



Variation of vegetative and floral traits in the alpine plant *Solidago minuta*: evidence for local optimum along an elevational gradient

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Abstract

Alpine plants growing along wide elevational gradients experience very different abiotic and biotic conditions across elevations. As a result of genetic differentiation and/or plastic response, conspecific plants growing in high elevations, as compared to low elevations, generally have shorter stems and lower number of flowers, but larger flower size. However, most often, detailed models of elevational variations were not examined. To reveal the pattern of elevational changes in a set of fitness-related morphological traits, tests of linear and unimodal models were performed based on measurements of 1047 *Solidago minuta* plants collected from 47 sites distributed along a 1000 m elevational gradient in the Tatra Mountains. Nearly all of the investigated floral traits, i.e. inflorescence and flower heads size, and number and size of individual flowers, expressed unimodal relationships with elevation having their maxima in the centre of the elevation range. This pattern suggests the existence of a local optimum with respect to sexual reproduction at the centre of the elevational range. Possible explanations of observed elevational variations are discussed in the context of pollinator selection and the ‘resource-cost compromise’ hypothesis. Best floral performance in the centre of the elevational range of *S. minuta* may also support the idea that the favourability of habitat conditions declines from the centre to the margin of the distribution, and species are expected to be more abundant, increase reproduction and perform better in the centre of the range.

Keywords Altitudinal gradient · ‘Centre-periphery’ hypothesis · Morphology · Phenotypic variation · Species range

Introduction

Plants growing along wide elevational gradients in mountains experience very different abiotic and biotic conditions, which change considerably over relatively small vertical distances. Environmental factors associated with the increase in elevation in mountains of temperate seasonal zones include reduction in mean temperature and CO₂ partial pressure, decrease in the length of the growth period and prolonged duration of snow cover, reduction in soil microbial activity and resource competition among plants, decrease in nutrient availability, increase in light intensity and UV radiation, increase in precipitation and wind velocity (Billings 1974; Körner 2003, 2007). Elevation in mountains is a complex ecological factor comprised of many abiotic and

biotic components which are vital for plant growth and cannot be easily separated. Therefore, the elevational gradient has been considered as the most important factor in studies on phenotypic variation of plant species in mountains (e.g. Stöcklin et al. 2009; Št’astná et al. 2012; Kim and Donohue 2013; Scheepens and Stöcklin 2013; Gugger et al. 2015; Hamann et al. 2016; Stöcklin and Armbruster 2016; Sakurai and Takahashi 2016; Takahashi and Matsuki 2016). Plants can respond to elevational changes based on their morphological and physiological plasticity and through local adaptations (Hirano et al. 2017). Alpine plant species, compared to lowland plants, have distinctly smaller overall size (e.g. Körner and Renhardt 1987; Blionis and Vokou 2002; Guo et al. 2010), allocate more biomass to underground organs (Körner and Renhardt 1987; Ma et al. 2010) and locate more of their aboveground biomass to flowers (Fabbro and Körner 2004). Morphological differences along elevational gradients are also visible at the intraspecific level in species distributed along wide elevational ranges. Plants growing in high elevation, as compared to low elevation, have shorter stems (Nishizawa et al. 2001; Alexander et al.

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2009; Takahashi and Yoshida 2009; Maad et al. 2013), lower numbers of flowers (Kelly 1998; Baret et al. 2004; Maad et al. 2013) and lower numbers of flower heads (Asteraceae family) (Kelly 1998; Alexander et al. 2009), but larger flower sizes (Kudo and Molau 1999; Malo and Baonza 2002; Herrera 2005; Maad et al. 2013). In addition, along with an increase in elevation, plants possess higher plasticity of flower longevity (Trunschke and Stöcklin 2017), increase clonality, tend to be older (Št'astná et al. 2012) and produce more flowering shoots (von Arx et al. 2006).

Although numerous studies have documented elevational variation in plant morphological traits, the nature of the relationship between traits and elevation has rarely been examined. Often, only the existence of linear relationships (i.e. straight line) between traits and elevation is tested by means of simple linear regression (e.g. Kelly 1998; von Arx et al. 2006; Alexander et al. 2009; Wirth et al. 2010; Montesinos-Navarro et al. 2011). Applying a simple linear regression model assumes the existence of a monotonic (only decreasing or increasing) relationship between plant traits and elevation, most often as a result of plant responses due to plasticity and/or adaptation to changes in climatic conditions along the elevation (e.g. von Arx et al. 2006; Alexander et al. 2009; Wirth et al. 2010; Montesinos-Navarro et al. 2011). However, plant species with wide elevational ranges are expected to be exposed to different selective pressures at low and high elevations (Frei et al. 2014a), and this may result in non-linear responses in some traits along the elevational gradient. For example, Malo and Baonza (2002) in their study on plant–pollinator interactions along an elevational gradient found that the *Cytisus scoparius* flower size in the mountains of Central Spain had a unimodal relationship with elevation and the maximum size occurred at the intermediate elevation. This curvilinear, unimodal relationship may be explained as a result of the trade-off between pollinator selection for larger flowers in higher elevations (e.g. Totland 2001, 2004; Malo and Baonza 2002; Maad et al. 2013) and the selection suggested by the ‘resource-cost compromise’ hypothesis, according to which smaller flowers are advantageous in unfavourable environmental conditions due to the lower cost of their development and maintenance (Herrera 2005). Hence, the abiotic selection for smaller flowers at higher elevations can prevent a response in flower size to selection from pollinators (Zhao and Wang 2015). The existence of a unimodal relationship between morphological traits and the elevational gradient may also be predicted based on the idea that populations from the centre of the species range perform better than marginal populations. According to this ‘centre-periphery’ hypothesis, the populations from the centre of the range should be more abundant and perform better than those from the periphery because habitat suitability decreases from the range centre to the periphery (Hengeveld and Haeck 1982; Brown 1984).

Similarly, the ‘abundant centre model’ (ACM, Vaupel and Matthies 2012), or ‘abundant centre distribution’ (ACD, Herrera and Bazaga 2008), predicts that the favourability of habitat conditions declines from the centre to the margin of the distribution and that species are expected to be more abundant, increase reproduction and perform better in the centre of their range (Jump and Woodward 2003; Vaupel and Matthies 2012).

To understand the role of environmentally induced phenotypic plasticity and genetic effects in plant intraspecific variation along elevational gradients, studies based on the results of the transplantation of plants (or growing them from seed), originating from different elevations, to the common garden (e.g. Neuffer and Bartelheim 1989; Hirano et al. 2017) or reciprocal transplantation to plots located at different elevations (e.g. Gonzalo-Turpin and Hazard 2009; Hautier et al. 2009; Scheepens et al. 2010; Hamann et al. 2016) are essential. However, knowledge on variations in morphological traits and plant performance in natural populations along elevational gradients is also important to understand the role of natural selection in plant adaptation to alpine environments and plant phenotypic responses to such conditions (Clausen et al. 1948; Gonzalo-Turpin and Hazard 2009; Bastida et al. 2015). Moreover, it has been emphasized that, in the context of present and predicted future climate changes, knowledge of plant performance along elevational gradients may contribute to an enhanced prediction of plant responses under an altered climate (Theurillat and Guisan 2001; Felde et al. 2012; Frei et al. 2014b).

The aim of this paper is to examine models of elevational changes in a set of fitness-related morphological traits of the alpine plant, *Solidago minuta* L., along a 1000 m elevational gradient in the Tatra Mountains in the Western Carpathians. Specifically, the paper addresses the following question: do the morphological traits of *S. minuta* change monotonically, i.e. only increasing or decreasing their values with an increase in elevation as a response to environmental gradients, or are there non-linear relationships between fitness-related traits and elevation with maxima at intermediate elevations suggesting the existence of a local optimum along an elevational gradient?

Materials and methods

Species and study area

Alpine goldenrod (*S. minuta* L., syn. *Solidago virgaurea* ssp. *minuta*, Asteraceae) is a perennial, yellow-flowered alpine plant growing in European high-mountain chains extending from the Sierra Nevada through the Pyrenees and Alps to the Carpathians and Dinaric Alps (Wagenitz 1979; Slavík 2004). Flowers gathered in flower heads are

insect-pollinated with outer female ligulate flowers and inner hermaphrodite tubular flowers. From the closely related *Solidago virgaurea* L. that is widespread in the lowlands throughout Europe, alpine *S. minuta* differs in many of its morphological traits, especially in those related to flower heads and flowers. *S. minuta*, as compared to *S. virgaurea*, has a smaller stature with a shorter stem, larger flower heads and considerably more tubular and ligulate flowers per head (Kiełtyk and Mirek 2014).

The investigated elevational gradient was located in the Polish area of the Tatra Mountains, (Fig. 1, the highest peak in the Slovak part is 2655 m a.s.l. and in the Polish part, 2499 m a.s.l.) which is the highest chain in the arc of the Carpathians. The mean annual temperature decreases from ca. +6 °C at the foothills of the Polish Tatras (ca. 900–1000 m a.s.l.) to –2 °C at 2200 m a.s.l., and –4 °C at the highest peaks. The mean annual sum of precipitation measured at the foothills at the weather station in Zakopane town at an elevation of 844 m a.s.l. is 1138 mm, and, at the weather station on the Kasprowy Wierch peak at an elevation of 1991 m a.s.l., it amounts to 1876 mm (Hess 1996). In the Polish Tatra Mountains, *S. minuta* has been found to grow at elevations from ca. 1100 to 2300 m a.s.l.; however, the main centre of the species range is at elevations from 1500 to 1900 m a.s.l. (Fig. 2), which in the Polish Tatra Mountains corresponds to the subalpine belt and the lowest part of the alpine belt. The phytosociological optimum of this species in the study area is in subalpine tall herb and tall grass vegetation (the *Mulgedio-Aconitetea* class) and grazed seminatural vegetation (Kiełtyk and Mirek 2017).

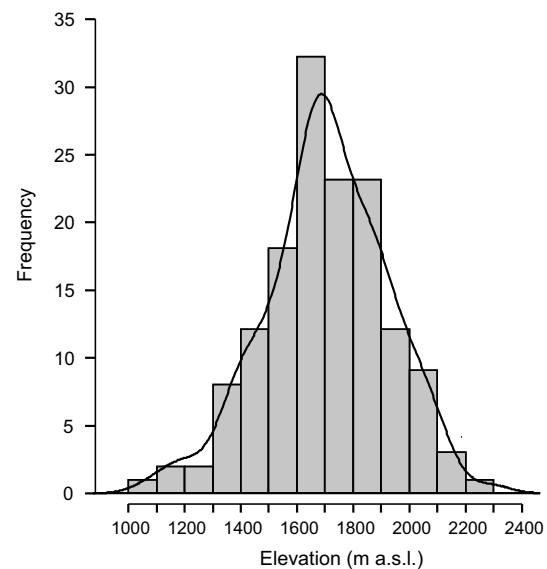
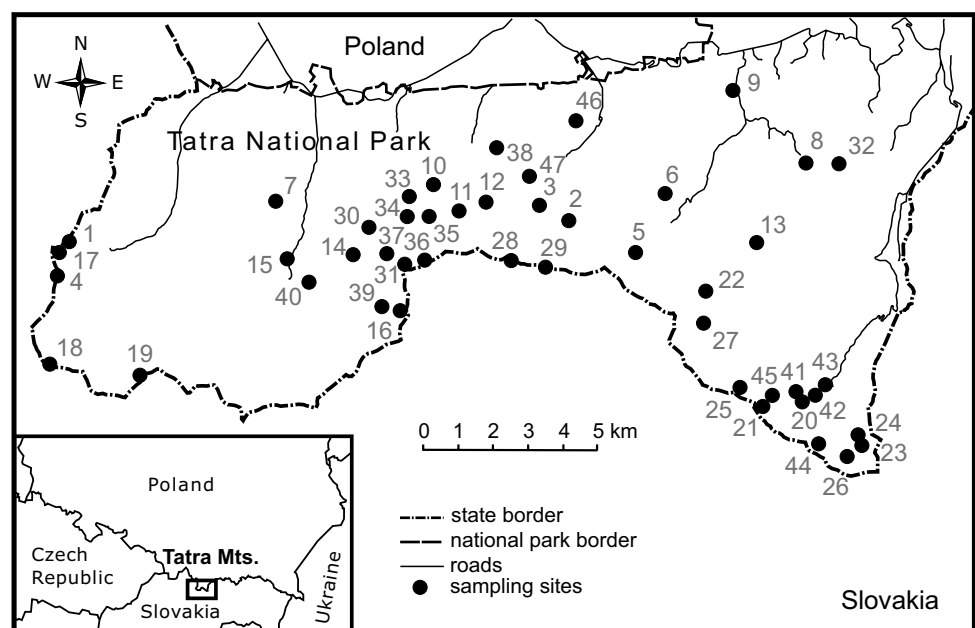


Fig. 2 Elevational distribution of *S. minuta* in Polish Tatra Mountains based on 147 quasi-random elevational records; line represents non-parametric kernel probability density function (modified from Kiełtyk and Mirek 2017)

Sampling and morphological measurements

For analysis of phenotypic variation, 1047 plants of *S. minuta* were collected from 47 sites distributed continuously along an elevational gradient of 1070–2120 m a.s.l. Sample sites were selected in a quasi-random fashion; an attempt was made to ensure that they were distributed approximately evenly along the elevational range of the species and that they were representative of all areas

Fig. 1 Location of the 47 sampled elevational sites of *S. minuta* in Polish Tatra Mountains, Western Carpathians. For geographic coordinates and elevations see Table 1



of the Polish-governed Tatra Mountains (Fig. 1; Table 1). The investigated elevational gradient extended from the lower montane belt (here up to 1250 m a.s.l.), through the upper montane (1250–1550 m a.s.l.), and the subalpine (1550–1800 m a.s.l.) to the alpine belt (1800–2300 m a.s.l.) (Mirek and Piękoś-Mirkowa 1992). Normally, each site sample consisted of 25 *S. minuta* flowering shoots, but fewer plants were collected in some localities. To ensure that the sampled shoots were separate genets, the minimal distance between the sampled plants was 1 m. Plants were collected in full flower head and flower development (blossom peak) from 2005 to 2008; 27 sites were sampled in 2005, 16 sites in 2006 and additional four in 2007 and 2008 (two sites per year). Morphological traits did not differ substantially between years, with the exception of the sites sampled in 2007 and 2008 due to sampling from different elevational belts in those years. Plants were collected on the sites from relatively small areas, up to ca. 15 m vertically and ca. 20 m horizontally. All sampled sites were situated in open, non-forested areas. Below tree line sampling sites were situated in glades or former mountain pastures and were not shaded by a tree canopy. Collected plants were dried and preserved as herbarium specimens for morphometric analyses. Elevational variation in *S. minuta* was examined for the following 12 vegetative and floral traits: plant height measured from the base to the top of inflorescence, middle stem leaf length, number of nodes of the stem from the base to the top of the plant, inflorescence length from the lowest stem node with developed flower head to the top of the inflorescence, inflorescence length relative to plant height, number of flower heads per plant, involucre height from the base of the flower head to the top of the highest bract apices, number of ligulate and tubular flowers per flower head, ligulate flower width and ligulate and tubular flower length. The number of flower heads per plant was counted directly for all sampled plants, whereas traits concerning flower head and flowers were obtained from one randomly chosen, well-developed head per plant from the upper part of the inflorescence, excluding the uppermost head on the shoot apex due to its larger size. The number of ligulate and tubular flowers was counted directly for the chosen flower head, whereas the size of ligulate and tubular flowers was measured for one randomly chosen flower from the head.

To characterize soil conditions associated with stands of *S. minuta*, soil for chemical analyses was sampled for 38 sites located along elevational gradient. Samples were taken from the topsoil to a depth of 15 cm in places, where *S. minuta* plants were rooted; three to five cores per site were combined to make each sample. The collected soil was air-dried, ground in a ceramic mortar, and passed through a 2-mm-mesh sieve. Soil was analyzed for basic nutrients and soil reaction. Total nitrogen was extracted using the Kjeldahl method, total organic carbon content was determined

Table 1 Sample sites of *S. minuta* in the Tatra National Park

| Site | Elevation (m a.s.l.) | Latitude (N) | Longitude (E) | Date |
|------|----------------------|--------------|---------------|------------|
| 1 | 1500 | 49°14'18.5" | 019°46'24.0" | 2005-07-26 |
| 2 | 1318 | 49°14'46.2" | 019°58'03.9" | 2005-07-28 |
| 3 | 1357 | 49°14'55.3" | 019°57'12.3" | 2005-07-28 |
| 4 | 1622 | 49°13'47.5" | 019°46'07.9" | 2005-08-18 |
| 5 | 1650 | 49°14'08.2" | 019°59'40.1" | 2005-08-03 |
| 6 | 1563 | 49°15'00.3" | 020°00'25.2" | 2005-08-03 |
| 7 | 1415 | 49°14'55.2" | 019°51'12.6" | 2005-08-09 |
| 8 | 1375 | 49°15'31.7" | 020°03'36.6" | 2005-08-10 |
| 9 | 1159 | 49°16'22.9" | 020°02'05.8" | 2005-08-10 |
| 10 | 1232 | 49°15'13.4" | 019°54'52.5" | 2005-08-12 |
| 11 | 1460 | 49°14'46.8" | 019°55'31.7" | 2005-08-12 |
| 12 | 1760 | 49°14'55.8" | 019°56'05.2" | 2005-08-12 |
| 13 | 1721 | 49°14'14.3" | 020°02'25.1" | 2005-08-13 |
| 14 | 1380 | 49°13'58.8" | 019°53'12.8" | 2005-08-14 |
| 15 | 1073 | 49°13'58.3" | 019°51'31.8" | 2005-08-16 |
| 16 | 1605 | 49°13'19.5" | 019°53'58.9" | 2005-08-16 |
| 17 | 1630 | 49°14'11.2" | 019°46'03.0" | 2005-08-18 |
| 18 | 2040 | 49°12'25.9" | 019°45'52.0" | 2005-08-18 |
| 19 | 2016 | 49°12'05.9" | 019°47'58.0" | 2005-08-18 |
| 20 | 1670 | 49°11'54.3" | 020°03'30.4" | 2005-08-22 |
| 21 | 2120 | 49°11'50.7" | 020°02'27.5" | 2005-08-22 |
| 22 | 1775 | 49°13'32.3" | 020°01'21.5" | 2005-08-24 |
| 23 | 1652 | 49°11'09.6" | 020°04'49.6" | 2005-08-25 |
| 24 | 1590 | 49°11'13.9" | 020°04'45.0" | 2005-08-25 |
| 25 | 1820 | 49°12'08.3" | 020°01'58.0" | 2005-08-29 |
| 26 | 1724 | 49°11'02.4" | 020°04'44.0" | 2005-08-30 |
| 27 | 2115 | 49°13'01.7" | 020°01'14.7" | 2005-08-31 |
| 28 | 1850 | 49°14'02.7" | 019°56'37.6" | 2006-08-12 |
| 29 | 1880 | 49°13'55.2" | 019°57'24.5" | 2006-08-12 |
| 30 | 1697 | 49°14'34.1" | 019°53'24.6" | 2006-08-16 |
| 31 | 2090 | 49°13'52.9" | 019°54'15.1" | 2006-08-16 |
| 32 | 1446 | 49°15'28.2" | 020°04'18.6" | 2006-08-18 |
| 33 | 1411 | 49°14'54.2" | 019°54'18.5" | 2006-08-21 |
| 34 | 1531 | 49°14'36.8" | 019°54'26.4" | 2006-08-21 |
| 35 | 1802 | 49°14'40.1" | 019°54'47.5" | 2006-08-22 |
| 36 | 2044 | 49°13'59.5" | 019°54'49.9" | 2006-08-22 |
| 37 | 1872 | 49°14'09.2" | 019°53'47.4" | 2006-08-22 |
| 38 | 1320 | 49°15'48.2" | 019°56'32.8" | 2006-08-24 |
| 39 | 1481 | 49°13'17.9" | 019°53'45.5" | 2006-08-26 |
| 40 | 1165 | 49°13'40.8" | 019°51'56.2" | 2006-08-26 |
| 41 | 1775 | 49°11'57.5" | 020°03'22.1" | 2006-08-28 |
| 42 | 1520 | 49°11'55.7" | 020°03'51.4" | 2006-08-28 |
| 43 | 1435 | 49°12'05.1" | 020°04'04.4" | 2006-08-28 |
| 44 | 1901 | 49°11'13.6" | 020°03'57.8" | 2007-08-22 |
| 45 | 1860 | 49°11'52.1" | 020°03'04.5" | 2007-08-27 |
| 46 | 1220 | 49°16'06.4" | 019°58'19.0" | 2008-08-17 |
| 47 | 1582 | 49°15'17.9" | 019°57'14.3" | 2008-08-21 |

Geographic coordinates are in accordance with WGS84 geodetic system

using a LECO CR-12 Carbon Analyzer and plant-available phosphorus was determined by the Egner-Riehm method. Metallic cations were leached in ammonium acetate solution; exchangeable potassium was determined using atomic emission spectrometry (AES), and exchangeable magnesium and exchangeable calcium using atomic absorption spectroscopy (AAS) with atomization by an air-acetylene flame (Mg) and by an acetylene–nitrous oxide flame (Ca).

Data analysis

Morphological variation in *S. minuta* along an elevational gradient was analyzed with linear mixed-effects models (Field et al. 2013). Morphological traits were averaged for each site, and mean values were used in models computation. To test whether the data were spatially auto-correlated, what could violate assumptions of linear models (Borcard et al. 2011), three methods for detection of autocorrelation were applied: (1) Moran's *I* spatial autocorrelation coefficient, (2) Mantel test for correlation between geographic distance and trait distance matrices (with $n = 9999$ permutations), and (3) building mixed-effects models without spatial structures and with spatial correlation structures (exponential and Gaussian) included and assessment fit of these models according to Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) (Zuur et al. 2009). Lower AIC and BIC values correspond to model better fitted to the data. Moran's *I* coefficient indicated that from the set of 12 morphological traits three, i.e. plant height, number of flower

heads, and number of tubular flower per head, were spatially auto-correlated (Table 2a). Mantel test for correlation between morphological traits and geographical distances did not detect existence of spatial correlation in the data, except for a slight spatial correlation in middle leaf length ($r = 0.1250$, p value = 0.044) (Table 2b). Comparison of null models with spatial structures for all traits, based on AIC and BIC values, indicated that including in model term for spatial correlation did not improve considerably goodness of fit of these models (Table 2c). Based on results of these three tests for spatial autocorrelation, the conclusion was made that morphological traits were not spatially auto-correlated. In the next step, the effect of elevation on morphological traits was tested by comparing model with linear fixed term $Y = a + b_1 \times (\text{elevation})$, and model with quadratic fixed term $Y = a + b_1 \times (\text{elevation}) + b_2 \times (\text{elevation})^2$, where a denotes an intercept and b_1 and b_2 denote regression coefficients. In both these models, year of sample collection was specified as a random effect to control for possible year effect. Because in 2007 and 2008 only four samples were collected (two per year), these samples were included in 2006 year. To compare linear and quadratic models, likelihood ratio test was calculated, in which p value < 0.05 expressed significant improvement of the linear model once the quadratic term was added. Additionally, for evaluation of both models Akaike's Information Criterion and Bayesian Information Criterion were calculated. To test whether soil characteristics of the sampled sites were correlated with elevation, Pearson correlation coefficients and simple linear regression were calculated for

Table 2 Results of spatial autocorrelation analyses

| Trait | a | | b | | c | | | | | |
|-----------------------------------|-----------|----------------|------------------|----------------|-------|-------|-------|-------|-------|-------|
| | Moran's I | <i>p</i> value | Mantel statistic | <i>p</i> value | AIC | | | BIC | | |
| | | | | | Null | Expon | Gauss | Null | Expon | Gauss |
| Plant height | 0.0774 | 0.0203 | 0.0485 | 0.2207 | 570.9 | 558.2 | 564.4 | 576.5 | 565.6 | 571.8 |
| Middle leaf length | 0.0045 | 0.5377 | 0.1250 | 0.0440 | 436.5 | 430.7 | 428.9 | 442.1 | 438.1 | 436.3 |
| No. stem nodes | 0.0467 | 0.1108 | 0.0738 | 0.1195 | 224.0 | 222.9 | 226.0 | 229.6 | 230.3 | 233.4 |
| Inflorescence length | 0.0163 | 0.3702 | −0.0107 | 0.5189 | 512.4 | 510.1 | 511.4 | 517.9 | 517.5 | 518.8 |
| Inflorescence length/plant height | 0.0166 | 0.3679 | 0.1157 | 0.0592 | −90.1 | −92.0 | −94.8 | −84.5 | −84.6 | −87.4 |
| No. flower heads | 0.0673 | 0.0377 | 0.0302 | 0.2751 | 372.6 | 370.9 | 374.2 | 378.2 | 378.3 | 381.6 |
| Involucre height | 0.0142 | 0.3990 | 0.0418 | 0.2537 | 73.4 | 70.7 | 72.9 | 79.0 | 78.1 | 80.3 |
| No. tubular flowers | 0.1054 | 0.0030 | 0.0358 | 0.2634 | 243.9 | 242.3 | 244.5 | 249.4 | 249.7 | 251.9 |
| No. ligulate flowers | 0.0608 | 0.0531 | 0.0173 | 0.3597 | 133.5 | 130.0 | 130.7 | 139.0 | 137.4 | 138.1 |
| Ligule width | 0.0065 | 0.5108 | 0.0014 | 0.4562 | −32.5 | −30.7 | −30.6 | −27.0 | −23.3 | −23.2 |
| Ligulate flower length | 0.0379 | 0.1626 | −0.0524 | 0.7781 | 103.9 | 100.5 | 103.8 | 109.5 | 107.9 | 111.2 |
| Tubular flower length | 0.0006 | 0.6039 | −0.0564 | 0.8236 | 27.1 | 27.0 | 28.9 | 32.6 | 34.4 | 36.3 |

a—Moran's *I* autocorrelation coefficient and *p* value of the test of null hypothesis of no spatial autocorrelation in morphological traits, b—Mantel test of the correlation between geographic distance and trait distance matrices and *p* value of the test of null hypothesis of no correlation between these matrices. c—Evaluation of goodness of fit of models with no term for spatial correlation (Null) and models with exponential (Expon), and Gaussian (Gauss) spatial correlation structures included

each soil parameter. All statistical analyses were performed in R version 3.4.2 (R Core Team 2017). Linear mixed-effects models were calculated using *lme()* function from the package ‘nlme’ (Pinheiro et al. 2017), Moran’s *I* spatial autocorrelation coefficient was calculated using *Moran.I()* function of the ‘ape’ package (Paradis et al. 2004), and Mantel test was calculated with the use of *mantel.rtest()* function from the ‘ade4’ package (Dray and Dufour 2007).

Results

Results of the analysis of soil characteristics of *S. minuta* sample sites indicated that none of the investigated soil parameters was significantly correlated with elevation (Fig. 3). Nearly all of the investigated morphological traits of *S. minuta* changed significantly along a 1000 m

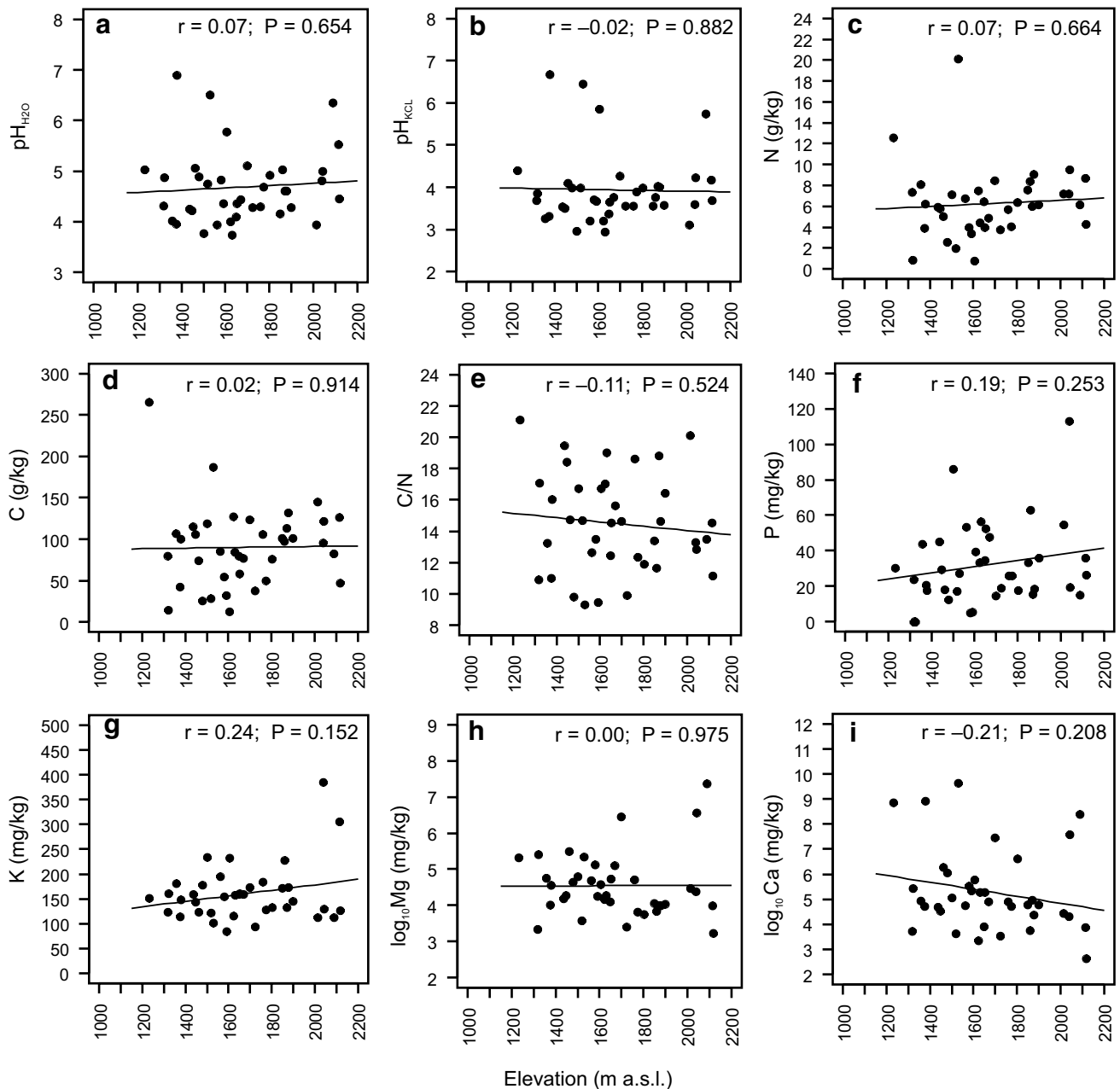


Fig. 3 Variation in soil parameters of *S. minuta* sites along elevational gradient; **a** acidity in H_2O solution, **b** acidity in KCL solution, **c** nitrogen content, **d** carbon content, **e** C/N ratio, **f** phosphorus content, **g** potassium content, **h** magnesium content, **i** calcium content.

r Pearson correlation coefficient, P p value of the significance test for the Pearson correlation coefficient. Line represents simple linear regression

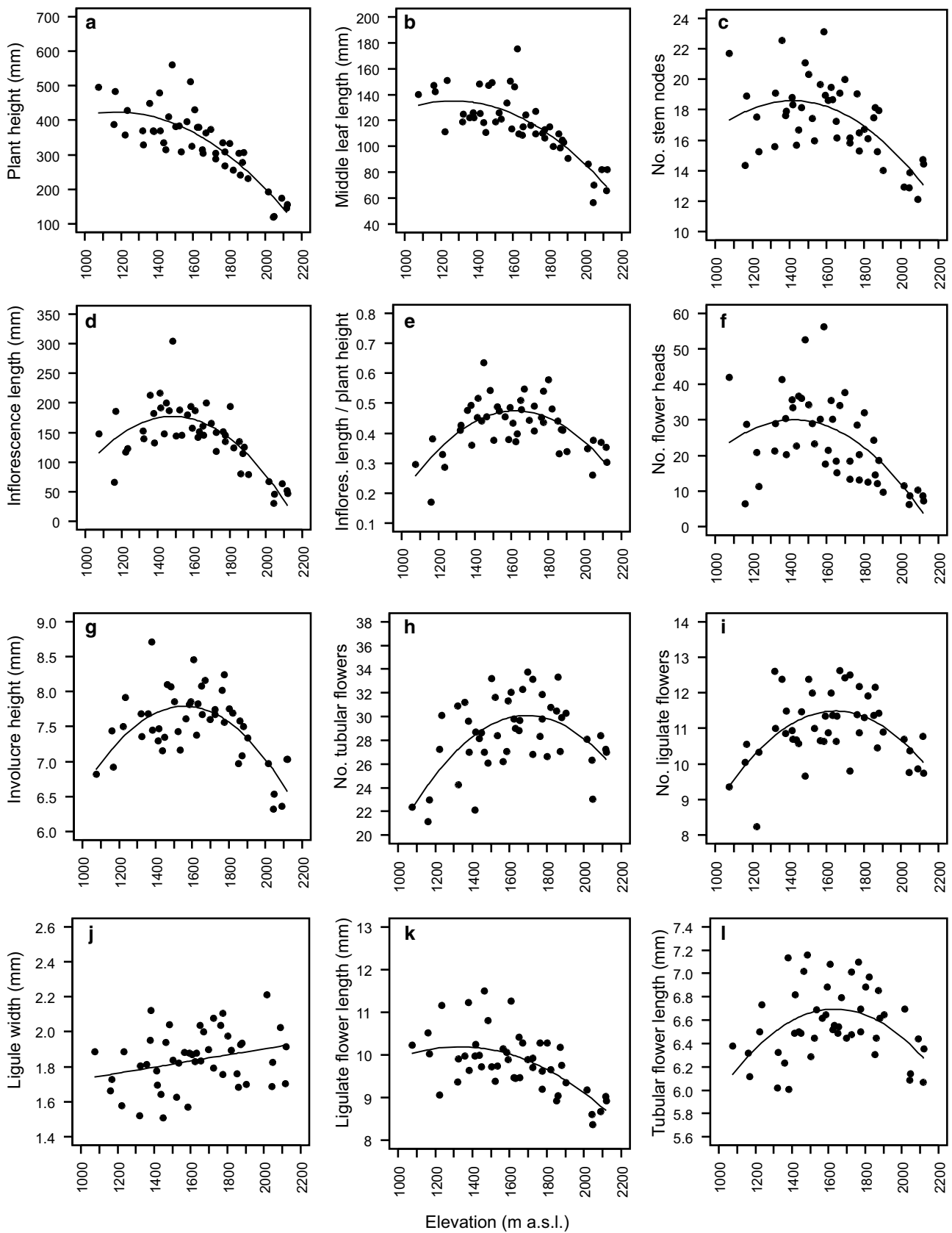


Fig. 4 Elevational variation in morphological traits of *S. minuta*; **a** plant height, **b** middle leaf length, **c** number of stem nodes, **d** inflorescence length, **e** inflorescence length/plant height ratio, **f** number of flower heads, **g** involu-

cre height, **h** number of tubular flowers, **i** number of ligulate flowers, **j** ligule width, **k** ligulate flower length, **l** tubular flower length. Dots represent traits averaged per elevational site; line represents fitted model

elevational gradient (Fig. 4). All of these traits, except one (Fig. 4j), were considerably better fitted to elevation by a model with the quadratic term than by a linear model (Table 3). Traits attributed to vegetative growth, such as plant height, leaf length and number of shoot nodes, did not change considerably from the lowest elevations up to ca. 1400–1500 m a.s.l., but, above 1500 m a.s.l., they began to decrease at a high rate with the increase in elevation (Fig. 4a–c). Linear model calculated for the elevational range of 1500–2120 m a.s.l. revealed that the fitted plant height decreased in this range from 418 to 146 mm, at the rate of 43.7 mm per every 100 m of increased elevation; that is equivalent to a decrease of 79.4 mm for a 1 K decrease of mean annual temperature, assuming a decrease in temperature by 0.55 K per every 100 m increase in elevation (Körner 2007). Size of inflorescence, as expressed by its length, was highest at the centre of the elevational range of the species. Absolute length of inflorescence increased from low elevational positions up to ca. 1500 m a.s.l. and began to decrease above this elevation (Fig. 4d), but inflorescence length relative to plant height continued to increase up to ca. 1600 m a.s.l., and above this elevation it began to decrease (Fig. 4e). The number of flower heads per plant decreased at higher elevations, having its maximum at the centre of the investigated gradient (Fig. 4f). Flower heads were largest at intermediate elevation. Involucre height and number of tubular and ligulate flowers had their maxima at elevations from 1400 to 1800 m a.s.l. (Fig. 4g–i). Ligule width varied greatly along elevational gradient; the linear model was significantly better fitted for this trait than the model with quadratic term (Fig. 4j). Ligulate flower length did not change considerably from low to intermediate elevations, but, above ca. 1600–1700 m a.s.l., a decrease with increasing elevation was observed

also in this trait (Fig. 4k). The size of tubular flowers, expressed by their length, was largest at the centre of the elevational range of the species, that is, from ca. 1500 to 1800 m a.s.l., and this decreased at higher and lower elevations (Fig. 4l).

Discussion

Results of the above ground performance analysis of the alpine plant *S. minuta* along a 1000 m elevational gradient in the Tatra Mountains show that nearly all of the investigated fitness-related floral traits of *S. minuta*, that is, relative size of inflorescence, number and size of flower heads, and number and size of individual flowers, were better fitted by the model with the quadratic term than by the linear model, and expressed unimodal relationships with elevation having their maxima in the centre of the elevational distribution of this species. This suggests the existence of a local optimum with respect to sexual reproduction at the centre of the elevational range of the species. Elevational variation in traits related to vegetative growth, such as plant height, leaf length and number of shoot nodes was also best fitted by the model with the quadratic term. Initially, from low to intermediate elevations, there was no considerable change in their values, but, from the intermediate elevation upwards, the reduction of plant size was observed. Measured soil parameters of *S. minuta* sample sites varied greatly and did not express any clear trend with elevation. This suggests that observed pattern of elevational variation in *S. minuta* was not influenced by soil characteristics.

The results presented here are in line with the results of Malo and Baonza (2002) who, in the study on plant–pollinator interactions along an elevational gradient, found that

Table 3 Linear mixed-effects models summaries; model 1 with linear fixed term $Y = a + b_1 \times (\text{elevation})$ and model 2 with quadratic fixed term $Y = a + b_1 \times (\text{elevation}) + b_2 \times (\text{elevation})^2$

| Y | Intercept (a) | b_1 | b_2 | AIC _{model1/model2} | BIC _{model1/model2} | Likelihood ratio test |
|-----------------------------------|---------------------------|--------------------------|-------------------------|------------------------------|------------------------------|-----------------------|
| Plant height (mm) | -268.23×10^{-01} | 766.84×10^{-03} | -3.26×10^{-04} | 525.3/517.0 | 532.7/526.2 | 10.29; $p = 0.0013$ |
| Middle leaf length (mm) | -113.56×10^{-01} | 231.35×10^{-03} | -9.1×10^{-05} | 400.7/391.1 | 408.1/400.4 | 11.56; $p = 0.0007$ |
| Number of stem nodes | -370.16×10^{-02} | 315.19×10^{-03} | -1.1×10^{-05} | 211.6/204.2 | 219.0/213.4 | 9.41; $p = 0.0022$ |
| Inflorescence length (mm) | $-637.73 \times 10^{+00}$ | 109.93×10^{-02} | -4.0×10^{-04} | 498.2/472.0 | 505.6/481.3 | 28.20; $p < 0.0001$ |
| Inflorescence length/plant height | -143.07×10^{-02} | 234.77×10^{-05} | -7.0×10^{-07} | $-88.1/-114.1$ | $-80.7/-104.9$ | 28.04; $p < 0.0001$ |
| No. of flower heads per plant | -787.91×10^{-01} | 153.15×10^{-03} | -5.0×10^{-05} | 361.7/354.6 | 369.1/363.8 | 9.105; $p = 0.0025$ |
| Involucre height (mm) | -158.91×10^{-02} | 120.38×10^{-04} | -3.9×10^{-06} | 69.2/40.7 | 76.6/49.9 | 30.57; $p < 0.0001$ |
| No. of tubular flowers per head | -286.67×10^{-01} | 693.55×10^{-04} | -2.0×10^{-05} | 243.0/227.3 | 250.4/236.6 | 17.70; $p < 0.0001$ |
| No. of ligulate flowers per head | -605.75×10^{-02} | 213.11×10^{-04} | -6.0×10^{-06} | 135.2/119.7 | 142.6/129.0 | 17.50; $p < 0.0001$ |
| Ligule width (mm) | 155.36×10^{-02} | 174.60×10^{-06} | – | $-36.4/-35.1$ | $-29.0/-25.8$ | 0.73; $p = 0.3941$ |
| Ligulate flower length (mm) | 592.33×10^{-02} | 641.20×10^{-05} | -2.0×10^{-06} | 88.4/84.5 | 95.8/93.8 | 5.86; $p = 0.0155$ |
| Tubular flower length (mm) | 191.59×10^{-02} | 584.75×10^{-05} | -1.8×10^{-06} | 29.1/18.9 | 36.5/28.2 | 12.13; $p = 0.0005$ |

Degree of freedom (df)—44 for model 1, and 43 for model 2

the flower size of *Cytisus scoparius* in the mountains of Central Spain had a unimodal relationship with elevation. The increase in flower size in conspecific populations of insect-pollinated plants with increasing elevation has been explained by pollinator selection for larger flowers at high elevation, where pollinators are rare but generally have a larger size (e.g. Malo and Baonza 2002; Maad et al. 2013). Such an increase in the size of floral structures, e.g. flowers, flower heads and inflorescences, is considered to be advantageous for insect-pollinated plants because this increases the chances of attracting pollinators and producing viable seeds (Ohara and Higashi 1994). However, Zhao and Wang (2015) found that, despite lower pollinator availability at high elevations and the existence of strong selection by pollinators for larger flowers, the flower size of *Trollius ranunculoides* decreased significantly towards higher elevations. This decrease in flower size was explained in the context of the ‘resource-cost compromise’ hypothesis, according to which smaller flowers are advantageous in unfavourable environmental conditions due to the lower cost of their development and maintenance (Herrera 2005). The abiotic selection for smaller flowers at higher elevations could prevent a response in flower size to selection from pollinators (Totland 2001, 2004; Zhao and Wang 2015). Perhaps, there is a trade-off between response to pollinator selection and adaptation to environmental, potentially selective factors associated with changes in elevation, such as, among others, low temperature, strong winds and short growing season at high elevations. Result of this trade-off may be responsible for the existence of unimodal relationships between floral traits of some species and elevation; from low to intermediate elevations, selection by pollinators for larger inflorescences and larger flower heads might prevail, whereas in environmental conditions of high elevations, plant growth and size may be constrained partly as a result of phenotypic plasticity, and partly by climatic selection for smaller phenotypes which are advantageous due to lower resource requirements, as proposed by the ‘resource-cost compromise’ hypothesis (Herrera 2005; Zhao and Wang 2015).

It is also worth noting that the results of this study seem to support the ‘centre-periphery’ hypothesis and the ‘abundant centre model’ (Hengeveld and Haeck 1982; Brown 1984; Jump and Woodward 2003; Herrera and Bazaga 2008; Vaupel and Matthies 2012), both predicting that populations from the centre of the species range perform better than marginal populations. Accordingly, *S. minuta* was found to be most frequent in the centre of its elevational distribution (Kieltyk and Mirek 2017) and produced its largest inflorescences, flower heads and flowers, as well as its highest number of flowers per head, in the centre of its elevational range. Although the reproductive success of *S. minuta* was not investigated in this study, the pattern of morphological variation in fitness-related

floral traits may suggest that the species performs best at the centre of its elevational range and achieves a local optimum there. This result is consistent, for example, with a recent study on elevational divergence in two *Aquilegia vulgaris* subspecies in the southern Iberian Peninsula in which both taxa performed better at their central elevational range than at the periphery (Bastida et al. 2015). Similarly, Angert and Schemske (2005) found that two species, *Mimulus cardinalis* and *M. lewisii*, growing at different elevation ranges in North America, were both best fitted in the centre of their elevational ranges. With regard to the elevational limits of *S. minuta* distribution, the upper limit, as with other alpine plants, is most probably determined by abiotic factors, while the lower limit is likely controlled predominantly by biotic factors, particularly high inter-specific competition at early stages, i.e. seedlings (Billings and Mooney 1968; Weppeler and Stöcklin 2005).

Significant unimodal relationships between fitness-related inflorescence and floral traits of *S. minuta* and elevation suggest that, at the centre of an elevational range, there exists a local optimum in terms of the development of floral structures for sexual reproduction. It should be noted, however, that this study cannot render a definitive statement as to the causes of the observed pattern of morphological variation and to what degree the observed changes represent genetic differences of locally adapted populations or plastic, environmentally induced responses across the elevation gradient. Moreover, in addition to climatic factors and pollinator selection pressure, there are other possible factors, e.g. herbivory, competition, or habitat and vegetation conditions and characteristics, which may also be responsible for the observed pattern of elevational variation in *S. minuta*. Models of elevational variations in morphological traits have rarely been the subject of previous studies, and it is difficult to determine if the unimodal changes in floral traits along the elevational gradient that were observed in *S. minuta* represent a wider pattern in alpine plants. It is possible that unimodal changes in morphological traits may be observed only in plant species with wide vertical ranges, as a result of different selection pressures operating at low and high elevations, whereas species with a narrow elevational range may exhibit only decreasing or increasing monotonic changes with elevation, as a result of dominant selection pressure at given elevations. Further studies investigating variations in plant species with wide, as well as narrow or more restricted elevational ranges are necessary to be able to comment on the generality of the revealed elevational patterns in alpine species.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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