Oecologia (2010) 162:853–863
DOI 10.1007/s00442-009-1515-6

PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Phylogenetically balanced evidence for structural and carbon isotope responses in plants along elevational gradients

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Received: 7 October 2008 / Accepted: 5 November 2009 / Published online: 9 December 2009

Abstract We tested three hypotheses related to the functioning of mountain plants, namely their reproductive effort, leaf surface structure and effectiveness of CO_2 assimilation, using archive material from contrasting elevations. Analysis of elevational trends is at risk of suffering from two major biases: a phylogenetic bias (i.e. an elevational change in the abundance of taxonomic groups), and covariation of different environmental drivers (e.g. water, temperature, atmospheric pressure), which do not permit a mechanistic interpretation. We solved both problems in a subcontinental survey of elevational trends in key plant traits in the European Alps and the high Arctic (northern Sweden, Svalbard), using herbarium samples of 147 species belonging to the genera *Carex*, *Saxifraga* and *Potentilla*. We used both species and phylogenetically independent contrasts as data points. The analysis revealed enhanced reproductive efforts at higher elevation in insect-pollinated taxa (not in wind-pollinated taxa), no increase in leaf pubescence at high elevation (as is often assumed), and a strong correlation between ^{13}C discrimination and elevation. Alpine taxa operate at a smaller mesophyll resistance to CO_2 uptake relative to diffusive resistance (stomata). By comparison with congeneric low altitude polar taxa (low temperature, but high atmospheric pressure), the response could be attributed to the elevational decline in atmospheric pressure rather than temperature (a mean increase in $\delta^{13}C$ by 1.4‰ km^{-1}). The signal is consistent within and across genera and within species, suggesting rapid adjustment of leaf physiology to reduced partial pressure of CO_2. These results offer answers to long-debated issues of plant responses to high elevation life conditions.

Keywords Elevation · Atmospheric pressure · Morphology · Reproduction · Temperature

Communicated by Kouki Hikosaka.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1515-6) contains supplementary material, which is available to authorized users.

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Introduction

Certain environments select for certain plant functional traits. These traits may be phenotypic (a result of physiological acclimatization or structural modification), or genotypic (selected in the course of evolution). However, evolutionary fixed traits may not necessarily be related to the actual environment of a species. Such traits may also be neutral with respect to plant functioning and, thus, may not have been selected against. Thus, traits related to the phylogenetic position of a taxon rather than the current environment may bias results of screening tests if taxa are unevenly represented in a given sample (e.g. Harvey and Pagel 1991; Westoby 1999). In order to identify specific trait–environment

linkages, data are required for a broad set of habitat conditions and for different phylogenetic lineages. Elevational gradients represent a particularly useful tool to test traits for their long-term adaptive nature, although it is not elevation per se which exerts selective pressure, but the environmental conditions associated with elevation (Körner 2007).

One problem with the study of plant traits along any elevational gradient is the gradual shift in species, genera and even plant family composition of vegetation. For instance, the graminoid life form is almost exclusively represented by Poaceae at low elevations, but at high elevations Cyperaceae contribute a significant fraction. Because Cyperaceae and Poaceae always differ in some traits, a species-based elevational trend in traits across graminoids would reflect the elevational shift in family abundance. Hence, the question is whether: (1) certain traits become more abundant with elevation because of phenotypic adjustment across taxa, or (2) these traits become more abundant because species with such traits are selected for, or (3) these traits are a neutral by-product of selection for certain phylogenetic groups for reasons not related to those traits. While (1) and (2) reflect important ecological responses, irrespective of whether phylogeny is involved (Westoby 1999), possibility (3) needs to be dismissed in an ecological context. This can be done by repeated testing (sampling) species within unrelated genera across the same environmental gradient and/or by statistically accounting for phylogenetic dependence in trait analyses. Here, we employed both strategies.

As plants get smaller with elevation, characteristic changes in allometry, anatomy and physiology take place (Körner et al. 1989; Körner 2003). Here we select one important trait from each of these three groups of characteristics in order to test associated hypotheses related to elevation. We used the relative size of inflorescences as a proxy for reproductive effort, leaf pubescence as an anatomical feature often related to climatic stress, and stable C isotope discrimination as an indicator of the specific constraints of CO_2 uptake. The three traits are proxies for key plant–environment responses, and they exemplify traits easily obtained from large plant archives (herbaria).

It is a long-debated issue, whether plants undertake less or more effort to reproduce sexually (by flowers) as elevation increases. Because the overall size of plants declines with elevation, this can only be tested relative to their body size and not in absolute terms. Using biometric relationships, we explored elevational changes in the relative size of inflorescences compared to total plant and leaf size. Showy flowers are likely to become relatively more important (across taxa) in cold environments given the greater likelihood of pollinator limitation (Fabbro and Körner 2004; Pluess et al. 2005, but see Zhao et al. 2006). Using a large sample size (high number of species) over a broad spectrum of climatic conditions, and, in contrast to earlier surveys, accounting for the possibility of "taxonomic bias" by congeneric comparisons, we ask whether there is such a general trend of larger inflorescences as elevation increases across the Alps.

Leaf pubescence is often assumed to increase with elevation, possibly because there exist a number of very prominent highly pubescent alpine taxa such as the edelweiss (i.e. various *Leontopodium* species) or several species of *Saussurea* in Central Asia (Yang et al. 2008). But many alpine plants show little pubescence, and it is quite unclear what the specific benefits of higher pubescence in an alpine setting might be (Körner 2003). Before speculating on such likely benefits, we need to know whether such a trend in leaf surface properties does exist in an unbiased sample.

For testing physiological adaptation to life conditions at high elevation, we selected C isotope discrimination by plants, preserved in plant dry matter. The heavier but similarly stable ^{13}C is discriminated compared to the normal ^{12}C when leaves assimilate CO_2. Expressed as the stable C isotope composition ($\delta^{13}C$), the degree of ^{13}C discrimination by leaves indicates the relative importance of stomatal versus biochemical limitations of CO_2 uptake, and thus, offers insight into photosynthetic adjustments to environmental conditions such as a cold climate or low partial pressure of ambient CO_2 at high elevations. Earlier assessments for humid regions and large enough ranges of elevation (avoiding any bias from water shortage or topography) indicated a reduced overall ^{13}C discrimination as altitude increases, suggesting a more efficient way of C fixation at high elevations (Körner et al. 1988, 1991). However, these earlier data could still reflect some bias introduced by the representation of different taxonomic groups at different elevations and could not resolve the question whether such trends are driven by temperature or atmospheric pressure. Here we offer data for a taxonomically balanced sample of species, covering 3 km of elevation and strictly humid life conditions during C fixation. The comparison with cold climate habitats at sea level pressure in the high Arctic permitted us to separate the influence of temperature and atmospheric pressure.

Since elevation itself is not biologically relevant (plants do not respond to metres), it is important to identify the actual climatic drivers that operate across elevational gradients. In humid areas, the elevational decline in temperature (besides the general drop in atmospheric pressure), is the predominant environmental driver, with secondary effects on atmospheric humidity, freezing events and snow cover as well as seasonality. However, this global temperature gradient is regionally confounded by a water availability gradient, with low elevations often dry and moisture increasing with elevation. In such cases, it is particularly dangerous to test for elevation effects, as if they represented

a uniform gradient of atmospheric influences (Körner 2007). Furthermore, the plants' microhabitat may vary so that species experience and adapt to, for instance, varying shade versus sunlit conditions or different soil moisture, not strictly related to elevation. Such microhabitat variation and species' preferences have to be taken into account should the analysis of elevation-related phenomena make sense.

An elegant tool for ranking species' environmental preferences within the European flora is the so-called indicator value. Indicator values reflect aggregated long-term expert experience on species–environment linkages and are expressed in a semi-quantitative manner by ranking those preferences on a scale of from one to five or from one to ten (Ellenberg 1974; Landolt 1977; Diekmann 2003). Here we applied these indicator values to segregate species by their temperature and moisture requirements and to group species by their shade preference. Combined, for the first time, with stable C isotope data, indicator values help in discriminating samples (species) which may exhibit traits not strictly related to elevation (e.g. microhabitat moisture or light peculiarities instead of the general elevational temperature or pressure effects). We further expanded our study to the European lowland Arctic, in order to separate effects of atmospheric pressure—from temperature-related phenomena.

Based on previous knowledge, the three selected aspects of plant adaptation to high elevations were explored by testing the following hypotheses:

1. The relative significance of reproductive organs (their size) increases with elevation in insect-pollinated species, but not in wind-pollinated species.
2. We argue that the alpine climate does not select for any specific leaf surface properties such as high leaf pubescence.
3. We further hypothesize that the CO_2 uptake efficiency reflected in $\delta^{13}CO_2$ increases with elevation in response to reduced atmospheric pressure (CO_2 partial pressure) and not in response to declining temperature.

While many previous attempts used phylogenetically unbalanced samples and/or had elevation effects confounded with moisture gradients (Körner 2007), the analysis presented here does, for the first time, provide unbiased, strictly temperature- and/or pressure-related signals for a large sample of plant species.

Materials and methods

Study areas

The study areas covered by our herbarium survey in south-central Europe include the Swiss Alps and the nearby French and Italian Alps. Most collections were made between 45°30′–47°30′N and 6°30′–10°30′E, which is an area c. 200 km long and c. 100 km wide. The elevational range covered by our data extends from 300 to more than 3,000 m a.s.l. The elevation of the treeline varies between 1,800 m in the front ranges and 2,300 m in the central ranges. The naturally treeless alpine belt with mostly closed vegetation covers a range of ca. 500–800 m above the treeline, with the nival belt above, extending beyond 3,000 m at many places. The natural flora below the treeline is conifer forest, yielding terrain to deciduous forests below 1,000 m elevation. Due to millennia of land use, the montane forest belt is fragmented, and formerly restricted low-stature vegetation now covers vast areas, home to many of the species studied here.

The climate of this area falls in the transition between the temperate zone of Central Europe and the northern edge of the Mediterranean. Annual mean temperatures at low elevation are around 9°C and the warmest month means are ca. 19°C, with a linear altitudinal lapse rate of temperature of ca. 0.55 K 100 m^{-1} during the growing season. Precipitation is between 700 and 1,000 mm at low elevation and increases with altitude.

For testing pressure versus temperature effects on C isotope discrimination, we also included herbarium material from northern Sweden (69°N; Abisko, ca. 300 m a.s.l.; largely *Carex* species) and the Svalbard archipelago (78–79°N; Spitzbergen, ca. 10–50 m a.s.l.; largely *Saxifraga* species). The polar climate in these regions offers an 8- to 12-week growing season, 24 h daylight in summer and mean air temperatures during the growing season of around 6–8°C, with northern Sweden more similar to the lower alpine belt in the Alps, and Svalbard more similar to the upper alpine belt. Moisture availability is not problematic in any of these polar areas, although annual precipitation is typically low.

Plant samples

Following the Flora Alpina (Aeschimann et al. 2004), we chose the three species-rich genera *Saxifraga*, *Potentilla* and *Carex* for our survey. Each genus is represented by more than 30 species in the herbaria of the Institute of Botany (University of Basel) and of the Basler Botanische Gesellschaft (Basel Botanical Society). On average, each species has been collected over the past 150 years mostly more than 30 times across the Alps. From these multiple collections per species we selected five well-preserved vouchers per species with complete geo-references, collection date, etc., which covered the highest and lowest collections as well as mid elevation collections for a given species. Most plants from the Alps were sampled between 1880 and 1980, with no historical sampling bias (collection

dates randomly spread across all elevations). The collections from Svalbard (herbarium at UNIS, Longyearbyen, Spitzbergen) were all made in the 1990s. The collections from Abisko, northern Sweden, were made in 2000 (personal collection by J. Stöcklin, Basel).

For the Alps, the total of 30 non-shade species of *Potentilla* comprises 137 valid samples (25 of the species had five suitable vouchers, a few had between one and four). There are 35 *Saxifraga* species, comprising a total of 155 vouchers (nine species with between two and four vouchers only), and for *Carex*, 82 species comprising 384 vouchers (nine species with between one and four vouchers only; Table S1). The arctic samples comprise 14 *Carex* and two *Saxifraga* species from northern Sweden, and two *Potentilla*, eight *Saxifraga* and three *Carex* species from Svalbard (Table S2).

Morphological and anatomical plant traits measured included leaf length, inflorescence size, plant height and leaf pubescence. In *Saxifraga*, leaf length was measured for rosette leaves only, and in the two other genera, study leaves were attached to stems/tillers. The inflorescence size of *Carex* refers to its spike length, and the diameter of individual inflorescences is used as inflorescence size of the other genera. The pubescence of the upper side of the leaf was checked by a magnification lens and was ranked into six classes (from 0 for no to 5 for extreme pubescence). Whole plant or leaf and inflorescence size can reflect the vegetative and reproductive effort of plants, respectively, with the ratio between inflorescence and leaf size or whole plant height representing a sort of reproductive effort in relative terms (Fabbro and Körner 2004): ratio = ln (inflorescence size/leaf length + 1). When the ratio was 0.693, namely ln(2), the length of inflorescence and leaf were the same. If the ratio was greater than 0.693, the inflorescence was longer than leaves, and vice versa. If the ratio increased with altitude, this means that, compared to the change in leaf length, the inflorescence is getting relatively bigger. The same equation applies to the ratio between inflorescence size and plant height or leaf size and plant height. Tissue density does not change significantly with elevation, hence these biometric relationships represent trends in plant biomass allocation (Fabbro and Körner 2004).

Indicator values of all species

Indicator values of species for temperature, moisture and light preferences were obtained from Ellenberg (1974) and Landolt (1977). The light indicator value was used to identify and eliminate the few taxa known to have a shade preference, so that the temperature and moisture gradients are not further confounded with light effects. The final sample uses species only with a light indicator value ≥3 (with 5 the maximum). The few shade species were treated as a separate group. The moisture indicator value was employed to test (but then also to eliminate from the further elevation-oriented analysis) all species with a moisture indicator value <3 (drought-adapted species). Through this procedure we lost only very few species from lower elevations. Had we not excluded these species, the results would have been hardly affected.

C isotope analysis

The isotopic value is expressed as the relative deviation from the international standard Vienna Pee Dee belemnite and is expressed in the delta notation: $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$ (‰), where R represents the $^{13}C/^{12}C$ ratio of the sample and the standard, respectively. The concentration of the heavy ^{13}C isotope in plants is less than that in the atmosphere. During photosynthesis the heavier $^{13}CO_2$ is discriminated against the lighter $^{12}CO_2$: (1) via diffusion of CO_2 from the ambient air into the intercellular spaces, where the diffusion velocity of the lighter isotope is faster than that of the heavier isotope; and (2) during the biochemical fixation by Rubisco, depending on the photosynthetic rate and the stomatal conductance. The organic plant material is therefore depleted in ^{13}C. Farquhar et al. (1982) formulated this relationship between photosynthesis and stomatal regulation, which results in a distinct isotopic ratio as $\Delta = a + (b - a) \times c_i/c_a$ with Δ as the discrimination of ^{13}C against ^{12}C, $a = 4.4$‰, the fractionation of CO_2 through diffusion, $b = 27$‰, the fractionation by Rubisco, c_i the substomatal and c_a the ambient CO_2 concentration. When plants are exposed to any environmental impact causing either a reduction in stomatal conductance or photosynthesis (drought, shade, etc.) resulting in a change of the c_i/c_a ratio, this will be reflected in a change of the $^{13}C/^{12}C$ isotope ratio in organic matter (e.g. increasing drought will lead to stomatal closure and a decreasing c_i/c_a ratio, reflected in a reduced Δ). Thus Δ or the $\delta^{13}C$ value are indicators for changes in photosynthesis and stomatal conductance in response to environmental changes. The $\delta^{13}C$ value is a powerful tool, which reflects the stomatal (water) versus carboxylation limitation of CO_2 uptake, and has therefore often been seen as a proxy for water limitation (frequent stomatal closure; Rundel et al. 1988; Saurer and Siegwolf 2007).

When elevational gradients without any significant moisture limitation were compared, the ^{13}C isotope discrimination of plants decreased with increasing elevation (either due to reduced temperature or atmospheric pressure; Körner et al. 1988, 1991). When low elevation moisture stress comes into play, this elevational trend in $\delta^{13}C$ can be equilibrated or even reverted. Hence, moisture gradients can drive $\delta^{13}C$ in any direction and must be accounted for in any analysis of elevational gradients. In order to separate possible pressure

from temperature influences, we included congeneric samples (in part the same species) from the polar region, which grow at high atmospheric pressure but at a similar low temperature to the high-elevation species in the Alps.

Within the five (in a few cases, fewer) vouchers per species, we pooled the 2–3 samples from a species' 'mid-range' of elevation for ^{13}C isotope analysis across genera (the replicate is the species). For intra-specific responses to elevation we took the lowest and highest elevation sample (the elevational range was at least 1 km) for four to ten species per genus, with light and moisture indicator values of 3 or higher). We used similar amounts of dry leaf material per voucher that was ground with a steel ball mill, and 0.6–0.8 mg of dry powder was weighed into tin capsules. The capsules were combusted to CO_2 under excess oxygen in an elemental analyser (EA-1110, Carlo Erba Thermoquest, Milan). The combustion products were transferred in the helium stream through a variable open-split interface (Conflo II, Finnigan Mat, Bremen), which was linked to a mass spectrometer (Delta S, Thermo Finnigan Mat), operating in the continuous flow mode (Werner et al. 1999).

Along with the increase in atmospheric CO_2 concentration over the last 150 years resulting from fossil fuel and increased biomass burning, the atmospheric $^{13}C/^{12}C$ isotope ratio has declined (Suess effect; cf. Keeling 1979). This gradual change in the $^{13}C/^{12}C$ isotope ratio of atmospheric CO_2 is reflected in the $\delta^{13}C$ of concurrently produced organic material. Therefore, we corrected all $\delta^{13}C$ values to pre-industrial values according to Francey et al. (1999), so that each sample with its specific age was corrected to the isotopic signal of the respective year when the sample was harvested. This correction allows the comparison of all samples with each other, irrespective of their year of harvest. Furthermore, the rise of atmospheric CO_2 concentration over the considered sampling period from 290 to 380 p.p.m. might have changed the CO_2 gradient across the leaf epidermis and with this, shifted $\delta^{13}C$ values to more negative values. Yet, based on results from tree ring studies, it was found that plants can compensate for the increasing CO_2 either with an increase in photosynthesis, or a decrease in stomatal conductance, or both (Saurer and Siegwolf 2007). Since sampling was completely randomly spread over the last 150 years (median around 1920, no significant year × elevation interaction), this might add noise to our signal, since different species might respond differently, but this would not affect the regression against elevation. Similarly, any change in climate over the sampling period would be random with respect to sampling elevation.

Data analysis

In a first analysis we used individual species as independent data points and used linear least square regression analysis to test for linear relationships between elevation and functional plant traits, namely $\delta^{13}C$, plant height, inflorescence size, leaf length, leaf pubescence, inflorescence size–plant height ratio, inflorescence size–leaf length ratio and leaf length–plant height ratio.

To assess the possible impact of phylogeny, we applied two approaches. First, we performed phylogenetic autocorrelation as proposed by Gittleman and Kot (1990) to test whether the elevational distribution of species, which represents the principle independent variable of the study, was influenced by phylogeny. Second, we calculated phylogenetic independent contrasts (PICs) across a phylogeny followed by a regression analysis with an intercept of zero that paralleled the analyses between plant traits and elevation using species as data points. We calculated average values for elevation and trait values across all samples analysed per species. A phylogenetic hypothesis was assembled based on the BIOFLOR database (Durka 2002; Fig. S1) including 77 of the 82 *Carex* species, 25 of 30 *Potentilla* and all 35 *Saxifraga* species. We used Grafen's method to calculate branch lengths with $\rho = 0.5$, and exchanged polytomies into branches of zero branch length. PICs were calculated with Felsenstein's (1985) method. Phylogenetic analyses were performed using functions of ape (Paradis 2006) in R.

Results

Plant indicator values and elevation

Since elevational gradients may include both temperature and moisture gradients, we first tested the actual elevational position of taxa and their temperature and moisture indicator values separately. In a second step we tested the temperature indicator values for all species that exhibit no preference for dry habitats (water indicator value 3 or larger). Indeed, there is a strong linear correlation between the mean elevation of species and the temperature indicator value taken from the literature, yielding, for the first time, a quantitative confirmation of indicator values (Fig. 1). The moisture indicator values in these species do not show any correlation with elevation when tested across the full range of elevations. A few low elevation taxa are attributed as preferentially dry habitat species by their indicator value. However, the absence or presence of these few taxa did not affect the correlation between the temperature indicator value and elevation (i.e. actual temperature; not shown), suggesting a dominant temperature and/or pressure effect on the species' elevational distribution in the given subcontinental region. Given the confidence that there is no systematic confounding influence of drought on our sample of species, we explored elevational plant responses.

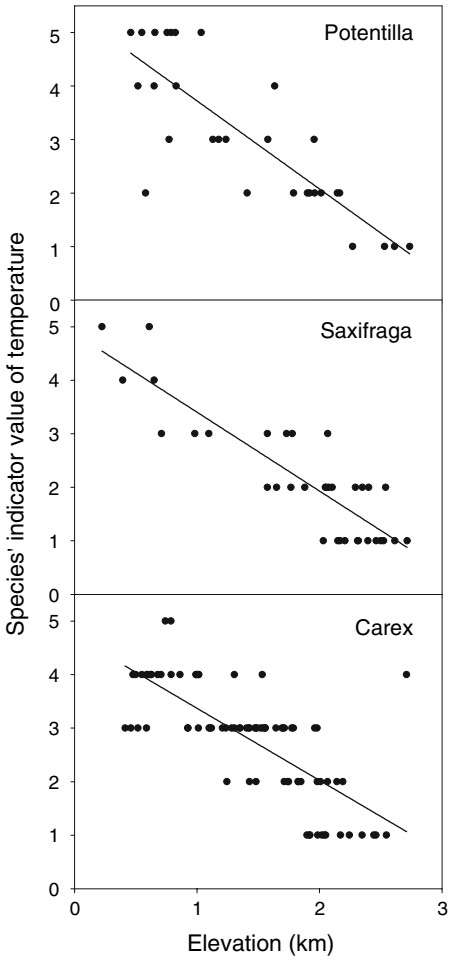

Fig. 1 The relationship between species' mean elevation, derived from five herbarium vouchers per species, and their temperature indicator value (linear least squares regression). *Potentilla,* 30 species ($y = -1.6x + 5.4$, $r^2 = 0.69$, $P < 0.0001$, $n = 30$); *Saxifraga,* 35 species ($y = -1.5x + 4.9$, $r^2 = 0.77$, $P < 0.0001$, $n = 35$); *Carex*, 82 species ($y = -1.3x + 4.7$, $r^2 = 0.55$, $P < 0.0001$, $n = 82$). All species selected are from open habitats (no shade species)

Phylogenetic autocorrelation analysis showed that within genera the elevational position of species was not confounded by phylogeny ($P = 0.178$, 0.736 and 0.994 for *Carex*, *Potentilla* and *Saxifraga*, respectively). However, across the whole data this was not the case ($P = 0.0007$), reflecting the fact that *Saxifraga* species, on average, were sampled from slightly higher elevations (1.86 km, SD 0.67) than *Carex* (1.44 km SD 0.57) or *Potentilla* (1.42 km, SD 0.69).

Elevational changes in morphological and anatomical traits

Plant height and leaf length significantly decrease with elevation in the three genera, while absolute inflorescence size decreases in *Saxifraga* and *Carex* but does not change in *Potentilla* (Fig. 2). Pubescence of leaves does not exhibit any trend with elevation in *Potentilla* and *Carex*, and shows a reduction with elevation in *Saxifraga*. In the two insect-pollinated genera *Potentilla* and *Saxifraga*, relative inflorescence size increases with elevation (asymmetric allometry), whereas in *Carex* (wind-pollinated) relative inflorescence size does not change with elevation (symmetric allometry). The PIC analysis at genus level confirmed the results. Out of the 14 significant species–trait correlations found, eight were confirmed by the PIC analysis, while for the rest, the same trend was observed with the sign of the correlation being identical but non-significant (Fig. S2). All non-significant relationships were also non-significant in the PIC analyses. The PIC analysis combining all species into one data set showed a general change with elevation of plant height, inflorescence size, leaf length, inflorescence/leaf ratio and inflorescence/height ratio but no change of pubescence and leaf/height ratio (Fig. S2).

To test for moisture-related changes in traits, we grouped the species for each genus into a warm and cold indicator value group (i.e. elevational groups) and tested within each group the correlation between traits and the moisture indicator values (Table 1). Plant height, leaf length and inflorescence size are getting larger with increasing moisture preference in *Carex* species with a warm habitat preference, but all other species across genera do not show any relationship between measures of size and moisture indicator values. There was also no trend in pubescence with species' moisture preference.

Elevation responses of $\delta^{13}C$

Values of $\delta^{13}C$ correlate significantly with elevation for all three genera (Fig. 3), which means the discrimination of the heavy C isotope decreases with elevation across taxa. The PIC analysis at genus level fully confirmed the positive correlation of $\delta^{13}C$ with elevation ($P < 0.001$; Figs. 3, S2). The increasing $\delta^{13}C$ values in *Potentilla* and *Carex* are nearly the same, about 1.2‰ km^{-1} of elevation. The increase in $\delta^{13}C$ in *Saxifraga* tended to be more pronounced, at about 1.8‰ km^{-1} elevation, the difference in the slope between *Saxifraga* and the two other genera being marginally significant ($P = 0.064$). The mean rate of change for all three genera is 1.4‰ km^{-1}.

The ranking of species by their indicator value for moisture does not correlate with $\delta^{13}C$ (not shown). The six *Carex* species ranked as shade species by their light indicator value were from 600 to 1,100 m elevation, and their mean $\delta^{13}C$ (-27.4 ± 1.0‰) is lower (more negative) than that of the 25 non-shade species of the same elevation (-26.2 ± 1.2‰; one-way ANOVA, $P < 0.05$). The sample did not include sufficient numbers of shade species of *Potentilla* and *Saxifraga* to permit such a comparison for these.

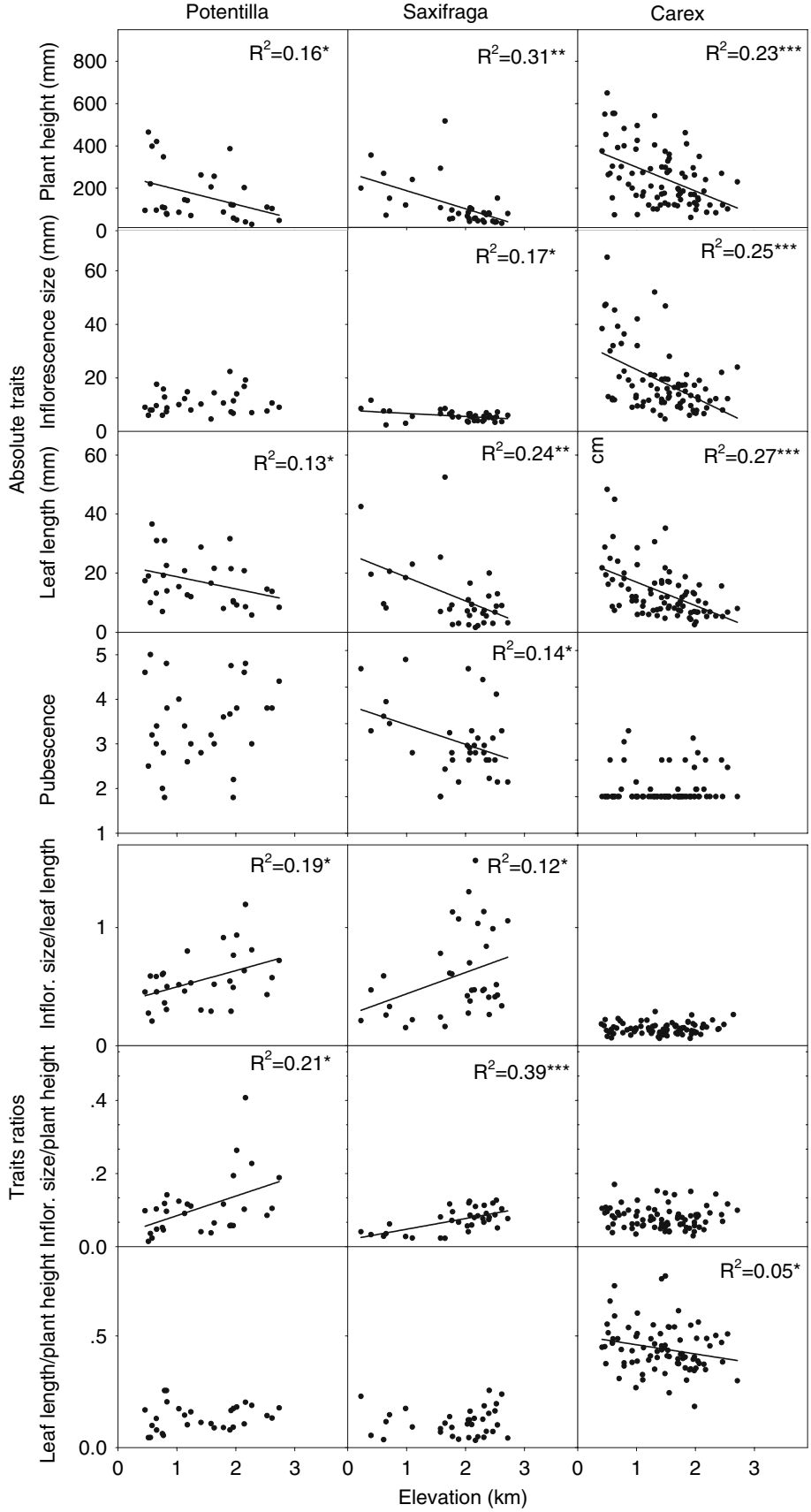

Fig. 2 Responses of plant functional traits to elevation (mean value of five vouchers per species). *Potentilla*, 30 species; *Saxifraga*, 35 species; *Carex*, 82 species. Note the scale change in *Carex* leaf length. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Note that a similar graph with phylogenetically independent contrasts (PIC) is available in the supplementary material as Fig. S2

Table 1 Correlations (r^2) between plant biometrics and the moisture indicator value in *Carex*

	Warm[a]	Cold[a]	Total
Plant height (*P*)	+0.41**	+0.38*	+0.38**
Inflorescence size (*I*)	+0.43**	n.s.	+0.37**
Leaf length (*L*)	+0.42**	n.s.	+0.38**
I/*L*	n.s.	−0.57**	n.s.
I/*P*	n.s.	−0.40*	n.s.
L/*P*	n.s.	n.s.	n.s.
Number of species	55	27	82

*$P < 0.05$, **$P < 0.01$, n.s. non-significant

[a] Species' temperature indicator values (between 1 and 2 for cold, and between 3 and 5 for warm)

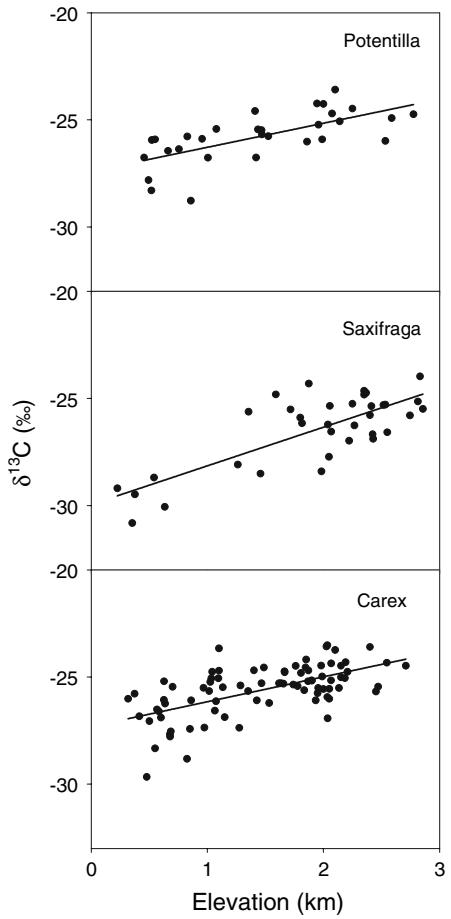

Fig. 3 Elevational responses of leaf stable C isotope composition (δ^{13}C). *Potentilla*, $y = 1.1x - 27$, $r^2 = 0.41$, $P < 0.0001$, $n = 30$; *Saxifraga*, $y = 1.8x - 30$, $r^2 = 0.50$, $P < 0.0001$, $n = 35$; *Carex*, $y = 1.2x - 27$, $r^2 = 0.34$, $P < 0.0001$, $n = 82$. Species are from open habitats only

Five *Potentilla*, nine *Saxifraga* and ten *Carex* species were selected for intra-specific comparisons (Table 2). The average increase in δ^{13}C within these species is ca. 0.95‰ km^{-1}, nearly one-third lower than in the all-genera inter-specific comparison (Fig. 3). Therefore, the elevational adjustment of CO_2 uptake efficiency is weaker at the individual plant and/or genotype level than at species level. However, particularly in *Saxifraga*, the intraspecific contrasts differ so much (−2.87 to +2.41‰ km^{-1}) that a larger sample would be needed.

Given the very clear relationship between elevation and inter-specific δ^{13}C and the absence of moisture gradients, the question remains unresolved whether temperature or pressure (partial pressure of CO_2) is controlling these trends. The data for the congeneric polar species provide strong evidence that pressure is the dominant factor. The δ^{13}C values for the samples from polar latitudes match those from warm, low elevations in the Alps (Table 3; Fig. 3). In *Carex* and *Potentilla*, values from only 11° south of the North Pole (near sea level) are not different from those obtained in warm, low elevation sites in southern

Table 2 Intra-specific differences of stable C isotope composition (δ^{13}C) across elevation (‰ km^{-1})

Species[a]	δ^{13}C difference
Potentilla anserina	1.26
Potentilla aurea	0.47
Potentilla crantzii	1.17
Potentilla erecta	0.47
Potentilla palustris	1.32
Mean ($n = 5$)	0.94 ± 0.4
Saxifraga androsacea	0.84
Saxifraga biflora spp. *macropetala*	−0.48
Saxifraga cotyledon	0.10
Saxifraga exarata spp. *moschata*	1.08
Saxifraga muscoides	2.26
Saxifraga mutata	2.41
Saxifraga sedoides	2.24
Saxifraga seguieri	−2.87
Saxifraga stellaris	1.22
Mean ($n = 9$)	0.76 ± 1.7
Carex appropinquata	0.74
Carex fimbriata	1.26
Carex flava	2.07
Carex lasiocarpa	−0.38
Carex nigra	−0.81
Carex paniculata	1.09
Carex paupercula	0.48
Carex pilulifera	3.54
Carex vesicaria	1.64
Carex viridula	1.21
Mean ($n = 10$)	1.11 ± 1.2

[a] All selected species are from open, non-water-limited habitats, which means the light and moisture indicator values of these species are 3 or higher

Table 3 The mean values of $\delta^{13}C$ (‰) of species in the Arctic compared with those from the Alps collected at three elevations

	Potentilla	*Saxifraga*	*Carex*
Arctic	−27.3 ± 0.7	−27.6 ± 1.0	−27.3 ± 1.3
Alps			
Altitude <1 km	−26.8 ± 1.1	−29.7 ± 0.8*	−26.8 ± 1.2
Altitude1–2 km	−25.6 ± 0.7*	−26.4 ± 1.6*	−25.6 ± 0.7*
Altitude >2 km	−24.7 ± 0.7*	−25.8 ± 0.9*	−24.7 ± 0.9*

*$P < 0.05$ (significant difference from the polar reference)

The number of species at low, mid and high elevation is ten, 12, eight for *Potentilla* in the Alps (two in the Arctic); five, nine, and 21 for *Saxifraga* (ten); and 21, 40, 21 for *Carex* (17). Two of the polar *Saxifraga* and 14 of the polar *Carex* species are from 69° latitude (northern Sweden, ca. 300 m a.s.l.), the other two *Potentilla*, eight *Saxifraga* and three *Carex* species from the polar group are from 78–79° latitude (Spitzbergen, ca. 30–50 m a.s.l.)

Europe (46°N). Only in *Saxifraga*, the species with the steepest elevational gradient in $\delta^{13}C$, does $\delta^{13}C$ differ slightly between low elevations in the Alps and the arctic sites. Overall, temperature does not exhibit a significant influence on $\delta^{13}C$, and air pressure remains the dominant driver of the elevational gradient in $\delta^{13}C$ in plant tissue.

Discussion

This study illustrates the power of large plant archives for exploring general patterns of plant adaptation to the environment (Spehn and Körner 2009). In the past, a lot of evidence from diverse species mixes helped to distinguish some trends of plant responses along elevational gradients (Körner et al. 1989, 1991; Fabbro and Körner 2004). However, the unresolved issue of potential phylogenetic bias remained. Closely related species may share both life history traits and preferred environmental conditions due to phylogenetic niche conservatism (Prinzing et al. 2001). For example, 50% of variation in the temperature niche position of European plant species as indicated by the temperature indicator is explained at higher taxonomic levels like genus and family (Prinzing et al. 2001). This may lead to biases in analyses of trait correlations, especially in analyses across a limited number of taxa. Alpine regions may be especially prone to such effects due to endemism and species-rich genera that predominantly radiated in alpine regions, like *Saxifraga*. Here, we offer the first assessment of elevational trends in both morphological and physiological traits across a large subcontinental region taking into account phylogenetic relationships. The PIC analysis underlines that the patterns found are not constrained by phylogeny at the species level. The existence of ecological indicator values for most of the studied species added value to our analysis, by permitting a stratification of samples by species' climate preference criteria. The combination of indicator values with morphological plant traits and stable isotope data across elevations of a large mountain area yielded very robust signals, unbiased by environmental drivers not universally related to elevation (water and light regime). The inclusion of arctic species permitted us to dismiss low temperature as a major driver of the observed elevational adjustment of the photosynthetic machinery as reflected by the increase in $\delta^{13}C$ with elevation.

The 147 species from three genera from three different plant families yielded consistent responses to the climatic changes associated with elevation, with a reduction in plant size and leaf length, a constant relative inflorescence size in the wind-pollinated genus *Carex* and an increase in inflorescence size relative to leaf and plant size in the two insect-pollinated genera *Saxifraga* and *Potentilla*. From other studies (Zhu et al. 2009; Krummen and Körner in preparation), we know that the trend seen in *Carex* is in line with that seen in Poaceae. These wind-pollinated taxa do not reduce their relative investment in sexual reproduction at higher altitudes. Wind-pollinated species are characterized by high pollen production. The maintenance of reproductive allometries in wind-pollinated species may also be a result of the constrained possibilities of mating system evolution as wind-pollinated species are generally less variable than insect-pollinated species (Michalski and Durka 2009). The patterns seen in *Saxifraga* and *Potentilla* confirm the trend found in a non-phylogenetically-balanced sample by Fabbro and Körner (2004). Hence, there is clear evidence for a relative enhancement of a plant's effort to have larger inflorescences as elevation increases if the plant depends on insect pollination. Moreover, increased reproductive investment into inflorescences seems to be based on the necessity for outcrossing, as it has been shown that the proportion of outcrossing plants increases with elevation (Kühn et al. 2006). Reproductive assurance, i.e. increased self-pollination, is one potential response to harsh environmental conditions and reduced resource and pollinator availability. However, for our alpine set of wind- and insect-pollinated species the maintenance or even the increase in relative inflorescence size disproved reproductive assurance, at least at the morphological level.

Leaf pubescence has often been claimed to be higher in alpine compared to lowland plants. This false belief must originate from the charismatic nature of some well-known species. However, most alpine plant species do not differ in this respect from lowland taxa (Körner 2003), and the current systematic search for such trends showed absolutely no increase in pubescence with elevation. The driving forces for leaf pubescence do not change with elevation and neither temperature as such nor temperature-related water relations appear to matter (smaller plants get warmer and thus,

exhibit steeper vapour pressure gradients to the free atmosphere; e.g. Smith and Geller 1979; Körner and De Moraes 1979). In *Saxifraga*, leaf pubescence is even reduced at high elevation, which may be associated with very small and compact plant size. Presumably, leaf herbivory or the risk of pathogen infections (facilitated by leaf wetting) also plays some role, but there is no indication that the significance of such influences changes with elevation across the taxa studied.

Stable isotopes have become an indispensable tool in functional ecology. Here we provide unconfounded evidence that plant discrimination of the heavy ^{13}C isotope decreases as elevation increases. We corrected for historical trends in atmospheric $\delta^{13}C$, and excluded—as far as possible—any potential bias by water shortage and by phylogeny. Previous surveys had already suggested a mean 1.1‰ increase in $\delta^{13}C$ km^{-1} in elevation (Körner et al. 1991), provided there was no confounding with drought gradients (Körner 2007). It appears that the overall signal we found is a combination of within-species adjustments (two-thirds of the signal; either acclimative or genotypic) and species-specific evolutionary responses (one-third of the signal, based on our subsample of within-species trends). The coherence of our congeneric sampling of species removed much of the noise that had been seen in earlier global data sets (Körner et al. 1988, 1991), and, with a 1.4‰ increase in $\delta^{13}C$ km^{-1}, the trend is in fact steeper than previously reported. We find it remarkable that the genus *Saxifraga* that reaches the highest elevations and highest polar latitudes also exhibits the steepest response of 1.8‰ km^{-1}. We do not have a good explanation for this, but presumably, the inherently greater leaf thickness in most species of this genus plays a role, and the steepness of the gradient is driven by the very negative values at low elevation species. Given water was eliminated as a driver by careful sampling, it remained to be shown whether the elevational changes in $\delta^{13}C$ seen across these 147 species are related to temperature or to atmospheric pressure (both changing in parallel with elevation)?

These new data permit us to resolve this question. The data from congeneric samples from low elevation in polar regions indicate that atmospheric pressure rather than temperature (both decreasing with elevation) is the driving factor. We cannot resolve whether partial pressure or total pressure causes the change, but adjustment of photosynthesis to reduced partial pressure at high elevation had been evidenced (a steeper initial A/c_i slope; Körner and Diemer 1987; Terashima et al. 1995).

If it were temperature that caused a reduction in ^{13}C discrimination with elevation, we should see a positive correlation between $^{13}CO_2$ discrimination and temperature, which is not the case. In fact, Saurer et al. (2008) had reported a negative relationship between ^{13}C discrimination and temperature, most likely related to a steeper leaf to air vapour pressure difference, enhancing transpiration. So plants may more often be reducing stomatal conductance to prevent excess water loss, which leads to a reduced c_i/c_a ratio and a reduced ^{13}C discrimination. In an arctic/alpine setting as chosen here, moisture stress is, however, not a likely explanation (Körner 2003). Moreover, the climatic relatedness of C isotope data in plants is based on the assumption that we know which climate and which period of the year had contributed most to the signal preserved in biomass. The smaller the plants are, the more decoupled they are aerodynamically from the free atmosphere and the more they "engineer" a microclimate that deviates substantially from conventional meteorological data (Körner 2003). For alpine plants it is known that their photosynthetic temperature optimum is at similar temperatures to their congeneric lowland relatives (Körner and Diemer 1987), thus reflecting physiological adjustment to the most favourable periods during the growing season. Timing of development and growth may cause C acquisition to be restricted to short warm periods which are not mirrored in longer term climatological records (cf. the recent observation by Helliker and Richter 2008). This means that cold climate plants have not necessarily fixed the C we can sample during cold periods, just as plants from dry regions may have fixed most of their C during brief, wet spells. With this in mind, temperature effects on $\delta^{13}C$ are even less likely. The fact that we found the steepest gradient in $\delta^{13}C$ in the genus *Saxifraga* with the smallest, most prostrate growth habit (greatest warming compared to free atmosphere) further reduces the likelihood that temperature per se plays a role in elevational trends in $\delta^{13}C$.

Should small compact plant size cause leaves to experience more ^{13}C depleted CO_2 respired from the soil, the trend should go in the opposite direction, i.e. show more negative values in small stature, high altitude plants, which is clearly not the case. It had been shown earlier across a broad sample of species that upright alpine plants do not differ in their $\delta^{13}C$ from prostrate plants (Körner et al. 1991). There is also no difference in plant size between the sampled alpine and arctic taxa.

This study has thus resolved a number of long-standing ecological questions related to plant life along elevational gradients. Insect-pollinated but not wind-pollinated plants increase their inflorescence size relative to body size, enhancing visibility at high elevation, leaves do not increase their surface roughness (pubescence) with elevation, thus exhibit no elevation specific structural adjustment of reflectivity, wettability or surface aerodynamics, etc., often associated with high pubescence. The adjustment of leaf gas exchange to a high elevation reflects a pressure- (presumably CO_2 partial pressure) rather than temperature-related adaptation. Well-selected herbarium material appeared to be an ideal tool with which to explore such adaptive responses over

large geographic areas, and the novel analytical tools such as mass spectrometry attribute new added value to such old collections. The information accumulated in such archives could not be collected today with reasonable effort and thus, these archives offer a unique source of samples for testing ecological theory over large geographical areas (Körner et al. 2007; Spehn and Körner 2009).

Acknowledgements We thank Heinz Schneider, the curator of the Institute of Botany Herbarium in Basel, for advice, and the Basel Botanical Society for permitting us to co-sample their collections. We thank Inger Alsos and Allan Bursas from Unis, Longyearbyen (Svalbard) for helping with samples from their herbarium. Jürg Stöcklin, Basel, made the *Carex* collections in northern Sweden. He, and two anonymous experts, and the handling editor Kouki Hikosaka provided most helpful comments. We also acknowledge laboratory and logistic help by Eva Spehn, Matthias Saurer, Martin Krnoul, Susanna Pelaez-Riedl and Olivier Bignucolo. The China Scholarship Council supported the first author during the visiting scholarship at the University of Basel that led to this work.

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Appendix

Fig. S1 Phylogeny of the *Carex*, *Potentilla* and *Saxifraga* species investigated.

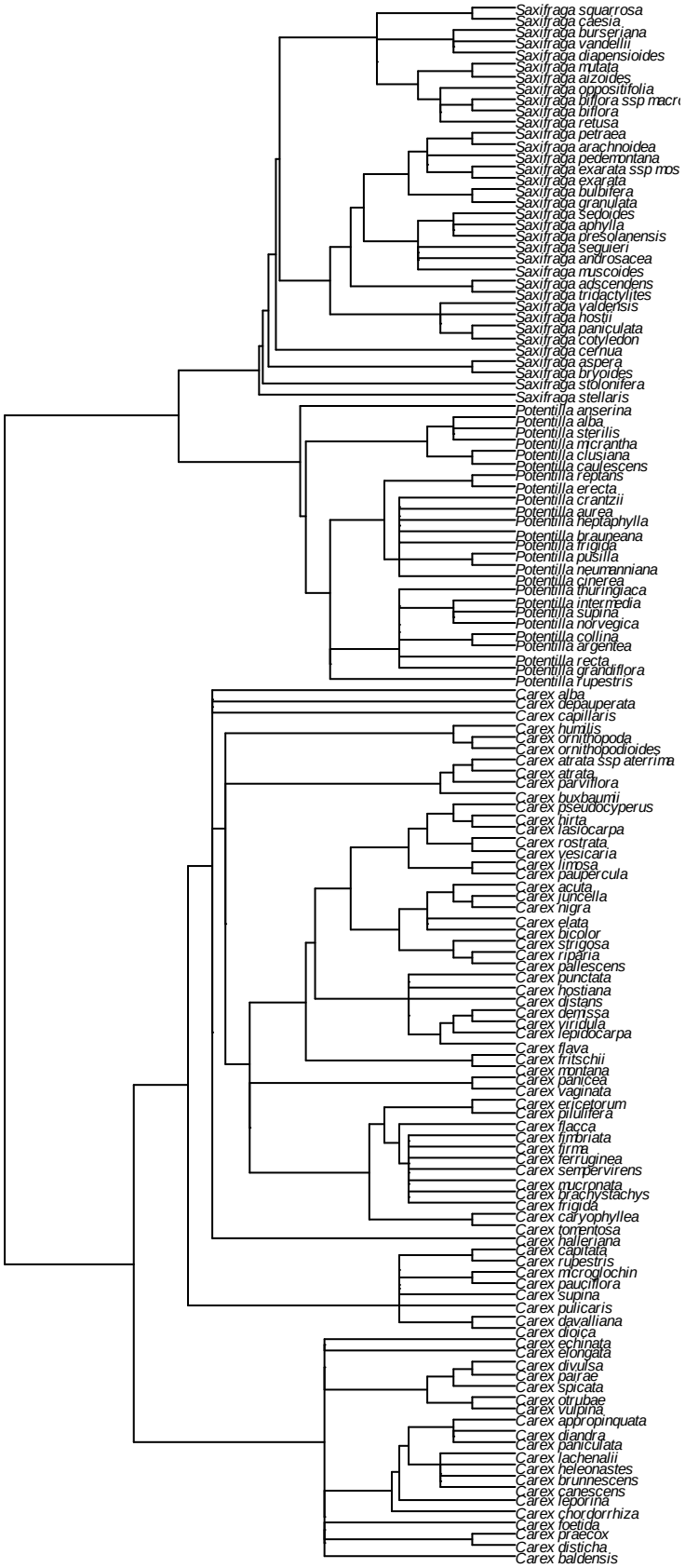

Fig. S2 Regression of phylogenetic independent contrasts of $\delta^{13}C$, plant height, inflorescence size, leaf length, pubescence, inflor. size/leaf length ratio, inflor. size/plant height ratio and leaf length/plant height ratio with phylogenetic independent contrasts of elevation for 25 *Potentilla*, 35 *Saxifraga*, 77 *Carex* and for all species. Regressions were forced through the origin, and only the significant regression lines were shown in the figures. *, ** and *** indicate significances at $p<0.05$, $p<0.01$ and $p<0.001$ respectively.

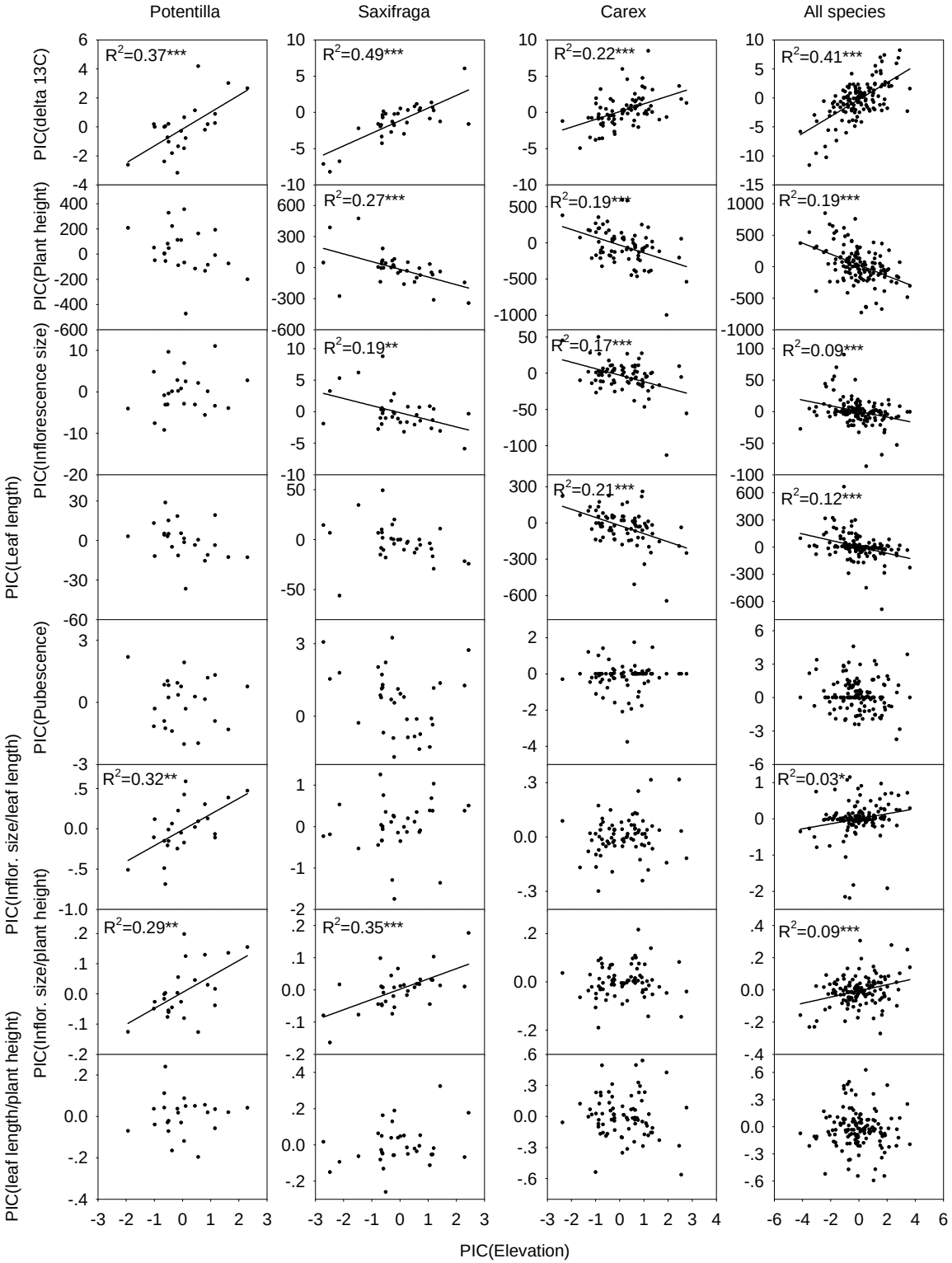

Table S1 Species collected from the Alps

Potentilla alba	*Saxifraga adscdendens*	*Carex acuta*
Potentilla anserina	*Saxifraga aizoides*	*Carex alba*
Potentilla argentea	*Saxifraga androsacea*	*Carex appropinquata*
Potentilla aurea	*Saxifraga aphylla*	*Carex atrata*
Potentilla brauneana	*Saxifraga arachnoidea*	*Carex atrata* ssp *aterrima*
Potentilla caulescens	*Saxifraga aspera*	*Carex atrofusca*
Potentilla cinerea	*Saxifraga biflora*	*Carex baldensis*
Potentilla clusiana	*Saxifraga biflora macropetala*	*Carex bicolor*
Potentilla collina	*Saxifraga bryoides*	*Carex brachystachys*
Potentilla crantzii	*Saxifraga bulbifera*	*Carex brunnescens*
Potentilla delphinensis	*Saxifraga burseriana*	*Carex buxbaumii*
Potentilla erecta	*Saxifraga caesia*	*Carex canescens*
Potentilla frigida	*Saxifraga cernua*	*Carex capillaris*
Potentilla grammopetala	*Saxifraga cotyledon*	*Carex capitata*
Potentilla grandiflora	*Saxifraga diapensioides*	*Carex caryophyllea*
Potentilla hetpaphylla	*Saxifraga exarata*	*Carex chordorrhiza*
Potentilla intermedia	*Saxifraga exarata moschata*	*Carex curvula*
Potentilla micrantha	*Saxifraga granulata*	*Carex davalliana*
Potentilla multifida	*Saxifraga hostii*	*Carex demissa*
Potentilla neumanniana	*Saxifraga muscoides*	*Carex depauperata*
Potentilla nitida	*Saxifraga mutata*	*Carex diandra*
Potentilla nivea	*Saxifraga oppositifolia*	*Carex dioica*
Potentilla norvegica	*Saxifraga paniculata*	*Carex distans*
Potentilla pusilla	*Saxifraga pedemontana*	*Carex disticha*
Potentilla recta	*Saxifraga petraea*	*Carex divulsa*
Potentilla reptans	*Saxifraga presolanensis*	*Carex echinata*
Potentilla rupestris	*Saxifraga retusa*	*Carex elata*
Potentilla sterilis	*Saxifraga sedoides*	*Carex elongata*
Potentilla supina	*Saxifraga seguieri*	*Carex ericetorum*
Potentilla thuringiaca	*Saxifraga squarrosa*	*Carex ferruginea*
	Saxifraga stellaris	*Carex fimbriata*
	Saxifraga stolonifera	*Carex firma*
	Saxifraga tridactylites	*Carex flacca*
	Saxifraga valdensis	*Carex flava*
	Saxifraga vandellii	*Carex foetida*
		Carex frigida
		Carex fritschii
		Carex halleriana
		Carex heleonastes
		Carex hirta
		Carex hostiana
		Carex humilis
		Carex juncella
		Carex lachenalii
		Carex lasiocarpa
		Carex lepidocarpa
		Carex leporina
		Carex limosa
		Carex liparocarpos

Carex maritima
Carex microglochin
Carex montana
Carex mucronata
Carex nigra
Carex norvegica
Carex ornithopoda
Carex ornithopodioides
Carex otrubae
Carex pairae
Carex pallescens
Carex panicea
Carex paniculata
Carex parviflora
Carex pauciflora
Carex paupercula
Carex pilulifera
Carex praecox
Carex pseudocyperus
Carex pulicaris
Carex punctata
Carex riparia
Carex rostrata
Carex rupestris
Carex sempervirens
Carex spicata
Carex strigosa
Carex supina
Carex tomentosa
Carex vaginata
Carex vesicaria
Carex viridula
Carex vulpina

Table S2 Species collected from the Arctics

Potentilla hyparctica	*Saxifraga cernua**	*Carex atrata**
Potentilla pulchella	*Saxifraga oppositifolia**	*Carex atrofusca**
	Saxifraga cernua	*Carex buxbaumii**
	Saxifraga cespitosa	*Carex canescens**
	Saxifraga flagellaris	*Carex capillaris**
	Saxifraga hieracifolia	*Carex chordorrhiza**
	Saxifraga hirculus	*Carex dioica**
	Saxifraga oppositifolia	*Carex vaginata**
	Saxifraga rivularis	*Carex lachenalii**
	Saxifraga tenius	*Carex lasiocarpa**
		*Carex limosa**
		*Carex norvegica**
		*Carex paupercula**
		*Carex rostrata**
		Carex rupestris
		Carex glaerosa
		Carex lachenalii

Species followed by * were collected from Abisko, and the others came from Svalbard.