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RESEARCH ARTICLE

Leveraging Natural History Collections to Understand the Impacts of Global Change

Resampling alpine herbarium records reveals changes in plant traits over space and time

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Abstract

1. Climate warming causes upward shifts in plant species distributions, resulting in an influx of species from lower elevations into alpine plant communities. Plant functional trait changes along elevation gradients and over time may reflect these changing conditions. Intraspecific trait variation measured from herbarium records offers a way to observe such changes in trait values over time.

2. We selected four species: *Poa alpina* and *Polygonum viviparum* found in alpine grasslands, and *Cardamine resedifolia* and *Ranunculus glacialis* found in high-alpine to subnival scree habitats. We measured several functional traits from (i) herbarium records collected between 1880 and 1950 and from (ii) individuals resampled in 2014 along an elevation gradient covering >1500 m within the same study region in the Swiss Alps. By comparing (i) against (ii) for each species separately, we analysed temporal changes in the distribution of traits along the studied elevation gradient.

3. After a century of climate warming, the change in the relationship linking plant functional traits with elevation was species dependent. Size-related and reproductive functional trait values for *P. viviparum* increased over time, increasing at lower, but not higher elevations. *Poa alpina*'s size-related traits increased consistently with time along the elevation gradient. Most of *C. resedifolia*'s size-related and flowering traits decreased over time at lower elevations and converged at higher elevations. Finally, *R. glacialis* traits did not respond to time alone—reproductive traits decreased over time at lower, and increased at higher elevations, reversing their historical trait distributions. The negative trend for vegetative trait values with elevation did not change over time, however. In 2014, at lower elevations, all species mainly occurred on their typical microhabitat types, but occurrence on other microhabitats increased with elevation for all species.

4. *Synthesis*: Contrasting temporal changes in the distribution of growth and reproductive trait values between alpine grassland and alpine-subnival scree species, especially at lower elevations, suggest that climate warming effects vary among species. Additionally, species' physiological constraints and availability of suitable

microhabitats may further impact species' distribution changes. Further warming may confine the distribution of high-alpine plant species to even higher elevations, or microclimates currently difficult to colonise by lower-alpine species.

1 | INTRODUCTION

Long-term studies have demonstrated that the global rise in temperature causes upward-range shifts of plant species distributions along the slopes of mountain ecosystems (Grabherr et al., 2010; Lenoir et al., 2008). This spatial redistribution of mountain plants is complemented by an increase in plant species richness in alpine ecosystems (Felde et al., 2012) as well as on mountain tops (Rixen & Wipf, 2017; Steinbauer et al., 2018), resulting in an influx of more competitive plants from lower elevations into previously specialised and sparsely vegetated alpine plant communities. Furthermore, shorter-term studies have illustrated that global warming results not only in distribution and abundance changes but also in shifts in plant species individual trait variability (Bjorkman et al., 2018).

The realised niche of plant species is restricted by the availability of environmental conditions along spatial gradients. Within this realised niche, plant performance and fitness, expressed through their functional traits, vary with abiotic conditions such as temperature (Bjorkman et al., 2018). Both at the leading and trailing edge of the range, the spatial distribution of species becomes increasingly patchy, often restricted to micro-sites or microrefugia (Hampe & Petit, 2005). However, the general decrease in the availability of suitable habitats with increasing elevation (and thus decreasing temperature) makes it relatively straightforward to assess plant functional trait changes at the leading edge because the leading edge is closer and even sometimes restricted to mountaintops and thus easier to identify and relocate. On the contrary, it is more complicated to assess plant functional trait changes at the trailing edge of a given plant species' elevational range because the patchy distribution of the trailing edge is spread out across a much larger surface area. Hence, most studies capture plant trait responses to climate change at one single point along a given environmental gradient, although some have repeated such measurements along several climatic gradients (see, for example, Guittar et al., 2016; Klanderud et al., 2015; Vandvik et al., 2020). Given that most plant species are shifting their elevational ranges upwards with climate warming, it is likely that the distribution pattern of their functional traits along elevational gradients will also change over time. Hitherto, and to the best of our knowledge, no study has investigated how the distribution of plant trait values along elevational gradients changes over time, and how this varies among species.

Species respond differently to one another under climate warming, with some species expanding faster than others, from graminoids and shrubs expanding faster in the Arctic tundra biome (Berner et al., 2020) to forbs and ferns expanding faster in the alpine and subnival vegetation belts (Steinbauer et al., 2018; Wipf et al., 2013). This trend is particularly pronounced in alpine environments, indicated by the ongoing widespread homogenisation of alpine plant communities and increasing extinction debt (Alatalo et al., 2022; Mitchell et al., 2017; Staude et al., 2022; Verrall et al., 2021). As climate warming pushes lowland species to expand to ever-higher elevations, the resident-specialised high-alpine plant species will not only encounter more and more individuals but also more vigorous neighbours with whom to compete for resources and limited space, triggering further changes in plant functional traits. The observed variation in occurrence frequency across alpine species on mountain summits suggests that not all alpine species present at high elevations will respond similarly to climate warming (Kulonen et al., 2018). However, although we know that species richness has accelerated in alpine environments over long periods of climate warming, we still cannot make clear predictions as to how plant functional traits will change along elevational gradients as climate warms.

Plant functional traits, such as morphological, physiological, chemical and phenological characteristics have been widely used as indicators of plant responses to climate change because examining plant traits could indicate the strength of environmental filters on plant communities (Venn et al., 2011). Some traits may be more responsive to the impact of climate change than others (Wright et al., 2004), and even if a species' distribution has been classified as stable, variations in their functional traits may vary over time to adjust to the new climatic conditions (Frei et al., 2014). For instance, plant height often shows clear patterns along environmental gradients and has already been used to track species responses to climate change (i.e. Bjorkman et al., 2018; Guittar et al., 2016). However, such directional patterns are not that clear for other plant traits and our basic understanding of trait patterns along environmental gradients remains relatively limited, thus inhibiting our ability to use space-for-time substitution to determine potential changes in functional traits in response to future environmental changes. Here, we have the chance to study a suite of growth and reproductive trait patterns along elevational gradients for several plant species and over a sufficiently long time period to test how these elevational patterns may have changed over time.

Most recent studies rely on field-based measurements of plant functional traits that have been collected during the recent acceleration period of anthropogenic climate change, after the onset of climate warming (Bjorkman et al., 2018; Elmendorf et al., 2015;

Gottfried et al., 2012). Hence, these studies fail to capture baseline values of plant functional traits that are representative of the conditions prior to the acceleration period. One approach to investigate changes in plant functional traits over a longer time period is to analyse specimens preserved in herbarium records, which can date back many centuries ago. Herbarium specimens supply a baseline source of information on functional traits, from which a wealth of field and observational studies may follow (Gallagher et al., 2009; Heberling, 2022). Herbarium records can be used to better understand the impact that climate change has had on plant communities by studying how the functional traits of specimens have changed over time and in space (Miller-Rushing et al., 2006). So far, herbarium records have been used to study plant invasions (Fuentes et al., 2013; Gassó et al., 2009), predict species' distributions (Elith et al., 2006) and determine phenological changes under climate change (Gallagher et al., 2009; Lavoie & Lachance, 2006; Primack et al., 2004). Only rarely have herbarium specimens been used to study traits and shifts in plant trait values over large environmental gradients (although see for example Hill et al., 2015). Few studies have measured traits from herbarium records to test for functional trait changes over time along geographical gradients (Hill et al., 2015; Kopp et al., 2020). Our study harnesses the opportunity to determine not only trait patterns over an elevation gradient but also how these patterns have changed over a long time period and for several species.

The Alps have been a hotspot for botanists for over a century, which has resulted in a vast source of historical records (Pauli et al., 2001; Rumpf et al., 2018; Steinbauer et al., 2018; Wipf et al., 2013). This, in combination with the strong collecting activity of early 20th-century botanists, has left a legacy of well-documented herbarium records. Using topographic position (elevation, slope and aspect) as a proxy for topoclimatic conditions as experienced by herbarium records with accurate locations and collection time, we can test for temporal changes in reproductive and vegetative plant traits, as well as for the magnitude of the change in relation to environmental change during the same time period. Here, we exploit the wealth of herbarium records collected between 1880 and 1985 in south-eastern Switzerland for a set of four alpine plant species. More specifically, we ask: (1) is there a relationship between environmental gradient (elevation, aspect and slope as a proxy for temperature) and the variation in plant functional traits? (2) do these trait distributions along the studied elevation gradients shift over time? and (3) can microhabitat conditions explain potential differences among species responses to climate change along the studied elevation gradients?

2 | MATERIALS AND METHODS

To assess temporal changes in the relationship between plant species traits and environmental conditions within a region where we do have old herbarium records, we established, in July 2014, two elevation transects on siliceous bedrock along hiking paths in two neighbouring valleys around Davos (Swiss Alps; 46°40′ to 46°47′ N, and 9°50′ to 9°57′ E). We focused on the elevation gradient ranging from the valley floor at 1500 m, dominated by subalpine conifer forests and grasslands, to mountain summits at 3146 m a.s.l., dominated by nival scree vegetation (Figure 1). Substrate types vary in relative proportions with elevation in this region, whereby organic soils are much less abundant at higher elevations and replaced by an increase in the relative abundance of scree (see Kulonen et al., 2018). A climate station at 1560 m in Davos, the nearest weather station in the vicinity of our study sites, has recorded an average total annual precipitation of 1044 mm/year and an average mean annual air temperature of 3.6°C since 1864 (Figure 1). Between 1880 and 1930, the average total annual precipitation and average mean annual air temperature at the same site were 939 mm/year and 2.1°C, respectively (Begert et al., 2005).

2.1 | Study species and specimen collection

We selected four plant species well represented in historical herbarium collections and with frequent known occurrences in the Davos region. The species had also been included in a different vegetation study (Kulonen et al., 2018) and showed varying patterns and success in terms of frequency and elevational change on alpine summits in the wider area over the past century (Table 1). Of the four species, one is a graminoid (*Poa alpina*) and three are herb species (*Cardamine resedifolia, Polygonum viviparum, Ranunculus glacialis*). *Cardamine resedifolia* and *R. glacialis* are species typical of alpine siliceous scree communities (Delarze et al., 2015). *Ranunculus glacialis* has a relatively narrow high-alpine to nival distribution and a relatively high tolerance for harsh conditions at high altitudes, while *C. resedifolia* has a wider distribution range occurring from acidic scree slopes at alpine altitudes up to subnival summits. Of the two species, over the past century, *C. resedifolia* has been more successful in colonising new summits and showed an upward shift of its upper range limit within the study region (Kulonen et al., 2018; Table 1). *Poa alpina* and *P. viviparum* are found in a range of different subalpine and alpine grassland communities (Delarze et al., 2015), and thus are more frequent at lower elevations as opposed to *R. glacialis* and *C. resedifolia*. Relative to the occurrences of these species on summits of the wider study region, *P. vivparum* has a lower-elevation distribution than the other three species, and has neither increased in frequency nor elevation over the past century (Kulonen et al., 2018, see also distribution maps for all four species at www.infoflora.ch). *Poa alpina* is a generalist pioneer species with a large elevation range reaching up to 4200 m elsewhere in the European Alps (Fischer et al., 2011), and has been one of the most successful species in terms of frequency and elevation gain on summits of the wider study region (Kulonen et al., 2018). The latter two species reproduce both sexually and vegetatively (by bulbils).

For each of the two transects, we selected sites along an elevation gradient with intervals of 50 m in elevation, where at least two of the target species were present with 5 or more individuals within a 20 m corridor from the path. If these criteria were not met, the
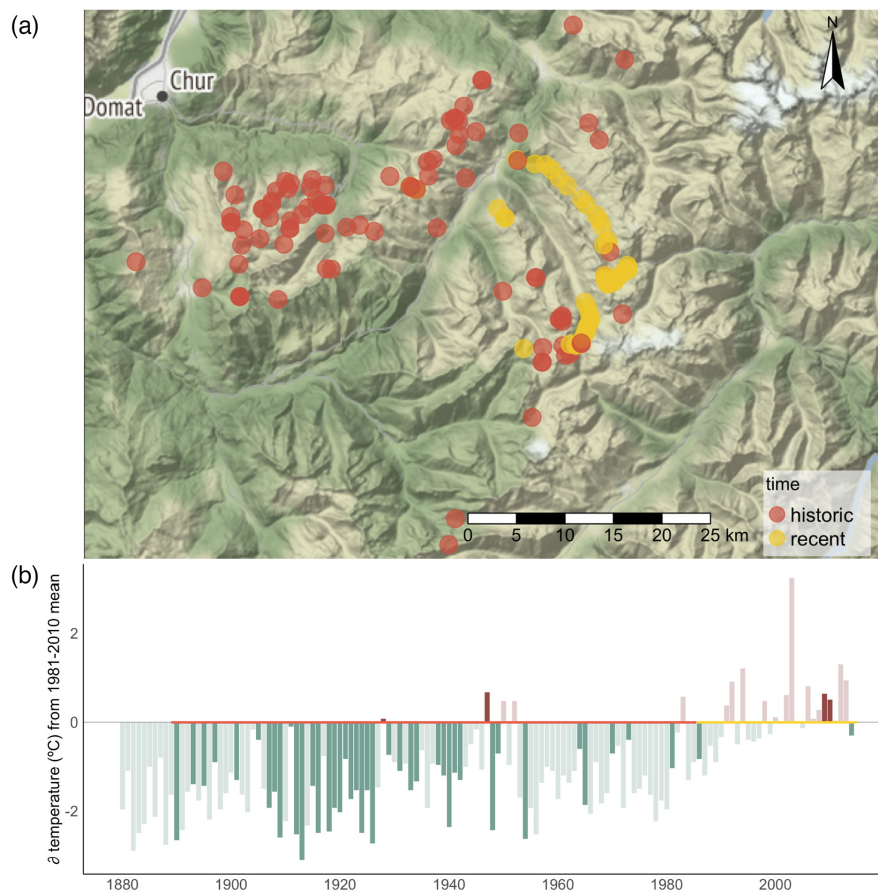
(a)

(b)

search continued uphill until sufficient individuals were identified. At each site, we selected a maximum of 8 individuals (or less if we did not find sufficient numbers) of each target species on each of three different microhabitat types (scree, rock and organic substrates; hereafter referred to as microhabitats; see Kulonen et al., 2018 for further details). An individual was defined as a specimen without visual connection to other specimens of the same species, with a distance of at least 1 m between collected individuals. Due to the tussock-forming nature of *Poa alpina*, tussocks were selected with as small a diameter as possible to reduce disturbance to the habitat. All specimens were collected at maturity (July–August 2014). After collection, plant specimens were pressed to herbarium standards, allowing reliable comparison with historical herbarium samples (see below; Perez et al., 2020).

2.2 | Trait measurements

To test whether a shift of trait distribution has occurred along the studied elevation gradients, we retrieved all herbarium specimens for the target species collected within an average of 10 km from the contemporary transect locations (Figure 1). We selected herbarium records covering the period 1880–1985 from several herbaria in Switzerland (herbaria of the University and ETH Zurich, Universities

of Basel and Neuchâtel and the Graubuenden Natural History Museum). Records were selected for subsequent analyses only when precise information on the botanist, location, date and elevation of the collected material were available (i.e. the name of the botanist who collected the plant material, a precise elevation and specified location and a date corresponding to the day, month and year of collection). Geographical locations were geo-referenced using contemporary maps from the respective time period of the collection, while elevation (unless exactly stated in the herbarium record), aspect and slope of the locations were retrieved from a digital terrain model at 20 m resolution (map.geo.admin.ch at 1:10000 resolution).

Finally, a number of functional traits were measured for each species (see Table 1). For each of the historical and newly collected herbarium records, we sampled traits linked to four growth strategies: (1) vegetative height, (2) vegetative growth characteristics, (3) reproductive height and (4) reproductive performance. These traits were chosen for their prior indication of environmental change and ease of measurement on herbarium samples (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). To avoid damaging the fragile herbarium specimens, different traits were measured for each species within the four growth and reproductive strategies according to feasibility of non-destructive handling. Thus, traits occasionally differ between species for the same growth or reproduction strategy (Table 1). Traits were measured directly from the herbarium

TABLE 1 Summary information on the four studied species' typical habitat (from Delarze et al., 2015) and traits measured. Due to the fragile nature of herbarium material, it was not possible to measure the same traits across all species without destroying the collected historic specimens. Thus, a suite of traits, sometimes differing between species, was selected to best represent predominant growth and reproductive traits easily measurable on herbarium material. Note that inflorescence length for *P. viviparum* corresponds to the total length including bulbils and flowers. Further details on trait selection can be found in the Supplementary Materials

Species	Community	Traits	Trait significance
Cardamine resedifolia (*n* = 844)	Alpine scree	Rosette leaf number	Vegetative biomass; indication of photosynthetic area
		Leaf length	Light interception; indication of photosynthetic area, with consequences for leaf energy and water balance
		Number of flowers	Reproductive output; effort into pollinator attraction
		Plant height	Surrogate for growth form, light reception, competitive vigour, reproductive size, whole-plant fecundity, and potential lifespan
Ranunculus glacialis (*n* = 736)	Alpine scree	Leaf width	Indication of photosynthetic area, with consequences for leaf energy and water balance
		Petiole length	Light interception; indication of photosynthetic area
		Number of flowers	Reproductive output; effort into pollinator attraction
		Flowering stem length	Effort into pollinator attraction
Poa alpina (*n* = 1564)	Low-alpine meadow	Basal leaf length	Light interception; indication of photosynthetic area, with consequences for leaf energy and water balance
		Inflorescence length	Reproductive output; effort into pollinator attraction
		Inflorescence stalk length-	Effort into pollinator attraction
Polygonum viviparum (*n* = 748)	Low-alpine meadow	Leaf area	Light interception; indication of photosynthetic area, with consequences for leaf energy and water balance
		Leaf length	Indication of photosynthetic area, with consequences for leaf energy and water balance
		Inflorescence length	Reproductive output; effort into pollinator attraction
		Inflorescence stalk length	Effort into pollinator attraction

sheets using digital callipers accurate to 0.01 mm. Leaf area was calculated as leaf length multiplied by leaf width.

2.3 | Climate

To estimate the regional climate and its change over time, we downloaded climate data from the nearest weather station in Davos Dorf, covering the period 1864–2014 (Begert et al., 2005). In the absence of both on-site temperature or precipitation measurements and reliable downscaled climate data for the historical sampling period, the central position of this singular climate station provides a reasonable climate proxy for all historical and contemporary records. Mean summer temperature (June, July, August) and cumulative precipitation from January to August were calculated for each year. We further calculated temperature and precipitation anomalies from the 1981–2010 reference period (Figure 1b). There is a significant difference in mean summer temperature and precipitation sum between the historical (1880–1985) and contemporary (1986–2014) collection periods (Supplementary Figure S3). Overall, summer temperatures have increased by 1.53°C, and precipitation by 45.3 mm, indicating a strong warming and a slight decrease in precipitation between the two sampling periods.

2.4 | Statistical analyses

Since the accuracy of the written comments from the botanists who collected old herbarium specimens varies, we indexed the herbarium specimens according to the quality and completeness of the accompanying written record, into low (location potentially varying by hundreds of metres, for example, due to geographical terms covering large areas), medium (location potentially varying by tens of metres) and high quality (location very exact). For this study, we ran two preliminary set of models on subsets of the data: (i) one set including only records of the highest quality and (ii) one set including both the medium and high-quality records. Since both sets of models returned similar results we chose to display results from the set of models using most of the data (ii) and report the final results in the paper based on both medium- and high-quality records. Low-quality records were systematically excluded beforehand.

We tested for temporal changes in the distribution of each of the studied plant traits along elevational gradients. Using generalised linear mixed-effects models, we estimated the significance of elevation (1515–3145 m; used as a scaled fixed effect term), time (a factor variable with two levels, being contemporary vs. historical; as fixed effect), their two-way interaction term (elevation×time; as

fixed effect) and topographical parameters used a covariates (slope, northness and eastness; as scaled fixed effects) on each of the studied reproductive and growth traits that we used as response variables (Table 1). We included transect ID and botanist ID as random intercept terms to account for potential regional effects and for collections strategies that could have varied between the different botanists who collected the old herbarium specimens. Our overall model formula was thus:

$$trait = elevation \times time + slope + northness + eastness$$
$$+ (1|transect) + (1|botanist).$$

All models had the same structure, except for *P. viviparum*'s inflorescence length and leaf area, and for *R. glacialis*' flowering stem length, fitted with a random effect for herbarium sheet because of singular model fit. Models were run following a Gaussian distribution, excepting flower number and leaf number which were run with a Poisson distribution that better fit count data. When the two-way interaction term between elevation and time was non-significant, we removed it from the model formula, leaving only the additive main effects.

To complement the comparison between recent and historical trends, we further tested for the effects of interannual temperature and precipitation on plant trait trends over the previous century. We ran generalised linear models following a Gaussian distribution, where each trait collected on a given year was allowed to vary in response to time and interannual temperature and precipitation between 1880 and 1985. These analyses are further detailed in the Supplementary Materials.

Finally, we tested whether the contemporary distribution of each of the four studied species varied along the studied elevational gradients between the three studied microhabitats (organic soil, scree, rock), to explore whether potential differences among species responses to climate change along the elevation gradient could be driven by microhabitat preferences. At each contemporary sampling elevation, we calculated the occurrence proportion of each species on the three microhabitats along the elevational gradients, being the ratio of individuals per species collected from each microhabitat at each sampling elevation. This time, we ran generalised linear models following a binomial distribution (cf. proportion data) to determine whether the proportion of individuals varied in response to microhabitat and elevation:

$$proportion = microhabitat \times elevation$$

where **proportion** varies as a function of the interaction between microhabitat and elevation. Each model was fitted with a weights argument to account for the total number of individuals collected per species and per sampling elevation.

We used R (R version 4.1.1) and the GGPLOT package for data visualisation (Wickham, 2016). Models were fitted using the LME4 package in R (Bates et al., 2015) and predictions made with the SJPLOT (Lüdecke, 2022) and GGEFFECTS (Lüdecke, 2018) package. More information on model outputs is available in the Supplementary Materials.
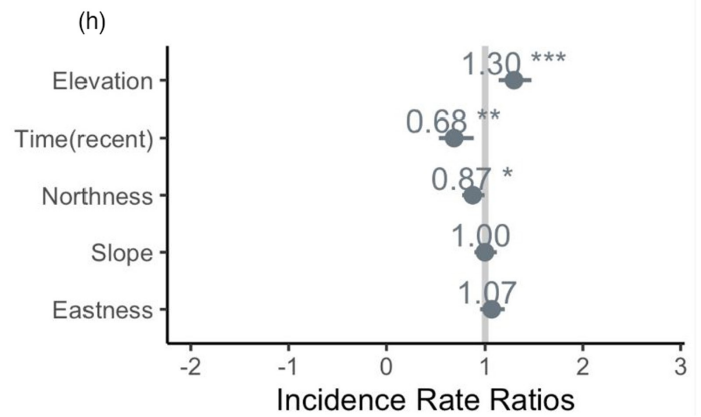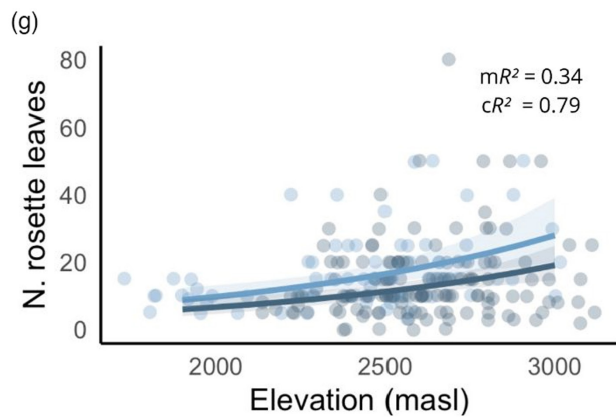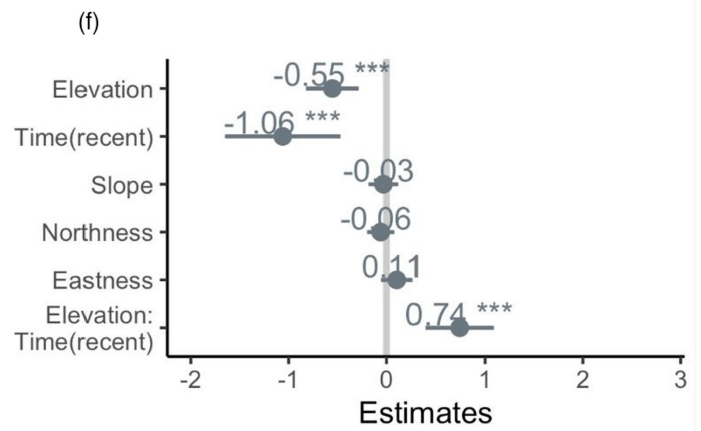
3 | RESULTS

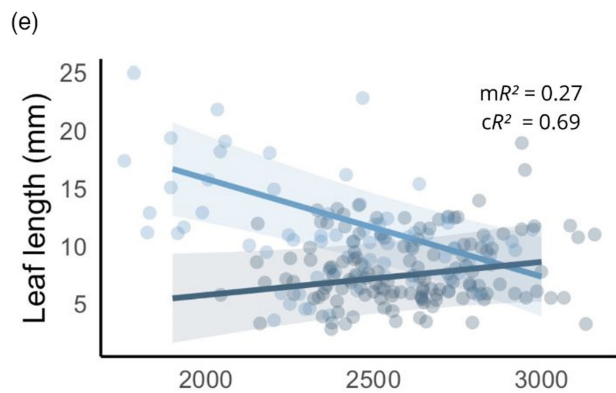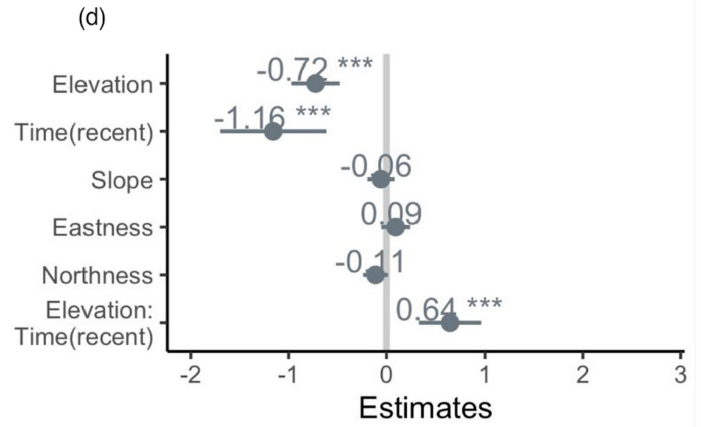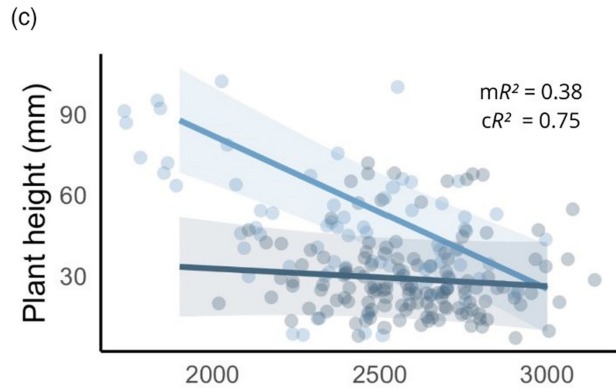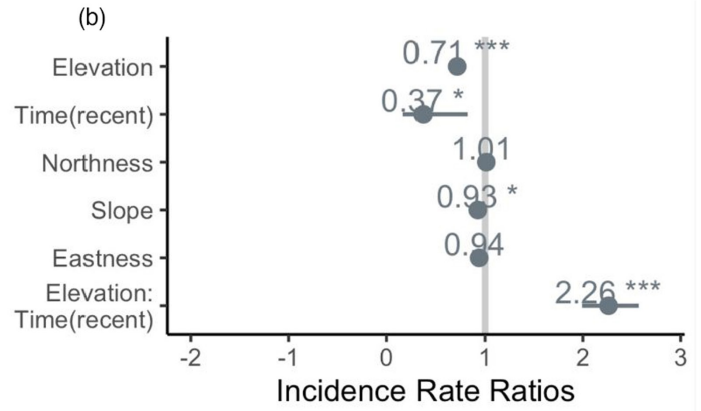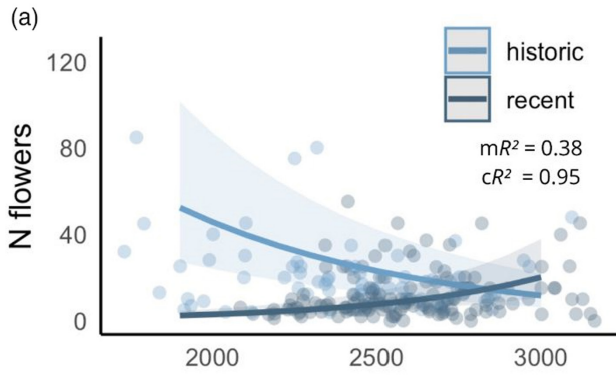### 3.1 | Relationship between environmental gradient and plant functional traits

We found that, in general, plant functional traits vary with elevation across all four studied species (Figures 2–5). In particular, we found clear elevational patterns for the height and size of the reproductive organs, with inflorescences generally reducing in length and height towards higher elevations for *Poa alpina* and *Polygonum viviparum* but generally increasing in size towards higher elevations for *Ranunculus glacialis* and *Cardamine resedifolia* (see Figures 2–5). Furthermore, we found that plant height and leaf size decline with elevation for *P. viviparum*, *P. alpina* and *C. resedifolia*, but not for *R. glacialis*. In addition, we found that plant functional traits are sensitive to aspect and slope (Figures 2–5), and species abundance to microhabitat type (Figure 6), which reinforces the relevance of using these as covariates in all our models.

3.1.1 | Cardamine resedifolia

The relationship of plant functional traits with elevation for *C. resedifolia* has changed significantly over time, since the beginning of the 20th Century, for at least three traits. While historically, plant height was higher at lower elevations, plants are now smaller at lower elevations (Figure 2b,f). Similarly, the number of flowers was historically decreasing with elevation while it is now increasing. Interestingly and irrespectively of the time period considered, *C. resedifolia* produces more rosette leaves at higher elevations, albeit now fewer rosette leaves are produced than 100 years ago throughout the studied elevational gradients (Figure 2d,h). These leaves were also historically longer at lower elevations while now the leaves tend to be longer at higher elevations (Figure 2c,g). Noteworthy, significantly more flowers are produced on steeper slopes (Figure 2a,e) and more rosette leaves are produced on northern aspects (see Figure 2h), although

FIGURE 2 Trait variation with elevation (m a.s.l.), time (historic vs. recent) and other covariates for *Cardamine resedifolia*. (a, c, e, g): Temporal changes in the relationship between traits and elevation. (b, d, f, h): Standardised forest plots of effect sizes or estimates (doubled standard deviation), where variables that deviate left of the solid grey line demonstrate a reduction in trait size/number with the corresponding variable (pale shade), and variables that deviate right of the line demonstrate an increase in trait size/number (dark shade). Significant variables are shown as *** = $p < 0.001$, ** = $p < 0.01$ and * = $p < 0.05$. Marginal (m) and conditional (c) R^2 are reported for each trait. Dark and pale shade ribbons on the left panels show the 95% confidence interval around the predicted lines.

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)

these effects are minor compared with the main effects of time and elevation.

3.1.2 | Ranunculus glacialis

In general, we found that *R. glacialis* showed weaker relationships between the investigated functional traits and elevation. More flowers are now produced at higher elevations after a century of climate warming while it was the opposite based on historical specimens (Figure 3a,e). In addition, these flowers are born on longer flower stems at higher elevations than a century ago (Figure 3b,f). Neither petiole length nor leaf width displayed significant trends along the studied elevational gradients or over time: their relationships remained similar across the two time periods and across the elevational gradients. Finally, *R. glacialis* produces significantly fewer flowers and narrower leaves on steeper slopes (Figure 3a,e,d,h), although these effects remain relatively minor.

3.1.3 | Poa alpina

Poa alpina demonstrates consistent and significant declines with elevation for all the investigated functional traits. More specifically, inflorescences reduce in size and height while basal leaves are shorter towards higher elevations. Flower stem length significantly changes over time along the elevational gradients whereby individuals now grow taller inflorescences than 100 years ago and display a stronger decline over the contemporary elevation gradient than the historical one (Figure 4). Basal leaves are longer now than in the past and this trend is consistent throughout the studied elevational gradients (Figure 4f). Furthermore, *P. alpina*'s vegetative height, inflorescence length and basal leaf length were more reduced on northern aspects than on southern aspects (Figure 4).

3.1.4 | Polygonum viviparum

Polygonum viviparum is the only species of the four studied plant species to display a significant interaction term between elevation and time across all four investigated traits, such that the relationship of all traits with elevation is significantly more negative today than in the past (Figure 5). The relative increase over time in these four studied traits has thus been greatest at lower elevations. Individuals now have a greater flowering height (cf. flower stem length) at lower elevations than 100 years ago, as well as a stronger decline in

reproductive height over the contemporary elevation gradient than the historical one (Figure 5b,f). *Polygonum viviparum* displayed a shift in distribution over time such that contemporary inflorescences are longer at lower elevations than historically and shorter at high elevations than historically (Figure 5a,e). Similarly, *P. viviparum* flowering stem length and leaf length are smaller on northern aspects than on southern aspects (Figure 5d,f).
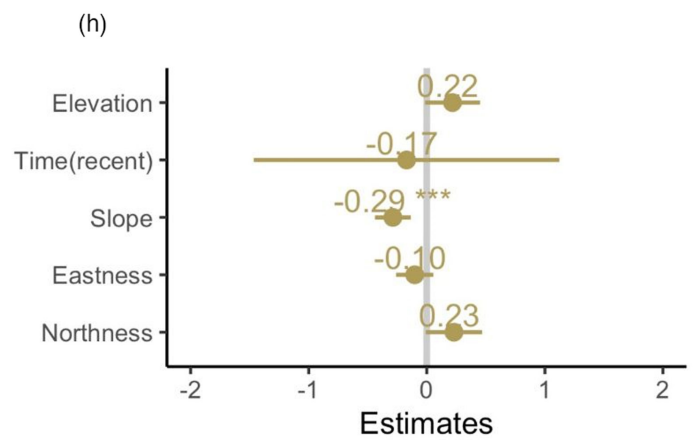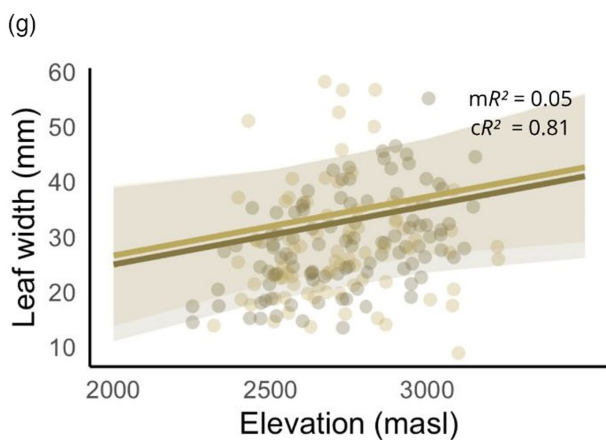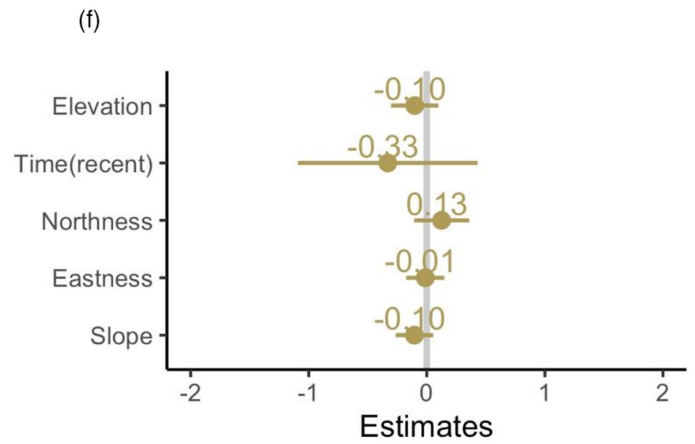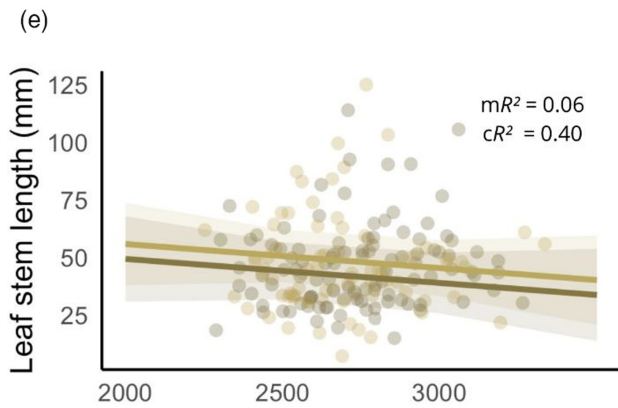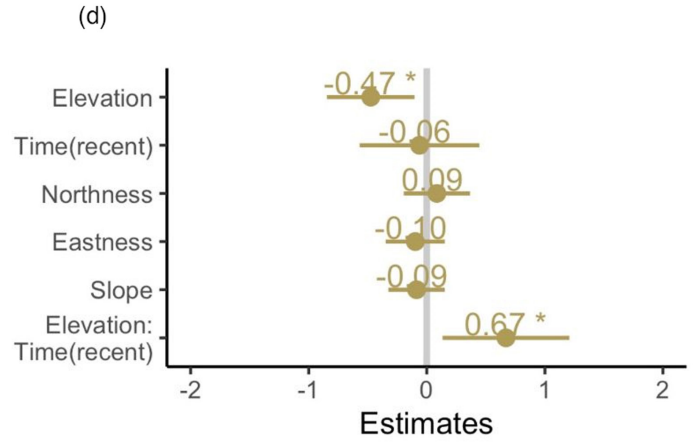
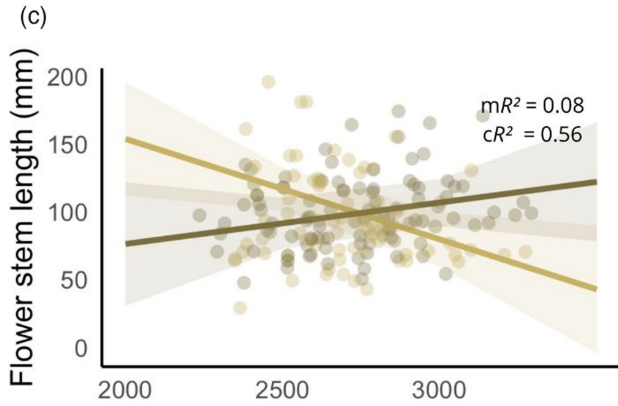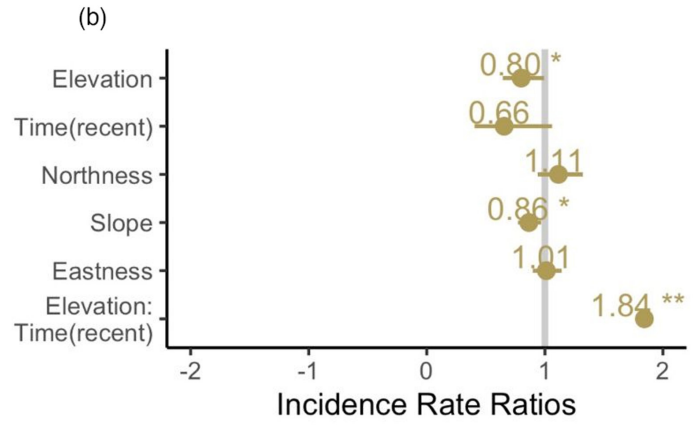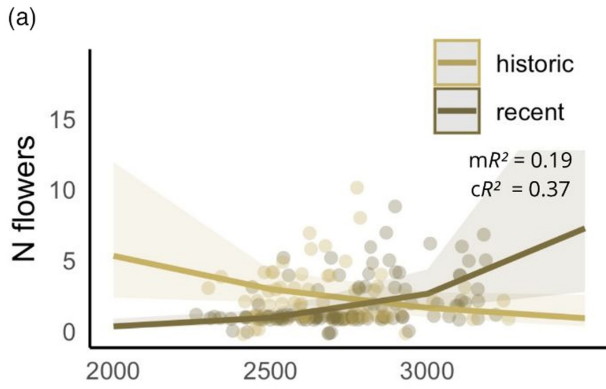### 3.2 | Divergent microhabitat preferences

We found that all four studied species have different microhabitat preferences. Along the contemporary elevation gradient, *P. viviparum* and *P. alpina* were almost exclusively found in organic substrates at lower elevations. At higher elevations, *P. alpina* was mostly found on scree, while *P. viviparum* was equivalently found on both scree and organic substrates (Figure 6). *Ranunculus glacialis* and *C. resedifolia* were most commonly collected on scree throughout the studied elevational gradients but the probability of finding these two species on scree decreased with elevation such that both species tended to be equivalently found on all three microhabitats (scree, organic substrates and rocks) at high elevations.

In our analyses, we treated time and elevation as proxies for changes in temperature (cf. climate change and the adiabatic lapse rate of temperature). Nevertheless, within the historical collection period alone, mean summer temperature varied between 5.4 and 15°C (see also Figure 1). By analysing the response of each of the plant functional traits to interannual variation in temperature and precipitation over the historical time period, we found that our findings are mostly supported (see Supplementary Materials for full model output). In general, inflorescence length increased during warmer summers for *P. alpina* and *P. viviparum*. Furthermore, leaf width for *R. glacialis* increased during warmer summers, whilst petiole length increased during warmer summers and during summers with more precipitations (see Supplementary Figure S2). All other traits did not vary significantly with interannual temperature and precipitation variation. While temperature, through elevation or interannual variability, proved to be a driver of some trait variability (although in varying directions for each species and trait), we found that precipitation was rather unimportant.

4 | DISCUSSION

Using herbarium records collected since 1889, we found that the trait distributions of four alpine plant species have shifted along elevational

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FIGURE 3 Trait variation with elevation (m a.s.l.), time (historic vs. recent) and other covariates for *Ranunculus glacialis*. (a, c, e, g): Temporal changes in the relationship between traits and elevation. (b, d, f, h): Standardised forest plots of effect sizes or estimates (doubled standard deviation), where variables that deviate left of the solid grey line demonstrate a reduction in trait size/number with the corresponding variable (pale shade), and variables that deviate right of the line demonstrate an increase in trait size/number (dark shade). Significant variables are shown as *** = $p < 0.001$, ** = $p < 0.01$ and * = $p < 0.05$. Marginal (m) and conditional (c) R^2 are reported for each trait. Dark and pale shade ribbons on the left panels show the 95% confidence interval around the predicted lines.

(a) N flowers vs Elevation (masl); historic and recent; mR^2 = 0.19, cR^2 = 0.37

(b) Incidence Rate Ratios: Elevation 0.80 *, Time(recent) 0.66, Northness 1.11, Slope 0.86 *, Eastness 1.01, Elevation:Time(recent) 1.84 **

(c) Flower stem length (mm) vs Elevation; mR^2 = 0.08, cR^2 = 0.56

(d) Estimates: Elevation −0.47 *, Time(recent) −0.06, Northness 0.09, Eastness −0.10, Slope −0.09, Elevation:Time(recent) 0.67 *

(e) Leaf stem length (mm) vs Elevation; mR^2 = 0.06, cR^2 = 0.40

(f) Estimates: Elevation −0.10, Time(recent) −0.33, Northness 0.13, Eastness −0.01, Slope −0.10

(g) Leaf width (mm) vs Elevation (masl); mR^2 = 0.05, cR^2 = 0.81

(h) Estimates: Elevation 0.22, Time(recent) −0.17, Slope −0.29 ***, Eastness −0.10, Northness 0.23

FIGURE 4 Trait variation with elevation (m a.s.l.), time (historic vs. recent) and other covariates for *Poa alpina*. (a, c, e): Temporal changes in the relationship between traits and elevation. (b, d, f): Standardised forest plots of effect sizes or estimates (doubled standard deviation), where variables that deviate left of the solid grey line demonstrate a reduction in trait size/number with the corresponding variable (pale shade), and variables that deviate right of the line demonstrate an increase in trait size/number (dark shade). Significant variables are shown as *** = $p < 0.001$, ** = $p < 0.01$ and * = $p < 0.05$. Marginal (m) and conditional (c) R^2 are reported for each trait. Dark and pale shade ribbons on the left panels show the 95% confidence interval around the predicted lines.
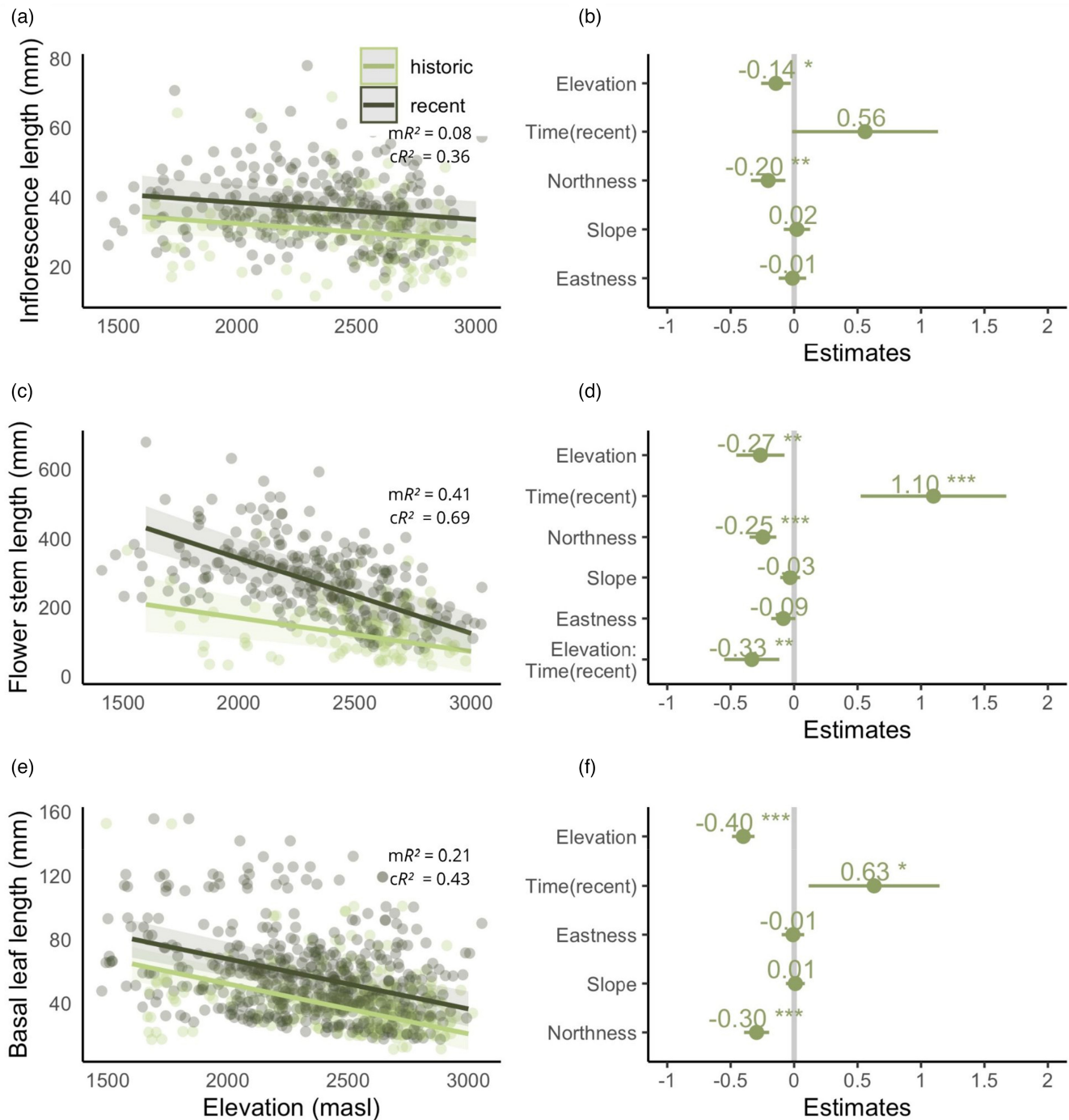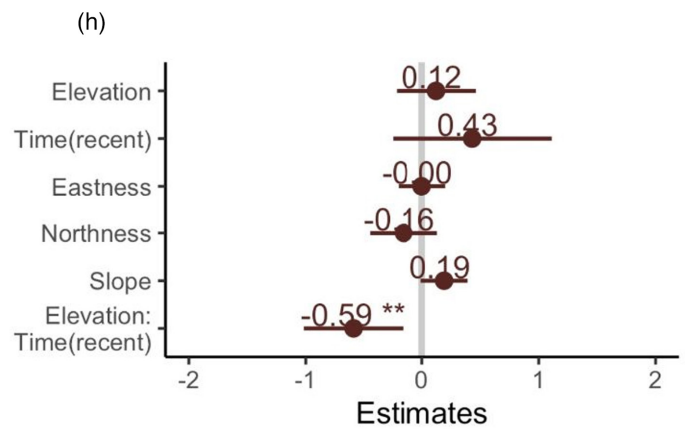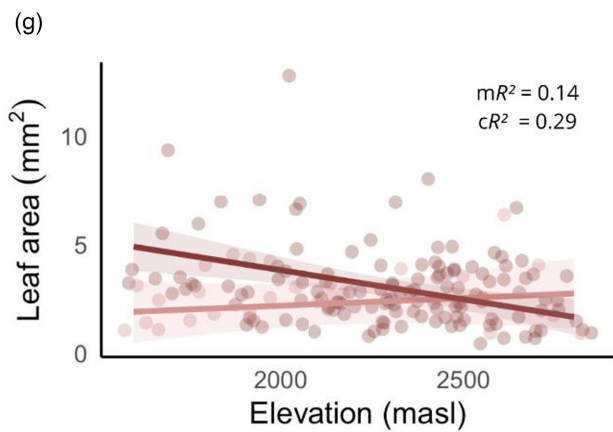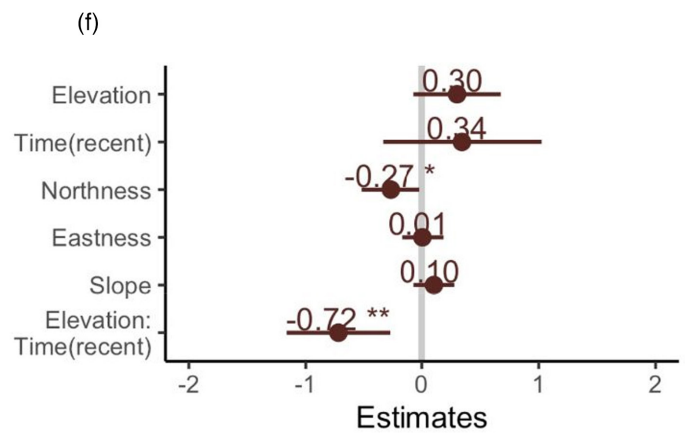
FIGURE 5 Trait variation with elevation (m a.s.l.), time (historic vs. recent) and other covariates for *Polygonum viviparum*. (a, c, e, g): Temporal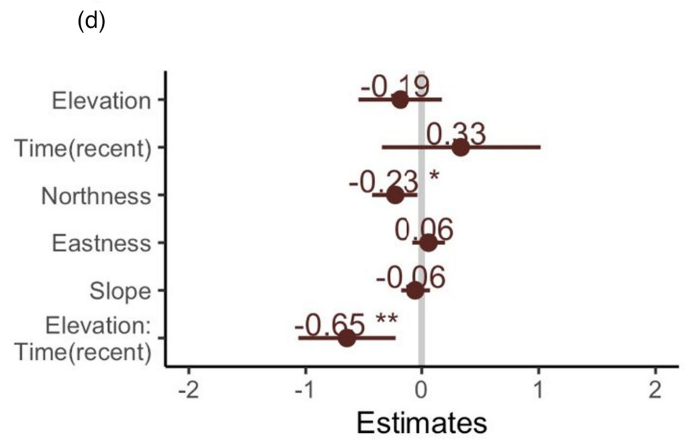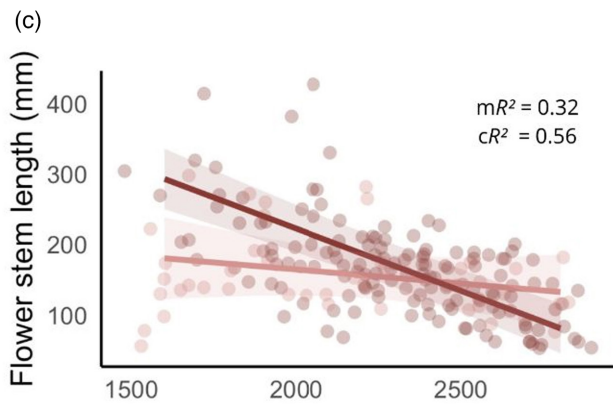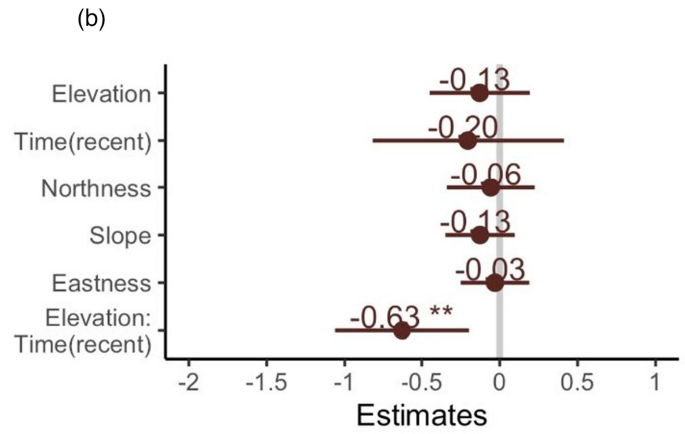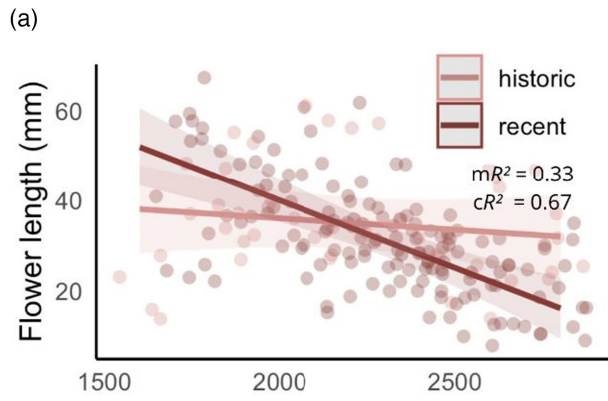 changes in the relationship between traits and elevation. (b, d, f, h): Standardised forest plots of effect sizes or estimates (doubled standard deviation), where variables that deviate left of the solid grey line demonstrate a reduction in trait size/number with the corresponding variable (pale shade), and variables that deviate right of the line demonstrate an increase in trait size/number (dark shade). Significant variables are shown as *** = $p < 0.001$, ** = $p < 0.01$ and * = $p < 0.05$. Marginal (m) and conditional (c) R^2 are reported for each trait. Dark and pale shade ribbons on the left panels show the 95% confidence interval around the predicted lines.
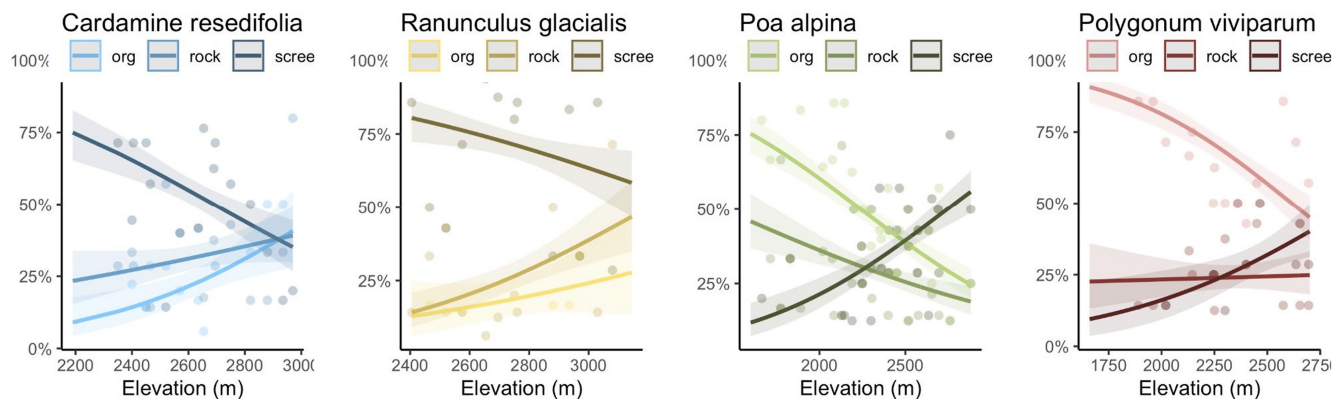
FIGURE 6 Percentage of individuals found on three microhabitats (organic soil, rock and scree) along an elevation gradient (m a.s.l) for *Cardamine resedifolia* (blue), *Ranunculus glacialis* (ochre), *Poa alpina* (green) and *Polygonum viviparum* (pink). These relationships are based on contemporary samples. The proportion of individuals of each species found on scree differs significantly with elevation ($p < 0.05$; an increase for *P. alpina* and *P. viviparum*, a decrease for the other two species). Additionally, *P. alpina* and *P. viviparum* are significantly more abundant on rock substrates with increasing elevation ($p < 0.05$), and significantly less abundant on organic soils with increasing elevation ($p < 0.05$). See Supplementary Materials for the full model output.

TABLE 2 Species elevation range, mean elevation, and summit presence on historical and contemporary surveys of the four studied alpine plant species. Data adapted from Kulonen et al. (2018) and Steinbauer et al. (2018)

Species	Summit frequency shift over 100 years (N summits)	Historical mean elevation (m)	Historical max. elevation (m)	Shift of max. elevation over 100 years (m)
Cardamine resedifolia	+19	2808	3142	+252
Ranunculus glacialis	+5	3027	3406	+3
Poa alpina	+35	2821	3265	+151
Polygonum viviparum	0	2745	2977	+3

gradients in the Swiss Alps and over a century-long period of climate warming. To our knowledge, this is the first study to use old herbarium records dating back to the late 1880s to determine how the relationship between plant traits and elevation has changed over a period of unprecedentedly rapid climate change. Our findings indicate that changes in trait patterns with elevation varied among species, suggesting that climate change can lead to different responses in plant species' trait characteristics. Furthermore, we found that species' microhabitat preferences largely corresponded to the habitat types they were classified for (Table 1, Delarze et al., 2015), whereby *P. viviparum* and *P. alpina* are predominantly found on organic soils, while *R. glacialis* and *C. resedifolia* are mostly found on scree or rocks.

4.1 | Intraspecific trait patterns with temperature

For both *P. viviparum* and *P. alpina*, we found a strong increase in vegetative size, in terms of plant height and leaf length, under warmer conditions, either obtained through a negative effect of elevation (i.e. warmer conditions at low elevations), a positive effect of time (i.e. climate warming) or a combination of both (i.e. interaction effect between time and elevation). This perfectly aligns with previous studies showing that plant height is one of the most sensitive traits to react

positively to warming (Bjorkman et al., 2018; Elmendorf et al., 2015). Yet, we found almost opposite patterns for *C. resedifolia*, with plant height and leaf length decreasing over time and especially so at lower elevations. Interestingly, leaf area (a trait closely related to leaf width and leaf length, collected from herbarium material in our study) did not show any directional pattern in a meta-analysis of intraspecific trait responses to elevation (Midolo et al., 2019), thus suggesting high variability in how vegetative traits relate to temperature. We found similar variability in leaf length and leaf width in our study. For example, while *P. alpina* has increased in leaf length consistently across the studied elevational gradients, *P. viviparum* has shown an increase in leaf length over time, but at lower elevations only. This suggests that *P. viviparum* is either more temperature limited at higher elevations than *P. alpina*, or co-limited by the availability of its preferred microhabitat. A combination of these two factors could explain the obvious difference in successful colonisation of alpine summits over the past century (Table 2; Kulonen et al., 2018) between the two species.

4.2 | Microhabitat preferences

One of the potential co-determinants of plant trait variation alongside temperature is microhabitat availability. In the case of the

predominantly scree-dwelling species *C. resedifolia*, microhabitat availability and the potentially increased competition from new upward-moving neighbours in organic soils might well have led to local disappearance of individuals at lower elevations (see historical and recent distribution with elevation in Figure 2). Similarly, the replacement of rock and scree microhabitats by organic soils (i.e. due to farmland melioration or by being overgrown over time) at lower elevations of the specialist species *R. glacialis's* distribution (Kulonen et al., 2018) may explain today's shift towards a positive relationship with elevation for three out of the four investigated traits. This reduction in suitable habitat quantity or quality at lower elevations may be a reason for reduced plant size with fewer flowers today than historically. We found a clear pattern for the two relatively more competitive species predominantly occurring on organic soils and in grassland communities, *P. alpina* and *P. viviparum*. Both species showed increases in almost all measured traits over time, with this effect strongest at sites located at the lower elevation margin of their elevation range, which reaches lower than that of the other two studied species. The reduction of preferred substrate at higher elevations (such as organic soil for the case of *P. viviparum*, where a coincidental reduction in trait size above 2200m and its increasing prevalence on scree is observed) may limit the establishment of these two grassland species in high-alpine environments. This confirms the findings of Kulonen et al. (2018) that microhabitat preference and availability, as well as mycorrhizal associations, along an elevation gradient is a strong determinant and constraint that determines species' long-term establishment success on alpine summits (Read & Haselwandter, 1981; Ruotsalainen et al., 2004).

4.3 | Functional traits respond differently to climate anomalies

We found that alpine plant trait values responded little to interannual summer temperature variation before 1986. During the period of historical collections, years with above-average summer temperatures were consistently followed by cooler years. Since 1986, however, there has been a clear and consistent warming trend. Many alpine species are long-lived and have below-ground storage capacities (Körner, 2021), providing a buffer against year-to-year variation but also the potential for a build-up of trait responses over time. Thus, the consistently above-average summer temperatures of the contemporary survey years could be an explanation for the much stronger effect of time (which we largely attribute to warming) compared with intra-annual variation within the historical period.

We demonstrated that plant functional trait values vary not only with elevation in mountain environments but also with aspect. *Poa alpina* in particular grows taller and invests more in reproduction at higher elevations and on southern aspects now than 100 years ago. This is in line with our expectations that traits will respond most strongly on the warmest aspects, and with previous findings that plant traits respond differently according to aspect (Kulonen et al., 2018; Winkler et al., 2016). Indeed, in alpine terrains, a

temperature range can be as large across small distances within the same elevational belt (cf. a microtopographic effect of opposing aspects) as across distant elevational belts (Scherrer & Körner, 2010). Thus, we can expect trait responses to climate change to differ depending on small-scale variability in topographical factors (Dubuis et al., 2013). The impact of climate change on alpine plants may be alleviated by topographic complexity and its associated microclimate heterogeneity offering short-distance escapes or microrefugia (Graae et al., 2018; Lenoir et al., 2013; Scherrer & Körner, 2010; Spasojevic et al., 2013).

However, specialist species such as cryophilic and dwarf-growing alpine species that are often already restricted in their range and that depend on extremely cold conditions are highly at risk of losing their microrefugia (Scherrer & Körner, 2011). Our findings suggest that this could be the case for *R. glacialis*, a high-alpine specialist known to be affected by recent climate change (Felde et al., 2012; Totland & Alatalo, 2002) and which is disappearing from the lower end of its elevation range in Norway (Klanderud & Birks, 2003). In parallel, for *R. glacialis*, we observed a significant increase in reproductive height and number of flowers at higher elevations, but not for petiole length or leaf width. This corresponds with findings from a warming experiment in Norway, where *R. glacialis* showed very little response to increasing temperatures (Diemer, 2002; Totland & Alatalo, 2002). These trait patterns for *R. glacialis* are also in line with a recent study of intraspecific trait variability across 66 species along 40 elevation gradients, showing that species with preference for highest elevations and with narrow elevation range are those with the lowest intraspecific trait variability and response to elevation (Rixen et al., 2022). As a cryophilic species, *R. glacialis* may suffer from direct effects of warming on its metabolism. The species has been found to have difficulties adapting rates of dark respiration to higher temperatures. Prolonged warm periods would lead to a rapid loss of stored carbohydrates (Cooper, 2004; Larigauderie & Körner, 1995). Under further warming, individuals at lower elevations may not be physiologically capable of survival.

Our finding of an increase in reproductive height only in the upper elevations, but not in the lower ones, could be a further signal of physiological deficiencies of *R. glacialis* at its lower range margins. This is confirmed by observations of continuing population decline, over the past 20 years, of virtually all high-elevation species, including *R. glacialis*, at a nearby site (Stubaier Alps) in the lower part of their range (Lamprecht et al., 2018; Steinbauer et al., 2020). This, however, occurred concurrently with an overall decrease in vegetation cover and therefore may also indicate physiological rather than competition effects, or a combination of both.

4.4 | The benefits and constraints of using herbarium material as a climate change response predictor

Comparing herbarium records with contemporary specimens to study temporal changes in trait distributions of alpine plants is a

relatively untapped technique. While we conclude that, overall, our approach is useful to detect and interpret species' variable responses to warming, we cannot exclude some bias arising from the way herbarium specimens have been collected in the past. It is likely that early 20th-century botanists, given their aim to assemble significant and reference collections, were biassed towards sampling larger, more productive, and flowering specimens (in the same way as photographers today would choose well-developed, large and flowering individuals to take a nice picture of). Thus, smaller and non-flowering individuals may not have been collected. We thus expect that the majority of specimens in the historical records would be generally taller and larger than the average individual available from the background population. For our contemporary collection, however, we randomly chose mature individuals in the field, thus avoiding a bias towards collecting larger plants (although still collecting mature, flowering individuals). In such a case, any reduction in plant size over time could be an artefact due to historical sampling bias while a significant increase in plant size over time would most likely be attributed to a true response to a change in the environment that might well be, in fact, underestimated given the underlying bias towards sampling larger individuals in the past. We would expect this potential bias to span over the whole altitudinal gradient, thus this alone would not account for an altitude x time effect such as in *R. glacialis*. However, we cannot discard the fact that reductions in trait sizes over time are not due to a collector bias (e.g. a negative effect of time on *C. resedifolia's* plant height in Figure 2b,f).

Despite taking a conservative approach in the recent sampling through random selection of individuals along a fixed elevation gradient (which in general explained little of the random effects variance), we still found a remarkably strong change over time in plant functional trait distributions for all four species, thus strengthening our conclusions. Herbarium records collected prior to the onset of, as well as during, climate change thus hold much potential for further uncovering long-term responses of plant performance to climate change, both before and during the recent acceleration in climate warming. This could provide validation for many of the shorter-term ecological studies that have only captured responses after the start of the warming acceleration in the 1980s.

Other environmental constraints may drive changes in the distribution of traits. For example, the availability of nutrients for growth has major implications for plant species in alpine environments (Körner et al., 1989). Atmospheric nitrogen (N) deposition has been observed across the Swiss Alps, which has been shown to affect alpine plant community composition (Hiltbrunner et al., 2005). Nitrogen depositions could play a role even in alpine-subnival zones, albeit less strong than in lowlands, since soil warming leads to greater nutrient availability, which may be especially important in temperature-limited habitats at high elevations (e.g. Staude et al., 2022). The uniform increase in the size of *P. alpina*, the only graminoid species in our study, across the elevation gradient, as well as its gain in frequency and elevation over time, fits this pattern. Hence, the impact of N deposition on our findings cannot be ruled

out and could actually be a compounding or even a confounding effect in addition to climate change. Impacts of these alternative drivers can, thus, not be excluded, and could be explored by investigating changes in plant chemical traits over time, for example through a collaboration with the NutNet network (Leff et al., 2015), albeit this would imply potential damage or even destruction of old herbarium specimens.

5 | CONCLUSIONS

Here, we combined herbarium with contemporary specimens for four alpine plant species to investigate temporal changes in trait distributions along an elevation gradient subjected to contemporary climate change. Our findings suggest that changes in plant trait patterns with elevation are species-specific. For the two alpine grassland species *P. alpina* and *P. viviparum*, we found that plant-size-related traits increased under warmer conditions, while for *R. glacialis* and *C. resedifolia*, the reverse was true. We corroborate previous studies that report increasing microhabitat restrictions for the high-alpine specialist species *R. glacialis*, suggesting that further warming may confine its distribution to higher elevations. Herbarium collections in future studies could thus aid in better understanding plant species' responses in a changing world.

AUTHOR CONTRIBUTIONS

Sonja Wipf and Christian Rixen designed the study with input from Sarah Woodin and Francesca Jaroszynska. Francesca Jaroszynska collected the data with help of Christian Rixen, Sonja Wipf and their field team. Francesca Jaroszynska conducted the data analyses with support from Jonathan Lenoir. Francesca Jaroszynska led the manuscript writing, with contributions from all authors.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14062.

DATA AVAILABILITY STATEMENT

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REFERENCES

Alatalo, J. M., Erfanian, M. B., Molau, U., Chen, S., Bai, Y., & Jägerbrand, A. K. (2022). Changes in plant composition and diversity in an alpine heath and meadow after 18 years of experimental warming. *Alpine Botany*, *132*, 181–193. https://doi.org/10.1007/s00035-021-00272-9

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Begert, M., Schlegel, T., & Kirchhofer, W. (2005). Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. *International Journal of Climatology*, *25*(1), 65–80. https://doi.org/10.1002/joc.1118

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., Burns, P., Zetterberg, P., D'Arrigo, R., & Goetz, S. J. (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications*, *11*(1), 4621. https://doi.org/10.1038/s41467-020-18479-5

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Cooper, E. J. (2004). Out of sight, out of mind: Thermal acclimation of root respiration in Arctic ranunculus. *Arctic, Antarctic, and Alpine Research*, *36*(3), 308–313. https://doi.org/10.1657/1523-0430(2004)036[0308:OOSOOM]2.0.CO;2

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Ter Steege, H., Morgan, H. D., Van Der Heijden, M. G. A., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380.

Delarze, R., Gonseth, Y., Eggenberg, S., & Vust, M. (2015). *Lebensräume der Schweiz-Ökologie-Gefährdung-Kennarten* (3. vollständig überarbeitete Ed.). Ott.

Diemer, M. (2002). Population stasis in a high-elevation herbaceous plant under moderate climate warming. *Basic and Applied Ecology*, *3*(1), 77–83. https://doi.org/10.1078/1439-1791-00079

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P., & Guisan, A. (2013). Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, *24*(4), 593–606. https://doi.org/10.1111/jvs.12002

Elith, J., Graham*, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M. M., Townsend Peterson, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Fosaa, A. M., Gould, W. A., Hermanutz, L., Hofgaard, A., Jónsdóttir, I. S., Jorgenson, J. C., Lévesque, E., Magnusson, B., Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Rixen, C., Tweedie, C. E., & Walker, M. D. (2015). Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(2), 448–452. https://doi.org/10.1111/j.1461-0248.2011.01716.x

Felde, V. A., Kapfer, J., & Grytnes, J. (2012). Upward shift in elevational plant species ranges in Sikkilsdalen, Central Norway. *Ecography*, *35*(10), 922–932. https://doi.org/10.1111/j.1600-0587.2011.07057.x

Fischer, M., Weyand, A., Rudmann-Maurer, K., & Stöcklin, J. (2011). Adaptation of Poa alpina to altitude and land use in the Swiss Alps. *Alpine Botany*, *121*(2), 91–105. https://doi.org/10.1007/s00035-011-0096-2

Frei, E. R., Ghazoul, J., Matter, P., Heggli, M., & Pluess, A. R. (2014). Plant population differentiation and climate change: Responses of grassland species along an elevational gradient. *Global Change Biology*, *20*(2), 441–455. https://doi.org/10.1111/gcb.12403

Fuentes, N., Pauchard, A., Sánchez, P., Esquivel, J., & Marticorena, A. (2013). A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions*, *15*(4), 847–858. https://doi.org/10.1007/s10530-012-0334-6

Gallagher, R. V., Hughes, L., & Leishman, M. R. (2009). Phenological trends among Australian alpine species: Using herbarium records to identify climate-change indicators. *Australian Journal of Botany*, *57*(1), 1–9. https://doi.org/10.1071/BT08051

Gassó, N., Sol, D., Pino, J., Dana, E. D., Lloret, F., Sanz-Elorza, M., Sobrino, E., & Vilà, M. (2009). Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distributions*, *15*(1), 50–58. https://doi.org/10.1111/j.1472-4642.2008.00501.x

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, *2*, 111–115. https://doi.org/10.1038/nclimate1329

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., Ehrlén, J., Speed, J. D., Klanderud, K., & Bråthen, K. A. (2018). Stay or go–how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 41–50. https://doi.org/10.1016/j.ppees.2017.09.008

Grabherr, G., Gottfried, M., & Pauli, H. (2010). Climate change impacts in alpine environments. *Geography Compass*, *4*(8), 1133–1153. https://doi.org/10.1111/j.1749-8198.2010.00356.x

Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, *97*(10), 2791–2801. https://doi.org/10.1002/ecy.1500

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*(5), 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Heberling, J. M. (2022). Herbaria as big data sources of plant traits. *International Journal of Plant Sciences*, *183*(2), 777–783. https://doi.org/10.1086/717623

Hill, K. E., Guerin, G. R., Hill, R. S., & Watling, J. R. (2015). Temperature influences stomatal density and maximum potential water loss through stomata of *Dodonaea viscosa* subsp. *angustissima* along a latitude gradient in southern Australia. *Australian Journal of Botany*, *62*(8), 657–665.

Hiltbrunner, E., Schwikowski, M., & Körner, C. (2005). Inorganic nitrogen storage in alpine snow pack in the Central Alps (Switzerland). *Atmospheric Environment*, *39*(12), 2249–2259. https://doi.org/10.1016/j.atmosenv.2004.12.037

Jaroszynska, F., Rixen, C., Woodin, S., Lenoir, J., & Wipf, S. (2022). Data from: Resampling alpine herbarium records reveals changes in plant traits over space and time. *Zenodo*. https://doi.org/10.5281/zenodo.7245342

Klanderud, K., & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, *13*(1), 1–6. https://doi.org/10.1191/0959683603hl589ft

Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS ONE*, *10*(6), e0130205. https://doi.org/10.1371/journal.pone.0130205

Kopp, C. W., Neto-Bradley, B. M., Lipsen, L. P. J., Sandhar, J., & Smith, S. (2020). Herbarium records indicate variation in bloom-time sensitivity to temperature across a geographically diverse region. *International Journal of Biometeorology*, *64*(5), 873–880. https://doi.org/10.1007/s00484-020-01877-1

Körner, C. (2021). *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer Nature.

Körner, C., Neumayer, M., Menendez-Riedl, S. P., & Smeets-Scheel, A. (1989). Functional morphology of mountain plants. Dedicated to Prof. H. Meusel, on the occasion of his 80th birthday. *Flora*, *182*(5), 353–383. https://doi.org/10.1016/S0367-2530(17)30426-7

Kulonen, A., Imboden, R. A., Rixen, C., Maier, S. B., & Wipf, S. (2018). Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Diversity and Distributions*, *24*(2), 252–261. https://doi.org/10.1111/ddi.12673

Lamprecht, A., Semenchuk, P. R., Steinbauer, K., Winkler, M., & Pauli, H. (2018). Climate change leads to accelerated transformation of high-elevation vegetation in the Central Alps. *New Phytologist*, *220*(2), 447–459. https://doi.org/10.1111/nph.15290

Larigauderie, A., & Körner, C. (1995). Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annals of Botany*, *76*(3), 245–252. https://doi.org/10.1006/anbo.1995.1093

Lavoie, C., & Lachance, D. (2006). A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany*, *93*(4), 512–516. https://doi.org/10.3732/ajb.93.4.512

Leff, J. W., Jones, S. E., Prober, S. M., Barberán, A., Borer, E. T., Firn, J. L., Harpole, W. S., Hobbie, S. E., Hofmockel, K. S., Knops, J. M. H., McCulley, R. L., La Pierre, K., Risch, A. C., Seabloom, E. W., Schütz, M., Steenbock, C., Stevens, C. J., & Fierer, N. (2015). Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(35), 10967. https://doi.org/10.1073/pnas.1508382112

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bergendorff, C., Birks, H. J. B., Bråthen, K. A., & Brunet, J. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*(5), 1470–1481.

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

Lüdecke, D. (2022). sjPlot: Data visualization for statistics in social science. R package version 2.8.12. https://CRAN.Rproject.org/package=sjPlot

Midolo, G., De Frenne, P., Hölzel, N., & Wellstein, C. (2019). Global patterns of intraspecific leaf trait responses to elevation. *Global Change Biology*, *25*(7), 2485–2498. https://doi.org/10.1111/gcb.14646

Miller-Rushing, A. J., Primack, R. B., Primack, D., & Mukunda, S. (2006). Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany*, *93*(11), 1667–1674. https://doi.org/10.3732/ajb.93.11.1667

Mitchell, R. J., Hewison, R. L., Britton, A. J., Brooker, R. W., Cummins, R. P., Fielding, D. A., Fisher, J. M., Gilbert, D. J., Hester, A. J., Hurskainen, S., Pakeman, R. J., Potts, J. M., & Riach, D. (2017). Forty years of change in Scottish grassland vegetation: Increased richness, decreased diversity and increased dominance. *Biological Conservation*, *212*, 327–336. https://doi.org/10.1016/j.biocon.2017.06.027

Pauli, H., Gottfried, M., & Grabherr, G. (2001). High summits of the Alps in a changing climate. In G.-R. Walther, C. A. Burga, & P. J. Edwards (Eds.), *"Fingerprints" of climate change: Adapted behaviour and shifting species ranges* (pp. 139–149). Springer US. https://doi.org/10.1007/978-1-4419-8692-4_9

Perez, T. M., Rodriguez, J., & Mason Heberling, J. (2020). Herbarium-based measurements reliably estimate three functional traits. *American Journal of Botany*, *107*(10), 1457–1464. https://doi.org/10.1002/ajb2.1535

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234.

Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J., & Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, *91*(8), 1260–1264. https://doi.org/10.3732/ajb.91.8.1260

Read, D. J., & Haselwandter, K. (1981). Oobservations on the mycorrhizal status of some alpine plant communities. *New Phytologist*, *88*(2), 341–352. https://doi.org/10.1111/j.1469-8137.1981.tb01729.x

Rixen, C., & Wipf, S. (2017). Non-equilibrium in alpine plant assemblages: Shifts in Europe's summit floras. In *High mountain conservation in a changing world* (pp. 285–303). Springer.

Rixen, C., Wipf, S., Rumpf, S. B., Giejsztowt, J., Millen, J., Morgan, J. W., Nicotra, A. B., Venn, S., Zong, S., Dickinson, K. J., Freschet, G. T., Kurzböck, C., Li, J., Pan, H., Pfund, B., Quaglia, E., Su, X., Wang, W., Wang, X., ... Deslippe, J. R. (2022). Intraspecific trait variation in alpine plants relates to their elevational distribution. *Journal of Ecology*, *110*, 860–875. https://doi.org/10.1111/1365-2745.13848

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., & Dullinger, S. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(8), 1848–1853. https://doi.org/10.1073/pnas.1713936115

Ruotsalainen, A. L., Väre, H., Oksanen, J., & Tuomi, J. (2004). Root fungus colonization along an altitudinal gradient in North Norway. *Arctic, Antarctic, and Alpine Research*, *36*(2), 239–243. https://doi.org/10.1657/1523-0430(2004)036[0239:rfcaaa]2.0.co;2

Scherrer, D., & Körner, C. (2010). Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, *16*(9), 2602–2613. https://doi.org/10.1111/j.1365-2486.2009.02122.x

Scherrer, D., & Körner, C. (2011). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, *38*(2), 406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x

Spasojevic, M. J., Bowman, W. D., Humphries, H. C., Seastedt, T. R., & Suding, K. N. (2013). Changes in alpine vegetation over 21 years: Are patterns across a heterogeneous landscape consistent with

predictions? *Ecosphere*, *4*(9), art117. https://doi.org/10.1890/ES13-00133.1

Staude, I. R., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., Van Calster, H., Vellend, M., Bjorkman, A. D., Brunet, J., De Frenne, P., Hédl, R., Jandt, U., Lenoir, J., Myers-Smith, I. H., Verheyen, K., Wipf, S., Wulf, M., Andrews, C., … Baeten, L. (2022). Directional turnover towards larger-ranged plants over time and across habitats. *Ecology Letters*, *23*(2), 266–482. https://doi.org/10.1111/ele.13937

Steinbauer, K., Lamprecht, A., Semenchuk, P., Winkler, M., & Pauli, H. (2020). Dieback and expansions: Species-specific responses during 20 years of amplified warming in the high Alps. *Alpine Botany*, *130*(1), 1–11. https://doi.org/10.1007/s00035-019-00230-6

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231–234. https://doi.org/10.1038/s41586-018-0005-6

Totland, Ø., & Alatalo, J. M. (2002). Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, Ranunculus glacialis. *Oecologia*, *133*(2), 168–175. https://doi.org/10.1007/s00442-002-1028-z

Vandvik, V., Halbritter, A. H., Yang, Y., He, H., Zhang, L., Brummer, A. B., Klanderud, K., Maitner, B. S., Michaletz, S. T., Sun, X., Telford, R. J., Wang, G., Althuizen, I. H. J., Henn, J. J., Garcia, W. F. E., Gya, R., Jaroszynska, F., Joyce, B. L., Lehman, R., … Enquist, B. J. (2020). Plant traits and vegetation data from climate warming experiments along an 1100 m elevation gradient in Gongga Mountains, China. *Scientific Data*, *7*(1), 189. https://doi.org/10.1038/s41597-020-0529-0

Venn, S. E., Green, K., Pickering, C. M., & Morgan, J. W. (2011). Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecology*, *212*(9), 1491–1499. https://doi.org/10.1007/s11258-011-9923-1

Verrall, B., Green, K., & Pickering, C. M. (2021). Dynamics in plant diversity and composition on Australian alpine summits over time. *Biodiversity and Conservation*, *30*(6), 1855–1880. https://doi.org/10.1007/s10531-021-02171-1

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York ISBN 978-3-319-24277-4. https://ggplot2.tidyverse.org

Winkler, M., Lamprecht, A., Steinbauer, K., Hülber, K., Theurillat, J.-P., Breiner, F., Choler, P., Ertl, S., Gutiérrez Girón, A., Rossi, G., Vittoz, P., Akhalkatsi, M., Bay, C., Benito Alonso, J.-L., Bergström, T., Carranza, M. L., Corcket, E., Dick, J., Erschbamer, B., … Pauli, H. (2016). The rich sides of mountain summits – A pan-European view on aspect preferences of alpine plants. *Journal of Biogeography*, *43*(11), 2261–2273. https://doi.org/10.1111/jbi.12835

Wipf, S., Stöckli, V., Herz, K., & Rixen, C. (2013). The oldest monitoring site of the Alps revisited: Accelerated increase in plant species richness on Piz Linard summit since 1835. *Plant Ecology & Diversity*, *6*(3–4), 447–455. https://doi.org/10.1080/17550874.2013.764943

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Model output for plant functional trait changes over time along an elevation gradient for *Ranunculus glacialis* (flower number, leaf stem length, flower stem length, and leaf width). T-statistics are reported for flower stem length, leaf stem length and leaf width. Z-statistics are reported for flower number. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S2. Model output for plant functional trait changes over time along an elevation gradient for *Polygonum viviparum* (inflorescence length, leaf length, inflorescence stem length and leaf area). T-statistics are reported for all traits. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S3. Model output for plant functional trait changes over time along an elevation gradient for *Poa alpina* (inflorescence length, basal leaf length and inflorescence stem length). T-statistics are reported for all traits. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S4. Model output for plant functional trait changes over time along an elevation gradient for *Cardamine resedifolia* (flower number, leaf length, plant height, number of rosette leaves). T-statistics are reported for leaf length and plant height. Z-statistics are reported for flower number and number of rosette leaves. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S5. Model output for reproductive height trait change to a century of temperature and precipitation variation for *Poa alpina* (inflorescence length, basal leaf length and inflorescence stem length). T-statistics are reported for all traits. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S6. Model output for reproductive height trait change to a century of temperature and precipitation variation for *Cardamine resedifolia* (flower number, leaf length, plant height, number of rosette leaves). T-statistics are reported for leaf length and plant height. Z-statistics are reported for flower number and number of rosette leaves. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S7. Model output for reproductive height trait change to a century of temperature and precipitation variation for *Polygonum viviparum* (inflorescence length, leaf length, inflorescence stem length and leaf area). T-statistics are reported for all traits. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S8. Model output for reproductive height trait change to a century of temperature and precipitation variation for *Ranunculus glacialis* (flower number, leaf stem length, flower stem length, and leaf width). T-statistics are reported for flower stem length, leaf stem length and leaf width. Z-statistics are reported for flower number. Significant variables are shown as *** $= p < 0.001$, ** $= p < 0.01$, * $= p < 0.05$.

Table S9. Marginal and conditional R-squared values for the models illustrated in Figures 2–5 of the main manuscript.

Figure S1. Observation frequency according to sampling orientation of four alpine plant species for historical (black) and contemporary (golden) herbarium collections.

Figure S2. Forest plots of estimates for *Cardamine resedifolia* (a, e, i, m, blue), *Ranunculus glacialis* (b, f, j, n, ochre), *Poa alpina* (c, g, k,

o, green), and *Polygonum viviparum* (d, h, l, p, pink), where variables that deviate left of the solid grey line demonstrate a reduction in trait size/number with the corresponding variable (pale shade), and variables that deviate right of the line an increase in trait size/number (dark shade). Significant variables are shown as *** = p < 0.001, ** = p < 0.01, * = p < 0.05.

Figure S3. Box plot illustrating the change in precipitation (left, mm/y) and temperature (right, °C) for the contemporary (1985-2015) and historical (1880-1985) sampling time periods.