



High-elevation plant species exhibit limited morphological variability across elevations, contrary to species with a wider elevational distribution

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Abstract

Plants along mountain slopes experience strong environmental variation, particularly declining air temperature with increasing elevation. Investigating intraspecific variation in morphological traits and biomass allocation across elevational gradients can reveal how plants adjust their life-history strategies to climatic conditions, improving our understanding of their resilience to climate change. We analysed variation in overall morphology and biomass allocation in two high-elevation species: *Campanula alpina* and *Doronicum stiriaceum*, both centred in the alpine belt. Their elevational responses were compared with three species exhibiting wider elevational occurrence: *Soldanella carpatica* (lower montane to subnival belt), *Bellidiastrum michelii* (lower montane to alpine belt), and *Senecio subalpinus* (lower montane to subalpine belt). All five species showed decreasing plant height with increasing elevation. However, high-elevation species maintained stable aboveground biomass and reproductive allocation, while species with wider elevational occurrence exhibited more than 50% reduction in aboveground biomass, and two of them showed significant decline in flower biomass with elevation. Our findings confirm that species with wider or lower elevational ranges exhibit greater trait variation than high-elevation specialists. These patterns suggest that mountain generalist species, with lower elevational preferences and wider elevational occurrence, may respond more strongly to rising temperatures, potentially increasing aboveground biomass and plant height under future climate change. In contrast, high-elevation species demonstrated the ability to persist across a wide temperature range while maintaining stable biomass, indicating physiological tolerance and potential to withstand warming in alpine environments. Further research is needed to understand how high-elevation specialists maintain stable growth and reproductive output, particularly their eco-physiological adaptations.

Keywords Aboveground plant mass · Alpine plants · Climate change · Elevation gradient · Intra- and interspecific variation · Tatra mountains

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Introduction

Plants encounter temporal and spatial variation in abiotic and biotic factors. To maintain population persistence and reproductive success, plants can adjust to spatial heterogeneity in environmental conditions through adaptive phenotypic plasticity (e.g., Frei et al. 2014; Dai et al. 2017; Hamann et al. 2017; Trunschke and Stöcklin 2017; Henn et al. 2018; Szukala et al. 2023) and through adaptive genetic differentiation of local populations (e.g., Scheepens et al. 2010; Frei et al. 2012; Hamann et al. 2016; Hirano et al. 2017; Knotek et al. 2020; Morente-López et al. 2020; Wos et al. 2022; Love and Ferris 2024). When ecologically relevant environmental factors appear as pronounced spatial

gradients, clinal adaptive variation in plant traits can emerge within species (Montesinos-Navarro et al. 2011; Wadgymar et al. 2022; Love and Ferris 2024). High mountain ecosystems offer such gradual environmental conditions, since steep abiotic gradients, primarily climatic gradients, are a defining feature (Körner 2021). Accordingly, in temperate mountain regions, several key abiotic conditions change with increasing elevation. These include decreasing mean air temperatures, carbon dioxide and oxygen concentrations, increasing light intensity and UV radiation, shorter growing seasons, more frequent strong winds and extreme weather events, and decreased nutrient availability (Nagy and Grabherr 2009; Takahashi 2014; Körner 2021). Biotic factors also vary with increasing elevation; for instance, resource competition between plants diminishes and herbivory pressure decreases at higher elevations (Rasman et al. 2014; Körner 2021). Conversely, competition for pollinators among insect-pollinated plants intensifies because of the reduced number of pollinators at higher elevations (Maad et al. 2013; Zhao and Wang 2015; Arroyo et al. 2017). Elevation, therefore, is an important proxy of several abiotic and biotic environmental factors that significantly influence plant life along mountain slopes (e.g. Scheepens and Stöcklin 2013; Takahashi and Matsuki 2017; Sakurai and Takahashi 2017; Kiełtyk 2018, 2021a, b, 2024; Paudel et al. 2019; Khatri et al. 2023; García-Rodríguez et al. 2024; Love and Ferris 2024).

The most noticeable consequences of the steep climatic gradients in high mountain ecosystems in temperate zones include the natural range limits of tree species observed at the alpine treeline ecotone (Körner 2012) and the vertical diversification of vegetation into distinct elevational zones (Leuschner and Ellenberg 2017). However, the same environmental factors contributing to the high interspecific and life form diversity and distribution of alpine floras across elevations also exert selective pressures on plants at the intraspecific level, generating elevational trait variation within species. Environmental factors along elevation gradients can drive clinal adjustments in plant physiology, morphology, and biomass allocation through either plastic or genetic responses (Halbritter et al. 2018). Elevational gradients have also been shown to repeatedly generate similar genetically based phenotypic clines across different mountain ranges, suggesting parallel evolutionary responses to comparable selection pressures. For example, strong directional selection on plant adaptive traits across elevation and the emergence of local ecotypes have been observed in *Arabidopsis arenosa* (Knotek et al. 2020; Wos et al. 2022) and *Heliosperma pusillum* (Szukala et al. 2023), where parallel independent adaptations to elevation gradients within these species were found in multiple mountain ranges. The emergence of phenotypically similar high-elevation ecotypes

in different mountain ranges, as seen in *A. arenosa* and *H. pusillum*, suggests that the most significant selective pressures related to elevation are those associated with climate variations that change similarly across elevations in mountains within a given climate zone (Körner 2007).

In recent years, increasing attention has been directed toward patterns of intraspecific phenotypic variation in plants along elevational gradients in mountainous regions (e.g., Halbritter et al. 2018; Olejniczak et al. 2018; Basnett et al. 2019; Rixen et al. 2022; Khatri et al. 2023; Spitzer et al. 2023; García-Rodríguez et al. 2024). Investigating how plant morphology and biomass allocation vary across elevation provides key insights into plant strategies for coping with steep environmental gradients. Furthermore, understanding how plants adjust their life histories in response to the pronounced climatic gradients typical of mountain slopes contributes to our broader understanding of their capacity to cope with climate change (e.g., Frei et al. 2014; Pfennigwerth et al. 2017; Blume-Werry et al. 2018; Midolo et al. 2019; Rixen et al. 2022).

Rixen et al. (2022) recently demonstrated that the degree and pattern of intraspecific trait variation may differ depending on a species' elevational range. High-elevation specialists with narrow vertical distribution tend to exhibit more conservative (i.e., less variable) trait responses compared to wide-ranging or lower-elevation species, suggesting a reduced capacity to respond plastically to climate-induced environmental changes. In contrast, mountain generalist species, with lower elevational preferences and wider elevational distribution, frequently show greater trait variability, reflecting higher adaptive flexibility. These patterns have important implications for predicting which species may persist or be outcompeted as warming progresses.

However, while Rixen et al. (2022), who analysed seven morphological traits (including vegetative and generative height, presence/absence of flowers, and plant basal area), focused primarily on general trait variability, relatively little is known about biomass investment and partitioning in high-elevation species. Although traits such as height and basal area can serve as proxies for plant size, they do not directly quantify biomass. In contrast, measuring plant mass provides a direct assessment of size, a trait closely linked to a plant's capacity for resource acquisition and overall biomass production. Importantly, patterns of biomass investment and partitioning can reveal distinct ecological strategies and resource allocation trade-offs (e.g., between vegetative growth and reproduction) across elevation. The allocation of dry matter to different plant structures reflects fundamental trade-offs, as resources devoted to one organ or function are unavailable to others (Weiner et al. 2009). Thus, biomass allocation patterns are not only indicative of growth constraints but also of adaptive strategies that

support survival and reproduction under the extreme conditions typical of high-elevation environments (Doležal et al. 2021, 2024). Studying these patterns may therefore yield valuable insights into how plants balance competing functional demands in mountain ecosystems.

Despite recognition that high-elevation species may be particularly vulnerable to climate change, empirical data on their intraspecific morphological variation and biomass allocation remain limited. Most previous research has focused on species with wide elevational distributions (e.g., Herrera 2005; Scheepens et al. 2010; Maad et al. 2013; Bucher et al. 2016; Khatri et al. 2023), while studies on high-elevation specialists are comparatively scarce (e.g., He et al. 2017; Seguí et al. 2018; Paudel et al. 2019). Moreover, many studies have sampled only a few elevation sites, limiting the ability to model continuous variation and detect nonlinear or threshold responses to elevation (cf. Kiełtyk 2024). This constrains our understanding of how plants respond across their full vertical distribution.

Our study addresses these gaps by examining patterns of morphological variation and biomass partitioning in *Campanula alpina* and *Doronicum stiriacum*, two high-elevation species with their elevational occurrence centred in the alpine belt of the Tatra Mountains in Central Europe. These results are compared with previously documented and reanalysed data from three species with wider or lower elevational ranges in the same region: *Soldanella carpat-ica*, occurring from the lower montane to the subnival belt; *Bellidiastrum michelii* (lower montane to alpine belt); and *Senecio subalpinus* (lower montane to subalpine belt). All five species were sampled across numerous elevational sites spanning their full vertical ranges in the Tatra Mountains, allowing us to model continuous patterns of trait variation and biomass allocation.

This study aims to identify potential differences in the elevational patterns of morphology and biomass partitioning between high-elevation specialists and species with wider elevational ranges. Specifically, we asked the following research questions: (1) Does plant size and mass in high-elevation species decrease with increasing elevation, as observed in species with wider elevational occurrence? (2) Do high-elevation species exhibit lower variability in morphological traits and biomass partitioning across elevation compared to species with wider or lower elevational distributions, suggesting reduced morphological plasticity?

Materials and methods

Study region

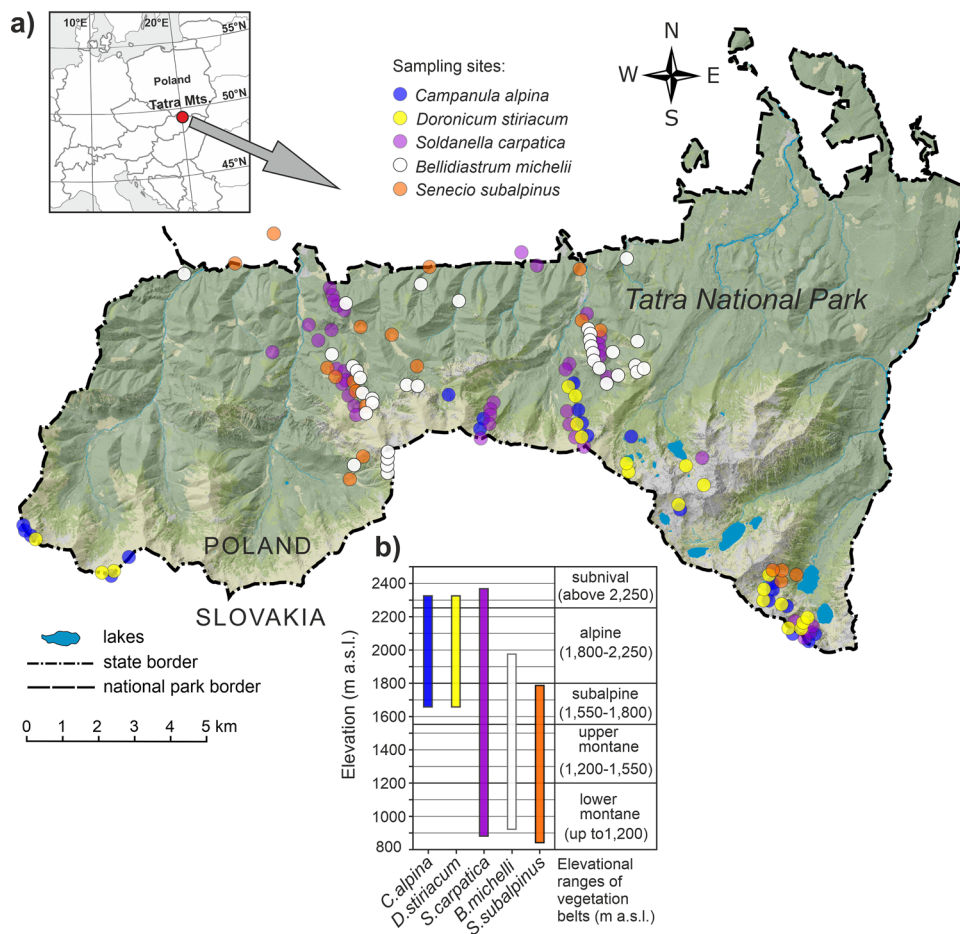
The research was conducted along an elevation gradient in the Polish part of the Tatra Mountains, within the protected area of the Tatra National Park (Fig. 1a). As the highest mountain range in the Carpathians (with the Gerlach peak reaching 2,655 m a.s.l. in the Slovak part), the Tatra Mountains represent the only alpine mountain system with a well-developed subnival zone between the Alps and the Caucasus (Mirek 1996). The main ridge of the Tatra Mountains forms a natural border between Poland and Slovakia. On the Polish side, the landscape is dominated by valleys and north-facing slopes, with elevations ranging from approximately 900 m to 2,499 m a.s.l. (Rysy peak). The mean annual temperature declines with elevation, from about +6 °C at the foothills to −4 °C at the highest peaks, while snow cover persists for approximately 100 days at the foothills and up to 290 days at the mountain summits (Hess 1996). Precipitation also increases with elevation, with an annual average of 1,138 mm at 844 m a.s.l. and 1,876 mm at 1,991 m a.s.l. The Tatra Mountains feature the occurrence of five distinct vegetation belts along their elevational gradient (Fig. 1b): the lower montane forest (extending up to 1,200 m a.s.l. in the Polish Tatra Mountains), the upper montane forest (1,200–1,550 m a.s.l.), the dwarf pine (subalpine) belt (1,550–1,800 m a.s.l.), the alpine belt (1,800–2,250 m a.s.l.), and the subnival belt (above 2,250 m a.s.l.) (Mirek 1996).

Study species

In this study, we investigated intraspecific trait variation along elevational gradients in two high-elevation species, *Campanula alpina* and *Doronicum stiriacum*, both of which have their elevational distributions centred in the alpine belt. We then compared their elevational responses with those of three species with wider or lower elevational ranges: *Soldanella carpat-ica*, which occurs from the lower montane to the subnival belt; *Bellidiastrum michelii*, found from the lower montane to the alpine belt; and *Senecio subalpinus*, distributed from the lower montane to the subalpine belt (Fig. 1b).

Campanula alpina Jacq. (Campanulaceae) (Fig. 2a) is a perennial herbaceous plant, (5–)10–20 cm tall, with basal rosettes of leaves and a leafy stem (Fedorov 1976). The leaves are linear-lanceolate, with basal leaves narrowed at the base, while the cauline leaves are liguliform. The simple or somewhat branched stems bear few or numerous bell-shaped blue-violet flowers, 10–20 mm in height (Aeschimann et al. 2004). The species blooms from July to September (Taciak 1971). *Campanula alpina* occurs in the

Fig. 1 Location of the sampling sites for the investigated species in the Polish Tatra Mountains, Western Carpathians (a), and their elevational distribution in the study region in relation to the elevational ranges of vegetation belts (b)



Carpathians and the Eastern Alps (Tacik 1971; Aeschimann et al. 2004). In Carpathians the species grows in alpine and subnival grasslands on base-poor substrates (Tacik 1971). In the study area, *C. alpina* was found and sampled at elevations ranging from 1,662 to 2,325 m a.s.l. (Supplementary Table S1).

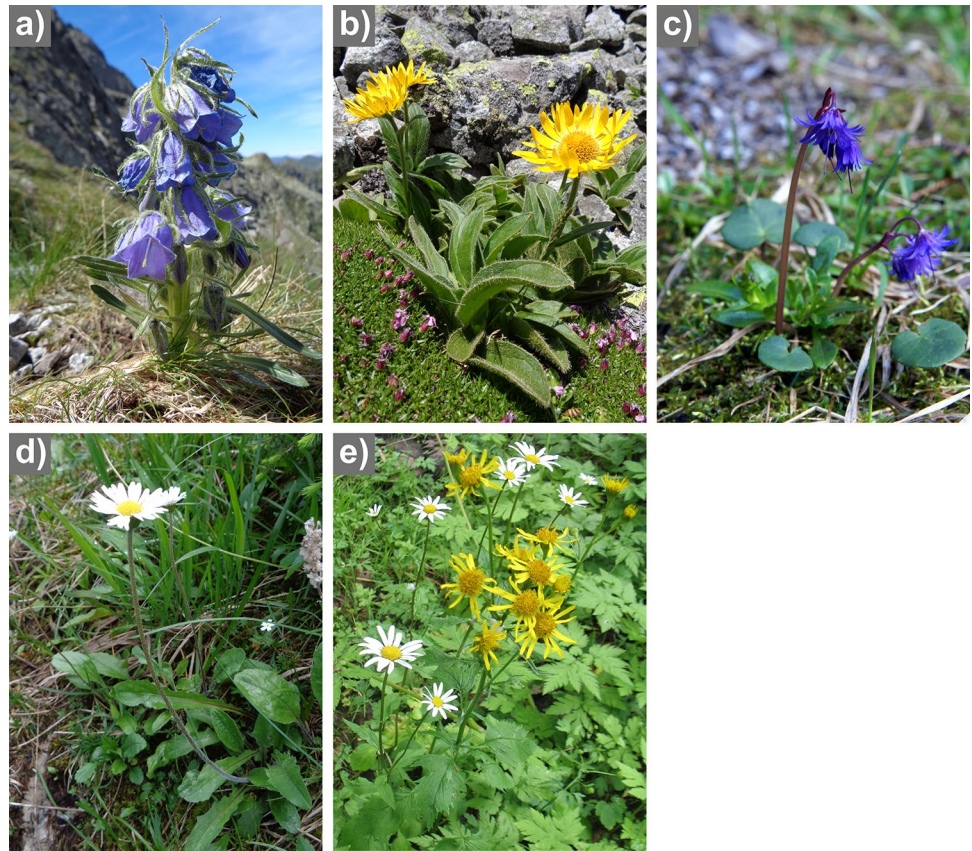
Doronicum stiriaceum (Vill.) Dalla Torre (Asteraceae, syn. *D. clusii* (All.) Tausch, *D. clusii* ssp. *vilosum*) (Fig. 2b) is a perennial herbaceous plant, 10–30(–40) cm tall (Kucowa 1971a; Aeschimann et al. 2004), with a sparsely leafed stem and basal leaves arranged in a rosette. The leaves are densely villous: the basal leaves are elliptic-oblong to elliptic-ovate, tapering to a petiole; the lower cauline leaves are similar but with shorter petioles; the middle cauline leaves are elliptic-lanceolate and amplexicaul, while the upper cauline leaves are lanceolate (Ferguson 1976). The flower head is solitary, 4.5–7.5 cm in diameter, and consists of yellow, insect-pollinated outer ligulate female flowers and inner tubular hermaphroditic flowers. The species blooms from July to September. *Doronicum stiriaceum* occurs in the Carpathians and the Eastern Alps (Kucowa 1971a; Aeschimann et al. 2004). In Carpathians the species grows in vegetation on siliceous rocks, screes, and moraines in the alpine and

subalpine belts (Kucowa 1971a). In the study area, *D. stiriaceum* was found and sampled at elevations ranging from 1,662 to 2,325 m a.s.l. (Supplementary Table S1).

Soldanella carpatica Vierh. (Primulaceae) (Fig. 2c) is a perennial herbaceous plant, (3–)5–15(–20) cm tall. The sub-orbicular leaves, with a leaf blade 0.8–3(–5) cm wide, are arranged in a basal rosette (Pawłowska 1963). The erect, leafless scape bears (1–)2–5 violet, insect-pollinated flowers in an inflorescence at the top (Pawłowska 1972). The species blooms from April to September (Zhang and Kadeireit 2002). *Soldanella carpatica* is endemic to the Western Carpathians (Zhang et al. 2001) and grows from the lower montane forest to the subnival belt on both base-rich and base-poor soils developed from a variety of bedrock types (Pawłowska 1972). *Soldanella carpatica* occurs in spruce and fir forests, subalpine tall-herb vegetation, alpine siliceous and calcicolous grasslands and swards, as well as snowbed communities. In the study area, *S. carpatica* was found and sampled at elevations ranging from 890 to 2,370 m a.s.l. (Kiełtyk 2024).

Bellidiastrum michelii Cass. (Asteraceae, syn. *Arnica bellidiastrum* All., *Aster bellidiastrum* (L.) Scop., *Doronicum bellidiastrum* L.) (Fig. 2d) is a perennial herbaceous

Fig. 2 Study species: *Campanula alpina* (a), *Doronicum stiriaceum* (b), *Soldanella carpatica* (c), *Bellidiastrum michelii* (d), and *Senecio subalpinus* (e, yellow flowers)



plant, 10–35 cm tall. The leaves, which are suborbicular, spatulate, obovate, or elliptical in shape, are arranged in a basal rosette. The erect, leafless scape bears a single flower head at the top. The flowers, gathered in the flower head, are insect-pollinated, with outer female white or pink ligulate flowers and inner tubular hermaphroditic yellow flowers. The species blooms from May to August (Rostański 1971). *Bellidiastrum michelii* is widespread in the mountain regions of Central and Southern Europe (Merxmüller and Schreiber 1976). The species grows predominantly in grasslands, pastures, rocks, and along springs on calcareous substrates from the lower montane forest to the alpine belt (Rostański 1971; Aeschimann et al. 2004). In the study area, *B. michelii* was found and sampled at elevations ranging from 920 to 2,075 m a.s.l. (Kieltyk 2021a).

Senecio subalpinus W.D.J. Koch (Asteraceae) (Fig. 2e) is a perennial herbaceous plant, (25–)30–70(–90) cm tall. The stem of *S. subalpinus* is erect, usually branched only at the inflorescences and leafy throughout, with leaves gradually decreasing in size toward the top of the stem (Kucowa 1971b; Chater and Walters 1976). The number of flower heads ranges from (3–)5 to 20, each 25–40 mm in diameter, and they form a corymb. The flowers are yellow or orange-yellow, gathered in a flower head with outer ligulate female and inner tubular hermaphroditic flowers, and are insect-pollinated. The species blooms from July to September

(Kucowa 1971b). *Senecio subalpinus* is widespread in the Carpathians, Eastern Alps, and the mountains of the Balkan Peninsula, mainly in the montane and subalpine vegetation belts (Kucowa 1971b; Chater and Walters 1976; Aeschimann et al. 2004). *Senecio subalpinus* grows predominantly in tall-herb vegetation, fresh meadows and pastures, along river and stream banks, and in forest glades and clearings, mostly on eutrophic and wet soils (Kucowa 1971b; Aeschimann et al. 2004). In the study area, *S. subalpinus* was found and sampled at elevations ranging from 840 to 1,792 m a.s.l. (Kieltyk 2021b).

Field sampling and morphological measurements

A total of 202 *Campanula alpina* plants from 21 sites and 185 *Doronicum stiriaceum* plants from 20 sites were collected at elevations ranging from 1,662 to 2,325 m a.s.l. Most of the plant material was collected in 2016, with five sites sampled in 2015 (Supplementary Table S1). An effort was made to sample the entire elevational range of the species in the area and to ensure that the sampled sites were distributed approximately evenly along the species' elevational ranges. At each site, 9–10 plants at peak bloom were sampled, although in some cases fewer, with a minimum distance of 1.5 m between sampled plants. The collected plants

showed no restrictions in growth or reproductive function, nor any symptoms of herbivory damage or fungal infection.

The corolla tube diameter and length of *Campanula alpina*, measured on one randomly selected flower per

plant, as well as the flower head diameter of *Doronicum stiriaceum*, were measured using a digital caliper (Powerfix Profi, Neckarsulm, Germany) immediately after collection, when the flowers were fresh and undeformed (Table 1).

Table 1 Traits of *Campanula alpina* (Ca) and *Doronicum stiriaceum* (Ds) analysed in the study

Trait	Measurement details	Accuracy / significant digits
Common traits		
<i>Plant height</i> —measured from the base of the plant to the highest point of the inflorescence, representing the maximum plant height.	Straightened stem was measured with a ruler on herbarium specimens.	0.5 cm
<i>Plant mass</i> —dry mass of the aboveground plant parts. Calculated as sum of leaf, stem and flower (flower head in Ds) mass weighed separately.	—	0.0001 g
<i>Leaf mass</i> —total dry mass of all plant leaves.	Weighed on an analytical balance after drying for 48 h at 80 °C	0.0001 g
<i>Stem mass</i> —dry mass of plant stem (including lateral branches in Ca).	As above.	0.0001 g
<i>Flower mass</i> —total dry mass of all flowers in the inflorescence (in the flower head in Ds).	As above.	0.0001 g
<i>Number of flowers</i> in the inflorescence (in the flower head in Ds).	In Ds: counted by stereomicroscopy at × 10 magnification after separation of the flower head into ligulate and tubular flowers.	—
<i>Individual flower mass</i> —in Ca: mean mass of three largest flowers in the inflorescence weighed separately; in Ds: calculated by dividing total flower mass in the flower head by number of flowers in the head.	—	0.0001 g
<i>Leaf mass fraction</i> —total leaf mass divided by plant aboveground mass.	—	—
<i>Stem mass fraction</i> —stem mass divided by plant aboveground mass.	—	—
<i>Flower (Flower head in Ds) mass fraction</i> —total flower mass (flower head mass in Ds) divided by plant aboveground mass.	—	—
<i>Campanula alpina</i> specific traits		
<i>Corolla tube diameter</i> —measured in the upper part of the tube beneath corolla lobes for one randomly chosen flower from the inflorescence.	Measured with a digital calliper on fresh plants in the field immediately after plant collection.	0.1 mm
<i>Corolla tube length</i> —measured perpendicularly to the floral axis from the calyx base to the top of the corolla for the chosen flower.	As above.	0.1 mm
<i>Doronicum stiriaceum</i> specific traits		
<i>Flower head mass</i> —dry mass of the flower head.	Weighed on an analytical balance after drying for 48 h at 80 °C.	0.0001 g
<i>Flower head diameter</i> —the maximum distance between the tips of two opposed petals.	Measured with a digital calliper on fresh plants in the field immediately after plant collection.	0.1 mm
<i>Ligulate flower length</i> —corolla length measured for one randomly chosen ligulate flower from the head.	Measured with stereomicroscopy at × 10 magnification after 1 h rehydration in water.	0.1 mm
<i>Ligulate flower width</i> —ligule width of the chosen flower.	As above.	0.1 mm
<i>Tubular flower length</i> —corolla length measured for one randomly chosen tubular flower from the head.	As above.	0.1 mm

Subsequently, the plants were dried in a botanical press and preserved for further laboratory analyses. Plant height was measured from the base of the plant to the highest point of the inflorescence, representing the maximum plant height. The plants were separated into three fractions (stem, leaves, and flowers/flower heads) and dried for 48 h at 80 °C in a laboratory drying oven with natural air circulation (Pol-Eko-Aparatura SLN 240, Wodzisław Śląski, Poland) to determine the dry matter content, following the procedure described by Pérez-Harguindeguy et al. (2013). The dry weight was obtained using an analytical balance (Radwag AS 60/220.X2 PLUS, Radom, Poland).

For *Doronicum stiriaceum*, after recording the dry weight of the single flower head per plant, it was soaked in water in a Petri dish for 1 h and then carefully separated into ligulate and tubular flowers. Rehydration was necessary to prevent damage to the brittle, dry flowers and to facilitate the straightening of the corollas for subsequent measurements. The total number of flowers in each flower head was counted. One ligulate and one tubular flower were then randomly selected from each head for size measurements. In ligulate flowers, the width of the ligule and the length of the corolla were measured, while in tubular flowers, only the corolla length was measured using a stereoscopic microscope (Delta Optical SZ-450T, Mińsk Mazowiecki, Poland). After measurement, the flowers were stored in paper envelopes, dried for 48 h at 80 °C in a forced-air drying oven (Binder FD 115, Tuttlingen, Germany) and their dry matter content subsequently weighed on an analytical balance. All weight measurements were conducted immediately after the samples were removed from the oven to minimize moisture absorption from ambient laboratory air. Raw measurement data for *C. alpina* are available in Supplementary Data File 1, and for *D. stiriaceum* in Supplementary Data File 2.

To compare elevational trait variation in the high-elevation species *Campanula alpina* and *Doronicum stiriaceum* with that of species with wider elevational distributions from the Tatra Mountains, we utilized our previously published data on 383 *Soldanella carpatica* plants from 40 elevational sites sampled in 2018 (Kieltyk 2024), 340 *Belldiastrum michelii* plants from 34 sites sampled in 2016 (Kieltyk 2021a), and 200 *Senecio subalpinus* plants from 20 sites sampled in 2017 and 2018 (Kieltyk 2021b). The methods for plant material collection and morphological measurements were consistent across all investigated species. Leaf mass fraction was calculated as the total leaf mass divided by the aboveground plant mass. Stem mass fraction was calculated as stem mass divided by aboveground mass. Flower mass fraction was calculated as the total flower mass (in *C. alpina* and *S. carpatica*) or the mass of all flower heads (in *D. stiriaceum*, *B. michelii*, and *S. subalpinus*) divided by aboveground plant mass. Species-specific details

on plant collection and trait measurements for *C. alpina* and *D. stiriaceum* are presented in Table 1, while corresponding information for *B. michelii*, *S. subalpinus*, and *S. carpatica* can be found in Kieltyk (2021a, b, 2024).

Statistical analyses

All analyses were conducted using the statistical programming environment R (version 4.4.1; R Development Core Team 2024). Variation in morphological and biomass partitioning traits within species along the elevational gradient was analysed using linear mixed-effects models (Field et al. 2013), implemented via the *lmer()* function from the *lme4* package (Bates et al. 2015). In these models, elevation was included as a continuous fixed effect, and sampling site was treated as a random effect. Elevational patterns of trait variation were assessed for 12 traits in *C. alpina*, 15 traits in *D. stiriaceum*, and 9 traits each in *S. alpina*, *B. michelii*, and *S. subalpinus* (Supplementary Table S2). To compare the effect of elevation on trait variation among species, we calculated the percentage change in trait values per 100 m increase in elevation, as well as across the full elevational range of each species (from the lowest to the highest recorded elevation). The following traits were analysed: plant height, plant mass, leaf mass, stem mass, flower mass, individual flower mass, leaf mass fraction, stem mass fraction, and flower mass fraction. These percentage changes were calculated based on model-estimated trait values at the lowest and highest sampling sites. Changes per 100 m were used to compare the magnitude of trait variation among species over a common elevational increment, while changes across the full elevational range reflected overall shifts within each species' elevational distribution.

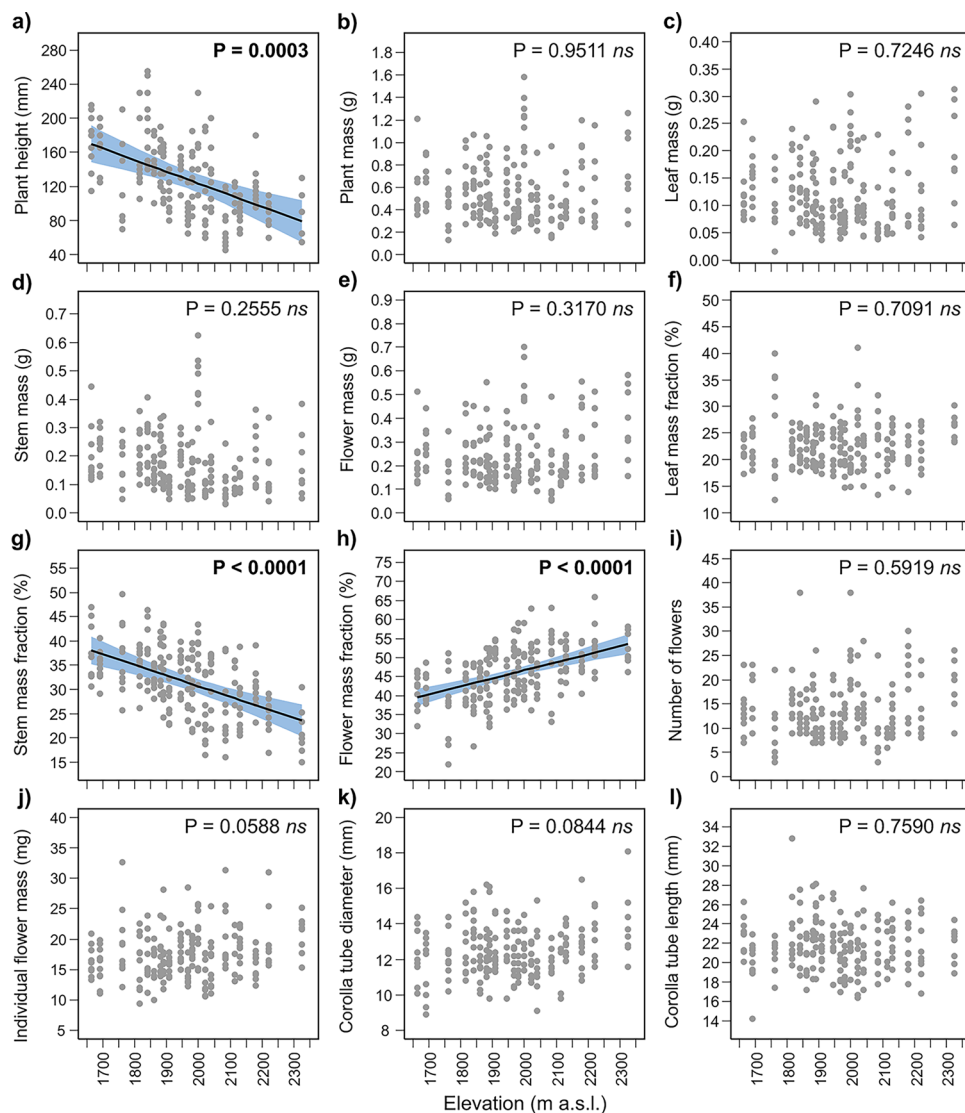
Results

Elevational trait variation in high-elevation species

In *C. alpina*, significant elevational variation was observed in three of the twelve investigated morphological traits (Supplementary Table S2). Plant height (Fig. 3a) and stem mass fraction (Fig. 3g) decreased, whereas flower mass fraction (Fig. 3h) increased with increasing elevation. The remaining traits of *C. alpina* showed no significant relationship with elevation.

In *D. stiriaceum*, significant elevational variation was observed in four of the fifteen investigated morphological traits (Supplementary Table S2). Plant height (Fig. 4a) and stem mass fraction (Fig. 4h) decreased, whereas leaf mass fraction (Fig. 4g) and tubular flower length (Fig. 4o) increased with increasing elevation. The remaining traits

Fig. 3 Elevational variation in morphological traits of *Campanula alpina*. **a** Plant height; **b** Plant mass; **c** Leaf mass; **d** Stem mass; **e** Flower mass; **f** Leaf mass fraction; **g** Stem mass fraction; **h** Flower mass fraction; **i** Number of flowers; **j** Individual flower mass; **k** Corolla tube diameter; **l** Corolla tube length. Solid lines represent the results of the mixed-effects models, with surrounding bands indicating the 95% confidence intervals. *P* p-value of model significance, *ns* non-significant at the 0.05 level



of *D. stiriicum* showed no significant relationship with elevation.

Elevational trait variation in high-elevation vs. wider elevation species

Plant height declined with increasing elevation in all species, with the steepest reductions observed in *C. alpina* and *B. michelii* (up to ~66% across their elevational ranges; per 100 m: Fig. 5a; across the elevational range: Fig. 6a). In the high-elevation species (*C. alpina* and *D. stiriicum*), above-ground biomass components, including leaf, stem, and flower mass, remained unchanged with elevation (Figs. 5b–f and 6b–f). In contrast, the wide-elevation (*S. carpatica*) and lower-elevation (*B. michelii*, *S. subalpinus*) species showed significant declines in plant mass, particularly in leaf and stem mass, with plant mass reductions exceeding 50% in all three species. Flower mass also declined in *S. carpatica*

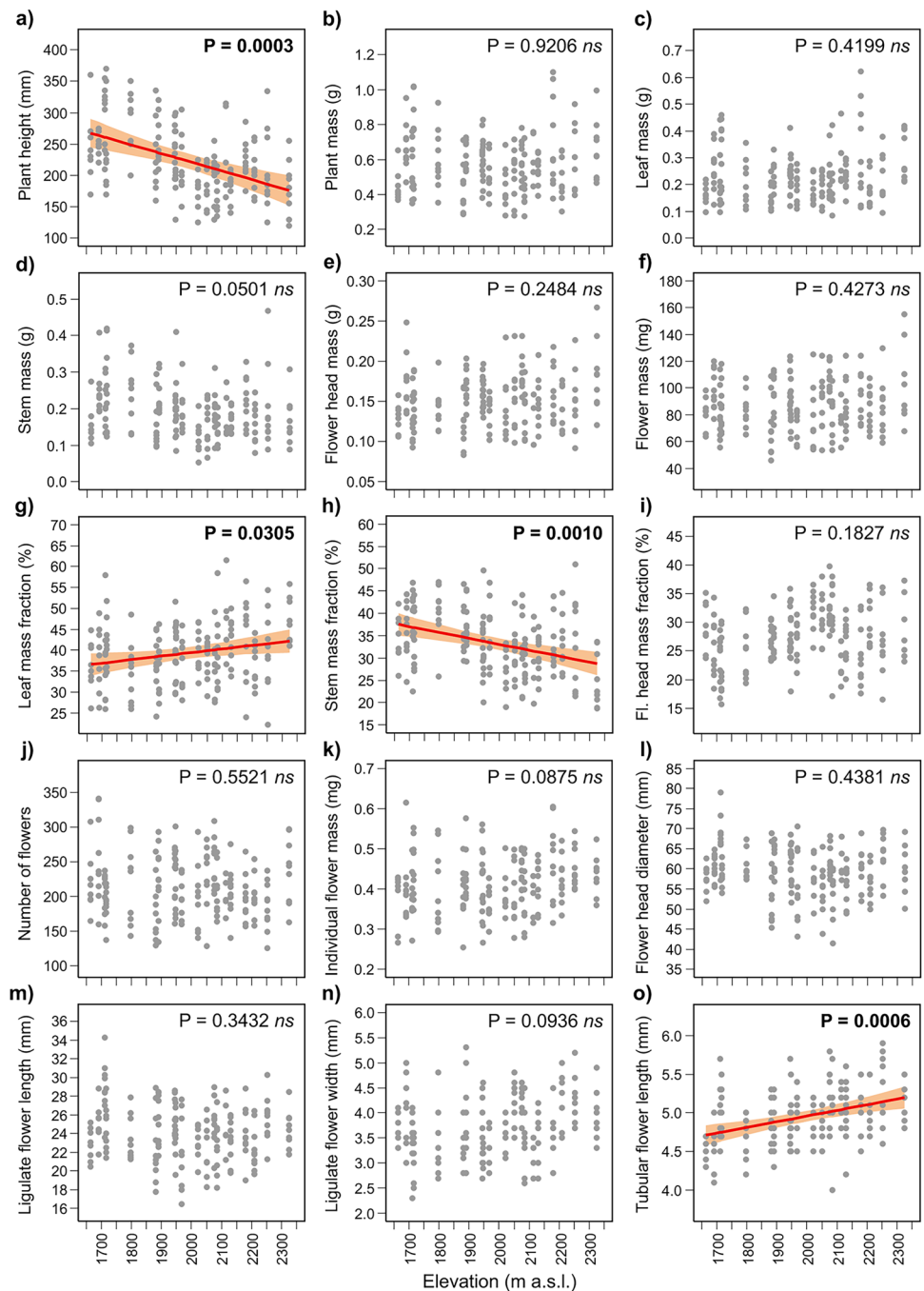
and *B. michelii*, but remained stable in *S. subalpinus*. Interestingly, individual flower mass decreased in *S. carpatica* and *B. michelii*, yet increased in *S. subalpinus*. Leaf mass fraction increased slightly only in *D. stiriicum* and declined marginally in *S. carpatica*. Stem mass fraction generally decreased with elevation in most species, except *S. carpatica*. Flower mass fraction increased in all species but *D. stiriicum*, with the strongest increase observed in *B. michelii* (Figs. 5g–i and 6g–i).

Discussion and conclusions

Plant mass response to the elevation gradient

Our results demonstrated substantial differences in how plant morphology and biomass partitioning varied with elevation among species with different elevational distribution.

Fig. 4 Elevational variation in morphological traits of *Doronicum stiriacum*. **a** Plant height; **b** Plant mass; **c** Leaf mass; **d** Stem mass; **e** Flower head mass; **f** Flower mass; **g** Leaf mass fraction; **h** Stem mass fraction; **i** Flower head mass fraction; **j** Number of flowers; **k** Individual flower mass; **l** Flower head diameter; **m** Ligulate flower length; **n** Ligulate flower width; **o** Tubular flower length. Solid lines represent the results of the mixed-effects models, with surrounding bands indicating the 95% confidence intervals. *P* p-value of model significance, *ns* non-significant at the 0.05 level

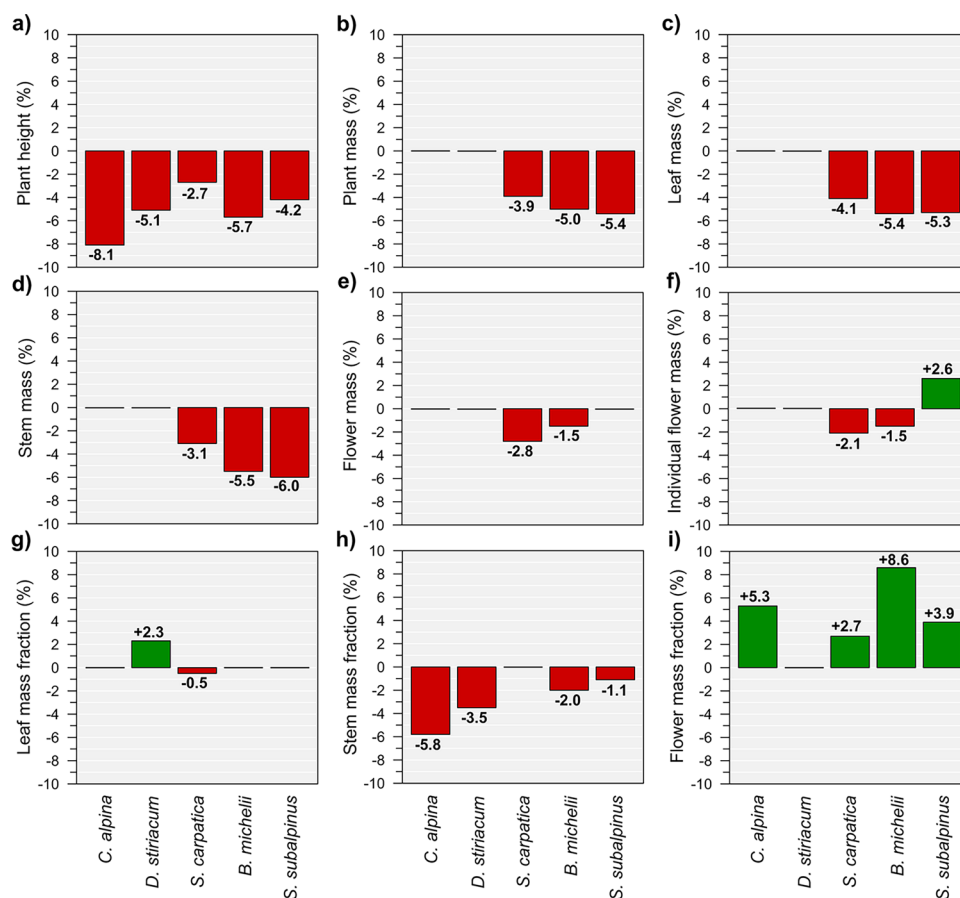


Analyses of phenotypic change per 100 m and across full elevational ranges showed consistent patterns. We hypothesized that high-elevation species would show more conservative responses to environmental changes along elevational gradients compared to wide or lower-elevation species. In line with this hypothesis, high-elevation specialists (*C. alpina* and *D. stiriacum*) maintained constant plant mass along the gradient, while species with wider or lower elevational ranges (*S. carpatica*, *B. michelii*, *S. subalpinus*) were more responsive to elevation. These findings fully support the hypothesis recently formulated and tested by Rixen and

colleagues (2022) that species specialized to high elevations display more conservative (i.e., less variable) trait responses across their elevational distribution than species with larger range sizes or from lower elevations.

The key finding is that high-elevation specialists maintained aboveground mass, leaf mass, flower mass and individual flower mass with increasing elevation, while species with lower or wider elevational distribution generally declined. Although the two high-elevation species are specialized for high-elevation environments and primarily grow in the alpine belt, their elevational ranges in the

Fig. 5 Percentage changes in trait values in *C. alpina*, *D. stiriicum*, *S. carpatica*, *B. michelii*, and *S. subalpinus* per 100 m increase in elevation. **a** Plant height; **b** Plant mass; **c** Leaf mass; **d** Stem mass; **e** Flower mass; **f** Individual flower mass; **g** Leaf mass fraction; **h** Stem mass fraction; **i** Flower mass fraction

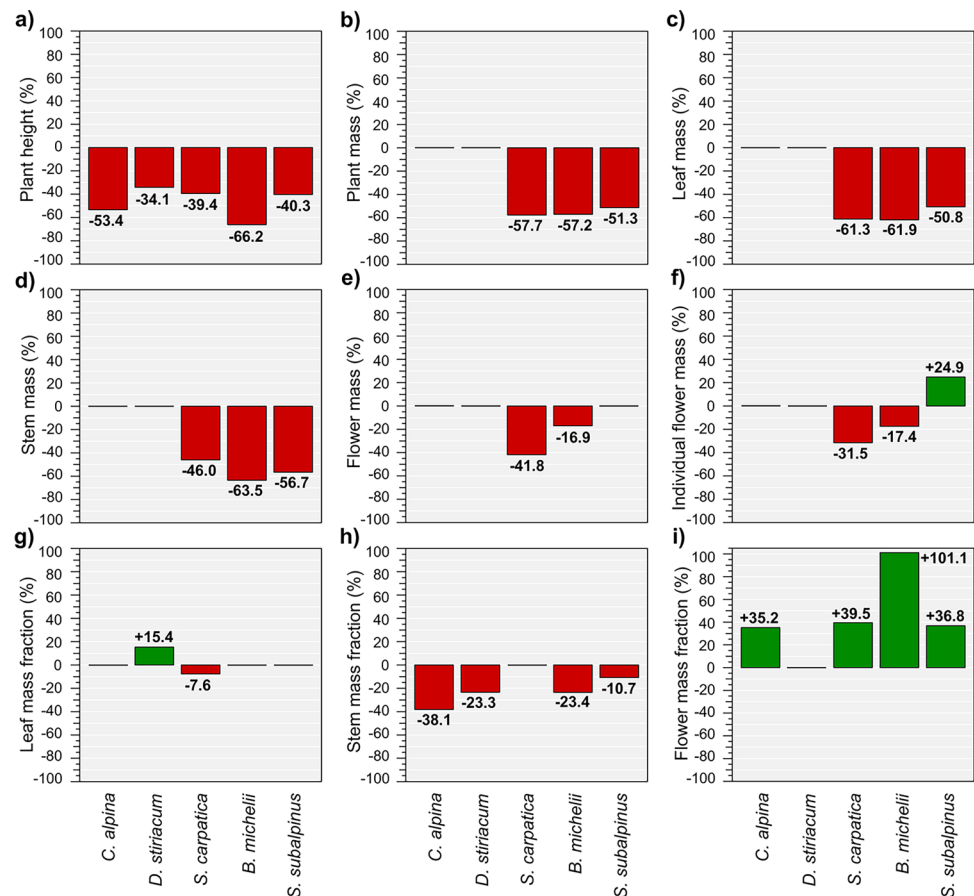


study area were not particularly narrow, spanning a 660 m elevational range and corresponding to a ~ 3.6 K decrease in temperature (assuming $0.55 \text{ K} \cdot 100 \text{ m}^{-1}$; Körner 2021). The ability of these high-elevation species to maintain constant aboveground biomass suggests that they are well adapted to high-elevation environments and that their growth is not constrained by abiotic environmental conditions. In contrast, species with wider or lower elevational ranges exhibited strong responses to increasing elevation. All species in this group experienced more than 50% reduction in aboveground mass and leaf mass from the lowest to the highest elevations. Moreover, unlike the high-elevation species, species with wide (*S. carpatica*) or lower (*B. michelii*) elevational distributions also showed a decline in flower mass with increasing elevation. Furthermore, individual flower mass decreased with elevation in *S. carpatica* and *B. michelii* (although it increased in *S. subalpinus*). The substantial reduction in plant mass and floral investment in the species with larger range sizes or lower elevations suggests that their growth is strongly constrained at high elevations, primarily due to climatic conditions.

Patterns of elevational changes in biomass partitioning did not reveal clear differences between high-elevation species and wider elevation range species. Leaf mass fraction

showed minimal variation with elevation, with notable changes observed only in *D. stiriicum* and *S. carpatica*. Stem mass fraction decreased in all species except *S. carpatica*, while flower mass fraction increased in all species except *D. stiriicum*. As our study focused solely on aboveground biomass allocation, specifically to leaves, stems, and flowers, and did not include belowground biomass or root/shoot ratio, this represents a relevant limitation given the important role of belowground allocation in plant resource-use strategies and stress tolerance in mountains (Reich et al. 2014; Blume-Werry et al. 2018; Doležal et al. 2021). Moreover, plant size and age have also been shown to interact with biomass allocation patterns and influence how resources are partitioned (Doležal et al. 2021, 2024). While our findings highlight important aboveground biomass patterns along elevation, future research incorporating belowground biomass, as well as plant size and age, is needed to fully understand the adaptive strategies of high-elevation specialists and species with wider elevational occurrence across elevational gradients.

Fig. 6 Percentage changes in trait values in *C. alpina*, *D. stiriaceum*, *S. carpatica*, *B. michelii*, and *S. subalpinus* across the species' ranges, from the lowest to the highest elevation. **a** Plant height; **b** Plant mass; **c** Leaf mass; **d** Stem mass; **e** Flower mass; **f** Individual flower mass; **g** Leaf mass fraction; **h** Stem mass fraction; **i** Flower mass fraction



Plant height response to the elevation gradient

Plant height decreased significantly with increasing elevation in both high-elevation specialists and species with wider or lower elevational ranges. This reduction was accompanied by a significant decrease in stem mass in the wider elevation species, whereas stem mass remained unchanged in the high-elevation species. The decline in plant height with increasing elevation has been observed in numerous other species (e.g., Kofidis et al. 2007; Alexander et al. 2009; Takahashi and Yoshida 2009; Zhu et al. 2010; Maad et al. 2013; He et al. 2017; Paudel et al. 2019; Cruz-Maldonado et al. 2021; Rathee et al. 2021) and is considered a common phenotypic adaptation to environmental conditions that change with elevation in mountains. Research in alpine environments has demonstrated that air temperature is highest near the ground, while wind speed increases logarithmically with distance from the surface (Körner 2021). For example, in the alpine zone of the European Alps, surface temperatures on dark humic soils can reach +80 °C at mid-day, while within a compact leaf canopy a few centimetres above the ground, it may be +27 °C, compared to only +4 °C at a nearby weather station (Körner 2021). These substantial variations in air temperature and wind speed across a small

vertical distance above ground level likely drive adaptive reductions in plant height for species growing on mountain slopes. Furthermore, because canopy height generally decreases with elevation (Leuschner and Ellenberg 2017), reduced plant height helps keep flowers within the relatively stable aerodynamic boundary layer near the ground, avoiding colder, more turbulent air above (Dietrich and Körner 2014). Thus, as elevation increases, it becomes increasingly important for plants to grow closer to the ground, where microclimatic conditions are relatively milder. Our results indicate that this adaptive response occurs in both high-elevation specialists and species with wider elevational occurrence. This aligns with findings by Rixen et al. (2022) from various mountain systems but contrasts with observations from the Tibetan Plateau, where reduced plant height with elevation was found only in low-elevation species, not in high-elevation specialists (Hu et al. 2024).

Possible causes of contrasting response patterns

The sharp reduction in aboveground biomass with increasing elevation in lower-elevation species with broader elevational distributions contrasted with the stable growth of high-elevation specialists across a substantial range

(~660 m), suggesting fundamentally different mechanisms of elevational response. To disentangle whether these patterns reflect phenotypic plasticity or genetically based local adaptation, a common garden experiment, ideally including environmental treatments across contrasting elevational groups, is essential to move beyond observational inference. The divergence in growth patterns suggests that generalist species may experience increasing environmental constraints at higher elevations, while high-elevation specialists are better adapted to such conditions. However, beyond absolute environmental harshness, differences in the predictability of environmental conditions across elevation may also contribute to the patterns observed. While high elevations are cold and resource-poor, they may offer relatively stable abiotic conditions from year to year. In contrast, lower elevations may be more variable, particularly in terms of biotic interactions such as competition or herbivory (Rixen et al. 2022). Indeed, empirical evidence suggests that populations and species from more variable environments tend to exhibit higher levels of plasticity (Chevin and Hoffmann 2017). Such differences in environmental predictability, both abiotic and biotic, can influence the evolution of plasticity and may help explain why species with wider or lower elevational ranges exhibit stronger trait responses to elevation than high-elevation specialists.

The ability of high-elevation plants to maintain stable plant mass across their elevational ranges may have multiple underlying causes. Alpine species are known to be highly adapted to tissue formation and growth under extremely low temperatures. Some alpine species, such as *Soldanella pusilla*, even develop flowering shoots at 0 °C in mid-winter beneath 2–3 m of snow (Körner et al. 2019). It is possible, therefore, that high-elevation species, having high metabolic and photosynthetic efficiency at low temperatures and a short growing season at the highest elevations, do not increase tissue production or biomass accumulation in the climatically milder, lower parts of their elevational distributions due to genetically based constraints on organ structure and size. This could explain why they show limited responsiveness to elevation across their ranges. Another not mutually exclusive mechanism for maintaining a stable phenotype in the high-elevation species across their elevational ranges may involve physiological responses such as increased metabolic efficiency and enhanced photosynthetic capacity with increasing elevation, thereby supporting sustained tissue formation.

Our results indicate that species occupying wider- or lower-elevation ranges display markedly greater morphological variability than the high-elevation specialists. This suggests they may be more responsive to rising temperatures, potentially increasing their height and mass, both of which declined with elevation and colder conditions in our

study. However, the high-elevation species demonstrated an ability to live and thrive across a wide range of temperatures, such as those encountered along the 660 m elevational gradient, while maintaining stable aboveground biomass. This suggests that high-elevation species may effectively tolerate and physiologically adjust to increased temperatures associated with predicted climate change in mountain regions (Engler et al. 2011; Mountain Research Initiative EDW Working Group 2015). Moreover, a well-documented example of the high temperature tolerance of alpine species is their ability to migrate downward along mountain streams and rivers. Alpine plants are often temporarily observed growing and flowering in competition-free sites on river gravels and banks at mountain foothills or adjacent lowlands, up to 2,000 m or more below their natural elevational range (Walas 1938). Thus, climate warming alone does not appear to pose a direct threat to alpine species; rather, the primary risk may stem from increased competition with species from lower elevations, which could be competitively superior under warmer conditions (Alexander et al. 2015; Rumpf et al. 2018).

Outlook for future research

Although elevational trait variation in plants is well studied, few studies have focused on high-elevation specialists or analysed whole-plant morphology and biomass. Our results from two high-elevation species confirm that their elevational trait variation differs fundamentally from that of three species with wider or lower elevational ranges. To determine whether these patterns are shaped by phenotypic plasticity or genetically based local adaptation, a common garden experiment across contrasting elevational groups is essential. Moreover, our results suggest that high-elevation species rely more on physiological rather than morphological responses to cope with environmental change. To understand how these specialists maintain stable aboveground biomass and flower production across elevations, studies on elevational variation in eco-physiological traits, particularly those linked to photosynthetic efficiency, are necessary.

Because our species sample is small (two high-elevation species and three species with wider or lower elevational ranges), any phylogenetic influence on trait variation could be confounded with elevational distribution. However, the three Asteraceae species span different elevational niches, which likely reduces the sole effect of shared ancestry on the observed patterns. Since most species were sampled in different years, the robustness of trait patterns across years could not be assessed. To further strengthen conclusions about differing patterns of elevational trait variation between high-elevation specialists and species with wider or lower elevational ranges, future studies should include

a larger number of species from contrasting elevational groups, measure root biomass, and ideally incorporate multi-year sampling alongside phylogenetically informed analyses.

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Author contributions PK, AO, and JFS designed the study. PK collected and processed the plant material. PK and JFS analysed the data. PK wrote the manuscript, with both co-authors contributing to revisions. All authors approved the manuscript.

Data availability All data supporting the findings of this study are available within the manuscript or supplementary information files. Raw data measurements for *Campanula alpina* are available in Supplementary Data File 1 (ESM_3), for *Doronicum stiriacum* in Supplementary Data File 2 (ESM_4), and for *Soldanella carpatica*, *Bellidiastrum michelii*, and *Senecio subalpinus* in the supplementary materials accompanying Kiełtyk 2024, Kiełtyk 2021a, and Kiełtyk 2021b, respectively.

Declarations

Conflict of interest The authors declare no competing interests.

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