

Chapter 12

Non-equilibrium in Alpine Plant Assemblages: Shifts in Europe's Summit Floras

Christian Rixen and Sonja Wipf

Abstract Climate warming has been more pronounced in Arctic and alpine areas, and changes in the mountain flora can be expected as the temperature envelope moves upslope. On the one hand, alpine habitats will shrink due to upward migration of species from lower areas, such as trees and tall plants. On the other hand, extinctions of summit plants may be slowed down considerably by the high diversity of microhabitats, the longevity of alpine plants and positive plant–plant interactions in extreme environments. This review chapter attempts to document and monitor vegetation changes on mountain summits. Vegetation surveys that repeat century-old historical vegetation records show considerable upward migration and subsequent increases in species on summits. This trend apparently has accelerated in recent decades. Detailed monitoring of the last decade in European mountain ranges, however, shows that this vegetation change may be at the cost of rare endemic species and alpine specialists in drier Mediterranean regions. This chapter furthermore reviews other factors than temperature influencing alpine vegetation, namely precipitation and snow, nutrients, atmospheric CO₂ concentrations and land use. A subsequent question is how threatened mountain flora is by the ongoing environmental changes. Finally, this chapter discusses options for conservation and land use in high-alpine areas.

Keywords Climate change · Alpine plants · Long-term monitoring · Warming · Snow · High mountain conservation

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12.1 Introduction

Mountain plant species are already showing strong responses to climate change, for instance through upwards shifts in distribution limits (Grabherr et al. 1994; Walther et al. 2002; Lenoir et al. 2008). Species distribution models predict that this will lead to a contraction or total loss of high-alpine species' distribution ranges in the longer term (Engler et al. 2011), as their potential new habitat decreases in area at higher altitude (Körner 2007), while they might become out-competed and replaced by species from lower elevations (Engler et al. 2011). Through these mechanisms, species distribution models predict losses of over one-third of all species of the alpine vegetation belt for some regions of the Alps, and even higher extinction rates in other European mountain ranges (Engler et al. 2011).

This chapter will give an overview of our current knowledge of vegetation change in alpine regions with a particular focus on mountain summits in the Swiss Alps and across Europe. First, results from different monitoring approaches will be reviewed. One way to study vegetation changes is to repeat historical surveys, as many historical species lists from mountain summits are available from about a century ago, in some cases even from 170 years ago. Another suitable approach is standardised monitoring that was initiated relatively recently but capture shorter term vegetation changes in great detail (e.g. Roth et al. 2014). The Global Observation Research Initiative in Alpine Environments (GLORIA) for instance was initiated in 2001 across many European mountains and has now research sites on summits all over the world (Grabherr et al. 2000). The first analyses from GLORIA have demonstrated rapid vegetation changes on European summits (Pauli et al. 2012; Gottfried et al. 2012).

This chapter will then focus on different factors influencing mountain vegetation. The most discussed cause for vegetation changes is climate warming, but it is important to take also other factors of global change into consideration, such as atmospheric CO₂ concentrations, nutrient availability, land use, etc. Although temperature is, without a doubt, an important climatic driver of alpine plant distribution, it probably strongly interacts with precipitation and soil moisture (Elmendorf et al. 2012a, b) especially in the form of snow (Grytnes et al. 2014).

Given ongoing climate and vegetation change, the question arises how threatened mountain flora actually is. On the one hand, habitat for high-alpine specialists will most likely shrink in a warming climate. On the other hand, the high diversity of microhabitats on mountains (Scherrer and Körner 2011) and the longevity of many mountain plants may prevent extinctions or at least result in a delayed extinction debt (Dullinger et al. 2012). This book chapter will outline our current knowledge about the extinction risk of alpine plants.

Finally, the key question remains whether humans can contribute to the preservation of alpine plants or to prevent their local extinctions. Hence, the final section of this chapter will outline opportunities for conservation, appropriate forms of land-use, conservation and restoration measures in high-alpine environments.

12.2 Rapid Climate Change in Arctic and Alpine Areas

Mountain ecosystems are projected to experience more dramatic climate warming than most other regions of the world (Pepin et al. 2015; IPCC 2014). The Swiss Alps, for instance, have already experienced a warming of 1.8 °C since the Little Ice Age in the mid-nineteenth century (Begert et al. 2005) (Fig. 12.1), and the warming during the past 30 years was twice as high compared with the Northern Hemisphere (Böhm et al. 2001; Rebetez and Reinhard 2008). Since then the duration of snow cover has decreased in many regions of the world (IPCC 2007), and glaciers in the Alps have lost about 35% of their surface area (Hoelzle et al. 2007). Migration of plants and animals to higher elevations are impressive indicators for these profound changes in climate (Walther et al. 2002; Seimon et al. 2007).

12.3 Re-surveys of Historical Vegetation Records on Summits

Several studies have used re-surveys of historical data of summits floras to study long-term vegetation changes in high-alpine regions (Grabherr et al. 1994; Klanderud and Birks 2003; Walther et al. 2005). Summits are easy to relocate, which makes them equivalent to permanent plots. Moreover, summits are particularly important in the context of climate change-driven upward shifts, as they represent the last resort before species go extinct due to the absence of suitable habitats at even higher altitudes. Summits might thus provide one of the most exact,

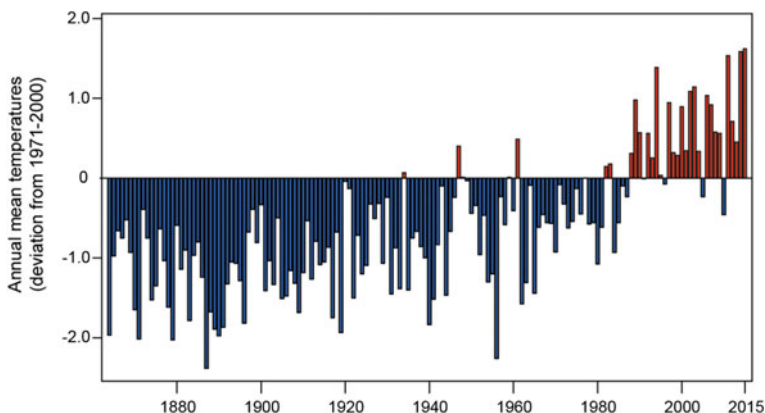


Fig. 12.1 Temperature anomalies (annual deviation from long-term mean) since the Little Ice Age at five climate stations (mean values) in Switzerland above 1000 m a.s.l. (Grand St. Bernard, Sils Maria, Davos, Engelberg, Säntis). Based on data from Begert et al. (2005)

most sensitive, and longest term indicators for floristic change and species loss due to climate change in the world. As a baseline for these re-survey studies serves plant species lists of mountain summits collected in the late nineteenth and early twentieth century by some of the most renowned botanists of their time, who were aiming to explore the elevation limits of vascular plant life (Stöckli et al. 2011). Europe is unique in harbouring a large number of such historical datasets, and Swiss botanists had a leading role. Almost 200 historical summit records of high quality (Stöckli et al. 2011) exist from Switzerland alone, and dozens more from the French and Italian Alps, the Pyrenees, the Scottish Highlands and the Scandes (e.g. Moen and Lagerstrom 2008; Odland et al. 2010; Grytnes et al. 2014; Klanderud and Birks 2003).

In general, previous re-survey studies on summits found an enrichment of the plant community and that species from lower elevation had been colonising higher elevations over the past century (see Fig. 12.2; Hofer 1992; Grabherr et al. 1994, 2001; Camenisch 2002; Walther et al. 2005; Holzinger et al. 2008; Kullman 2010; Wipf et al. 2013a). The rate of upward migration of plant species varied between studies, ranging from 4 (Grabherr et al. 2001) to 28 m per decade (Walther et al. 2005). However, these results were based on studies with relatively few samples (approx. 30 summits). While most studies suggest climate warming as a main driver of these changes, changes in winter precipitation might be an additional factor that fosters high-alpine community change (Grytnes et al. 2014).

Analyses of species traits indicated that species with seeds adapted to long-distance dispersal (i.e. with wings or similar) were particularly successful new

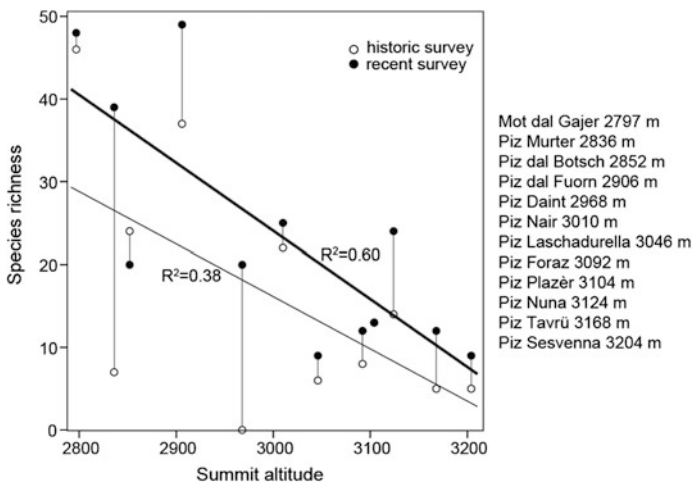


Fig. 12.2 Species numbers on 12 summits in the Swiss National Park region along a gradient in elevation as recorded in historical times by Josias Braun-Blanquet (1911–1927, *thin line*) (Braun-Blanquet 1958) and in recent times (2010–2012, *bold line*). Based on Wipf et al. (2013a)

colonisers (Holzinger et al. 2008; Vittoz et al. 2009; Matteodo et al. 2013). Generally, trait characteristics of new colonisers on summits were similar to those of lowland communities (Matteodo et al. 2013), further illustrating the general upwards trend of plants in mountain areas. Also, there is evidence that the biodiversity change has accelerated during the past 30 years comparable to recent temperature increase (Wipf et al. 2013b; Walther et al. 2005).

The single most prominent example for long-term vegetation change on a mountain summit is certainly Piz Linard in South East Switzerland (Wipf et al. 2013b; see Fig. 12.3). This mountain was first visited and botanized by Oswald Heer in 1835. He then recorded only a single plant species at the summit (*Androsace alpina*, Alpine Rock-Jasmine, Primulaceae) but noted many other plant species at a lower elevation of the same mountain (Fig. 12.3). Piz Linard was then re-visited and re-botanized eight times, the last time in 2011, making a total of nine botanical records in 176 years (Table 12.1). Species numbers had increased due to

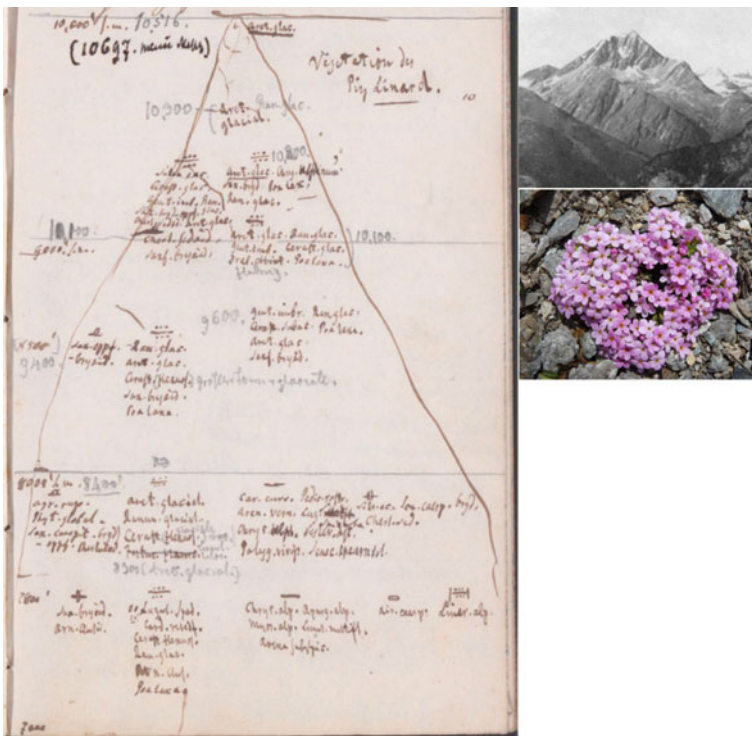


Fig. 12.3 Excerpt from Oswald Heer’s 1835 notebook (Heer 1835). Diagram of species occurrences on Piz Linard with *Aretia glacialis* = *Androsace alpina* (small photo; C. Rixen) at the summit. A transcript of this figure with modern species names is available in Wipf et al. (2013b). The photo of Piz Linard was taken by Josias Braun-Blanquet (Braun-Blanquet 1957), one of the re-surveys in the 1930s and 1940s. Reprinted by permission of the publisher (Taylor & Francis Ltd, <http://www.tandfonline.com>)

Table 12.1 Species occurrences and abundances on Piz Linard summit (3410 m a.s.l.; uppermost 30 m) from 1835–2011. Abundances are indicated by colour: light grey, low (<5 individuals); intermediate grey, intermediate (<10 individuals); dark grey, high (>10 individuals). No abundances are available for the 1864 and 1895 records. Species present in the uppermost 10 m are indicated with *double asterisks*. Highest observations of the species elsewhere in south-eastern Switzerland up to 1911 are listed for comparison. See details in Wipf et al. (2013b). In 2014, *Doronicum clusii* was rediscovered on the summit, but no full species record was taken (Wipf et al. personal communication)

Species	Presence on Piz Linard summit								Highest historical observation elsewhere			
	1835	1864	1895	1911	1937	1947	1992	2003	2011	Altitude (m)	Location	Year
<i>Androsace alpina</i> (L.) Lam.	**	**	**	**	**	**	**	**	**	3400 ⁺	Piz Kesch ¹	1894
<i>Leucanthemopsis alpina</i> (L.) Heywood	**	**	**	**	**	**	**	**	*	3400 ⁺	Piz Tschierva ²	1906
<i>Ranunculus glacialis</i> L.	**	**	**	**	**	**	**	**	**	3500	Piz Tschierva ²	1906
<i>Saxifraga bryoides</i> L.	**	**	**	**	**	**	**	**	**	3418	Piz Kesch ¹	1894
<i>Saxifraga oppositifolia</i> L.	**	**	**	**	**	**	**	**	**	3465	Piz Palü ³	1835
<i>Poa laxa</i> Haenke	**	**	**	**	**	**	**	**	**	3400 ⁺	Piz Kesch ¹	1894
<i>Draba fladnizensis</i> Wulfen	**	**	**	**	*	*	*	*	*	3400 ⁺	Piz Kesch ¹	1894
<i>Gentiana bavarica</i> L.	*	*	*	*	*	*	*	*	*	3400	Piz Tschierva ²	1906
<i>Cerastium uniflorum</i> Clairv.	*	*	*	*	*	*	*	**	**	3400	Piz Kesch ¹	1894
<i>Saxifraga exarata</i> Vill.	*	*	*	*	*	*	*	**	**	3380	Piz Kesch ¹	1894
<i>Luzula spicata</i> (L.) DC.	*	*	*	*	*	*	*	*	*	3262 ⁺	Piz Languard ⁴	1905
<i>Cardamine resedifolia</i> L.	*	*	*	*	*	*	*	*	*	3280	Piz Julier ⁴	1910
<i>Sedum alpestre</i> Vill.	*	*	*	*	*	*	*	*	*	3250	Piz Languard ⁴	1905
<i>Doronicum clusii</i> (All.) Tausch	*	*	*	*	*	*	*	*	*	3260 ⁺	Piz Languard ⁴	1905
<i>Cerastium pedunculatum</i> Gaudin	*	*	*	*	*	*	*	**	**	3100 ⁺	Munt Cotschen ³	1835
<i>Erigeron uniflorus</i> L.	*	*	*	*	*	*	*	*	*	3262 ⁺	Piz Languard ⁴	1905
<i>Gnaphalium supinum</i> L.	*	*	*	*	*	*	*	*	*	3262 ⁺	Piz Languard ⁴	1905
Total species number	1	3	4	8	10	10	10	12	16			

⁺ found at higher altitude on Piz Linard in 1911.
 Source: ¹Schibler (1897, 1929); ²Rübel (1912); ³Heer (1885); ⁴Braun (1913).

upward migration to a total of 16 species in 2011. Interestingly, the species number stagnated (at ten species) during three records between 1937 and 1992 but then increased considerably to 16 species in the past decades, which matches well the recent temperature increase. Most already present species increased in abundance and colonised new areas of the summit, while new arrivals mainly established at sites with already high species richness (Wipf et al. 2013b). Species that appeared after 1992 differed from species already present previously by having had a 200 m lower maximum altitude in the region during the early twentieth century. Although the conclusions that can be drawn from one single mountain are limited, the example of Piz Linard is nevertheless highly illustrative of ongoing vegetation changes on summits that are also supported by larger studies.

12.4 Extensive Monitoring of Recent Changes in Summit Plants

Re-sampling of historical vegetation surveys proved to be a very useful tool to study long-term vegetation changes on summits, but has the downside of some methodological uncertainties (Stöckli et al. 2011; Burg et al. 2015). This problem

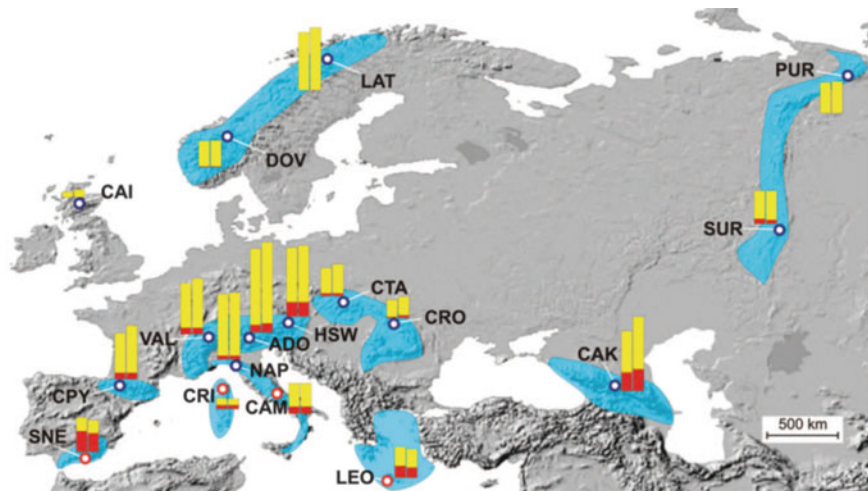


Fig. 12.4 GLORIA network (Pauli et al. 2012). Vascular plant species numbers in 17 European study regions. *Blue circles* indicate boreal and temperate, *red circles* indicate Mediterranean species. Bars show the number of species found in 2001 (*left bar*) and 2008 (*right bar*); the proportion of endemic species is shown in *red*. Species number (endemic number) per region in 2001/in 2008: LAT (N-Scandes/Sweden, 109(0)/118(0)); PUR (Polar Urals/Russia), 58(0)/60(0); DOV (S-Scandes/Norway), 49(1)/50(1); CAI (Cairngorms/UK), 10(0)/14(0); SUR (S-Urals/Russia), 62(9)/62(7); CTA (High Tatra/Slovakia), 53(5)/60(5); HSW (NE-Alps/Austria), 130(27)/134(27); CRO (E-Carpathians/Romania), 33(2)/40(5); ADO (S-Alps/Italy), 158(14)/170(17); VAL (W-Alps/Switzerland), 96(12)/105(12); NAP (N-Apennines/Italy), 123(7)/126(7); CPY (Central Pyrenees/Spain), 87(12)/101(12); CAK (Central Caucasus/Georgia), 113(35)/140(41); CRI (Corsica/France), 20(7)/19(7); CAM (Central Apennines/Italy), 57(13)/57(13); SNE (Sierra Nevada/Spain), 65(39)/60(35); LEO (Lefka Ori-Crete/Greece), 58(22)/54(19). *Blue-shaded areas* indicate the respective maximum distribution of species defined as endemic (12); most endemics have a far more narrow distribution area. From Pauli et al. (2012). Reprinted with permission from AAAS

was addressed in the Global Observation Research Initiative in Alpine Environments (GLORIA, <http://www.gloria.ac.at>), which provides a detailed protocol to record summit vegetation (Grabherr et al. 2000). Within less than a decade, significant changes in vegetation were already found in monitoring sites across Europe that were set up in 2001 and repeated in 2008 (Pauli et al. 2012; Gottfried et al. 2012) (and very recently in 2015). In the boreal-temperate mountain regions of Europe, species number had increased by nearly four species on average (Fig. 12.4; Pauli et al. 2012). In Mediterranean mountain regions, however, species number had decreased by ca. 1.5 species, possibly because recent climatic trends have decreased the availability of water in the European south.

Another interesting analysis of the same GLORIA data set looked at how much the vegetation change indicated warmer conditions, i.e. if species migrating upwards reported a warmer environment than before (so-called thermophilisation, Gottfried et al. 2012). Across the entire data set, the vegetation indicated

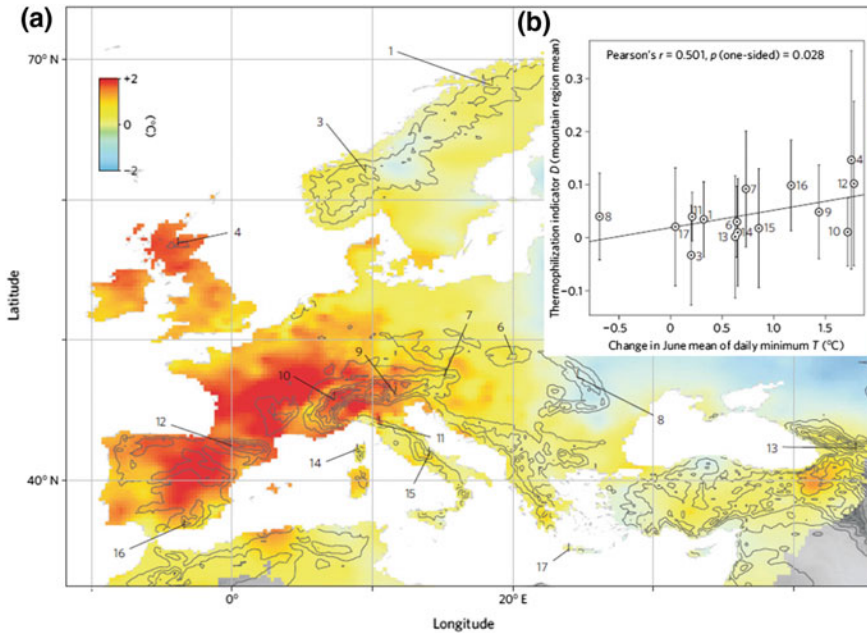


Fig. 12.5 Summit thermophilisation. The thermophilisation indicator D of mountain regions is correlated with temperature change. **a** Change in June mean of daily minimum temperature (map prepared from data provided by E-OBS (Haylock et al. 2008), resolution 0.25°), calculated as the difference between the averages of two time periods that precede plant data recording: prior 2008 (2003–2007)–prior 2001 (1996–2000). The numbers indicate the mountain regions and are referenced in (Gottfried et al. 2012). **b** Correlation of D with the change in June mean of daily minimum temperature (prior 2008–prior 2001) in the study regions (data derived from the map in a), using a one-sided test following the null hypothesis of no positive correlation. Vertical lines are 95% confidence intervals of D for the mountain regions, and a linear regression line is shown. Reprinted by permission from Macmillan Publishers Ltd: Nature, Gottfried et al. (2012)

thermophilisation, however, differences between mountain ranges were considerable. Most importantly, regions with most pronounced warming during the study period showed the highest thermophilisation (Fig. 12.5). These results illustrate how relatively rapid vegetation changes to climate warming can be.

12.5 Global Change, Not Only Climate Change: Snow Versus Temperature, Impacts of Nutrients, CO_2 Concentration, Land Use, Grazing

Temperature is one of the most important factors influencing high-alpine vegetation (Körner 2003). However, it always needs to be considered in combination with precipitation and, more specifically, snow. Temperature and light are responsible

for most physiological processes in alpine plants (Körner 2003), however, while snow is lying on the ground, warm atmospheric temperatures are of little effect on the plants below the snow (but see Starr and Oberbauer 2003; Palacio et al. 2015). Furthermore, there is evidence that with climate warming precipitation in the form of snow can actually increase and subsequently delay the timing of snowmelt and hence shorten the vegetation period (Bjorkman et al. 2015). Hence, to understand climate effects on alpine vegetation, we need to know summer temperatures and the timing of snowmelt.

Unfortunately, detailed snow information with high temporal and spatial resolution is often not easy to obtain. One possible approach is to use information of climate stations that not only record temperature but also snow cover below the stations. This approach has been used in the Swiss Alps where more than 100 metro stations have been employed since 1998 (Jonas et al. 2008; Rammig et al. 2010; Fontana et al. 2008). Plant phenology and productivity were analysed between stations and between years, and variables related to precipitation and snowmelt explained as much variance or more than temperature variables (Jonas et al. 2008). Also, vegetation change on Piz Linard (see above, Wipf et al. 2013b) and on Scandinavian mountains (Grytnes et al. 2014) seemed to be partly driven by the snow distribution on the summit. Furthermore, the small-scale distribution of snow in complex alpine terrain is extremely important for the distribution of plants: within the same elevation, the date of snowmelt can differ by more than a month within a few metres depending on topography (Rixen et al. 2010), which influences vegetation and plant populations considerably (for studies on the snowbed species *Salix herbacea* see Wheeler et al. 2015; Sedlacek et al. 2015; Cortes et al. 2014). Hence, future efforts should clearly focus on not only explaining vegetation changes by temperature but by a combination of temperature and precipitation/snow cover.

Apart from temperatures and precipitation, also factors such as nutrient input, elevated atmospheric CO₂, extreme events, land use, grazing, etc. need to be taken into consideration as drivers of vegetation change. Although nitrogen input is usually smaller (Hiltbrunner et al. 2005) and land-use less intensive at high elevation compared to lowlands, they are by no means negligible (Boutin et al. 2015). There is evidence that nitrogen deposition could affect alpine plants more than climate warming (Bobbink et al. 2010). Grazing by sheep can be observed up to the highest alpine grasslands e.g. in the Alps or the Pyrenees, and might over the long term have changed alpine vegetation composition profoundly. Abandonment of remote or steep areas, which is common e.g. in the Pyrenees and the Alps, is hence likely to change vegetation again, but in combination with climate change it is unlikely that vegetation will change back to its previous composition. Elevated atmospheric CO₂ concentrations did not enhance plant growth in alpine grasslands (Inauen et al. 2012; Körner et al. 1997) but in shrub communities at treeline (Anadon-Rosell et al. 2014; Dawes et al. 2013, 2014) where the bilberry (*Vaccinium myrtillus*) showed more growth, possibly at the cost of smaller or less responsive plant species.

12.6 Alpine Plants on the Verge to Extinction or Safe in Cold Microhabitats?

Although most studies demonstrate an impressive increase in species numbers and local colonisations, only relatively little local extinction, and no particular traits or species groups that were mainly affected by local extinctions, were found in long-term vegetation surveys in European alpine ecosystems (Hofer 1992; Walther et al. 2005; Wipf et al. 2013b; Grabherr et al. 2001; Matteodo et al. 2013). Moreover, the summit flora has been found to become more similar in composition over time, and there is evidence that many high-alpine species that were already present on few summits have meanwhile also colonised further summits (Kammer et al. 2007; Jurasinski and Kreyling 2007). Thus, up to now, we see many winners, but few losers on Europe's mountain summits even after several decades of ongoing climate warming.

Species distribution models recently predicted mountain flora to be threatened unequally across Europe in the twenty-first century (Engler et al. 2011). Specifically, temperature increase and precipitation decrease are expected to be more pronounced in e.g. the Alps and the Pyrenees than, e.g. in the Norwegian Scandes (Engler et al. 2011), which can be seen, in part, already in the temperature changes occurred in the recent past (Gottfried et al. 2012). Short-term floristic changes on European summits analysed by the GLORIA initiative indeed indicate a signal towards an increased prevalence of species with higher temperature preferences over 8 years that correlates with the magnitude of recent warming (see above, Gottfried et al. 2012).

While most studies agree that species upwards shifts are already happening, there is little consensus on potential losses of alpine biota due to future climate change. At first glance, the modelled projections of massive extinction rates in high-alpine species, and the observational findings of strong increase in summits species numbers even contradict each other. However, as the expected local extinctions are thought to be driven by competition through species rising to higher altitudes, it could be expected that an initial enrichment with new colonisers will be followed by an extinction of the formerly local species after a certain time lag (Dullinger et al. 2012; Engler et al. 2009). On the other hand, evidence for competitive replacement of high-alpine species is, at best, weak, even after decades of ongoing climate warming. Also, species in cold habitats are assumed to be less affected by competition (Pellissier et al. 2013) and their niches to be more closely related to their physiological limits (Normand et al. 2009). However, these studies do not take into account that some alpine species are true cold species, i.e. that they are not able to adapt their physiology (dark respiration) to a warmer temperature (Larigauderie and Körner 1995).

In contrast to the massive range contractions and high extinction rates among high-alpine plants predicted by species distribution models, recent micrometeorological studies show that due to the large variety of different microhabitats on a small spatial scale, the alpine belt offers a large number of small-scale "refugia" that

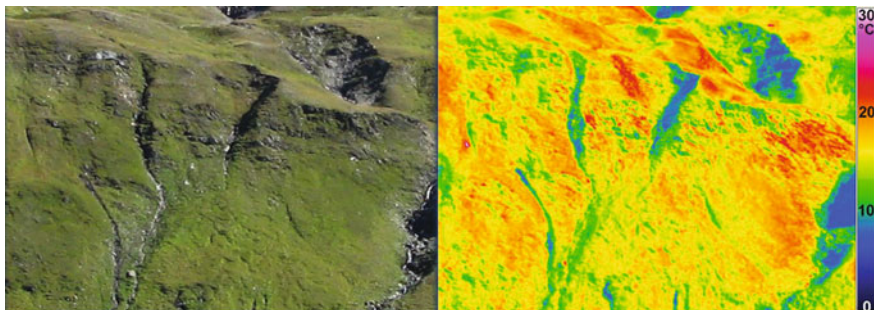


Fig. 12.6 Topography and surface temperatures on an NNW exposed slope at the Furka Pass in the Swiss Alps (elevation gradient of c. 100 m at c. 2450 m asl) on 29 August 2008, under full direct solar radiation (12–18 h). Topography, slope and aspect create a mosaic of habitats with very different temperatures. During one growing season temperature means of different microhabitats can differ by more than 10 °C

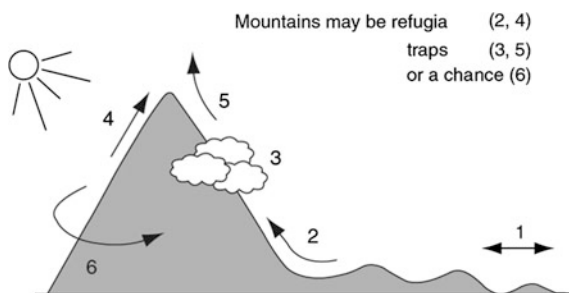


Fig. 12.7 Where to go in a warmer climate? Species from the lowlands may have difficulties to find suitable habitat as migration distances are long (1). Mountains can be refugia (2, 4) or traps (3, 5 if cloud forests shrink or mountains are too low). But often appropriate habitat can be nearby due to the mosaic of microhabitats on mountains (6). Reprinted from Körner (2013), with permission from Elsevier

could potentially meet the climatic requirements of high-altitude plants under warmer climate (Fig. 12.6, Scherrer and Körner 2011). Warmer “current micro-sites” and colder “future refugia” can persist at the same altitude, thus within a small distance of each other (Fig. 12.7). According to these studies, high-alpine plants should be well buffered against climate change, as they will only have to disperse over small distances to reach microsites that correspond with their climatic niche, rather than over large altitudinal distances as assumed by species distribution models. The point, however, is not so much about dispersion but about finding favourable sites to install and to grow when the place is already occupied. Many alpine species are in fact pioneer plants.

Support for the hypothesis of co-existence in separate microsites also arises from species distribution models themselves: if they operate with a spatial resolution too large to reflect small-scale microclimatic variability in the terrain, their predictions

of extinction risks will be too high, and models with finer scales end up with strikingly lower losses of high-alpine species (Randin et al. 2009). Thus, in alpine terrain with its high microsite diversity, coexistence between new colonisers and persisting high-alpine species may be possible if they do not show any niche overlap nor occupy the same microsites.

Even if species occupy the same microsite, they do not automatically out-compete each other. Neighbour facilitation, whereby plant individuals benefit from the presence of their interspecific neighbours, is a widespread phenomenon, especially under harsh environmental conditions (Brooker et al. 2008; Callaway et al. 2002; Choler et al. 2001; Wipf et al. 2006). Positive neighbour interactions can affect alpine plant diversity as much as climate (Cavieres et al. 2014). Neighbours can, e.g. ameliorate the microclimatic, environmental, and soil conditions while competing for the same resources at the same time (space, light, nutrients). If this facilitative force outbalances the competition, then facilitation fosters the coexistence of plant species on a small spatial scale (Kikvidze et al. 2001; Rixen and Mulder 2009) and could also play a major role in the colonisation of new sites through species from lower altitudes. There is even evidence that positive species interactions can extend species distributions into otherwise unfavourable habitats (le Roux et al. 2012). Hence, it is conceivable that facilitative neighbour interactions enable the coexistence of high-alpine species and new colonisers on mountain summits, which could counterbalance projected extinctions. Nevertheless, shifts in net interactions with environmental severity may differ among indicators of severity, growth forms and scales (Dullinger et al. 2007). Ongoing and future research will need to target at understanding if upward migration of plant species will lead to a loss of high-alpine specialists, or if the mosaic of microhabitats within one elevation range will provide enough buffer to prevent species loss, or if facilitation between neighbours enables the coexistence in the same microhabitat.

12.7 From Knowledge to Action? Towards Conservation of High Mountain Flora

Facing ongoing climate and vegetation change, the question remains if plants can adapt to new conditions and if humans can preserve alpine plants and prevent extinctions. We have seen above that the small-scale heterogeneity of the alpine landscape may provide habitat for alpine plants in a changing climate (Scherrer and Körner 2011). Adaptation of alpine plants through gene flow may also provide mechanisms to withstand changing environmental conditions (Cortes et al. 2014).

Nevertheless, upward migration of trees and plants from lower elevation will reduce the area with high-alpine habitat, and, in mountain ranges with human land use, measures for conservation and restoration need to be considered. On the one hand, moderate grazing can prevent or slow down tall competitive plants from outcompeting small alpine plants. On the other hand, if grazing pressure increases because alpine habitat decreases, erosion in steep areas might be the consequence. Also, pressures

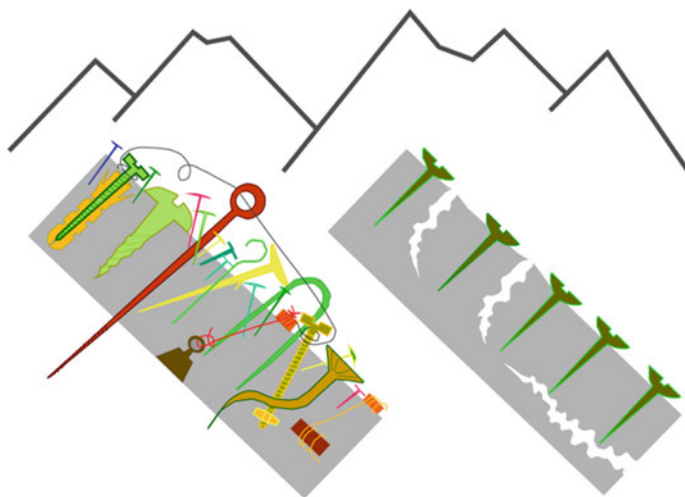
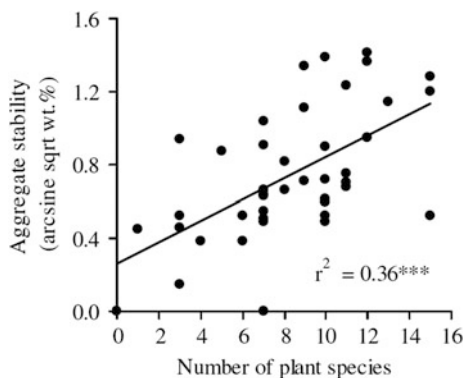


Fig. 12.8 Plants, with their diverse root systems, can be seen as the screws and nails of mountain ecosystems. From Körner and Spehn (2002) and Körner (2004) with permission of Springer Nature

Fig. 12.9 Relationship between aggregate stability (weight percent, arcsine square root transformed) and number of plant species on ski slopes (Pohl et al. 2009). Reprinted with permission of Springer



related to tourism (trampling, skiing, etc.) might become more severe if the alpine area shrinks (Pickering et al. 2003; Rixen and Rolando 2013; Rixen et al. 2011).

An important aspect to prevent erosion in alpine areas is that biodiversity provides an ecosystem function that is particularly relevant in steep terrain, namely soil aggregate stability. Figure 12.8 illustrates the idea that a high number of species and growth forms might be more likely to stabilise the uppermost soil horizons than a monoculture (Körner and Spehn 2002; Körner 2004). Although intuitive, this concept and the hypothesis have not often been tested in alpine vegetation. On disturbed ski slopes in the Swiss Alps, however, it was indeed shown that plant diversity explained soil aggregate stability better than all another measured plant, root and soil parameters (Fig. 12.9, Pohl et al. 2009). Hence, it is important to avoid

severe disturbance in sensitive alpine areas and, if necessary, to restore disturbed areas with seeds of adapted plants from high altitudes and with a large number of plant species to provide high plant diversity (Locher Oberholzer et al. 2008).

It clearly remains a challenge for future research to fully understand and appreciate if and how humans can provide conservation measures, appropriate intensities of grazing, etc. in alpine areas to prevent or reduce extinctions of alpine plant species. The established monitoring initiatives to document changes in alpine vegetation (see above) clearly need to be continued to improve our understanding of risks for alpine flora and possibly provide solutions for the future. Mountains are biodiversity hotspots, which provide numerous ecosystem services also for the lowlands, and hence we have a responsibility to maintain their precious habitats and flora.

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