relationship between SLA and elevation likely reflects the increasing divergence of daytime to night time leaf-to-air temperature differences with increasing elevation (Wright et al. 2017). While the climatic factors that drive variation in SLA are also likely to affect LDMC, we found high interspecific variability and no overall trend in LDMC values with elevation. This ratio of dry to fresh leaf weight is likely to be strongly affected by plant available water, which is more responsive to regional gradients, such as continentality, than to elevation (Marshall and Zhang 1994, Körner 2007). We saturated leaves before LDMC measurements to control for water availability as recommended (Perez-Harguindeguy et al. 2013), but nevertheless LDMC did not show consistent patterns in our study. Likewise, we found high variability and no overall trend in patch size over elevation, with both significant positive and negative relationships for species of the same growth form and mountain range (e.g., the forbs *Leucanthemopsis alpina* and *Campanula scheuchzeri* from the Swiss Alps; see Supplementary Information). Despite high interspecific variation, the number of flowering individuals increased with elevation, and there was no evidence for an optimum curve as may have been expected based on previous work (Kieltyk 2018). This pattern could be a stress-response (Malkinson and Tielbörger 2010), or may indicate a trade-off between vegetative and generative traits for alpine species: although individuals at high elevation tend to be shorter and have smaller leaves, the probability of flowering, which is ultimately an important fitness trait, is greater at higher elevations than at lower elevations, where species may experience more benign biotic growing conditions, but are also likely to experience more negative biotic interactions (Callaway et al. 2002). Such negative interactions may in particular be exerted through shading, which often a cause for suppressed flowering. Although numerous traits show trends in elevation, most marginal R^2 values are low, indicating that elevation only explains a small fraction of variation in the data. This is not surprising as alpine habitats are usually heterogenous at a very fine scale, and, for instance, temperature differences can differ by several degrees within a few meters in complex terrain (Scherrer and Körner 2011). Furthermore, elevation is merely a proxy for other factors that change along a mountain slope (Körner 2007). Only air pressure changes universally along elevation, but many other factors, such as moisture, may not be related to elevation or show non-linear relationships. Nevertheless, our gradients studied do not show strong moisture gradients, and elevation can be assumed to be a reasonable (even if not perfect) proxy for temperature. Therefore, despite much unexplained variation in our data set we believe that our analyses can indicate important ecological processes along elevation. Interestingly, mountain region did not affect trait patterns significantly when added to the statistical model as a fixed effect. Despite considerable climatic and geographical differences between the studied mountain regions, the results shown in our study apparently apply across larger scales.

Trait variation for species with different elevational preferences or ranges

We showed that patterns of trait variation over elevation depended upon the elevational preferences and ranges of alpine plant species. In particular, the decline in vegetative and generative heights, SLA and patch area over elevation was mainly driven by plant species with lower elevation preferences. Likewise, the slight overall increase in the probability of flowering with elevation was driven by species with higher elevational preference. Collectively, these results suggest that alpine specialist species may be subjected to trade-offs in vegetative and generative traits differently than alpine species with lower elevational preference. While these observations must be interpreted cautiously given the high residual variance left unexplained in our probability of flowering model (i.e., low marginal R^2 values), this significant effect is consistent with the stress gradient hypothesis (Bertness and Callaway 1994, Maestre et al. 2009). Alpine plant species that specialise in high elevation habitats are likely to experience more abiotic stress but less interspecific competition relative to species that prefer lower elevations. This may enable them to increase resource allocation to flowering, while maintaining overall conservative growth strategies by remaining short and small. In contrast, species that prefer lower alpine environments are likely to experience more variable interspecific competition from a higher diversity of neighbours. The variability of interspecific competition experienced by alpine plants with lower elevational preference is likely to select for the maintenance of vegetative trait flexibility, as demonstrated by the strong decline in vegetative and generative heights, SLA and patch area over elevation for these species. However, our data revealed no significant negative relationship between the presence of flowers and elevation for species with lower elevational preference. Thus, our data may suggest that a maintenance of vegetative trait flexibility may come at the expense of flexibility of flowering for alpine plant species with lower elevational preference. However, given the low statistical explanatory power of some of our models, trade-offs between vegetative and reproductive traits deserve further investigation.

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

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

Intraspecific height variation among alpine plants

Visualising plant species as a function of their range and elevational preferences allowed us to distinguish two alpine plant groups, with distinct patterns of intraspecific trait variation in response to elevation. Namely, the alpine habitat generalists were those species that demonstrated high variation in vegetative height over elevation, being tallest near their elevational minima and rapidly declining in height near their elevational maxima. In contrast, the high alpine specialist species, which occupied narrow elevational ranges at the highest relative elevations, showed no consistent response of vegetative height to elevation, again supporting the view that these species express a conservative range of trait values with elevation. Finally, it was interesting to observe that plant species with both low elevational preference and range of occurrence, which may be the subset of species that are likely to experience the greatest interspecific competition as sub-alpine species advance into alpine zones, were generally similar to the habitat generalist species in expressing mostly significantly negative relationships between vegetative height and standardised elevation. Such differentiations in trait variation between different species groups may help us in the long term to understand the future of alpine plants (Guisan and Theurillat 2001).While our analysis of traits at the species-level is limited by a small sample size, this finding may suggest that the low-alpine flora retains significant vegetative height flexibility, which may serve these species well in rapidly changing climates (Loveys et al. 2003). We suggest that verification of this pattern through the analysis of intraspecific trait variation of many more alpine species, different evolutionary lineages and growth forms, and from more geographic regions, is a high priority for future research.

Height of plants relative to neighbouring species

Plant traits respond to both abiotic and biotic drivers, therefore we wished to learn how the vegetative heights of our target species changed in relation to their nearest neighbours standardising for elevation, and whether these patterns would differ among species according to their elevational preferences and range. We found that species with higher elevational preference were smaller than their neighbours (belonging to different species) near their elevational minima and became taller relative to their neighbours near their elevational maxima, where few other species were likely to be present. This agrees with our finding that species with higher elevational preference showed relatively little height variation over elevation and maintained conservative height values while their neighbours became taller at lower elevations (see SFig. 3). In contrast, we found that target species with lower elevational preferences maintained a more constant height ratio with their neighbours throughout their elevational distributions, indicating that they were able to increase their vegetative heights apace with their neighbours near their elevational minima. These findings may in part be explained by net facilitative plant-plant interactions in harsh high alpine conditions and net competitive interactions at lower elevations (Callaway et al. 2002). Due to the net facilitative species interactions at high elevation, growing tall might be less necessary (and effective) as a means of competition with neighbours. However, to compete at lower elevations the ability to grow taller is probably a relevant survival mechanism.. The ratio of target plant to neighbour plant height over elevation varied for species with different range sizes. Species with narrower ranges were tallest relative to their neighbours in the upper half of their elevational distributions but declined in relative height near their elevational minima. Conversely, species with wider range of occurrence showed constant or increasing heights relative to their neighbours as they approached their elevational maxima. These findings provide additional evidence that plant species with wider range of occurrence and a preference for lower elevation express considerable variation in height over elevation, which permits them to grow taller in less stressful environments, and potentially enhances their competitive outcomes with neighbours. Equally, our data suggest that species that prefer high alpine environments or have narrow range of occurrence, achieve peak heights relative to their neighbours only in the upper reaches of their elevational distributions, but are unable to maintain their relative stature at lower elevations, where competition from neighbours is likely to be the greatest (Alexander et al. 2015). As neighbours in our study belong to different species (whichever species grew in the vicinity of our target plant), the comparison to neighbours holds for the species composition at a given site/elevation and does not represent direct interactions between specific species.

Conclusions

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

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Conflict of Interest statement

None of the authors have a conflict of interest.

Author Contributions statement

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

Data archiving statement

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

References

Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology **24**:1192-1201.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species' responses to climate change. Nature **525**:515-+.

Atkin, O. K., B. R. Loveys, L. J. Atkinson, and T. L. Pons. 2006. Phenotypic plasticity and growth temperature: understanding interspecific variability. Journal of Experimental Botany **57**:267-281.

Barton, K. 2019. MuMIn: Multi-Model Inference. R package version xx. https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1-48.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution **9**:191-193.

Bjorkman, A. D., I. H. Myers-Smith, S. C. Elmendorf, S. Normand, N. Ruger, P. S. A. Beck, A. Blach-Overgaard, D. Blok, J. H. C. Cornelissen, B. C. Forbes, D. Georges, S. J. Goetz, K. C. Guay, G. H. R. Henry, J. HilleRisLambers, R. D. Hollister, D. N. Karger, J. Kattge, P. Manning, J. S. Prevey, C. Rixen, G. Schaepman-Strub, H. J. D. Thomas, M. Vellend, M. Wilmking, S. Wipf, M. Carbognani, L. Hermanutz, E. Levesque, U. Molau, A. Petraglia, N. A. Soudzilovskaia, M. J. Spasojevic, M. Tomaselli, T. Vowles, J. M. Alatalo, H. D. Alexander, A. Anadon-Rosell, S. Angers-Blondin, M. te Beest, L. Berner, R. G. Bjork, A. Buchwal, A. Buras, K. Christie, E. J. Cooper, S. Dullinger, B. Elberling, A. Eskelinen, E. R. Frei, O. Grau, P. Grogan, M. Hallinger, K. A. Harper, M. Heijmans, J. Hudson, K. Hulber, M. Iturrate-Garcia, C. M. Iversen, F. Jaroszynska, J. F. Johnstone, R. H. Jorgensen, E. Kaarlejarvi, R. Klady, S. Kuleza, A. Kulonen, L. J. Lamarque, T. Lantz, C. J. Little, J. D. M. Speed, A. Michelsen, A. Milbau, J. Nabe-Nielsen, S. S. Nielsen, J. M. Ninot, S. F. Oberbauer, J. Olofsson, V. G. Onipchenko, S. B. Rumpf, P. Semenchuk, R. Shetti, L. S. Collier, L. E. Street, K. N. Suding, K. D. Tape, A. Trant, U. A. Treier, J. P. Tremblay, M. Tremblay, S. Venn, S. Weijers, T. Zamin, N. Boulanger-Lapointe, W. A. Gould, D. S. Hik, A. Hofgaard, I. S. Jonsdottir, J. Jorgenson, J. Klein, B. Magnusson, C. Tweedie, P. A. Wookey, M. Bahn, B. Blonder, P. M. van Bodegom, B. Bond-Lamberty, G. Campetella, B. E. L. Cerabolini, F. S. Chapin, W. K. Cornwell, J. Craine, M. Dainese, F. T. de Vries, S. Diaz, B. J. Enquist, W. Green, R. Milla, U. Niinemets, Y. Onoda, J. C. Ordonez, W. A. Ozinga, J. Penuelas, H. Poorter, P. Poschlod, P. B. Reich, B. Sande, B. Schamp, S. Sheremetev, and E. Weiher. 2018. Plant functional trait change across a warming tundra biome. Nature **562**:57-+.

Bonnier, G. 1890. Cultures expérimentales dans les Alpes et les Pyrénées. Revue Générale de Botanique **2**:513–546.

Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. Ecology **82**:18-32.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer, New York.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. L. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature **417**:844-848.

Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science **333**:1024-1026.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany **51**:335-380.

Cornelissen, J. H. C., P. M. van Bodegom, R. Aerts, T. V. Callaghan, R. S. P. van Logtestijn, J. Alatalo, F. S. Chapin, R. Gerdol, J. Gudmundsson, D. Gwynn-Jones, A. E. Hartley, D. S. Hik, A. Hofgaard, I. S. Jonsdottir, S. Karlsson, J. A. Klein, J. Laundre, B. Magnusson, A. Michelsen, U. Molau, V. G. Onipchenko, H. M. Quested, S. M. Sandvik, I. K. Schmidt, G. R. Shaver, B. Solheim, N. A. Soudzilovskaia, A. Stenstrom, A. Tolvanen, O. Totland, N. Wada, J. M. Welker, X. Q. Zhao, and M. O. L. Team. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters **10**:619-627.

Crepaz, H., G. Niedrist, J. Wessely, M. Rossi, and S. Dullinger. 2020. Resident vegetation modifies climate-driven elevational shift of a mountain sedge. Alpine Botany.

Engler, R., C. F. Randin, W. Thuiller, S. Dullinger, N. E. Zimmermann, M. B. Araujo, P. B. Pearman, G. Le Lay, C. Piedallu, C. H. Albert, P. Choler, G. Coldea, X. De Lamo, T. Dirnbock, J. C. Gegout, D. Gomez-Garcia, J. A. Grytnes, E. Heegaard, F. Hoistad, D. Nogues-Bravo, S. Normand, M. Puscas, M. T. Sebastia, A. Stanisci, J. P. Theurillat, M. R. Trivedi, P. Vittoz, and A. Guisan. 2011. 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology **17**:2330-2341.

Floder, S., J. Yong, T. Klauschies, U. Gaedke, T. Poprick, T. Brinkhoff, and S. Moorthi. 2021. Intraspecific trait variation alters the outcome of competition in freshwater ciliates. Ecology and Evolution **11**:10225-10243.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography **27**:1268-1276.

Freschet, G. T., C. Roumet, L. H. Comas, M. Weemstra, A. G. Bengough, B. Rewald, R. D. Bardgett, G. B. De Deyn, D. Johnson, J. Klimesova, M. Lukac, M. L. McCormack, I. C. Meier, L. Pages, H. Poorter, I. Prieto, N. Wurzburger, M. Zadworny, A. Bagniewska-Zadworna, E. B. Blancaflor, I. Brunner, A. Gessler, S. E. Hobbie, C. M. Iversen, L. Mommer, C. Picon-Cochard, J. A. Postma, L. Rose, P. Ryser, M. Scherer-Lorenzen, N. A. Soudzilovskaia, T. Sun, O. J. Valverde-Barrantes, A. Weigelt, L. M. York, and A. Stokes. 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytologist **232**:1123-1158.

Freschet, G. T., C. Violle, M. Y. Bourget, M. Scherer-Lorenzen, and F. Fort. 2018. Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. New Phytologist **219**:1338-1352.

Giejsztowt, J., A. T. Classen, and J. R. Deslippe. 2020. Climate change and invasion may synergistically affect native plant reproduction. Ecology **101**.

Guisan, A., and J.-P. Theurillat. 2001. Assessing alpine plant vulnerability to climate change: a modeling perspective. Integrated Assessment **1**:307–320.

Halbritter, A. H., S. Fior, I. Keller, R. Billeter, P. J. Edwards, R. Holderegger, S. Karrenberg, A. R. Pluess, A. Widmer, and J. M. Alexander. 2018. Trait differentiation and adaptation of plants along elevation gradients. Journal of Evolutionary Biology **31**:784-800.

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

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

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

Shiodera, B. Shipley, T. A. Shovon, A. Siebenkas, C. Sierra, V. Silva, M. Silva, T. Sitzia, H. Sjoman, M. Slot, N. G. Smith, D. Sodhi, P. Soltis, D. Soltis, B. Somers, G. Sonnier, M. V. Sorensen, E. E. Sosinski, N. A. Soudzilovskaia, A. F. Souza, M. Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K. Steinbauer, J. G. Stephan, F. Sterck, D. B. Stojanovic, T. Strydom, M. L. Suarez, J. C. Svenning, I. Svitkova, M. Svitok, M. Svoboda, E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U. Tappeiner, R. Tarifa, S. Tauugourdeau, C. Tavsanoglu, M. te Beest, L. Tedersoo, N. Thiffault, D. Thom, E. Thomas, K. Thompson, P. E. Thornton, W. Thuiller, L. Tichy, D. Tissue, M. G. Tjoelker, D. Y. P. Tng, J. Tobias, P. Torok, T. Tarin, J. M. Torres-Ruiz, B. Tothmeresz, M. Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk, J. L. Tsakalos, I. Tsiripidis, N. Tysklind, T. Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi, F. Valladares, J. Vamosi, P. M. van Bodegom, M. van Breugel, E. Van Cleemput, M. van de Weg, S. van der Merwe, F. van der Plas, M. T. van der Sande, M. van Kleunen, K. Van Meerbeek, M. Vanderwel, K. A. Vanselow, A. Varhammar, L. Varone, M. Y. Valderrama, K. Vassilev, M. Vellend, E. J. Veneklaas, H. Verbeeck, K. Verheyen, A. Vibrans, I. Vieira, J. Villacis, C. Violle, P. Vivek, K. Wagner, M. Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang, F. Wang, W. Q. Wang, H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. P. Wei, P. Weigelt, E. Weiher, A. W. Wells, C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White, M. Whitten, M. Williams, D. E. Winkler, K. Winter, C. Womack, I. J. Wright, S. J. Wright, J. Wright, B. X. Pinho, F. Ximenes, T. Yamada, K. Yamaji, R. Yanai, N. Yankov, B. Yguel, K. J. Zanini, A. E. Zanne, D. Zeleny, Y. P. Zhao, J. M. Zheng, J. Zheng, K. Zieminska, C. R. Zirbel, G. Zizka, I. C. Zo-Bi, G. Zotz, C. Wirth, and N. Nutrient. 2020. TRY plant trait database - enhanced coverage and open access. Global Change Biology **26**:119-188.

Kichenin, E., D. A. Wardle, D. A. Peltzer, C. W. Morse, and G. T. Freschet. 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Functional Ecology **27**:1254-1261.

Kieltyk, P. 2018. Variation of vegetative and floral traits in the alpine plant Solidago minuta: evidence for local optimum along an elevational gradient. Alpine Botany **128**:47-57.

Körner, C. 2003. Alpine plant life. 2nd edition. Springer Verlag, Berlin.

Körner, C. 2007. The use of 'altitude' in ecological research. Trends in Ecology & Evolution **22**:569-574.

Lamprecht, A., P. R. Semenchuk, K. Steinbauer, M. Winkler, and H. Pauli. 2018. Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. New Phytologist **220**:447-459.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology **16**:545-556.

Loveys, B. R., L. J. Atkinson, D. J. Sherlock, R. L. Roberts, A. H. Fitter, and O. K. Atkin. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. Global Change Biology **9**:895-910.

MacLean, S. A., and S. R. Beissinger. 2017. Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. Global Change Biology **23**:4094-4105.

Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology **97**:199-205.

Malkinson, D., and K. Tielbörger. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. Oikos **119**:1546-1552.

Marshall, J. D., and J. W. Zhang. 1994. Carbon-istope discrimination and water-use efficiency in native plants of the North-Central Rockies. Ecology **75**:1887-1895.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution **21**:178-185.

Midolo, G., P. De Frenne, N. Holzel, and C. Wellstein. 2019. Global patterns of intraspecific leaf trait responses to elevation. Global Change Biology **25**:2485-2498.

Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J. Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J. Kollar, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L. Nagy, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, A. O. Syverhuset, J. P. Theurillat, M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent Plant Diversity Changes on Europe's Mountain Summits. Science **336**:353-355.

Pauli, H., M. Gottfried, K. Reiter, C. Klettner, and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. Global Change Biology **13**:147-156.

Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change **3**:673-677.

Pellissier, L., B. Fournier, A. Guisan, and P. Vittoz. 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. Plant Ecology **211**:351-365.

Perez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N. Buchmann, G. Funes, F. Quetier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. G. A. van der Heijden, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany **61**:167-234.

Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist **182**:565-588.

R Development Core Team. 2021. R Foundation for Statistical Computing.*in* R. D. C. Team, editor., Vienna, Austria.

Read, Q. D., L. C. Moorhead, N. G. Swenson, J. K. Bailey, and N. J. Sanders. 2014. Convergent effects of elevation on functional leaf traits within and among species. Functional Ecology **28**:37-45.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. Journal of Applied Ecology **45**:218-227.

Rumpf, S. B., K. Hulber, G. Klonner, D. Moser, M. Schutz, J. Wessely, W. Willner, N. E. Zimmermann, and S. Dullinger. 2018. Range dynamics of mountain plants decrease with elevation. Proceedings of the National Academy of Sciences of the United States of America **115**:1848-1853.

Rumpf, S. B., K. Hulber, N. E. Zimmermann, and S. Dullinger. 2019. Elevational rear edges shifted at least as much as leading edges over the last century. Global Ecology and Biogeography **28**:533-543.

Scherrer, D., and C. Körner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography **38**:406-416.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. D. Dantas, F. de Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerstrom, Y. Le Bagousse-Pinguet, Y. Z. Li, N. Mason, J. Messier, T. Nakashizuka, J. McC Overton, D. A. Peltzer, I. M. Perez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schob, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters **18**:1406-1419.

Staude, I. R., H. M. Pereira, G. N. Daskalova, M. Bernhardt-Römermann, M. Diekmann, P. H., and al. 2021. Directional temporal turnover toward plant species with larger ranges across habitats. Ecology Letters **00**:000-000.

Steinbauer, M. J., J. A. Grytnes, G. Jurasinski, A. Kulonen, J. Lenoir, H. Pauli, C. Rixen, M. Winkler, M. Bardy-Durchhalter, E. Barni, A. D. Bjorkman, F. T. Breiner, S. Burg, P. Czortek, M. A. Dawes, A. Delimat, S. Dullinger, B. Erschbamer, V. A. Felde, O. Fernandez-Arberas, K. F. Fossheim, D. Gomez-Garcia, D. Georges, E. T. Grindrud, S. Haider, S. V. Haugum, H. Henriksen, M. J. Herreros, B. Jaroszewicz, F. Jaroszynska, R. Kanka, J. Kapfer, K. Klanderud, I. Kuhn, A. Lamprecht, M. Matteodo, U. M. di Cella, S. Normand, A. Odland, S. L. Olsen, S. Palacio, M. Petey, V. Piscova, B. Sedlakova, K. Steinbauer, V. Stockli, J. C. Svenning, G. Teppa, J. P. Theurillat, P. Vittoz, S. J. Woodin, N. E. Zimmermann, and S. Wipf. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature **556**:231-234.

Sundqvist, M. K., N. J. Sanders, and D. A. Wardle. 2013. Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change. Pages 261-280 *in* D. J. Futuyma, editor. Annual Review of Ecology, Evolution, and Systematics, Vol 44.

Thomas, H. J. D., A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, J. Kattge, S. Diaz, M. Vellend, D. Blok, J. H. C. Cornelissen, B. C. Forbes, G. H. R. Henry, R. D. Hollister, S. Normand, J. S. Prevey, C. Rixen, G. Schaepman-Strub, M. Wilmking, S. Wipf, W. K. Cornwell, P. S. A. Beck, D. Georges, S. J. Goetz, K. C. Guay, N. Ruger, N. A. Soudzilovskaia, M. J. Spasojevic, J. M. Alatalo, H. D. Alexander, A. Anadon-Rosell, S. Angers-Blondin, M. te Beest, L. T. Berner, R. G. Bjork, A. Buchwal, A. Buras, M. Carbognani, K. S. Christie, L. S. Collier, E. J. Cooper, B. Elberling, A. Eskelinen, E. R. Frei, O. Grau, P. Grogan, M. Hallinger, M. Heijmans, L. Hermanutz, J. M. G. Hudson, J. F. Johnstone, K. Hulber, M. Iturrate-Garcia, C. M. Iversen, F. Jaroszynska, E. Kaarlejarvi, A. Kulonen, L. J. Lamarque, T. C. Lantz, E. Levesque, C. J. Little, A. Michelsen, A. Milbau, J. Nabe-Nielsen, S. S. Nielsen, J. M. Ninot, S. F. Oberbauer, J. Olofsson, V. G. Onipchenko, A. Petraglia, S. B. Rumpf, R. Shetti, J. D. M. Speed, K. N. Suding, K. D. Tape, M. Tomaselli, A. J. Trant, U. A. Treier, M. Tremblay, S. E. Venn, T. Vowles, S. Weijers, P. A. Wookey, T. J. Zamin, M. Bahn, B. Blonder, P. M. van Bodegom, B. Bond-Lamberty, G. Campetella, B. E. L. Cerabolini, F. S. Chapin, J. M. Craine, M. Dainese, W. A. Green, S. Jansen, M. Kleyer, P. Manning, U. Niinemets, Y. Onoda, W. A. Ozinga, J. Penuelas, P. Poschlod, P. B. Reich, B. Sandel, B. S. Schamp, S. N. Sheremetiev, and F. T. de Vries. 2020. Global plant trait relationships extend to the climatic extremes of the tundra biome. Nature Communications **11**.

Thuiller, W., C. Albert, M. B. Araujo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgely, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008.

Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology Evolution and Systematics **9**:137-152.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology & Evolution **27**:244-252.

Walther, G. R., S. Beissner, and C. A. Burga. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science **16**:541-548.

Weemstra, M., N. Kiorapostolou, J. van Ruijven, L. Mommer, J. de Vries, and F. Sterck. 2020a. The role of fine-root mass, specific root length and life span in tree performance: A whole-tree exploration. Functional Ecology **34**:575-585.

Weemstra, M., K. G. Peay, S. J. Davies, M. Mohamad, A. Itoh, S. Tan, and S. E. Russo. 2020b. Lithological constraints on resource economies shape the mycorrhizal composition of a Bornean rain forest. New Phytologist **228**:253-268.

Wiens, J. J. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLoS Biology **14**.

Winkler, M., A. Lamprecht, K. Steinbauer, K. Hülber, J.-P. Theurillat, F. Breiner, P. Choler, S. Ertl, A. Gutiérrez Girón, G. Rossi, P. Vittoz, M. Akhalkatsi, C. Bay, J.-L. Benito Alonso, T. Bergström, M. L. Carranza, E. Corcket, J. Dick, B. Erschbamer, R. Fernández Calzado, A. M. Fosaa, R. G. Gavilán, D. Ghosn, K. Gigauri, D. Huber, R. Kanka, G. Kazakis, M. Klipp, J. Kollar, T. Kudernatsch, P. Larsson, M. Mallaun, O. Michelsen, P. Moiseev, D. Moiseev, U. Molau, J. Molero Mesa, U. Morra di Cella, L. Nagy, M. Petey, M. Pușcaș, C. Rixen, A. Stanisci, M. Suen, A. O. Syverhuset, M. Tomaselli, P. Unterluggauer, T. Ursu, L. Villar, M. Gottfried, and H. Pauli. 2016. The rich sides of mountain summits – a pan-European view on aspect preferences of alpine plants. Journal of Biogeography **43**:2261-2273.

Wright, I. J., N. Dong, V. Maire, I. C. Prentice, M. Westoby, S. Diaz, R. V. Gallagher, B. F. Jacobs, R. Kooyman, E. A. Law, M. R. Leishman, U. Niinemets, P. B. Reich, L. Sack, R. Villar, H. Wang, and P. Wilf. 2017. Global climatic drivers of leaf size. Science **357**:917-921.