Elevational variation in morphology and biomass allocation in carpathian snowbell *Soldanella carpatica* (Primulaceae)

Piotr Kiełtyk [Corresp. 1]

[1] Institute of Biological Sciences, Cardinal Stefan Wyszyński University in Warsaw, Warsaw, Poland

Corresponding Author: Piotr Kiełtyk
Email address: kieltyk@wp.pl

Plants growing along wide elevation gradients in mountains experience considerable variations in environmental factors that vary across elevations. The most pronounced elevational changes are in climate conditions with characteristic decrease in air temperature with an increase in elevation. Studying intraspecific elevational variations in plant morphological traits and biomass allocation gives opportunity to understand how plants adapted to steep environmental gradients that change with elevation and how they may respond to climate changes related to global warming. In this study, phenotypic variation of an alpine plant *Soldanella carpatica* Vierh. (Primulaceae) was investigated on 40 sites distributed continuously across a 1,480-m elevation gradient in the Tatra Mountains, Central Europe. Mixed-effects models, by which plant traits were fitted to elevation, revealed that on most part of the gradient total leaf mass, leaf size and scape height decreased gradually with an increase in elevation, whereas dry mass investment in roots and flowers as well as individual flower mass did not vary with elevation. Unexpectedly, in the uppermost part of the elevation gradient overall plant size, including both below- and above-ground plant parts, decreased rapidly causing abrupt plant miniaturization. Despite the plant miniaturization at the highest elevations, biomass partitioning traits changed gradually across the entire species elevation range, namely, the leaf mass fraction decreased continuously, whereas the flower mass fraction and the root:shoot ratio increased steadily from the lowest to the highest elevations. Observed variations in *S. carpatica* phenotypes are seen as structural adjustments to environmental changes across elevations, by means of plastic, environmentally induced responses and/or genetic differences among locally adapted populations, that increase chances of plant survival and reproduction at different elevations.

1 **Elevational variation in morphology and biomass**

2 **allocation in carpathian snowbell *Soldanella carpatica***

3 **(Primulaceae)**

5 Piotr Kiełtyk

6 Institute of Biological Sciences, Cardinal Stefan Wyszyński University in Warsaw, Warsaw,

7 Poland

9 Corresponding Author:

10 Piotr Kiełtyk

11 Wóycickiego 1/3, 01-938 Warsaw, Poland

12 Email address: kieltyk@wp.pl

13 p.kieltyk@uksw.edu.pl

Abstract

Plants growing along wide elevation gradients in mountains experience considerable variations in environmental factors that vary across elevations. The most pronounced elevational changes are in climate conditions with characteristic decrease in air temperature with an increase in elevation. Studying intraspecific elevational variations in plant morphological traits and biomass allocation gives opportunity to understand how plants adapted to steep environmental gradients that change with elevation and how they may respond to climate changes related to global warming. In this study, phenotypic variation of an alpine plant *Soldanella carpatica* Vierh. (Primulaceae) was investigated on 40 sites distributed continuously across a 1,480-m elevation gradient in the Tatra Mountains, Central Europe. Mixed-effects models, by which plant traits were fitted to elevation, revealed that on most part of the gradient total leaf mass, leaf size and scape height decreased gradually with an increase in elevation, whereas dry mass investment in roots and flowers as well as individual flower mass did not vary with elevation. Unexpectedly, in the uppermost part of the elevation gradient overall plant size, including both below- and aboveground plant parts, decreased rapidly causing abrupt plant miniaturization. Despite the plant miniaturization at the highest elevations, biomass partitioning traits changed gradually across the entire species elevation range, namely, the leaf mass fraction decreased continuously, whereas the flower mass fraction and the root:shoot ratio increased steadily from the lowest to the highest elevations. Observed variations in *S. carpatica* phenotypes are seen as structural adjustments to environmental changes across elevations, by means of plastic, environmentally induced responses and/or genetic differences among locally adapted populations, that increase chances of plant survival and reproduction at different elevations.

Introduction

Elevation gradients in mountains are characterised by rapid environmental changes over very short distances and increasing elevation in temperate seasonal zones is associated with changes in many factors crucial for plant growth, survival and reproduction (Körner, 2021). As elevation increases there is a decrease in temperature, atmospheric pressure, CO_2 content and length of the growing season, whereas precipitation, solar radiation, as well as number of weather-related extreme events, for example, frequencies of strong winds and frost during growing season, increase with an increase in elevation (Billings, 1974; Nagy & Grabherr, 2009; Takahashi, 2014;

62 Körner, 2021). Moreover, at high elevations soil depth, microbial activity, nutrients availability,

63 soil resource competition and herbivory pressure are generally lower (Rasmann et al., 2014;

64 Körner, 2021), whereas competition for pollinator services increases with elevation because the

65 number and activity of pollinators declines in low temperature environment of high elevations

66 (Maad, Armbruster & Fenster, 2013; Zhao & Wang, 2015; Arroyo, Pacheco & Dudley, 2017).

67 Therefore, elevation is an important indicator of abiotic and biotic variations which influence

68 plant performance and survival and may significantly alter functional characteristics of a plant

69 species (Hautier et al., 2009; Scheepens & Stöcklin, 2013; He et al., 2017; Trunschke &

70 Stöcklin, 2017; Kiełtyk, 2018; Miljković et al., 2019; Paudel et al., 2019; Kiełtyk, 2021a;

71 Kiełtyk, 2021b; Rathee et al., 2021; Ahmad et al., 2023).

72 The intraspecific elevational variation observed in many plants can result from their

73 adaptive plasticity (Dai et al., 2017; Hamann et al., 2017; Henn et al., 2018) and/or their genetic

74 adaptation to local conditions (Byars, Papst & Hoffmann, 2007; Gonzalo-Turpin & Hazard,

75 2009; Hirano, Sakaguchi & Takahashi, 2017; Morente-López et al., 2020) because the

76 environment selects for the optimal phenotype adapted to local resource availability and habitat

77 conditions (Midolo et al., 2019). To alleviate stress levels and increase the uptake of the limiting

78 resources or reduce the need for these limiting resources, plants can respond to variation in the

79 environment by adjusting their physiology, morphology and biomass allocation (Nicotra et al.,

80 2010; Freschet et al., 2018). Hence, different elevational stresses across elevation gradients may

81 select for different ecological strategies among individuals of the same species that are reflected

82 in distinct patterns of morphological variation and biomass allocation along elevational gradients

83 (Seguí et al., 2018).

84 Allocation of dry matter to different plant structures implies existence of investment trade-

85 offs, because resources allocated to one organ or function are unavailable for other organs or

86 functions (Weiner et al., 2009). For example, in herbaceous perennials much allocation to stem

87 and leaves is advantageous for competition for photosynthetic light capture but less allocation to

88 belowground parts is disadvantageous for water and nutrients acquisition as well as for

89 assimilates storage (Takahashi & Matsuki, 2017). According to the optimality theory the

90 relationship between dry mass allocation in below- and above-ground organs (the root:shoot

91 ratio) varies with range of resource supply and plants allocate more of their dry mass to organs

92 that capture the most limiting resource (Reich et al., 2014; Blume-Werry et al., 2018). There is a

93   prediction that plants growing in cold and low nitrogen availability environments, should invest

94   more of their biomass to below ground organs, as compared to plants growing at low elevations,

95   where temperatures are higher and soil richer in nutrients (Bloom, Chapin & Mooney, 1985;

96   McConnaughay & Coleman, 1999). The resource-retentive or the stress-tolerant life strategy

97   demonstrated by increased below ground allocation, particularly in storage organs (Grime,

98   2001), can increase the chance of plants survival and population persistence in abiotically

99   stressful and unpredictable environments of high elevations, by provisioning plants with stored

100   reserves in particularly severe years when the amount of assimilated carbohydrates is not

101   sufficient for year-to-year survival (Chapin, Schulze & Mooney, 1990; von Arx, Edwards &

102   Dietz, 2006; Guo et al., 2012). Conversely, the opposite pattern of allocation is expected for

103   plants growing in denser and taller vegetation at low elevations, where climatic conditions are

104   milder but competition for resources, particularly for light, is stronger (Callaway et al., 2002;

105   Read et al., 2014). In such environment selection should promote more the resource-acquisitive

106   strategy manifested in increased plant growth that results from higher allocation in aboveground

107   parts, namely, stem and leaves (Grime, 2001). Other important life-history adjustment in plants

108   growing along elevation gradients is associated with variations in flower size and floral

109   allocation (Arroyo, Pacheco & Aguilera, 2013; Dai et al., 2017; Basnett, Ganesan & Devy,

110   2019). In entomophilous species, increasing flower size can be correlated with higher

111   reproductive success. It is expected, that at high elevations where pollinators are scarce and

112   competition for pollinator services increase (Malo & Baonza, 2002; Maad, Armbruster &

113   Fenster, 2013; Zhao & Wang, 2015; Arroyo, Pacheco & Dudley, 2017) plants produce larger

114   flowers because they are preferred by insect pollinators (Malo & Baonza, 2002; Maad,

115   Armbruster & Fenster, 2013; Totland, 2001; Totland, 2004). And this, in turn, increases the

116   chances of pollen deposition and producing viable seeds, and finally, achieving reproductive

117   success (Arroyo, Primack & Armesto, 1982; Ohara & Higashi, 1994; Bingham & Orthner,

118   1998). However, other selective pressures can promote opposite adjustment in flower size across

119   elevations. In fact, it has been suggested that producing smaller flowers as found in some species

120   can be advantageous in resource limited and climatically severe environment of high elevations

121   because smaller flowers have lower cost of their structural development and physiological

122   maintenance (Herrera, 2005). Consequently, different selective pressures, abiotic and biotic, can

123   influence plant phenotypes along elevation gradients and studying variations in plant

124 morphology and dry mass allocation is important to understand environmental adaptations of

125 plants (Takahashi & Matsuki, 2017). Accordingly, common trends in plant intraspecific

126 variations with increasing elevation include, among others, reduced overall size, height and

127 biomass (Alexander et al., 2009; Zhu et al., 2010; Maad, Armbruster & Fenster, 2013; He et al.,

128 2017; Paudel et al., 2019; Kiełtyk, 2021a; Kiełtyk, 2021b), reduced leaf size (Byars, Papst &

129 Hoffmann, 2007; Kiełtyk, 2018; Miliković et al., 2019; Paudel et al., 2019) and leaf mass

130 (Kiełtyk, 2021a; Kiełtyk, 2021b), lower number of flowers (Kelly, 1998; Baret et al., 2004;

131 Šťastná, Klimešová & Doležal, 2012; Maad, Armbruster & Fenster, 2013; Gabel, Sattler &

132 Reisch, 2017), increased flower size and mass (Kudo & Molau, 1999; Malo & Baonza, 2002;

133 Herrera, 2005; Maad, Armbruster & Fenster, 2013; Kiełtyk, 2021b), and increased seed mass

134 (Kudo & Molau, 1999; Alexander et al., 2009; Wu et al., 2011; Qi et al., 2015). However, the

135 opposite patterns with decreases in flower size (Totland, 2001; Zhao & Wang, 2015; Hattori et

136 al., 2016) and seed mass (Totland, 2004; Wirth et al., 2010; Gabel, Sattler & Reisch, 2017) with

137 an increase in elevation have also been reported for some species. Furthermore, in the Asteraceae

138 family a shift in floral allocation patterns was observed in some species despite steady gross dry

139 mass investment in flowers across elevation gradients. Namely, plants growing at high elevations

140 had smaller numbers of larger flower heads with larger numbers of flowers as compared to low-

141 elevation plants that had larger numbers but smaller flower heads with smaller numbers of

142 flowers (Takahashi & Matsuki, 2017; Kiełtyk, 2021b). Overall, the variety of elevational

143 adjustments reported for different plant species suggests, that there are no general patterns of

144 plant intraspecific elevational variations, but plant phenotypic responses to elevation may be

145 species specific and context dependent (e.g. Olejniczak et al., 2018).

146   Patterns of intraspecific phenotypic variation in plants growing along elevation gradients in

147 mountains are drawing increased research interest (e.g. Halbritter et al., 2018; Olejniczak et al.,

148 2018; Basnett, Ganesan & Devy, 2019; Paudel et al., 2019; Cruz-Maldonado et al., 2021; Rathee

149 et al., 2021; Rixen et al., 2022; Ahmad et al., 2023; Khatri et al., 2023; Spitzer et al., 2023).

150 Studying variations in morphology and biomass allocation among plant organs across elevations

151 provides relevant insights for understanding plant adaptive responses to biotic and abiotic

152 variations along steep environmental gradients. Moreover, knowledge on life-history adjustments

153 in steep climatic gradients as found along mountain slopes contributes to our understanding of

154 how plants may cope with present and predicted future climate changes (e.g. Frei et al., 2014;

155 Pfennigwerth, Bailey & Schweitzer, 2017; Blume-Werry et al., 2018; Midolo et al., 2018; Rixen

156 et al., 2022).

157   The current study concerns variation in the alpine herb *Soldanella carpatica* Vierh.

158 (Primulaceae) across a 1,480 m elevation gradient in the Tatra Mts. The large elevation range of

159 the species in this region provides a good opportunity to look at the effects of elevation on plant

160 morphological variation and biomass allocation pattern. The aim of this study was to reveal the

161 overall effects of elevation on variations in set of fitness-related vegetative and reproductive

162 traits of *S. carpatica*. In particular, the following questions were addressed: (1) does plant size

163 expressed by plant dry mass and leaf size decrease with increasing elevation?, (2) do total flower

164 mass as well as individual flower mass change with elevation?, (3) does increasing elevation is

165 positively correlated with the root : shoot ratio?

166

Material & Methods

Study species

169 *S. carpatica* is a herbaceous perennial plant endemic to the West Carpathians. The scape of *S.*

170 *carpatica* is erect, (3)5–15(20) cm tall, not leafy, with (1)2–5- violet insect-pollinated flowers

171 gathered at the top inflorescence (Pawłowska, 1972). Suborbicular leaves are gathered in a basal

172 rosette (Fig. 1). Leaf blade is 8-50 mm wide, dark green, usually violet beneath with basal sinus

173 narrow and shallow (Pawłowska, 1963). The species blooms from April to September and fruits

174 from May to October (Zhang & Kadereit, 2002). *S. carpatica* is common in the Tatra Mountains

175 growing on various habitats along wide elevation gradient from lower montane forest floor

176 vegetation to scattered vegetation on rocky substrate in high elevations of subnival belt

177 (Pawłowska, 1963).

178

Study area

180 The research was conducted along the 890–2,370 m a.s.l. elevation gradient in the Tatra

181 Mountains, southern Poland, within the protected area of the Tatra National Park (Fig. 2).

182 Permission for the study was obtained from the Tatra National Park (Bot/380 DBN.503/28/18).

183 The Tatra Mountains, located in the centre of the Western Carpathians, constitute the highest

184 mountain massif within the Carpathian Range. The general elevational range in the Polish Tatras

185 extends from ca. 900 m to 2,500 m a.s.l. and crosses five climatic-vegetation belts. These are:

186   lower montane forest (up to 1,200 m a.s.l.), occupied by beech-fir forest, with temperate cool

187   climate (mean annual air temperature - MAT from +4 to +6 °C); upper montane forest (1,200–

188   1,550 m a.s.l.), dominated by spruce forest, with cool climate (MAT from +2 to +4 °C); dwarf

189   pine (=subalpine) belt (1,550–1,800 m a.s.l.), with very cool climate (MAT from 0 to +2 °C);

190   alpine belt (1,800–2,250 m a.s.l.), occupied by high-mountain grasslands, with temperate cold

191   climate (MAT from 0 °C to –2); subnival belt (above 2,250 m a.s.l.), characterized by scattered

192   poor vegetation, with cold climate (MAT from –2 to –4 °C) (Mirek, 1996).

193

194   Field sampling and traits measurements

195   The flowering plants of *S. carpatica* were collected in 2018, from the end of April to the

196   beginning of July, from 40 sites distributed from 890 m a.s.l. to 2,370 m a.s.l. (Table 1). The

197   elevation at each site was determined in the field using a GPS receiver with built-in barometric

198   altimeter (Garmin GPS MAP 76s, Olathe, USA). An attempt was made to sample entire

199   elevational range of the species in the area and ensure that the sampled sites were distributed

200   approximately evenly along the species elevational range. At each site, 9-10 plants in blossom

201   peak with single stalk were sampled and carefully excavated with roots. To ensure that the

202   sampled plants were separate genets, the minimal distance between the sampled plants was 2 m.

203   Sampled individuals were well-developed and did not show restriction in growth and

204   reproductive function as well as symptoms of fungal infection nor herbivory damages. Roots

205   were roughly cleaned of soil and plants were preserved as dry material for laboratory analyses.

206   Scape height was assessed as a distance between the plant base just below rosette leaves and the

207   top of inflorescence; during the measurement the scape was straightened. Leaf blade diameter,

208   the trait that assess size of photosynthetically active leaf part, was averaged for two largest plant

209   leaves; on each leaf blade width was measured in two perpendicular directions and averaged per

210   plant. In the next step plants were separated into four fractions, namely roots, scape, leaves and

211   flowers, and final cleaning of roots was performed over a 0.6 mm mesh sieve under running

212   water. Next, all the fractions were dried for 48 h at 80 °C in a laboratory drying oven with

213   natural air circulation (Pol-Eko-Aparatura SLN 240, Wodzisław Śląski, Poland) to obtain the dry

214   matter content (Pérez-Harguindeguy et al., 2013) by weighing on an analytical balance (Radwag

215   AS 60/220.X2 PLUS, Radom, Poland). All weight measurements were carried out immediately

216   after the samples were removed from the oven.

217

Statistical analyses

219 All analyses were conducted in the statistical programming environment R version R-4.1.1 (R

220 Development Core Team, 2021). Elevational variations in traits of *S. carpatica* (Table 2) were

221 analysed with the linear mixed-effect models (Field, Miles & Field, 2013) using the *lmer()*

222 function in the *lme4* package (Bates et al., 2015). In these analyses, elevation was used as a

223 continuous fixed effect and sample site was set as a random model component. Because

224 preliminary data analysis revealed that above 2,000 m a.s.l. there were considerable rapid

225 changes in values of some traits that could heavily influence the overall elevational variations,

226 analyses were run for two elevation ranges independently; the first model for each trait was

227 constructed for the full investigated elevation gradient 890–2,370 m a.s.l. (mod_{2370}), whereas the

228 second model, constructed for elevation gradient 890–1,980 m a.s.l. (mod_{1980}), did not contain

229 plants from the highest sites above 2,000 m a.s.l. To account for non-straight-line responses of

230 traits to elevation two mixed-effect models were constructed and evaluated for the both

231 examined elevation ranges. The first model included elevation as a linear fixed effects ($Y=$

232 $a+b_1 \times (elevation)$, where a denotes an intercept and b_1 regression coefficient) while the second

233 model included elevation and elevation with quadratic term ($Y=$

234 $a+b_1 \times (elevation)+b_2 \times (elevation)^2$, where a denotes an intercept and b_1 and b_2 denote regression

235 coefficients). Comparison of these models allowed to determine whether plant traits had a linear

236 or nonlinear relationship with elevation. Fits of these two models to the data were evaluated

237 based on a likelihood ratio test and *Chi-Squared* statistic where a significant $P_{model\ selection}$ value at

238 0.05 significance level (Table 3) indicated significant improvement in the straight-line model

239 upon addition of the quadratic term for elevation (Dalgaard, 2008). Comparisons of model fit

240 were carried out using the *anova()* function from the base R installation.

241

Results

Elevational variation in morphological traits

244 Models of traits elevational variations fitted to the 890–1,980 m a.s.l. and the 890–2,370 m a.s.l.

245 ranges (Table 3) differed considerably between these both ranges for many morphological traits

246 indicating significant change in *S. carpatica* morphology occurring at the highest sites located at

247 elevations 2,085–2,370 m a.s.l (Fig. 3). In the 890–1,980 m a.s.l. range aboveground plant mass

248   ($P_{1980} = 0.0436$, Fig. 3A), total leaf mass ($P_{1980} = 0.0201$, Fig. 3C), scape height ($P_{1980} = 0.0144$,

249   Fig. 3G) and leaf blade diameter ($P_{1980} = 0.0001$, Fig. 3H) decreased with an increase in

250   elevation, whereas root mass ($P_{1980} = 0.8583$, Fig. 3B), scape mass ($P_{1980} = 0.8536$, Fig. 3D),

251   total flower mass ($P_{1980} = 0.9112$, Fig. 3E) and individual flower mass ($P_{1980} = 0.4336$, Fig. 3F)

252   did not vary across elevations. However, in the 890–2,370 m a.s.l. range all the traits had

253   significant relationship with elevation (Table 3). Aboveground plant mass ($P_{2370} = 0.0067$, Fig.

254   3A), root mass ($P_{2370} = 0.0270$, Fig. 3B), total leaf mass ($P_{2370} = 0.0275$, Fig. 3C), scape mass

255   ($P_{2370} = 0.0009$, Fig. 3D), total flower mass ($P_{2370} < 0.0001$, Fig. 3E) and individual flower mass

256   ($P_{2370} = 0.0001$, Fig. 3F) did not have elevational trend or slightly decreased from 890 m to ca.

257   2,000 m a.s.l., whereas above 2,000 m a.s.l. values of these traits decreased very considerably.

258   Scape height ($P_{2370} < 0.0001$, Fig. 3G) decreased in a straight-line manner with an increase in

259   elevation in the 890–2,370 m range, whereas leaf blade diameter ($P_{2370} = 0.0059$, Fig. 3H)

260   decreased slightly from 890 m to ca. 2,000 m a.s.l., and above 2,000 m a.s.l. values of this trait

261   were reduced more considerably.

262   Generally, all traits reduced considerably their values with an increase in elevation from

263   890 m a.s.l. to 2,370 m a.s.l. (Table 4). In this range aboveground plant mass decreased with an

264   increase in elevation by 77.5%, total leaf mass decreased by 78.9%, scape mass decreased by

265   73.6%, total flower mass decreased by 68.5%, individual flower mass decreased by 46.3%, scape

266   height decreased by 37.2% and leaf blade diameter decreased by 56.4% (Table 4).

267   The reductions in size of plant organs occurred almost merely at the highest elevations

268   above 2,000 m a.s.l., at sites located at elevations 2,085–2370 m a.s.l., which constitutes ca. 20

269   % uppermost portion of the investigated elevation gradient. From 890 m to 1,980 m a.s.l. total

270   leaf mass decreased by 2.7%, leaf blade diameter decreased by 2.3%, aboveground plant mass

271   decreased by 2.1% and plant height decreased by 1.8% per every 100 m increase in elevation.

272   Percent changes in other traits in this elevation range were small and models used to their

273   calculations were statistically not significant (Table 4). Contrary, from 1,980 m to 2,370 m a.s.l.

274   rates of changes in all traits were very considerable; aboveground plant mass decreased by

275   12.1%, root mass decreased by 11.3%, total leaf mass decreased by 11.2%, scape mass decreased

276   by 16.2%, total flower mass decreased by 15.0%, individual flower mass decreased by 9.1%,

277   scape height decreased by 3.6% and leaf blade diameter decreased by 7.2% per every 100 m

278   increase in elevation (Table 4).

279

280 **Elevational variation in dry mass allocation traits**

281 Overall, *S. carpatica* plants allocated on average 39.8% of their total dry mass to root, 45.2% to

282 leaves, 10.4% to scape, and 4.7% to flowers. Of the aboveground plant mass, 74.7% was

283 allocated to leaves, 17.3% to scape and 8.0% to flowers.

284   All the dry mass partitioning traits were significantly fitted to elevation by straight-line

285 models (Table 3, Fig. 4). Models constructed for both elevation ranges, the 890–1,980 m and the

286 890–2,370 m a.s.l. were almost identical for these traits. The root:shoot ratio increased with

287 increasing elevation (P_{1980} = 0.0022, P_{2370} < 0.0001, Fig. 4A), whereas leaf mass fraction

288 decreased with an increase in elevation (P_{1980} = 0.0001, P_{2370} < 0.0001, Fig. 4B). Moreover,

289 flower aboveground mass fraction increased with an increase in elevation (P_{1980} = 0.0029, P_{2370} =

290 0.0009, Fig. 4C).

291   Within the entire elevation range from 890 m to 2,370 m a.s.l. the root:shoot ratio

292 increased by 61.0%, leaf mass fraction decreased by 24.3%, and flower aboveground mass

293 fraction increased by 42.8% (Table 4). The rates of these traits changes per 100 m increase in

294 elevation had similar values in the 890–1,980 m a.s.l. and 1,980–2,370 m a.s.l. elevational

295 ranges. In the 890–1,980 m a.s.l. range the root:shoot ratio increased by 3.4%, leaf mass fraction

296 decreased by 1.7% and flower aboveground mass fraction increased by 3.3% per 100 m increase

297 in elevation. Concurrently, in the 1,980–2,370 m a.s.l. range the root:shoot ratio increased by

298 5.3%, leaf mass fraction decreased by 1.5% and flower aboveground mass fraction increased by

299 2.2% per 100 m increase in elevation (Table 4).

300

301 **Discussion**

302 *Soldanella carpatica* varied across the elevation gradient adjusting its morphological and dry

303 mass traits to environmental factors correlated with elevation. Along most part of the studied

304 elevation gradient, from the base at 890 m a.s.l. to 2,000 m a.s.l., total dry mass of photosynthetic

305 tissue, leaf size and scape height decreased steadily in a clinal manner with an increase in

306 elevation, whereas dry mass investment in roots and flowers as well as individual flower mass

307 did not vary with elevation. However, at the highest elevations considerable changes occurred in

308 most of the traits leading to abrupt plant miniaturization. Accordingly, plants growing at

309 elevations above 2,000 m a.s.l. were distinctly smaller in size, had lower aboveground dry mass,

310   reduced leaf size and mass, reduced root, scape, total as well as individual flower mass, as

311   compared to plants from sites at elevations below 2,000 m a.s.l.

312

313   **Elevational variation in aboveground vegetative organs**

314   Maintaining relatively unchanged phenotype by *S. carpatica* across a wide 1,100-m elevation

315   range from 890 m to 2,000 m a.s.l. that corresponds approximately to ca. 6 K decrease in mean

316   annual temperature with an increase in elevation suggests that this species is particularly well

317   adapted to live across wide elevation gradients. Such specialised adaptations were found recently

318   in a closely related alpine species *Soldanella pusilla* that grows in the European Alps. *S. pusilla*

319   is a species extremely adapted to tissue formation and growth under conditions of very low

320   temperatures (Körner et al., 2019). That species resumes growth in mid-winter being at the time

321   covered by a 2-3 m thick snowpack and develops its entire flowering shoot under snow at 0 °C.

322   Moreover, *S. pusilla* has an enormous carbohydrate reserves, mainly stored in below ground

323   tissue, that would support basic metabolism for at least two entire years under snow (Körner et

324   al., 2019). Although no similar studies are available for *S. carpatica*, it can be assumed that this

325   species due to its phylogenetic and ecological relatedness to *S. pusilla* (Zhang & Kadereit, 2002)

326   has similar physio-ecological characteristics and its growth is not significantly limited by low

327   temperatures across the studied elevation gradient. Therefore, reductions in leaf size and total

328   leaf mass in *S. carpatica* as observed from low to high elevations can represent rather adaptation

329   to environmental conditions that change across elevations rather than restriction in growth

330   caused by harsh environment of high elevations. Accordingly, reduction of alpine plant size with

331   an increase in elevation is a well-known elevational trend (e.g. Alexander et al., 2009; Zhu et al.,

332   2010; Maad, Armbruster & Fenster, 2013; He et al., 2017; Paudel et al., 2019; Kiełtyk, 2021a;

333   Kiełtyk, 2021b) that contrasts with high metabolic capacity of tissues, especially leaves (Körner,

334   2021). The fact that root, stem and flowers of *S. carpatica* were unresponsive to the 1,100-m

335   elevation gradient from 890 m to ca. 2,000 m a.s.l. despite continuous reduction in dry mass of

336   photosynthetically active tissue could be explained by increased photosynthetic leaf tissue

337   efficiency that guarantees adequate assimilates supply for producing and maintaining unchanged

338   rest of plant organs in harsher climatic conditions associated with increasing elevation. It could

339   be therefore assumed, that because reduced photosynthetic organ size and mass at higher

340   elevations fully satisfy plant demand for products of photosynthesis and plant produces and

341   stores enough assimilates for growth, reproduction and year-to-year survival due to high

342   metabolic efficiency of leaf tissue, there is no advantage in allocation in high elevations as much

343   of dry mass to leaves as in low elevations, where inter-specific competition for light is stronger

344   (Weppler & Stöcklin, 2005; Callaway et al., 2002; Read et al., 2014) and where increased

345   investment in photosynthetically active tissue may be essential for capture and utilization of

346   sufficient light quantity. Moreover, the reduction in plant aboveground size with an increase in

347   elevation, that in *S. carpatica* is caused by reduction in leaf size and mass, can be advantageous

348   adaptation to decreased nutrients availability in soils (Sveinbjörnsson et al., 1995) and climatic

349   constraints at high elevations because smaller plants have lower resource requirements, as

350   proposed by the 'resource-cost compromise' hypothesis (Herrera, 2005; Zhao & Wang, 2015).

351   Additionally, the smaller are plants with smaller leaf rosettes growing close to the ground the

352   more they decouple their climate from the ambient due to reduction in surface area that is

353   exposed to cold air (Körner, 2021). Being closely attached to the ground also increases plant

354   resistance to environmental factors such as strong winds as well as to freezing events due to heat

355   accumulation by the leaf canopy close the ground (Fabbro & Körner, 2004; Cruz-Maldonado et

356   al., 2021). Therefore, decreasing plant aboveground size with an increase in elevation can

357   represent adaptive adjustment allowing local populations to efficiently use limited resources

358   under increasingly less favourable climatic conditions associated with increasing elevation.

359

360   **Elevational variation in reproductive organs**

361   Dry mass investment in flowers as well as flower size expressed by mean flower mass were not

362   affected by elevation along a 1,100-m elevation gradient ranging from 890 m a.s.l. to 2,000 m

363   a.s.l. Despite increasingly more growth limiting conditions due to reduced temperature and

364   resource limitation with an increase in elevation, *S. carpatica* retained steady dry mass

365   investment in flowers across the wide elevation range. Similar pattern of elevational variation in

366   flower mass was found in *Bellidiastum michelii*, where flower head mass, total flower mass as

367   well as individual flower mass did not change considerably along ca. 900-m elevation gradient

368   and decreases in these traits were visible only at the highest elevations of the species range

369   (Kiełtyk, 2021a). Furthermore, unchanged floral mass investment across the wide 950-m

370   elevation gradient was found in total mass of *Senecio subalpinus* flower heads, however, at the

371   level of an individual flower head both total tubular flower mass as well as total ligulate flower

372   mass increased toward high elevations (Kiełtyk, 2021b). Maintaining unchanged total mass of *S.*

373   *carpatica* flowers along with reduction in total leaf mass with an increase in elevation in the

374   890–2,000 m elevation range resulted in the increase in flower aboveground mass fraction.

375   Meanwhile, the increased portion of dry mass allocated to flowers may suggest that reproductive

376   investment is increasingly important strategy for local *S. carpatica* populations persistence with

377   an increase in elevation.

378   The plant height, a trait being related with species competitiveness for light in species with

379   leafy stems, that is often used as a proxy for plant size, was commonly found to decrease with an

380   increase in elevation in studies on intraspecific plant variations (e.g. He et al., 2017; Paudel et al.,

381   2019; Kiełtyk, 2021b). However, in case of *S. carpatica* plant height as expressed by the scape

382   height is not related to plant size nor competitive ability for light because the species has all its

383   leaves gathered in basal rosette and the only function of scape is to give support for flowers and

384   eventually fruits clustered at the top of scape. Thus, height of scape in *S. carpatica* defines

385   elevation on which flowers are positioned above the ground, and functionally this trait is related

386   to reproductive process by exposing flowers above the ground to attract pollinators and support

387   fruits when dispersing seeds. With an increase in elevation from 890 m to 2,000 m a.s.l. height of

388   *S. carpatica* scape decreased steadily, whereas amount of dry mass allocated to scape remained

389   unchanged, what resulted in producing thicker and tougher scapes with flowers elevated lower

390   above the ground toward higher elevations. Because height of leaf canopy of surrounding

391   vegetation generally also decrease with an increase in elevation (Leuschner & Ellenberg, 2017)

392   reduced scape height prevents flowers to protrude too high into well-stirred cold air above the

393   calm aerodynamic boundary layer created by leaf canopy (Dietrich & Körner, 2014). It has been

394   shown in the alpine environment that the closer the ground the higher air temperatures are

395   whereas wind speed rises logarithmically with distance from the ground (Körner, 2021).

396   Therefore, reducing the scape height toward higher elevations follows the general vegetation

397   trend of reduced foliage layer height and can enhance decoupling flowers from the colder free

398   atmosphere. Meanwhile, it has been shown that warmer flowers can more efficiently attract

399   pollinators as pollinators besides flower colour are also sensitive on flower temperature (Creux et

400   al., 2021), in colder climates preferring warmer flowers (Norgate et al., 2010). Additionally,

401   warmer flowers have thermal benefits during maturation of sexual organs, pollen germination

402   and pollen tube growth (Dietrich & Körner, 2014) and it has been found that experimentally

403 increased temperature and sheltering from wind of alpine plant *Ranunculus acris* resulted in

404 increased seed production (Totland & Eide, 1999). Thus, decreasing scape height in *S. carpatica*

405 with an increase in elevation can be a selective advantage of developing flowers in milder micro-

406 climate closer to the ground as maintaining higher floral temperatures in cool alpine environment

407 is often critical for the successful reproduction of high-mountain plants (Dietrich & Körner,

408 2014).

409

410 **Elevational variation in root mass**

411 Elevational variation in root mass of *S. carpatica* was analogous to that in flower mass as there

412 was no significant change in root mass in a wide range of elevations between 890–2,000 m a.s.l.

413 whereas above 2,000 m a.s.l. this trait decreased significantly. Steady root mass investment

414 across ca. 1,100-m elevation range accompanied by decrease in total leaf mass with increasing

415 elevation resulted in increasing the root:shoot ratio from low to high elevations. Because plants

416 can adjust their morphological traits such as root length, density, branching as well as proportion

417 of fine to coarse roots (Weemstra et al., 2021) to micro-mosaics of belowground conditions such

418 as water and nutrient availability or soil rockiness, the increased *S. carpatica* belowground mass

419 fraction toward high elevations may indicate an increased importance of resource acquisition

420 and/or assimilates storage in resource limited and climatically more growth restricting and

421 unpredictable environmental conditions of high elevations. Moreover, the decreased availability

422 of nutrients may result not only from decreasing soil nutrients content toward high elevations

423 (Körner, 2021) but also from increased belowground competition between plants for limited

424 resources. It has been suggested that in abiotically severe environments of high elevations

425 competition strength decreases as a result of reduced number of species that withstand

426 unfavourable conditions as well as due to restrictions in resource acquisition by plants caused by

427 severe physical conditions (Callaway, 1998). This relation may characterize aboveground plant

428 competition for space and light as height of leaf canopy decrease and vegetation becomes less

429 dense with increasing elevation (Nagy & Grabherr, 2009). However, because soil nutrients

430 content and soil depth generally decrease with an increase in elevation (Sveinbjörnsson et al.,

431 1995; Körner, 2021) nutrients availability for plants also decreases what can result in increasing

432 belowground resource competition. Thus, dry mass investment in roots can be increasingly

433 important for resource foraging with an increase in elevation as evidenced by unreduced *S.*

434 *carpatica* root mass from 890 m to 2,000 m a.s.l. despite accompanying continuous reduction in

435 aboveground plant mass. Furthermore, increasing the root:shoot ratio with an increase in

436 elevation supports the hypothesis that in colder and harsher environments plants tend to allocate

437 greater portion of their mass in belowground organs (Bloom, Chapin & Mooney, 1985;

438 McConnaughay & Coleman, 1999). Increased root mass fraction may be advantageous

439 adjustment in *S. carpatica* to acquire and/or store enough resources for growth, survival and

440 completing its life history cycle in high elevation environments.

441

442 **Plant miniaturization at the highest elevations**

443 The most pronounced pattern of elevational variation in *S. carpatica* is abrupt plant

444 miniaturization on sites located in the 20% uppermost part of the studied elevation gradient.

445 Rapid reduction in overall plant size may suggests that this species encounters considerably more

446 growth limiting conditions above 2,000 m a.s.l. as compared to lower elevations. Similar pattern

447 of rapid change in plant size across elevations was found in alpine taxon of the *Solidago*

448 *virgaurea* L. complex, where plants growing at the highest elevations had distinctly lower plant

449 height and rosette diameter (Takahashi & Matsuki, 2017) as well as lower number of flower

450 heads (Sakurai & Takahashi, 2017) as compared to plants from lower elevations. The reduction

451 in *S. carpatica* size cannot be explained merely by plant response, by means of phenotypic

452 plasticity and/or genetic adaptation, to limiting climatic conditions of high elevations because

453 climate factors change gradually with an increase in altitude (Nagy & Grabherr, 2009), as

454 exemplified by mean annual temperature decrease by 0.55 K per every 100 m increase in

455 elevation in mountains of temperate regions (Körner, 2021). Therefore, it could be other than

456 climatic factors alone that trigger off morphological changes in *S. carpatica* at the highest

457 elevations of the studied gradient. It is likely that the plant miniaturization above 2,000 m a.s.l.

458 was related to changes in orography, i.e. increased steepness and rockiness of mountain slopes

459 toward high mountain tops. The five highest sites on which size of *S. carpatica* was considerably

460 reduced were located at elevations 2,085–2,370 m a.s.l. on steep rocks of Czarny

461 Mięguszowiecki Wierch peak (2,405 m a.s.l.). The environment of such high peaks is

462 characterized by harsh climatic conditions and lack of accumulated snow cover in winter due to

463 frequent strong winds and high slopes inclination. Thus, *S. carpatica* growing on rocky initial

464 soils at the highest elevations of the studied gradient was exposed to particularly unfavourable

465   conditions caused by strong winds and lack of protective snowpack in winter, that was found to

466   be important for development and growth of closely related species *S. pusilla* in the European

467   Alps (Körner et al., 2019). Miniaturization of *S. carpatica* at the highest elevations could be,

468   therefore, a plastic or/and genetically based response to abrupt deterioration in growing

469   conditions caused by simultaneous interactions of climate, soil and orographic conditions.

470   It is important to note that environmental conditions that can cause abrupt changes in

471   morphology of alpine plants may also hinder predictions on plants upward migrations in

472   mountains (Frei, Bodin & Walther, 2010; Wipf et al., 2013; Steinbauer et al., 2018) as well as

473   plant phenotypic responses to climate warming if local orographic conditions or topographic

474   microhabitat diversity are not considered (Kulonen et al., 2018). It is likely that increased

475   rockiness and steepness of slopes and walls at high elevations of young mountains with glacial

476   landforms shaped by geomorphic processes of physical weathering and denudation (Kotarba,

477   1996) coupled with lack of snowpack during dormant season, that causes freezing stress (Körner,

478   2021), increased frequency of strong winds, shallow initial soils and increased patchiness of

479   fragmented vegetation (Leuschner & Ellenberg, 2017) may not constitute suitable habitats for

480   plant species from lower elevations migrating upward mountain slopes despite the increase in

481   mean annual temperature as predicted by future climate warming scenarios (Engler et al., 2011;

482   Mountain Research Initiative EDW Working Group, 2015). Moreover, diversity of microhabitats

483   in alpine landscapes creates mosaic of micro-environmental and life conditions, with range of

484   thermal niches that can differ in mean temperature by as much as 8 K at the same elevation, and

485   this exceeds around twice the worst climate warming scenario for the same region, as recently

486   shown in the European Alps by Körner and Hiltbrunner (2021). Furthermore, the difference in

487   temperature by 8 K corresponds to ca. 1,450 m difference in elevation, what equals

488   approximately to the differences in mean air temperature across the elevation range investigated

489   in the present study. Such diversity of thermal conditions at given elevation may ensure

490   availability of suitable conditions for cold adapted plants under warmed climate conditions.

491   This study revealed pattern of elevational variation in *S. carpatica* caused by

492   environmental factors correlated with elevation. However, to identify drivers of elevational

493   changes in plants analyses including set of environmental factors would be helpful. Moreover, to

494   disentangle the contributions of plastic, environmentally induced responses, and of genetic

495   differences among locally adapted populations, to morphological variation across elevation

496 gradients studies involving reciprocal plant transplantations to different elevations are required

497 (eg. Scheepens, Frei & Stöcklin, 2010; Hamann et al., 2016).

498

Conclusions

500 *Soldanella carpatica* overall size, leaf size and mass, and scape height decreased gradually with

501 an increase in elevation along most part of the elevation gradient, whereas in the uppermost part

502 of the gradient plant size decreased rapidly causing abrupt plant miniaturization. Despite the

503 plant miniaturization at the highest elevations, biomass partitioning traits changed gradually

504 across the entire species elevation range, namely, the leaf mass fraction decreased continuously,

505 whereas the flower mass fraction and the root:shoot ratio increased steadily from the lowest to

506 the highest elevations. Thus, the abrupt changes in *S. carpatica* morphology on the highest

507 elevation sites suggest that overall plant size as expressed by leaf size, scape height and plant dry

508 mass traits are strongly influenced by local environmental conditions to which they respond

509 considerably, whereas steady trajectory of dry mass partitioning changes across entire elevation

510 gradient suggests that mass partitioning and adjustive changes in organs mass fractions in

511 response to environmental conditions represent a stable evolutionary solution of the species.

512 While the continuous changes in plant morphology on most part of the gradient are likely to

513 represent plant adaptation or/and plastic phenotypic responses to gradual changes that occur in

514 climate conditions across elevations, the rapid plant miniaturization in the highest elevations may

515 reflect changes in orographic conditions such as increased rockiness and steepness of mountain

516 slopes at the highest elevations. On such steep, rocky slopes, there are no steady protective

517 snowpack during winter and plants are exposed to particularly low temperatures causing freezing

518 stress. Therefore, when predicting plants phenotypic responses across elevations in mountains or

519 possibility of upward plant species migrations caused by climate warming it is important to

520 consider local dominant orographic as well as topographic conditions, e.g. slope inclination,

521 exposition, rockiness, terrain relief, because they can substantially modify the climate conditions

522 experienced by plants at given elevation (e.g. Graae et al., 2018).

523

Acknowledgements

525 The support of collecting the material in the field by Wiesława Kiełtyk and Anna Delimat is

526 highly appreciated.

527

References

529

Ahmad M, Rosbakh S, Bucher SF, Sharma P, Rathee S, Uniyal SK, Batish DR, Singh HP. 2023. The role of floral traits in community assembly processes at high elevations in the Himalayas. *Journal of Ecology* **111**:1107–1119 DOI 10.1111/1365-2745.14083.

Alexander JM, Edwards PJ, Poll M, Parks CG, Dietz H. 2009. Establishment of parallel clines in traits of native and introduced forbs. *Ecology* **90**:612–622 DOI 10.1890/08-0453.1.

Arroyo MTK, Pacheco DA, Aguilera P. 2013. Floral allocation at different altitudes in highly autogamous alpine *Chaetanthera euphrasioides* (Asteraceae) in the central Chilean Andes. *Alpine Botany* **123**:7–12 DOI 10.1007/s00035-012-0109-9.

Arroyo MTK, Pacheco DA, Dudley LS. 2017. Functional role of long-lived flowers in preventing pollen limitation in a high elevation outcrossing species. *AoB Plants* **9**:plx050 DOI 10.1093/aobpla/plx050.

Arroyo MTK, Primack R, Armesto J. 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany* **69**:82–97 DOI 10.2307/2442833.

Baret S, Maurice S, Le Bourgeois T, Strasberg D. 2004. Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* Poiret (Rosaceae), on Réunion island. *Plant Ecology* **172**:265–273 DOI 10.1023/B:VEGE.0000026345.67250.d2.

Basnett S, Ganesan R, Devy SM. 2019. Floral traits determine pollinator visitation in *Rhododendron* species across an elevation gradient in the Sikkim Himalaya. *Alpine Botany* **129**:81–94 DOI 10.1007/s00035-019-00225-3.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software* **67**:1–48 DOI 10.18637/jss.v067.i01.

Billings WD. 1974. Arctic and alpine vegetation: plant adaptations to cold summer climates. In: Ives JD, Barry RG, eds. *Arctic and alpine environments*. London: Methuen, 403–443.

Bingham RA, Orthner AR. 1998. Efficient pollination of alpine plants. *Nature* **391**:238–239 DOI 10.1038/34564.

Bloom AJ, Chapin III FS, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics* **16**:363–392 DOI 10.1146/annurev.es.16.110185.002051.

Blume-Werry G, Lindén E, Andresen L, Classen AT, Sanders NJ, von Oppen J, Sundqvist MK. 2018. Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra. *Journal of Vegetation Science* **29**:226–235 DOI 10.1111/jvs.12605.

Byars SG, Papst W, Hoffmann AA. 2007. Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution* **61**:2925–2941 DOI 10.1111/j.1558-5646.2007.00248.x.

Callaway R. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* **82**:561–573 DOI 10.2307/3546376.

Callaway R, Brooker R, Choler P, Kikvidze Z, Lortie ChJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* **417**:844–848 DOI 10.1038/nature00812.

Chapin III FS, Schulze E, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**:423–447 DOI 10.1146/annurev.es.21.110190.002231.

Creux NM, Brown EA, Garner AG, Saeed S, Scher CL, Holalu SV, Yang D, Maloof JN, Blackman BK, Harmer SL. 2021. Flower orientation influences floral temperature, pollinator visits and plant fitness. *New Phytologist* **232**:868–879 DOI 10.1111/nph.17627.

Cruz-Maldonado N, Weemstra M, Jiménez L, Roumet C, Angeles G, Barois I, de los Santos M, Morales-Martines MA, Palestina RA, Rey H et al. 2021. Aboveground-trait variations in 11 (sub)alpine plants along a 1000-m elevation gradient in tropical Mexico. *Alpine Botany* **131**, 187–200 DOI 10.1007/s00035-021-00260-z.

Dai WK, Amboka GM, Kadiori EL, Wang QF, Yang CF. 2017. Phenotypic plasticity of floral traits and pollination adaptation in an alpine plant *Pedicularis siphonantha* D. Don when transplanted from higher to lower elevation in Eastern Himalaya. *Journal of Mountain Science* **14**:1995–2002 DOI 10.1007/s11629-017-4481-1.

Dalgaard P. 2008. *Introductory Statistics with R*, 2nd ed. New York: Springer Science+Business Media DOI 10.1007/978-0-387-79054-1.

Dietrich L, Körner Ch. 2014. Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alpine Botany* **124**:27–35 DOI 10.1007/s00035-014-0123-1.

Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araújo MB, Pearman PB, Le Lay G, Piedallu C, Albert CH et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology* **17**:2330–2341 DOI 10.1111/j.1365-2486.2010.02393.x.

Fabbro T, Körner Ch. 2004. Altitudinal differences in flower traits and reproductive allocation. *Flora* **199**:70–81 DOI 10.1078/0367-2530-00128.

Field A, Miles J, Field Z. 2013. *Discovering statistics using R*. London: Sage Publications.

Frei E, Bodin J, Walther GR. 2010. Plant species' range shifts in mountainous areas—all uphill from here? *Botanica Helvetica* **120**:117–128 DOI 10.1007/s00035-010-0076-y.

600 **Frei ER, Ghazoul J, Matter Ph, Heggli M, Pluess AR. 2014.** Plant population differentiation
601   and climate change: responses of grassland species along an elevational gradient. *Global*
602   *Change Biology* **20**:441–455 DOI 10.1111/gcb.12403.

603 **Freschet GT, Violle C, Bourget MY, Scherer-Lorenzen M, Fort F. 2018.** Allocation,
604   morphology, physiology, architecture: the multiple facets of plant above- and below-
605   ground responses to resource stress. *New Phytologist* **219**:1338–1352 DOI
606   10.1111/nph.15225.

607 **Gabel ER, Sattler J, Reisch Ch. 2017.** Genetic variation and performance of the alpine plant
608   species *Dianthus callizonus* differ in two elevational zones of the Carpathians. *Alpine*
609   *Botany* **127**:65–74 DOI 10.1007/s00035-016-0177-3.

610 **Gonzalo-Turpin H, Hazard L. 2009.** Local adaptation occurs along altitudinal gradient despite
611   the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*
612   **97**:742–751 DOI 10.1111/j.1365-2745.2009.01509.x.

613 **Graae BJ, Vandvik V, Armbruster WS, Eiserhardt WL, Svenning J-Ch, Hylander K,**
614   **Ehrlén J, Speed JDM, Klanderud K, Bråthen KA et al. 2018.** Stay or go – how
615   topographic complexity influences alpine plant population and community responses to
616   climate change. *Perspectives in Plant Ecology, Evolution and Systematics* **30**:41–50 DOI
617   10.1016/j.ppees.2017.09.008.

618 **Grime JP. 2001.** *Plant strategies, vegetation processes, and ecosystem properties*. 2nd ed.
619   Chichester: John Wiley and Sons.

620 **Guo H, Weiner J, Mazer SJ, Zhao Z, Du G, Li B. 2012.** Reproductive allometry in
621   *Pedicularis* species changes with elevation. *Journal of Ecology* **100**:452–458 DOI
622   10.1111/j.1365-2745.2011.01884.x.

623 **Halbritter AH, Fior S, Keller I, Billeter R, Edwards PJ, Holderegger R, Karrenberg S,**
624   **Pluess AR, Widmer A, Alexander JM. 2018.** Trait differentiation and adaptation of
625   plants along elevation gradients. *Journal of Evolutionary Biology* **31**:784–800 DOI
626   10.1111/jeb.13262.

627 **Hamann E, Kesselring H, Armbruster GFJ, Scheepens JF, Stöcklin J. 2016.** Evidence of
628   local adaptation to fine- and coarse-grained environmental variability in *Poa alpina* in the
629   Swiss Alps. *Journal of Ecology* **104**:1627–1637 DOI 10.1111/1365-2745.12628.

630 **Hamann E, Scheepens JF, Kesselring H, Armbruster GFJ, Stöcklin J. 2017.** High
631   intraspecific phenotypic variation, but little evidence for local adaptation in *Geum reptans*
632   populations in the Central Swiss Alps. *Alpine Botany* **127**:121–132 DOI 10.1007/s00035-
633   017-0185-y.

634 **Hattori M, Nagano Y, Shinohara Y, Itino T. 2016.** Pattern of flower size variation along an
635   altitudinal gradient differs between *Impatiens textori* and *Impatiens noli-tangere*. *Journal*
636   *of Plant Interactions* **11**:152–157 DOI 10.1080/17429145.2016.1226437.

637 **Hautier Y, Randin ChF, Stöcklin J, Guisan A. 2009.** Changes in reproductive investment with
638   altitude in an alpine plant. *Journal of Plant Ecology* **2**:125–134 DOI 10.1093/jpe/rtp011.

639 **He JD, Xue JY, Gao J, Wang J, Wu Y. 2017.** Adaptations of the floral characteristics and
640   biomass allocation patterns of *Gentiana hexaphylla* to the altitudinal gradient of the eastern
641   Qinghai-Tibet Plateau. *Journal of Mountain Science* **14**:1563–1576 DOI 10.1007/s11629-
642   017-4424-x.

643 **Henn JJ, Buzzard V, Enquist BJ, Halbritter AH, Klanderud K, Maitner BS, Michaletz ST,**
644   **Pötsch Ch, Seltzer L, Telford RJ et al. 2018.** Intraspecific trait variation and phenotypic
645   plasticity mediate alpine plant species response to climate change. *Frontiers in Plant*
646   *Science* **9**:1548 DOI 10.3389/fpls.2018.01548.

647 **Herrera J. 2005.** Flower size variation in *Rosmarinus officinalis*: individuals, populations and
648   habitats. *Annals of Botany* **95**:431–437 DOI 10.1093/aob/mci041.

649 **Hirano M, Sakaguchi S, Takahashi K. 2017.** Phenotypic differentiation of the *Solidago*
650   *virgaurea* complex along an elevational gradient: insights from a common garden
651   experiment and population genetics. *Ecology and Evolution* **7**:6949–6962 DOI
652   10.1002/ece3.3252.

653 **Kelly CA.** 1998. Effects of variable life history and insect herbivores on reproduction in
654   *Solidago macrophylla* (Asteraceae) on an elevational gradient. *The American Midland*
655   *Naturalist* **139**:243–254 DOI 10.1674/0003-0031(1998)139[0243:EOVLHA]2.0.CO;2.

656 **Khatri K, Negi B, Bargali K, Bargali SS. 2023.** Phenotypic variation in morphology and
657   associated functional traits in *Ageratina adenophora* along an altitudinal gradient in
658   Kumaun Himalaya, India. *Biologia* **78**:1333–1347 DOI 10.1007/s11756-022-01254-w.

659 **Kiełtyk P.** 2018. Variation of vegetative and floral traits in the alpine plant *Solidago minuta*:
660   evidence for local optimum along an elevational gradient. *Alpine Botany* **128**:47–57 DOI
661   10.1007/s00035-017-0197-7.

662 **Kiełtyk P.** 2021a. Intraspecific morphological variation of *Bellidiastrum michelii* (Asteraceae)
663   along a 1,155 m elevation gradient in the Tatra Mountains. *PeerJ* **9**:e11286 DOI
664   10.7717/peerj.11286.

665 **Kiełtyk P.** 2021b. Patterns of floral allocation along an elevation gradient: variation in *Senecio*
666   *subalpinus* growing in the Tatra Mountains. *Alpine Botany* **131**:117–124 DOI
667   10.1007/s00035-021-00247-w.

668 **Kotarba A.** 1996. Present-day geomorphic processes. In: Mirek Z, ed. *The nature of the Tatra*
669   *National Park*. Zakopane, Kraków: Tatrzański Park Narodowy, 125–137.

670 **Körner Ch. 2021.** *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems*.
671   3rd ed. Berlin: Springer DOI 10.1007/978-3-030-59538-8.

672 **Körner Ch, Hiltbrunner E. 2021.** Why is the alpine flora comparatively robust against climatic
673   warming? *Diversity* **13**:383 DOI 10.3390/d13080383.

674 **Körner Ch, Riedl S, Keplinger T, Richter A, Wiesenbauer J, Schweingruber F,**
675   **Hiltbrunner E. 2019.** Life at 0 °C: the biology of the alpine snowbed plant *Soldanella*
676   *pusilla*. *Alpine Botany* **129**:63–80 DOI 10.1007/s00035-019-00220-8.

677 **Kudo G, Molau U. 1999.** Variations in reproductive traits at inflorescence and flower levels of
678   an arctic legume, *Astragalus alpinus* L.: comparisons between a subalpine and an alpine
679   population. *Plant Species Biology* **14**:181–191 DOI 10.1046/j.1442-1984.1999.00012.x.

680 **Kulonen A, Imboden RA, Rixen Ch, Maier SB, Wipf S. 2018.** Enough space in a warmer
681   world? Microhabitat diversity and small-scale distribution of alpine plants on mountain
682   summits. *Diversity and Distributions* **24**:252–261 DOI 10.1111/ddi.12673.

683 **Leuschner Ch, Ellenberg H. 2017.** *Ecology of Central European non-forest vegetation: coastal*
684   *to alpine, natural to man-made habitats. Vegetation ecology of Central Europe,* vol. II.
685   Cham: Springer International Publishing DOI 10.1007/978-3-319-43048-5.

686 **Maad J, Armbruster WS, Fenster CB. 2013.** Floral size variation in *Campanula rotundifolia*
687   (Campanulaceae) along altitudinal gradients: patterns and possible selective mechanisms.
688   *Nordic Journal of Botany* **31**:361–371 DOI 10.1111/j.1756-1051.2013.01766.x.

689 **Malo JE, Baonza J. 2002.** Are there predictable clines in plant–pollinator interactions along
690   altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de
691   Guadarrama (Central Spain). *Diversity and Distributions* **8**:365–371 DOI 10.1046/j.1472-
692   4642.2002.00161.x.

693 **McConnaughay KDM, Coleman JS. 1999.** Biomass allocation in plants: ontogeny or
694   optimality? A test along three resource gradients. *Ecology* **80**:2581–2593 DOI
695   10.1890/0012-9658(1999)080[2581:BAIPOO]2.0.CO;2.

696 **Midolo G, De Frenne P, Hölzel N, Wellstein C. 2019.** Global patterns of intraspecific leaf trait
697   responses to elevation. *Global Change Biology* **25**:2485–2498 DOI 10.1111/gcb.14646.

698 **Miljković D, Stefanović M, Orlović S, Stanković Nedić M, Kesić L, Stojnić S. 2019.** Wild
699   cherry (*Prunus avium* (L.)L.) leaf shapes and leaf variations in natural populations at
700   different elevations. *Alpine Botany* **129**:163–174 DOI 10.1007/s00035-019-00227-1.

701 **Mirek Z. 1996.** The Tatra Mountains and the Tatra National Park – general information. In:
702   Mirek Z, ed. *The nature of the Tatra National Park*. Zakopane, Kraków: Tatrzański Park
703   Narodowy, 17–26.

704 **Morente-López J, Scheepens JF, Lara-Romero C, Ruiz-Checa R, Tabarés P, Iriondo JM.**
705   **2020.** Past selection shaped phenological differentiation among populations at contrasting
706   elevations in a Mediterranean alpine plant. *Environmental and Experimental Botany*
707   **170**:103894 DOI 10.1016/j.envexpbot.2019.103894.

708 **Mountain Research Initiative EDW Working Group. 2015.** Elevation-dependent warming in
709   mountain regions of the world. *Nature Climate Change* **5**:424–430 DOI
710   10.1038/nclimate2563.

711 **Nagy L, Grabherr G .2009.** *The biology of alpine habitats*. New York: Oxford University
712   Press.

713 **Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P,**
714   **Purugganan MD, Richards CL, Valladares F et al. 2010.** Plant phenotypic plasticity in a
715   changing climate. *Trends in Plant Science* **15**:684–692 DOI 10.1016/j.tplants.2010.09.008.

716 **Norgate M, Boyd-Gerny S, Simonov V, Rosa MGP, Heard TA, Dyer AG. 2010.** Ambient
717   temperature influences Australian native stingless bee (*Trigona carbonaria*) preference for
718   warm nectar. *PLoS ONE* **5**:e12000 DOI 10.1371/journal.pone.0012000.

719 **Ohara M, Higashi S. 1994.** Effects of inflorescence size on visits from pollinators and seed set
720   of *Corydalis ambigua* (Papaveraceae). *Oecologia* **98**:25–30 DOI 10.1007/BF00326086.

721 **Olejniczak P, Czarnoleski M, Delimat A, Majcher BM, Szczepka K. 2018.** Seed size in
722   mountain herbaceous plant changes with elevation in species-specific manner. *PloS ONE*
723   **13**:e0199224 DOI 10.1371/journal.pone.0199224.

724 **Paudel BR, Dyer AG, Garcia JE, Shresta M.** 2019. The effect of elevational gradient on alpine
725   gingers (*Roscoea alpina* and *R. purpurea*) in the Himalayas. *PeerJ* **7**:e7503 DOI
726   10.7717/peerj.7503.

727 **Pawłowska S. 1963.** *Soldanella* L., Urdzik. In: Pawłowski B, ed. *Flora Polska. Rośliny*
728   *naczyniowe Polski i ziem ościennych*, vol. 10. Warszawa, Kraków: Państwowe
729   Wydawnictwo Naukowe, 53–59.

730 **Pawłowska S. 1972.** *Soldanella* L. In: Tutin TG, Heywood VH, Burges NA, Moore DM,
731   Valentine DH, Walters SM, Webb DA eds. *Flora Europaea*, vol. 3. London: Cambridge
732   University Press, 23–24.

733 **Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-**
734   **Harte MS, Cornwell WK, Craine JM, Gurvich DE et al. 2013.** New handbook for
735   standardised measurement of plant functional traits worldwide. *Australian Journal of*
736   *Botany* **61**:167–234 DOI 10.1071/BT12225.

737 **Pfennigwerth AA, Bailey JK, Schweitzer JA. 2017.** Trait variation along elevation gradients in
738   a dominant woody shrub is population-specific and driven by plasticity. *AoB Plants*
739   **9**:plx027 DOI 10.1093/aobpla/plx027.

740 **Rasmann S, Pellissier L, Defossez E, Jactel H, Kunstler G. 2014.** Climate-driven change in
741   plant-insect interactions along elevation gradients. *Functional Ecology* **28**:46–54 DOI
742   10.1111/1365-2435.12135.

743 **Rathee S, Ahmad M, Sharma P, Singh HP, Batish DR, Kaur S, Kaur A, Yadav SS, Kohli**
744   **RK. 2021.** Biomass allocation and phenotypic plasticity are key elements of successful
745   invasion of *Parthenium hysterophorus* at high elevation. *Environmental and Experimental*
746   *Botany* **184**:104392 DOI 10.1016/j.envexpbot.2021.104392.

747 **Read QD, Moorhead LC, Swenson NG, Bailey JK, Sanders NJ. 2014.** Convergent effects of
748   elevation on functional leaf traits within and among species. *Functional Ecology* **28**:37–45
749   DOI 10.1111/1365-2435.12162.

750 **Reich PB, Luo YJ, Bradford JB, Poorter H, Perry CH, Oleksyn J. 2014.** Temperature drives
751   global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the*
752   *National Academy of Sciences of the United States of America* **111**:13721–13726 DOI
753   10.1073/pnas.1216053111.

754 **Rixen Ch, Wipf S, Rumpf SB, Giejsztowt J, Millen J, Morgan JW, Nicotra AB, Venn S,**
755   **Zong S, Dickinson KJ et al. 2022.** Intraspecific trait variation in alpine plants relates to
756   their elevational distribution. *Journal of Ecology* **110**:860– 875 DOI 10.1111/1365-
757   2745.13848.

758 **Qi W, Bu H, Cornelissen JHC, Zhang C, Guo S, Wang J, Zhou X, Li W, Du G. 2015.**
759   Untangling interacting mechanisms of seed mass variation with elevation: insights from the
760   comparison of inter-specific and intra-specific studies on eastern Tibetan angiosperm
761   species. *Plant Ecology* **216**:283–292 DOI 10.1007/s11258-014-0435-7.

762 **Sakurai A, Takahashi K. 2017.** Flowering phenology and reproduction of the *Solidago*
763   *virgaurea* L. complex along an elevational gradient on Mt Norikura, central Japan. *Plant*
764   *Species Biology* **32**:270–278 DOI 10.1111/1442-1984.12153.

765 **Scheepens JF, Stöcklin J. 2013.** Flowering phenology and reproductive fitness along a
766   mountain slope: maladaptive responses to transplantation to a warmer climate in
767   *Campanula thyrsoides*. *Oecologia* **171**:679–691 DOI 10.1007/s00442-012-2582-7.

768 **Scheepens JF, Frei ES, Stöcklin J. 2010.** Genotypic and environmental variation in specific
769   leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia*
770   **164**:141–150 DOI 10.1007/s00442-010-1650-0.

771 **Seguí J, Lázaro A, Traveset A, Salgado-Luarte C, Gianoli E. 2018.** Phenotypic and
772   reproductive responses of an Andean violet to environmental variation across an
773   elevational gradient. *Alpine Botany* **128**:59–69 DOI 10.1007/s00035-017-0195-9.

774 **Spitzer CM, Sundqvist MK, Wardle DA, Gundale MJ, Kardol P. 2023.** Root trait variation
775   along a sub-arctic tundra elevational gradient. *Oikos* **2023**:e08903 DOI 10.1111/oik.08903.

776 **Šťastná P, Klimešová J, Doležal J. 2012.** Altitudinal changes in the growth and allometry of
777   *Rumex alpinus*. *Alpine Botany* **122**:35–44 DOI 10.1007/s00035-012-0099-7.

778 **Steinbauer MJ, Grytnes JA, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen Ch,**
779   **Winkler M, Bardy-Durchhalter M, Barni E et al. 2018.** Accelerated increase in plant
780   species richness on mountain summits is linked to warming. *Nature* **556**:231–234 DOI
781   10.1038/s41586-018-0005-6.

782 **Sveinbjörnsson B, Davis J, Abadie W, Butler A. 1995.** Soil carbon and nitrogen mineralization
783   at different elevations in the Chugach Mountains of South-Central Alaska, U.S.A. *Arctic*
784   *and Alpine Research* **27**:29–37 DOI 10.1080/00040851.1995.12003094.

785 **Takahashi K. 2014.** Effects of wind and thermal conditions on timberline formation in central
786   Japan: a lattice model. *Ecological Research* **29**:121–131 DOI 10.1007/s11284-014-1129-2.

787 **Takahashi K, Matsuki S. 2017.** Morphological variations of the *Solidago virgaurea* L. complex
788   along an elevational gradient on Mt Norikura, central Japan. *Plant Species Biology*
789   **32**:238–246 DOI 10.1111/1442-1984.12148.

790 **Totland Ø. 2001.** Environment-dependent pollen limitation and selection on floral traits in an
791   alpine species. *Ecology* **82**:2233–2244 DOI 10.1890/0012-
792   9658(2001)082[2233:EDPLAS]2.0.CO;2.

793 **Totland Ø. 2004.** No evidence for a role of pollinator discrimination in causing selection on
794   flower size through female reproduction. *Oikos* **106**:558–564 DOI 10.1111/j.0030-
795   1299.2004.12991.x.

796 **Totland Ø, Eide W. 1999.** Environmentally-dependent pollen limitation on seed production in
797   alpine *Ranunculus acris*. *Ecoscience* **6**:173–179 DOI 10.1080/11956860.1999.11682518.

798 **Trunschke J, Stöklin J 2017.** Plasticity of flower longevity in alpine plants is increased in
799   populations from high elevation compared to low elevation populations. *Alpine Botany*
800   **127**:41–51 DOI 10.1007/s00035-016-0176-4.

801 **von Arx G, Edwards PJ, Dietz H. 2006.** Evidence for life history changes in high-altitude
802   populations of three perennial forbs. *Ecology* **87**:665–674 DOI 10.1890/05-1041.

803 **Weemstra M, Freschet GT, Stokes A, Roumet C. 2021.** Patterns in intraspecific variation in
804   root traits are species-specific along an elevation gradient. *Functional Ecology* **35**:342–356
805   DOI 10.1111/1365-2435.13723.

806 **Weiner J, Campbell LG, Pino J, Echarte L. 2009.** The allometry of reproduction within plant
807   populations. *Journal of Ecology* **97**:1220–1233 DOI 10.1111/j.1365-2745.2009.01559.x.

808 **Weppler T, Stöcklin J. 2005.** Variation of sexual and clonal reproduction in the alpine *Geum
809   reptans* in contrasting altitudes and successional stages. *Basic and Applied Ecology* **6**:305–
810   316 DOI 10.1016/j.baae.2005.03.002.

811 **Wipf S, Stöckli V, Herz K, Rixen Ch. 2013.** The oldest monitoring site of the Alps revisited:
812   accelerated increase in plant species richness on Piz Linard summit since 1835. *Plant
813   Ecology and Diversity* **6**:47–455 DOI 10.1080/17550874.2013.764943.

814 **Wirth LR, Graf R, Gugerli F, Landergott U, Holderegger R. 2010.** Between-year variation in
815   seed weights across altitudes in the high-alpine plant *Eritrichum nanum*. *Plant Ecology*
816   **207**:227–231 DOI 10.1007/s11258-009-9667-3.

817 **Wu G, Tian F, Ren G, Liu Z. 2011.** Seed mass increase along altitude within four *Saussurea*
818   (Asteraceae) species in Tibetian Plateau. *Polish Journal of Ecology* **59**:617–622.

819 **Zhang L-B, Kadereit JW. 2002.** The systematics of *Soldanella* (Primulaceae) based on
820   morphological and molecular (ITS, AFLPs) evidence. *Nordic Journal of Botany* **22**:129–
821   169 DOI 10.1111/j.1756-1051.2002.tb01360.x.

822 **Zhao Z-G, Wang Y-K. 2015.** Selection by pollinators on floral traits in generalized *Trollius*
823   *ranunculoides* (Ranunculaceae) along altitudinal gradients. *PLoS ONE* **10**:e0118299 DOI
824   10.1371/journal.pone.0118299.

825 **Zhu Y, Siegeolf RTW, Durka W, Körner Ch. 2010.** Phylogenetically balanced evidence for
826   structural and carbon isotope responses in plants along elevational gradients. *Oecologia*
827   **162**:853–863 DOI 10.1007/s00442-009-1515-6.

828

Study sites of *Soldanella carpatica* in the Polish Tatra Mountains.

Geographic coordinates were determined with a WGS84 geodetic system.

Site	Elevation (m a.s.l.)	Latitude (N)	Longitude (E)	Date
1	890	49°16'54.8"	19°57'27.2"	2018-05-02
2	920	49°16'44.8"	19°57'43.6"	2018-05-02
3	948	49°15'47.7"	19°52'14.2"	2018-04-28
4	1025	49°16'18.2"	19°52'49.6"	2018-04-29
5	1075	49°15'52.4"	19°58'55.8"	2018-05-03
6	1080	49°15'40.0"	19°53'07.7"	2018-04-28
7	1083	49°16'10.1"	19°52'48.6"	2018-04-29
8	1099	49°16'10.7"	19°52'52.3"	2018-04-29
9	1120	49°15'21.0"	19°51'25.4"	2018-04-29
10	1170	49°16'03.6"	19°52'55.2"	2018-04-28
11	1175	49°15'27.8"	19°59'31.8"	2018-05-29
12	1240	49°15'16.6"	19°52'51.9"	2018-05-01
13	1242	49°15'24.9"	19°59'37.2"	2018-05-03
14	1255	49°15'56.5"	19°53'08.3"	2018-04-28
15	1280	49°15'17.8"	19°59'38.9"	2018-05-03
16	1315	49°15'07.7"	19°59'41.4"	2018-05-29
17	1340	49°15'01.3"	19°58'29.3"	2018-04-30
18	1359	49°15'05.0"	19°58'29.8"	2018-04-30
19	1390	49°15'02.6"	19°53'04.8"	2018-05-01
20	1448	49°15'00.2"	19°53'12.6"	2018-05-01
21	1450	49°15'05.8"	20°00'03.2"	2018-05-29
22	1483	49°14'51.8"	19°53'13.8"	2018-05-01
23	1520	49°14'49.3"	19°53'11.3"	2018-05-01
24	1580	49°14'19.2"	19°56'34.6"	2018-05-28
25	1618	49°14'40.2"	19°53'17.4"	2018-05-26
26	1635	49°14'16.4"	19°56'30.3"	2018-05-28
27	1650	49°14'15.5"	19°56'32.5"	2018-06-14
28	1700	49°14'31.4"	19°53'25.9"	2018-05-26
29	1746	49°14'25.9"	19°53'28.5"	2018-05-26
30	1750	49°14'09.5"	19°56'23.7"	2018-06-14
31	1800	49°14'13.9"	19°58'41.0"	2018-05-25
32	1860	49°14'07.8"	19°58'43.4"	2018-05-25
33	1863	49°14'03.5"	19°56'18.6"	2018-06-14
34	1925	49°13'59.3"	19°58'49.9"	2018-05-28
35	1980	49°13'55.1"	19°58'53.5"	2018-05-25
36	2085	49°13'38.7"	20°01'51.8"	2018-07-10
37	2175	49°11'04.1"	20°04'10.1"	2018-07-07
38	2214	49°11'02.4"	20°04'08.0"	2018-07-07
39	2280	49°11'02.7"	20°04'01.2"	2018-07-07
40	2370	49°10'58.1"	20°04'01.0"	2018-07-07

Soldanella carpatica traits used in the study.

Trait	Measurement details	Accuracy / significant digits
Aboveground plant mass – total dry mass of the aboveground plant parts. Calculated as sum of leaves, stalk and flowers masses weighed separately.	Plant parts weighed on an analytical balance after drying for 48 h at 80 °C.	0.0001 g
Root mass – dry mass of all plant roots.	Roots washed on the 0.6 mm sieve under running water and weighed on an analytical balance after drying for 48 h at 80 °C.	0.0001 g
Total leaf mass – total dry mass of all plant leaves.	Weighed on an analytical balance after drying for 48 h at 80 °C.	0.0001 g
Scape mass - dry mass of plant scape.	Weighed on an analytical balance after drying for 48 h at 80 °C.	0.0001 g
Total flower mass – total dry mass of all plant flowers.	Weighed on an analytical balance after drying for 48 h at 80 °C.	0.00001 g
Individual flower mass – total flower mass divided by number of flowers in the inflorescence.	–	0.00001 g
Scape height – measured from the plant base to the top of the inflorescence.	Straightened scape was measured with a ruler on herbarium specimens.	1 mm
Leaf blade diameter – mean value of the two perpendicular blade width measurements. This trait was measured and averaged for two largest plant leaf blades.	Measured with a digital calliper on herbarium specimens.	0.1 mm
Root : Shoot ratio – root mass divided by plant aboveground mass.	–	–
Leaf mass fraction – total leaf mass divided by total plant mass.	–	–
Flower aboveground mass fraction – total flower mass divided by plant aboveground mass.	–	–

Summaries of linear mixed-effects models for fitting *Soldanella carpatica* traits to elevation.

Elevational model range - mod_{2370}: 890–2370 m a.s.l., mod_{1980}: 890–1980 m a.s.l.; $P_{model\ selection}$ – test between straight line and curvilinear line models; t, P – test of model significance at the significance level of 0.05.

	Elevational model range	$P_{\text{model selection}}$	Intercept a	Slope b_1	Slope b_2	t	P
Aboveground plant mass (g)	mod_{2370}	0.0048	7.340×10^{-2}	3.389×10^{-4}	-1.447×10^{-7}	-2.858	0.0067
	mod_{1980}	0.4402	3.368×10^{-1}	-6.000×10^{-5}	–	-2.099	0.0436
Root mass (g)	mod_{2370}	0.0212	3.236×10^{-3}	2.435×10^{-4}	-8.918×10^{-8}	-2.299	0.0270
	mod_{1980}	0.9100	1.579×10^{-1}	3.729×10^{-6}	–	0.180	0.8583
Total leaf mass (g)	mod_{2370}	0.0217	9.614×10^{-2}	2.156×10^{-4}	-9.961×10^{-8}	-2.288	0.0275
	mod_{1980}	0.4140	2.800×10^{-1}	-6.098×10^{-5}	–	-2.444	0.0201
Scape mass (mg)	mod_{2370}	0.0005	$-1.684 \times 10^{+1}$	8.759×10^{-2}	-3.207×10^{-5}	-3.587	0.0009
	mod_{1980}	0.9431	$3.934 \times 10^{+1}$	8.811×10^{-4}	–	0.1860	0.8536
Total flower mass (mg)	mod_{2370}	<0.0000	-6.663×10^{0}	3.683×10^{-2}	-1.337×10^{-5}	-5.656	< 0.0001
	mod_{1980}	0.2335	$1.747 \times 10^{+1}$	1.322×10^{-4}	–	0.112	0.9112
Individual flower mass (mg)	mod_{2370}	<0.0000	1.323×10^{0}	6.539×10^{-3}	-2.462×10^{-6}	-4.353	0.0001
	mod_{1980}	0.2902	5.780×10^{0}	-2.286×10^{-4}	–	-0.793	0.4336
Scape height (mm)	mod_{2370}	0.0833	$2.012 \times 10^{+2}$	-4.333×10^{-2}	–	-5.472	< 0.0001
	mod_{1980}	0.8607	$1.820 \times 10^{+2}$	-2.842×10^{-2}	–	-2.583	0.0144
Leaf blade diameter (mm)	mod_{2370}	0.0041	$1.821 \times 10^{+1}$	1.262×10^{-2}	-6.600×10^{-6}	-2.912	0.0059
	mod_{1980}	0.2017	$3.061 \times 10^{+1}$	-5.873×10^{-3}	–	-4.435	0.0001
Root : Shoot ratio	mod_{2370}	0.1649	3.407×10^{-1}	2.643×10^{-4}	–	5.000	< 0.0001
	mod_{1980}	0.7610	4.210×10^{-1}	2.020×10^{-4}	–	3.088	0.0022
Leaf mass fraction	mod_{2370}	0.8786	5.733×10^{-1}	-8.149×10^{-5}	–	-5.878	< 0.0000
	mod_{1980}	0.4429	5.791×10^{-1}	-8.600×10^{-5}	–	-4.463	0.0001
Flower aboveground mass fraction	mod_{2370}	0.6018	5.234×10^{-2}	1.832×10^{-5}	–	3.590	0.0009
	mod_{1980}	0.5847	4.715×10^{-2}	2.234×10^{-5}	–	3.216	0.0029

Fitted values of *Soldanella carpatica* traits and percentage traits changes across elevations.

All percentage changes in trait values are referred to fitted values at the base of elevational gradient at 890 m a.s.l. Trait values at 890 m a.s.l. were fitted by linear mixed-effects models constructed for the 890–1,980 m a.s.l. elevational ranges, values at 2370 m a.s.l. were fitted by models constructed for the 890–2370 m a.s.l. elevational ranges, and values at 1,980 m a.s.l. were averaged based on the fitted values from the both models; *ns* – not significant model used for fitted values estimation.

	Fitted value at 890 m a.s.l.	Fitted value at 1,980 m a.s.l.	Fitted value at 2,370 m a.s.l.	Change per 100 m increase in elevation in the 890–1,980 m a.s.l. range (%)	Change per 100 m increase in elevation in the 1,980–2,370 m a.s.l. range (%)	Total change with an increase in elevation from 890 m to 2,370 m a.s.l. (%)
Aboveground plant mass (g)	0.2834	0.1976	0.0639	− 2.1	− 12.1	− 77.5
Root mass (g)	0.1612	0.1505	0.0794	+ 0.2 *ns*	− 11.3	− 50.7
Total leaf mass (g)	0.2257	0.1459	0.0476	− 2.7	− 11.2	− 78.9
Scape mass (mg)	40.12	35.97	10.60	+ 0.2 *ns*	− 16.2	− 73.6
Total flower mass (mg)	17.58	15.79	5.54	+ 0.1 *ns*	− 15.0	− 68.5
Individual flower mass (mg)	5.58	4.97	2.99	− 0.4 *ns*	− 9.1	− 46.3
Scape height (mm)	156.7	120.6	98.5	− 1.8	− 3.6	− 37.2
Leaf blade diameter (mm)	25.4	18.2	11.1	− 2.3	− 7.2	− 56.4
Root : Shoot ratio	0.6008	0.8425	0.9671	+ 3.4	+ 5.3	+ 61.0
Leaf mass fraction	0.5025	0.4104	0.3802	− 1.7	− 1.5	− 24.3
Flower aboveground mass fraction	0.0670	0.0900	0.0958	+ 3.3	+ 2.2	+ 42.8

Figure 1

Soldanella carpatica habit.

Figure 2

Location of the 40 elevational sites sampled for *Soldanella carpatica* in the Polish Tatra Mts., Western Carpathians.
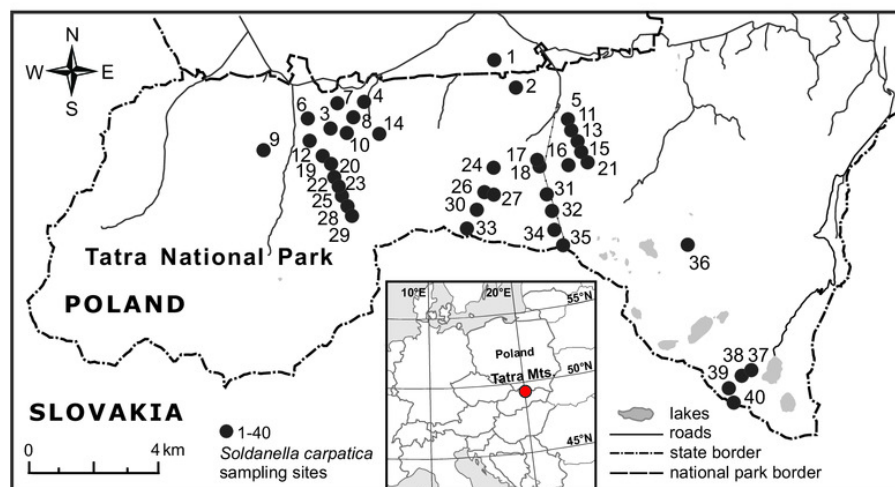
Figure 3

Elevational variation in morphological traits of *Soldanella carpatica*.

Solid lines represent the result of the mixed-effect models fitted to the 890–1,980 m a.s.l. range, interrupted lines represent models fitted to the entire 890–2,370 m a.s.l. range, the surrounding bands represent the 95% confidence intervals; P_{1980}, P_{2370} – p-value of model significance fitted for 890–1,980 m a.s.l. and 890–2,370 m a.s.l. elevation ranges, respectively; ns – non significant model at 0.05 significance level.
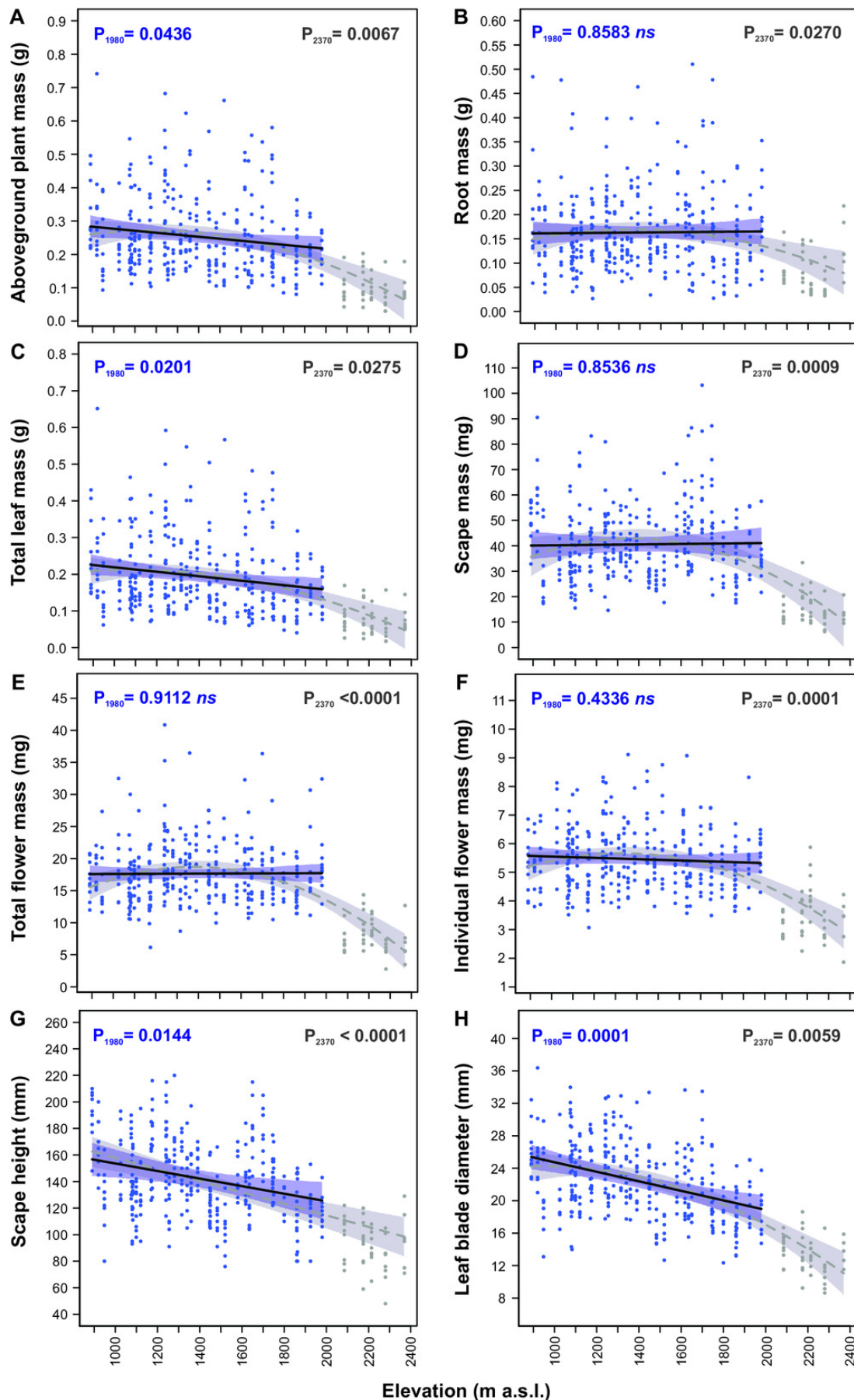
Figure 4

Elevational variation in *Soldanella carpatica* dry mass allocation traits.

Solid lines represent the result of the mixed-effect models fitted to the 890–1,980 m a.s.l. range, interrupted lines represent models fitted to the entire 890–2,370 m a.s.l. range, the surrounding bands represent the 95% confidence intervals; P_{1980}, P_{2370} – p-value of model significance fitted for 890–1,980 m a.s.l. and 890–2,370 m a.s.l. elevation ranges, respectively.

Elevation (m a.s.l.)