

Plant species' range shifts in mountainous areas—all uphill from here?

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Abstract Species from many different habitats are responding to recent climate change. Mountainous areas are of particular interest as they provide pronounced gradients and have experienced above-average temperature increases. Data from the beginning of the 20th century of both the upper and lower range limits of plants of the European Alps were updated a century later and analyzed in order to identify common trends and deviating patterns of shifts at opposing ends of species' ranges. At the upper

limit, there was a strong trend towards an increase in species richness per summit, including 33 species that were recorded for the first time on any of the investigated summit areas. The species experienced a consistent upward shift exceeding 100 elevational meters, and 49 out of the 125 investigated species shifted upwards to a present altitude which is higher than any reported occurrence in the region one century ago. The response at the lower range limit was more heterogeneous and suggests species-specific differences in responsiveness and response patterns. With this approach of the combined analysis of upper and lower range limits along elevational gradients, it is possible to identify candidate species that might not keep pace with climate change, and thus, might face an increased risk of extinction with continued global warming.

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Zusammenfassung Tier- und Pflanzenarten aus den verschiedensten Lebensräumen zeigen bereits Reaktionen auf den Klimawandel. Gebirgslebensräume sind in diesem Zusammenhang von besonderem Interesse, da sie ausgeprägte Gradienten aufweisen und eine im Vergleich zum globalen Durchschnitt stärkere Erwärmung erfahren haben. Detaillierte Angaben zu den höchst- und tiefstgelegenen Vorkommen von Pflanzenarten in den Alpen liegen von anfangs des 20. Jahrhunderts vor. Diese Angaben dienten als Grundlage für die vorliegende Arbeit. Sie wurden ein Jahrhundert später aktualisiert und im Hinblick auf gemeinsame Trends bzw. divergierende Veränderungsmuster an den jeweiligen Arealgrenzen ausgewertet. An der Arealobergrenze war ein deutlicher Trend zu einer höheren

Artenzahl pro Gipfel zu verzeichnen, darunter 33 Arten, welche zum ersten Mal überhaupt auf den untersuchten Gipfelbereichen nachgewiesen werden konnten. Die Arten erfuhren eine deutliche Aufwärtsverschiebung, die in manchen Fällen mehr als 100 Höhenmeter betragen kann, und 49 der 125 untersuchten Arten kommen mittlerweile in einer Höhe vor, die oberhalb der früher dokumentierten regionalen Höchstgrenze liegt. Die Veränderungen an der Untergrenze zeigen hingegen ein deutlich heterogeneres Bild und weisen auf unterschiedliche, artspezifische Reaktionsgeschwindigkeiten und -muster hin. Allerdings zeigte sich im Gegensatz zur Arealobergrenze kein deutlicher Aufwärtstrend der Arealuntergrenze bei den untersuchten Arten. Mit dem Ansatz der kombinierten Analyse der Veränderungen an der Arealober- und untergrenze lassen sich Arten erkennen, welche möglicherweise nicht mit dem Klimawandel Schritt halten können und damit einem erhöhten Aussterberisiko im Zusammenhang mit der fortschreitenden Erderwärmung ausgesetzt werden.

Introduction

Ecological ‘fingerprints’ of climate change (Walther et al. 2001; Parmesan and Yohe 2003; Root et al. 2003) appear across a wide range of taxonomic groups and geographic regions (Walther et al. 2002; Rosenzweig et al. 2007) and are being identified with increasing frequency (Walther et al. 2005b; Parmesan 2006). In this context, mountain ranges are of particular interest. Mountainous regions tend to warm more rapidly than the northern hemisphere average (Rebetez and Reinhard 2008) and the projected rate of warming in mountain systems is expected to be up to three times higher than the global average rate of warming recorded during the 20th century (Nogués-Bravo et al. 2007). Furthermore, mountain ecosystems as centers of endemism are important for biodiversity (Nogués-Bravo et al. 2007) and provide important ecosystem services for erosion control and water supply beyond their geographical limits including also the surrounding lowlands (Körner 2003; Becker et al. 2007).

The European Alps provide a long history of ecological data collection. Historical inventories of the Alpine flora proved to be a useful reference for detecting effects of climate change of the recent past and present (Hofer 1992; Grabherr et al. 1994, 2001; Camenisch 2002; Walther et al. 2005b; Cannone et al. 2007; Holzinger et al. 2008; Parolo and Rossi 2008; Vittoz et al. 2008). The comparison of recent and past inventories showed striking increases in species richness on mountain tops, and also suggested an increase of the floristic similarity of the summits (Jurassinski and Kreyling 2007). Hence, there is evidence

for a widespread upward movement of species along elevational gradients (Krajick 2004). However, there may also be species with opposing trends, i.e. resisting this general upward movement and remaining in place or even moving downwards. In these cases, effects such as gravitational mass movements (rock fall, avalanches, etc.) that push the range margin downhill may prevail.

We here compile and synthesize data of plant distributions on 25 summits of the Alps, which were re-inventoried recently (Grabherr et al. 2001; Camenisch 2002; Walther et al. 2005b). We compare the altitude of the present occurrences on mountain tops with information of species’ upper distributional limits at the beginning of the 20th century, to quantify their responsiveness to environmental change. Whereas these shifts reflect changes at the upper limit of plant elevational distributions (Walther et al. 2005b), we also analyze, for the first time to our knowledge, data of the same region for potential shifts at the lower-elevational range limit. Thus, we are able to compare findings from the upper range margins with those from the lower range margins of species in the same area, in order to assess whether all, upper and lower, range margins are moving uphill in parallel or if there are deviating patterns of range shifts at opposite ends of species’ elevational distributions.

Materials and methods

Rübel (1912) and Braun (1913) published data on the distribution of the alpine and nival flora in the region of Engadine valley in south-eastern Switzerland. These historical sources provide information on both the species’ upper range limits and localities of lowest detected occurrences in the past within the whole study region. These publications also served as historical source and baseline data for comparison with recent re-inventories of high-mountain summit vegetation (Grabherr et al. 2001; Camenisch 2002; Walther et al. 2005a). We here combine and analyze available data from the literature (Grabherr et al. 2001; Camenisch 2002) and our own data (Walther et al. 2005a; Burga et al. 2007) regarding the upper limit of species distribution on mountain summits in the Swiss Alps, and contrast these findings with new data for the species’ lower elevational limit in the same region in summer 2006, resurveying the surrounding area of the localities where the species’ lowermost occurrences were described in the historical literature (Rübel 1912). This allows us to study shifts at both the upper and lower ends of species distributions that have occurred since the beginning of the 20th century along elevational gradients. The altitudes of recent occurrences of the species were measured using barometric altimeters (Thommen pocket altimeter,

Revue Thommen AG, Switzerland, and Suunto Vector altimeter, Suunto Oy, Finland), which were calibrated against the relevant topographic map during field work. Given the precision of the altimeter and considering the discrepancy of a few meters in summit heights provided in the maps at the beginning and the end of the 20th century, differences between historic and present altitudes of the same species of <15 m were considered as to be within the range of uncertainty. We tested mean shifts for statistical significance by one sample *t*-tests using SAS for Windows 9.1. The nomenclature for species names in all records was standardized and updated following Aeschmann et al. (2004).

Shifts at the upper range margin

Usually, the summit area for investigation was defined as the uppermost 10 elevational meters (Rübel 1912), and the same delimitation was applied for all the recent re-inventory data. On Piz Languard (3,262 m at the summit), the uppermost 30 m were investigated, in agreement with the historical survey (for details see Walther et al. (2005b)). In total, we compiled available data of the floras of 25 summits with altitudes between 2,836 m and 3,418 m a.s.l., including 17 siliceous peaks and 8 calcareous peaks (cf. Fig. 1). For those summits where data are given in both Grabherr et al. (2001) and Walther et al. (2005b) we assembled the data of the two independent resurveys in one merged data set. Differences in the number of summits colonized by each species in the past compared to the present were calculated in order to identify changes in species' frequency on summits. Furthermore, for all species recorded on a summit in a recent inventory, we searched the historical literature for information on the historic highest detected occurrences of the same species in order to quantify range shifts that occurred in the course of the last century. These range shifts were analyzed at both the local scale, i.e. the difference between present and past species' upper limit on the same mountain (provided that information on the highest detected occurrence of the same species on the slope of the particular mountain was available in the historical literature), and the regional scale, i.e. the difference between the present and past uppermost limit of the same species on any mountain in the entire region (i.e. the Engadine).

The aforementioned analyses were restricted for methodological reasons to species that succeeded in reaching the defined summit area (usually the 10 uppermost elevational meters of each summit) in any of the recent inventories, but for Piz Languard (3,262 m a.s.l.), additional information is available for the uppermost occurrence of all species detected between 3,000 m a.s.l. and the summit (Braun 1913; Braun-Blanquet 1955).

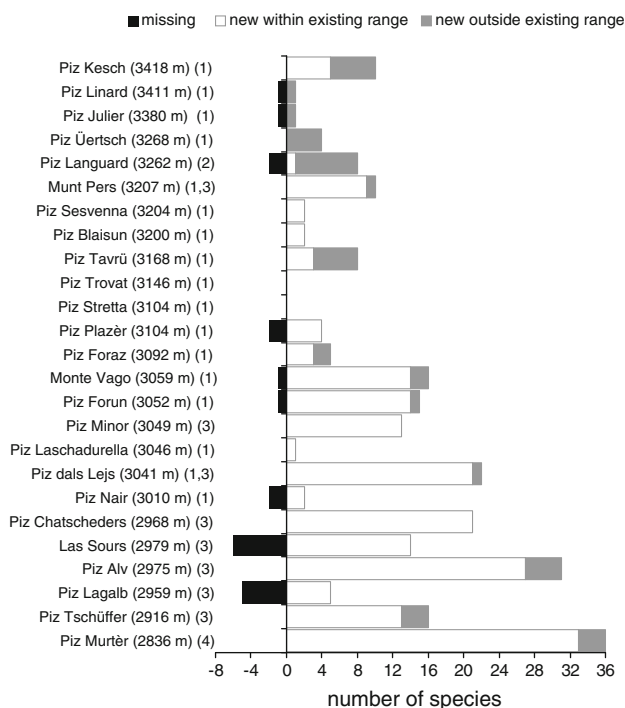


Fig. 1 Change in species richness of each investigated summit; new species are differentiated between those occurring on summits of lower altitudes than the species' historical upper limit (i.e. within existing range) and those above the former upper-elevational limit (outside existing range). Data sources for the different summits are indicated by numbers: (1) Grabherr et al. (2001), (2) Burga et al. (2007), (3) Walther et al. (2005a), and (4) Camenisch (2002)

Hence, we use here also the updated data from summer 2005 screening the area from 3,000 m a.s.l. to the summit and recording the uppermost present occurrence of each species found in the resurvey (for details see Burga et al. 2007).

Shifts at the lower range margin

For the lower range limits, information on the locality, usually the names of local areas that are indicated in topographic maps of 1:50,000 resolution or finer, and altitude (given in meters above sea level) was taken from Rübel (1912) for a set of 57 species in the study region. The species were selected based on the precision of the records from the historical data set and the phenological status during the period of field work (if possible, while in flower). This resulted in a list of localities between 1,715 and 2,700 m a.s.l. where lowest occurrences of one or several species had been recorded in the past. The surrounding areas of these localities were resurveyed in summer 2006. The area of the re-surveyed localities was between some square meters and around 250 m² depending on the topographical details of each locality. As for some

species several localities with low occurrences within the investigated region were listed in Rübél (1912), 81 species-locality pairs were verified in the field. In a similar manner as for the upper limit, we calculated species shifts separately for the local and regional scales. On the local scale, they resulted from differences between present and past lower limits for species found at the same locality (e.g. on the slope of the same mountain or in the same valley) as reported in the past. When a species was not found at the same locality as reported in the historical literature, but elsewhere in the region, the lowest site was used to calculate species shifts at the regional scale, i.e. the difference between present and past lowest occurrence of a species in the entire region.

Comparing range shifts at the lower and upper limit of the same species

Despite the fact that the re-inventories on upper and lower range limits were carried out independently, a set of 14 species resulted with information on both range margins at the local scale, and of 27 species with information on the coarser regional scale. These species sets could then be compared in terms of common trends and deviating patterns of shifts at opposing ends of elevational species ranges.

Results

Shifts at the upper range margins of species reaching the summit areas

Across all the 25 investigated summits, there was a strong trend towards an increase in species richness per summit (Fig. 1), but also a significant increase in the mean number of summits colonized by each species (+1.75, SD = 1.66, $p < 0.0001$, $n = 125$ species) in the course of the 20th century. Furthermore, 75 species with historical information on their uppermost occurrence on the same mountain, but at that time not occurring on the summit, succeeded in reaching the top, which underlines the upward trend of upper range margins (Fig. 2). For the species with range shifts >15 m in either direction, there is a significant mean upward shift of +145.3 m (SD = 156.4 m, $p < 0.0001$, $n = 172$ species-summit pairs) for the species on all summits; when excluding Piz Languard from the summit set (due to different delimitation of the summit area, see “Materials and methods”): +138.4 m (SD = 120.4 m, $p < 0.0001$, $n = 119$ species-summit pairs), and for Piz Languard only: +161 m (SD = 217.3 m, $p < 0.0001$, $n = 53$ species). For the 49 species listed in Table 1, reaching the top of one of the investigated higher-elevation summits also means a new uppermost elevational record

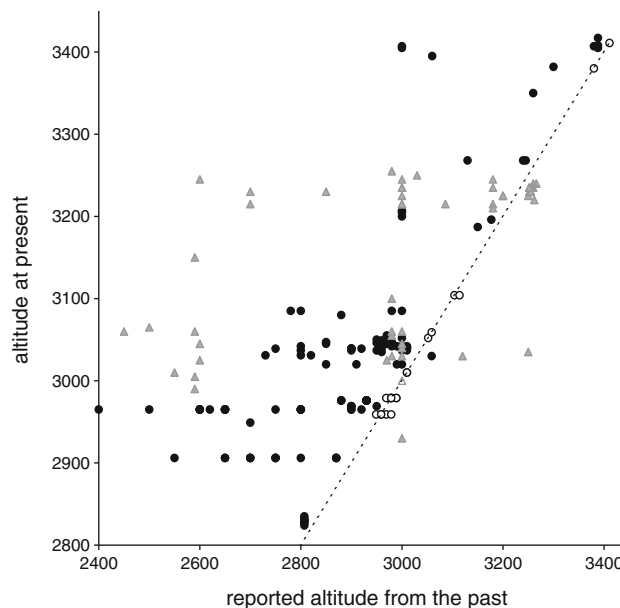


Fig. 2 Elevational range shifts of the species with information on their historical occurrence at the same mountain (only species with shifts >15 elevational meters are shown). In general, the investigated summit area at present was delimited to the uppermost 10 meters of elevation, except Piz Languard, where information from 3,000 m to the summit (3,262 m a.s.l.) was available. *Grey symbols* show the data from Piz Languard and *black symbols* from all the other summits excluding Piz Languard, *open symbols* show the historical altitude of the species that were not found in the investigated area of the same mountain in the resurveys, the *broken line* indicates the line of equal altitude

for the entire region; among them, 33 species were recorded for the first time on any of the investigated summit areas.

However, not all the species followed this trend towards higher altitudes and increasing numbers of summit colonizations. Three species fluctuated in the number of summits on which they were found, and experienced an equal number of losses and gains (=‘fluctuating species’ in Table 2); seven species did not change at all their number of summit occurrences (=‘stable species’ in Table 2); and finally, there were also three species with a declining trend in the number of summits on which they are occurring, relative to the first survey at the beginning of the 20th century (=‘declining species’ in Table 2).

Shifts of the upper range margins along the upper slopes of Piz Languard (3,000–3,262 m a.s.l.)

Whereas the previous analyses are based on the species which successfully reached the top of the mountains, the broader elevational range covered by the historical data set for Piz Languard (3,262 m a.s.l.) offers the possibility to analyze all 68 species, that occurred above an altitude of 3,000 m on this mountain at the beginning of the 20th

Table 1 List of species with new uppermost elevational records [m a.s.l.] in descending order according to the elevational shift for the region

Species name	Highest record in the past (Rübel 1912/Braun 1913) in the region	Highest record in the past (Rübel 1912/Braun 1913) on the same mountain	Altitude of new highest record	Locality	Upward shift at the same mountain	Elevational difference for the region
Species with new record on the same mountain as in the past:						
<i>Botrychium lunaria</i>	3,000	3,000	3,215	Piz Languard	215	215
<i>Cerastium latifolium</i>	3,130	3,130	3,268	Piz Üertsch	138	138
<i>Agrostis rupestris</i>	3,260	3,260	3,350	Piz Julier	90	90
<i>Luzula spicata</i>	3,300	3,300	3,382	Piz Linard	82	82
<i>Juniperus communis</i>	3,180	3,180	3,245	Piz Languard	65	65
<i>Juncus jacquinii</i>	3,180	3,180	3,215	Piz Languard	35	35
<i>Juncus trifidus</i>	3,180	3,180	3,210	Piz Languard	30	30
<i>Pritzelago alpina</i>	3,240	3,240	3,268	Piz Üertsch	28	28
<i>Saxifraga exarata</i>	3,380	3,380	3,407	Piz Kesch	27	27
<i>Linaria alpina</i>	3,200	3,200	3,225	Piz Languard	25	25
Species with new record on a different mountain than reported from the past:						
<i>Avenella flexuosa</i>	2,600		3,043	Piz Forun		443
<i>Hieracium villosum</i>	2,650	2,600	2,965	Piz Alv	365	315
<i>Adenostyles leucophylla</i>	2,940	2,700	3,230	Piz Languard	530	290
<i>Arnica montana</i>	2,800	2,500	3,065	Piz Languard	565	265
<i>Agrostis alpina</i>	3,010	3,000	3,245	Piz Languard	245	235
<i>Trollius europaeus</i>	2,600		2,820	Piz Murtèr		220
<i>Carduus defloratus</i>	2,600		2,814	Piz Murtèr		214
<i>Artemisia umbelliformis</i>	3,020	2,700	3,230	Piz Languard	530	210
<i>Leontodon hispidus</i>	2,620		2,827	Piz Murtèr		207
<i>Potentilla frigida</i>	3,200	3,000	3,405	Piz Kesch	405	205
<i>Gnaphalium hoppeanum</i>	2,762	2,650	2,965 ^b	Piz Alv	315	203
<i>Artemisia genipi</i>	3,208	3,000	3,407	Piz Kesch	407	199
<i>Anthoxanthum alpinum</i>	3,045	3,000	3,235	Piz Languard	235	190
<i>Draba dubia</i>	3,206		3,392	Piz Kesch		186
<i>Lloydia serotina</i>	3,050	2,850	3,230	Piz Languard	380	180
<i>Solidago virgaurea</i>	2,790	2,650	2,965 ^b	Piz Alv	315	175
<i>Crepis kernerii</i>	2,650		2,820	Piz Murtèr		170
<i>Selaginella selaginoides</i>	2,650		2,810	Piz Murtèr		160
<i>Sedum atratum</i>	3,000		3,153	Piz Tavrü		153
<i>Arabis bellidifolia</i>	3,009 ^a		3,158	Piz Tavrü		149
<i>Nardus stricta</i>	2,900		3,041	Piz Forun		141
<i>Antennaria dioica</i>	3,020	2,590	3,150	Piz Languard	560	130
<i>Phyteuma hemisphaericum</i>	3,098 ^a	3,000	3,215	Piz Languard	215	117
<i>Helianthemum alpestre</i>	2,850	2,600	2,965 ^b	Piz Alv	365	115
<i>Cardamine resedifolia</i>	3,280	3,060	3,395	Piz Linard	335	115
<i>Geum montanum</i>	3,120	3,000	3,235	Piz Languard	235	115
<i>Cirsium spinosissimum</i>	2,985	2,980	3,100	Piz Languard	120	115
<i>Poa alpina</i>	3,300		3,405	Piz Kesch		105
<i>Taraxacum alpinum</i>	3,150	3,030	3,250	Piz Languard	220	100
<i>Trisetum distichophyllum</i>	3,072 ^a		3,156	Piz Tavrü		84
<i>Saxifraga caesia</i>	3,010 ^a		3,087	Piz Foraz		77
<i>Elyna myosuroides</i>	3,010	2,980	3,085	Piz Stretta	105	75
<i>Minuartia verna</i>	3,200		3,268	Piz Uertsch		68
<i>Moehringia ciliata</i>	3,100		3,158	Piz Tavrü		58
<i>Campanula cochleariifolia</i>	3,020		3,069	Piz Foraz		49
<i>Achillea atrata</i>	2,980		3,025	Piz Laschadurella		45

Table 1 continued

Species name	Highest record in the past (Rübel 1912/Braun 1913) in the region	Highest record in the past (Rübel 1912/Braun 1913) on the same mountain	Altitude of new highest record	Locality	Upward shift at the same mountain	Elevational difference for the region
<i>Arabis caerulea</i>	3,130		3,159	Piz Tavrü		29
<i>Cerastium cerastoides</i>	3,000	2,600	3,025	Piz Languard	425	25
<i>Salix herbacea</i>	3,230	2,980	3,255	Piz Languard	275	25

^a Highest occurrence in the past according to the information provided in Grabherr et al. (2001)

^b No precise altitude within investigated summit area is available, therefore the lower limit of the investigated area is used for the calculation of the upward shift

Table 2 Species occurring on the same number or fewer summits than in the historical survey (for details see text)

Species name	Number of summits where species was recorded either in the past or present		
	New (recorded only in the present)	Stable (recorded in past and present)	Missing (recorded only in the past)
Fluctuating species:			
<i>Cardamine resedifolia</i>	1	7	1
<i>Cerastium pedunculatum</i>	1		1
<i>Elyna myosuroides</i>	1		1
Stable species:			
<i>Androsace alpina</i>		12	
<i>Saxifraga aphylla</i>		6	
<i>Primula hirsuta</i>		4	
<i>Sempervivum montanum</i>		3	
<i>Androsace helvetica</i>		3	
<i>Juncus trifidus</i>		1	
<i>Sesleria caerulea</i>		1	
Declining species:			
<i>Luzula alpinopilosa</i>		1	1 ^a
<i>Achillea erba-rota</i> ssp. <i>moschata</i>		2	1 + 1 ^a
<i>Achillea nana</i>			1 ^a

^a Missing within the investigated summit area, but recorded on the same mountain below the summit area

century (Fig. 2). On this summit, 9 species descended slightly (−15 to −35 m) in the upper part of the investigated range, whereas three species descended to considerably lower areas (*Luzula alpinopilosa*: −215 m; *Achillea nana*: −90 m; *Androsace obtusifolia*: −70 m). *Festuca violacea* was recorded in the past above 3,000 m, but was not detected in the latest survey. 36 species were observed at the same altitude (i.e. within the defined uncertainty range of ±15 m) and 37 higher than reported in the past. Among them, 19 species were recorded for the first time above 3,000 m on this mountain.

Shifts at the lower range margin

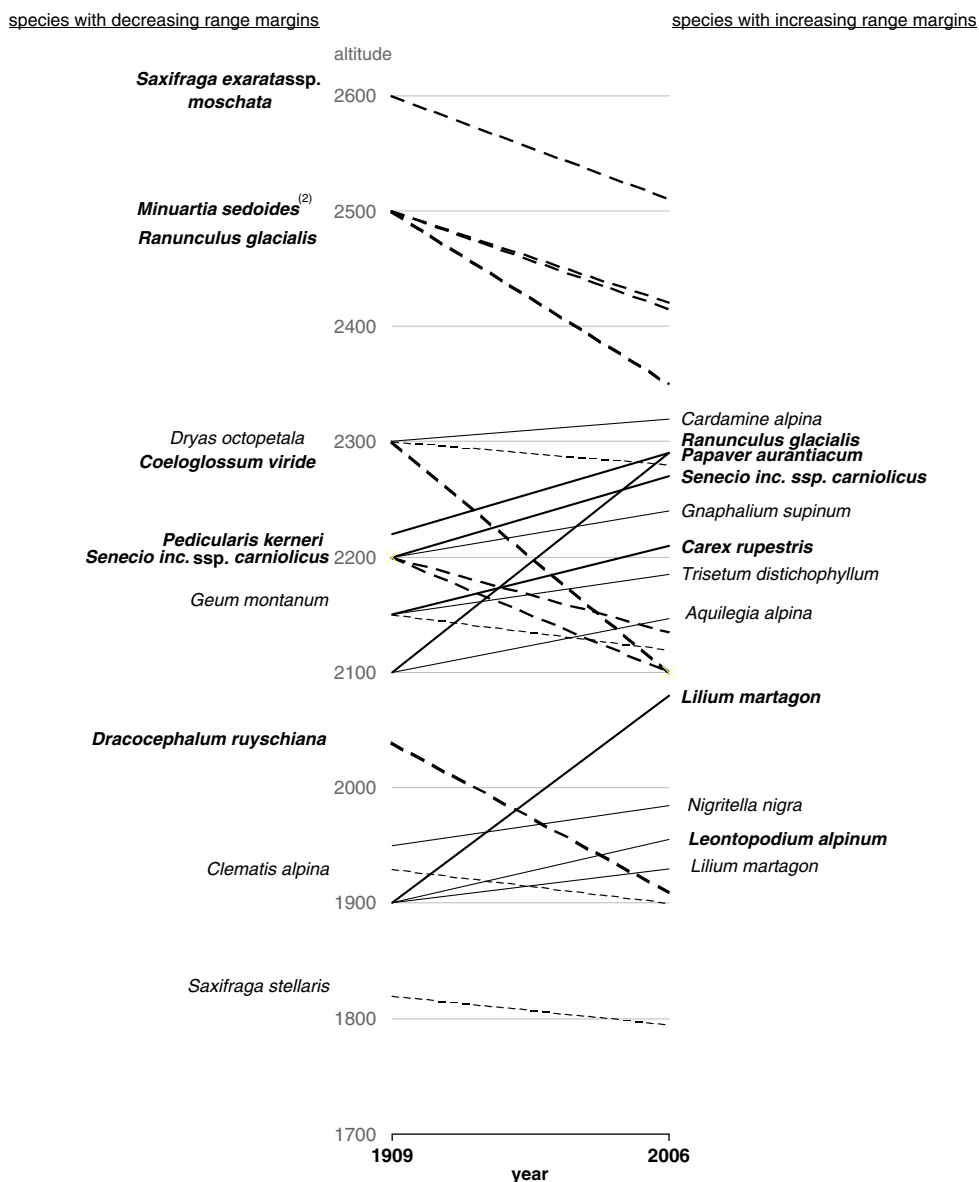
At the lower range limit, 35 out of the 57 resurveyed species were found at the same localities but sometimes at

different altitudes than reported in the past (Table 3; Fig. 3) and resulted in 46 species-locality pairs. 20 species at 22 localities remained at the same altitude whereas an equal number of 11 species at 12 localities shifted upwards or downwards, respectively. On average, there was no significant difference in elevation (mean shift = −2.4 m; SD = 68.6 m, $p = 0.82$, $n = 46$ species-locality pairs) for the resurveyed species at their lower-elevation boundary (Fig. 4). However, when splitting the dataset into two groups, species that were found at an altitude lower than 2,250 m revealed a positive but non-significant upward trend (mean shift = +14.2 m; SD = 59.4 m, $p = 0.17$, $n = 35$ species-locality pairs), while for species with a lower elevational limit at higher (>2,250 m) altitudes, there was a significant downward shift (mean shift = −55.0 m; SD = 72.2 m, $p = 0.03$, $n = 11$ species-locality pairs).

Table 3 Comparison of lowest-elevation occurrences of plant species in recent (2006) and historical (Rübel 1912; Braun 1913) surveys (the same species may show different trends at different localities)

	Same locality (35 species, 46 species-locality pairs)	Region (in total: 45 species)
Shift towards lower altitudes	11 species at 12 localities	7 species
Change only within range of uncertainty (± 15 m)	20 species at 22 localities	17 species
Shift towards higher altitudes	11 species at 12 localities	21 species

Fig. 3 Shifts at the lower distribution limit of species found at the same locality as reported in the past (only species with differences >15 m are shown; *dashed lines* decreases in altitude of range margin and *solid lines* increases in range margin, **bold** species with shifts >50 m. For *Minuartia sedoides*, information for two localities is available)



When a species was not found near the same locality but, for example, in a neighboring valley or on the slope of a different mountain than reported in the past, the range shift was interpreted on a regional scale. This approach resulted in data for 45 species and a mean shift on the regional scale that was significantly positive: +55.8 m (SD = 161.0 m, $p = 0.0254$, $n = 45$ species).

Shifts at opposite range margins of the same species

For 14 species, data are available to analyze trends on both upper and lower range margins of the same species at the local scale (Table 4a). Again, shifts at the upper range limit showed a more consistent trend (11 species with a marked upward shift, three species within the range of uncertainty),

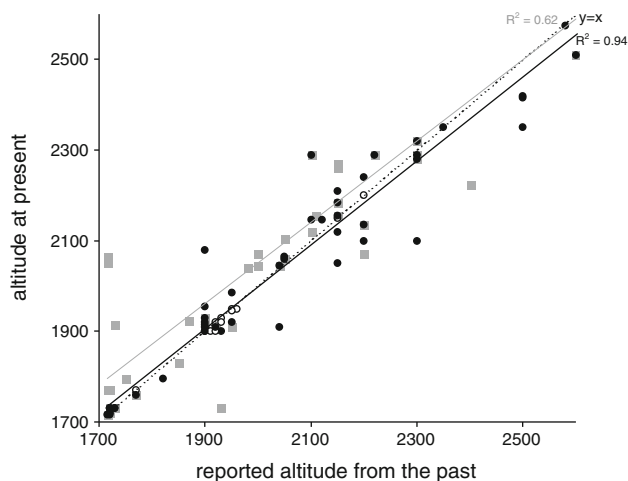


Fig. 4 Elevational shifts of the species at their lower range margins for species found at the same localities as reported in the past (black symbols and linear trendline) and on the regional scale (grey symbols and linear trendline). Open symbols show the historical altitude of the species that were not found in the resurvey, the broken line indicates the line of equal altitude

whereas at the lower range limit the pattern was more heterogeneous and included all three options (two species moved upward, seven showed no shift, five moved downward).

On the regional scale, the comparison of the direction of range shifts at upper and lower range limits is possible for 27 species (Table 4b). At this coarser resolution, the parallel upward shift of both range margins is more frequent than on the local scale (12 species, 44%), followed by

species exhibiting an upward shift of the lower range boundary but with a stable upper limit (6 species, 22%). Four species (15%) showed a stable lower limit but an expanding upper limit, while 2 species (7%) expanded their range at either end. The remaining three species showed no shift at the upper limit, whereas the lower limit remained stable for one species (4%) and showed a downward shift for 2 species (7%). For the species that showed a downward shift at their upper limit on Piz Languard, no information is available so far for their lower range limit.

Discussion

Although the historical data (Rübel 1912; Braun 1913) used in this study were not primarily intended to serve as baseline data for later resurveys, they have already proven to provide valuable information for analyses of floristic changes (Hofer 1992; Grabherr et al. 1994; Camenisch 2002; Walther et al. 2005a; Vittoz et al. 2008; see also Tingley and Beissinger 2009). As in many other cases (for reviews see e.g. Walther et al. 2001, 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006; Rosenzweig et al. 2007), we depend upon these detailed historical records or long-term monitoring series, dating as far back as before the increase in global average temperature of the recent past, in order to detect changes due to recent global warming.

For the upper range limit, the upward shift of alpine plant species was not only reflected in the increasing species richness on the summits as reported in previous studies

Table 4 Matrix for the comparison of the directions of range shift at opposite range margins of the same species found a) at the same localities as reported in the past and b) on the regional scale (for details see text)

	Upper range margin	
	Upward shift	Within range of uncertainty (<15 m)
<i>a. Lower range margin</i>		
Upward shift	<i>Gnaphalium supinum</i>	<i>Trisetum distichophyllum</i>
Within range of uncertainty (<15 m)	<i>Geum montanum</i> , <i>Gentiana punctata</i> , <i>Phyteuma globulariifolium</i> , <i>Carex sempervirens</i> , <i>Carex firma</i> , <i>Juncus trifidus</i>	<i>Androsace alpina</i>
Downward shift	<i>Senecio incanus ssp. carniolicus</i> , <i>Ranunculus glacialis</i> , <i>Dryas octopetala</i> , <i>Pedicularis kernerii</i>	<i>Minuartia sedoides</i>
<i>b. Lower range margin</i>		
Upward shift	<i>Salix herbacea</i> , <i>Gnaphalium supinum</i> , <i>Achillea atrata</i> , <i>Luzula spicata</i> , <i>Eritrichium nanum</i> , <i>Geum montanum</i> , <i>Ranunculus glacialis</i> , <i>Phyteuma globulariifolium</i> , <i>Oreochloa disticha</i> , <i>Veronica bellidioides</i> , <i>Carex sempervirens</i> , <i>Primula hirsuta</i>	<i>Saxifraga oppositifolia</i> , <i>Trisetum distichophyllum</i> , <i>Helictotrichon versicolor</i> , <i>Papaver aurantiacum</i> , <i>Carex rupestris</i> , <i>Carex curvula</i>
Within range of uncertainty (<15 m)	<i>Gentiana punctata</i> , <i>Dryas octopetala</i> , <i>Carex firma</i> , <i>Juncus trifidus</i>	<i>Androsace alpina</i>
Downward shift	<i>Senecio incanus ssp. carniolicus</i> , <i>Pedicularis kernerii</i>	<i>Minuartia sedoides</i> , <i>Saxifraga exarata ssp. moschata</i>

(Hofer 1992; Grabherr et al. 1994; Camenisch 2002; Walther et al. 2005a), but—as we show here—also in the colonization of on average nearly two more summits per species within a century among the investigated species. However, it has been questioned to what degree this floristic enrichment should be interpreted as upward migration due to recent climate change, or simply as recolonization after the end of the Little Ice Age (Kammer et al. 2007). Nonetheless Kammer et al. (2007) consider species that were discovered at elevations higher than their former uppermost occurrences as the first signs of an upward migration due to recent climate change. In particular they refer to species typical for alpine heaths and meadows that were for the first time discovered in the nival range (e.g. *Arnica montana*, *Avenella flexuosa*, *Nardus stricta*, and *Vaccinium myrtilus*). Therefore, this aspect deserves particular attention in the data set analyzed here. Ten species were found on the same mountain as their highest-elevation record was recorded in the past, but at higher altitudes, and another 39 species reached the peak of a mountain with an altitude that is higher than the uppermost occurrence of the species reported historically for the region. Furthermore, 33 species were recorded for the first time within the uppermost ten elevational meters on any of the investigated summits. Overall, there was a significant mean upward shift of approx. 150 elevational meters (depending on the specific data set used for calculation) of the upper margin of species distributions in the region compared to the occurrences reported one century ago. These results strongly suggest that, indeed, alpine/nival plants have been moving uphill from where they were in the past (Krajick 2004) and reached new height records in the investigated region. Thus, species close to their upper elevational limit seem highly responsive to changing environmental conditions, especially temperature (Salzer et al. 2009). From a physiological point of view, temperature is one of the major constraints on plant growth (Körner 2003). Hence, increasing average temperatures are likely to reduce this constraint, whereas other factors may have also facilitated the uphill movement of plant species (e.g. soil development and eutrophication).

However, focusing only on species that reached the top does not cover those that do not successfully move upwards until the summit areas. In this regard, the results from Piz Languard, where data is available on a much larger elevational range than just the summit area, provide a more-balanced picture of the situation at the upper range limit. Within this extended dataset, only a few species showed a downward shift of their upper range limit, while the general upward shift on this mountain was as strongly pronounced as on all the other summits. Hence, the majority of high alpine plants are indeed moving uphill, but not all species seem equally responsive. From the 125

species analyzed here at their upper range limit, 5 species (*Androsace alpina*, *Saxifraga aphylla*, *Sempervivum montanum*, *Androsace helvetica* and *Sesleria caerulea*) retained stable distributions in terms of both maximum altitude and number of summits they had colonized. *Androsace alpina* is also listed among the species with decreasing species cover between 1994 and 2004 in a recent analysis of permanent plots along an elevational gradient at the Schrankogel (Austria) (Pauli et al. 2006). Further species that show a shift in the downward direction, and thus, behave contrary to the general trend, include *Luzula alpinopilosa*, found on the same mountains but partly at considerably lower altitude than in the past (−215 m on Piz Languard), and in particular *Achillea erba-rota* ssp. *moschata* and *Achillea nana*, which both decreased in the number of summits they occupied as well as the altitude of their occurrence on particular mountains. Whereas climate change, resulting in warmer temperatures and prolonged growing seasons, supports an upward shift of plants and the colonization of former unsuitable habitats at higher altitudes, other factors affecting species ranges in the opposite direction may explain the response in the downward direction. Mechanical forces driven by gravity, such as erosion, snow- and landslides, expose plants to downslope processes and may counteract upward driving forces. In this dynamic balance between upward and downward acting forces, according to the data analyzed here, the upward forces seem to dominate with only few species having shifted their upper range margins to lower altitudes than recorded in the past.

At the lower range limit, the species differ much more in terms of the direction of range shifts and their responsiveness to climate change than at the upper range limit. On the local scale, the majority of the species remained at the same altitude or were detected at lower altitudes than reported in the past, resulting in a non-significant overall difference in elevation for the resurveyed species at their lower range limit. Furthermore, the subset of species with a lower elevational limit at altitudes higher than 2,250 m a.s.l. experienced a significant downward shift. Only on the coarse, regional scale, there is a trend towards higher altitudes, which would support the hypothesis of a parallel upward shift of both lower and upper range limits (cf. Hampe and Petit 2005). The 12 species that were not found in our survey, but are still present in the region (Reinalter 2004), may have left the areas that were searched for the lower range margins towards higher altitudes. This would be in concert with the observed recent decline of arctic-alpine plants at or near the southern periphery of their continuous geographic range in northwest Montana (Lesica and McCune 2004).

Alternatively, the (up to now) smaller responsiveness of lower range limits might also be a consequence of lagged

impacts of climate change. As it is typical for a local extinction process, environmental change at the lower range margin will first affect a species' population dynamics, and thus its demography, but only later its biogeography (Walther et al. 2010). Furthermore, both abiotic environmental conditions and biotic interactions may affect alpine plant population dynamics (Klanderud 2005). As a consequence, simulations of climatic warming in arctic zones suggested an increase in shrub biomass at the expense of other plant functional types (Epstein et al. 2000, but see Post and Pedersen 2008), a process that might also be expected in the longer term in alpine areas. Hence, with continued global warming, alpine species may be exposed to more competitive plant species or 'new' animal species migrating upwards from lower altitudes (Kullmann 2002, but see Price and Waser 2000). As a result, the available space for alpine species will be diminished within constant or even expanding elevational ranges (cf. also Breshears et al. 2008).

However, as the areas re-surveyed to detect a species' lower range limit were much larger than the well-defined summit areas sampled for the upper limit, species may have been overlooked in the difficult terrain. Moreover, methodological factors such as different sampling periods and sampling efforts (cf. Miller-Rushing and Primack 2008), or individual observer skills and experience (Tingley and Beissinger 2009) play an increasingly important role with larger investigation areas. Therefore, the results about lower range limits must be interpreted cautiously. Nonetheless, as we focus here on presence-only data from the past (cf. Tingley and Beissinger 2009), the comparison of historical with modern data in those locations where species once occurred, allows an estimate of local disappearance or persistence over the time span between the two surveys. In this regard, the lower limit of species' ranges was fairly constant over the course of the last century. The dynamic balance between upward and downward drivers seems less dominated by the upward forces compared to the situation at the upper limit.

Climate change (i.e. increasing temperatures and longer vegetation periods) is not necessarily in itself a reason to shift lower range margins upwards, but fosters replacement by other more competitive species. However, certain ecological niches may remain and allow species, at least for a certain time, to survive on the same altitude even in a changed climate, e.g. on a slope with different aspect on the same mountain.

However, there is also variability in the pattern of species' range shifts, which is revealed when looking at the responses in more detail, i.e. comparing corresponding localities in the past and present, or comparing upper and lower range limits of the same species. Almost all combinations of upward, stable and downward shifts are

represented, except those with downward shifts of the upper limit (cf. Table 4). Since only presence/absence data of the summit areas were collected, potential downward movements could not be observed in this study. An exception is Piz Languard, where the larger elevational range studied revealed 12 species with a downward movement. However, no data are available (so far) for the lower range limit of these species, as they were not included in the initial set of species selected for resurveying the lower limit. These patterns suggest highly species-specific behavior depending on the ecophysiology, habitat preferences, and dispersal capacity of the individual species (Lenoir et al. 2008; Le Roux and McGeoch 2008; Vittoz et al. 2009; Walther 2010). They may result in shifting dominances of species within communities, but also in the formation of non-analogue communities, where existing species will co-occur, but in new combinations (Huntley 1991; Walther 2004; Kullmann 2006).

Future research should continue searching the range limits of the species not detected here. Additionally, of the candidates identified as less-responsive species, not only the range limits should be monitored, but also populations at localities within their range in order to verify the trends presented at their limits of distribution. Furthermore, we should strive to substantially extend the list of species resurveyed in parallel at both their upper and lower range margins. Despite the methodological difficulties, this would broaden the spectrum of species and allow to reassess the information for general trends at opposite range limits. Elevational gradients are powerful 'natural experiments' for testing ecological responses to environmental change (Körner 2007). The combined analysis of upper and lower range limits along elevational gradients is an effective tool to identify candidate species that might not keep pace with global warming, i.e. species that for their limited dispersal potential migrate slower than the temperature increase would require. Such species would finally be exposed to the risk of being replaced by more competitive ones.

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