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Unchanged risk of frost exposure for subalpine and alpine plants after snowmelt in Switzerland despite climate warming

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Abstract

The length of the snow-free season is a key factor regulating plant phenology and shaping plant community composition in cold regions. While global warming has significantly advanced the time of snowmelt and the growth period at all elevations in the Swiss Alps, it remains unclear if it has altered the likelihood of frost risk for alpine plants. Here, we analyzed the influence of the snowmelt timing on the risk of frost exposure for subalpine and alpine plants shortly after snowmelt, i.e., during their most vulnerable period to frost at the beginning of their growth period. Furthermore, we tested whether recent climate warming has changed the risk of exposure of plants to frost after snowmelt. We analyzed snow and air temperature data in the Swiss Alps using six weather stations covering the period 1970–2016 and 77 weather stations covering the period 1998–2016, spanning elevations from 1418 to 2950 m asl. When analyzed across all years within each station, our results showed strong negative relationships between the time of snowmelt and the frequency and intensity of frost during the most vulnerable period to frost for subalpine and alpine plants, indicating a higher frost risk damage for plants during years with earlier snowmelt. However, over the last 46 years, the time of snowmelt and the last spring frost date have advanced at similar rates, so that the frequency and intensity of frost during the vulnerable period for plants remained unchanged.

Keywords Air temperature · Alpine plants · Frost risk · Global warming · Snowmelt · Snow cover

Introduction

In mountainous regions, a significant decline of the snow cover has been reported worldwide over the last decades (Park et al. 2012; Pederson et al. 2013; Xu et al. 2016), including the European Alps (Klein et al. 2016; Marty 2008; Valt and

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Cianfarra 2010). Since the beginning of the 1970s in the Swiss Alps, the shortening of the snow cover duration found at elevations greater than 1100 m asl was mainly caused by earlier snowmelt in spring, and, to a lower extent, by later snow onset in autumn (Klein et al. 2016), in connection with a stronger temperature warming in spring than in autumn (Rebetez and Reinhard 2008; Serquet et al. 2013).

The timing of snowmelt, which greatly fluctuates from year to year irrespective of elevation (Klein et al. 2016; Wheeler et al. 2014), is the main driver triggering the onset of growth of most alpine plant species in spring (Gerdol et al. 2013; Inouye 2008; Jonas et al. 2008; Sherwood et al. 2017; Vitasse et al. 2017). The snow depth accumulated during winter was also found to play a role in the abundance of flowers, as well as in the probability of frost damage in spring when the snow becomes too thin to sufficiently protect overwintering plant tissues against extreme low temperatures (Inouye et al. 2002). Conversely, a deeper snow cover tends to delay the time of snowmelt, and therefore shifts alpine plant growth to a warmer period of the year with possibly fewer frost events (Jonas et al. 2008).

The beginning of the growing season for alpine plants is primarily controlled by the timing of snowmelt and the



subsequently air temperatures (Vitasse et al. 2017). On average, a duration of 2 to 3 weeks after the time of snowmelt was observed before the beginning of plant height growth in the Swiss Alps in snowbed conditions, corresponding roughly to an accumulation of 100 growing degree days (abbreviated GDD 100 thereafter) (Vitasse et al. 2017). Hence, the few days following the time of snowmelt are critical for alpine plants, as it is the period when plants lose progressively their freezing resistance acquired during winter and thus, when they become most vulnerable to freezing damages (Rixen et al. 2012; Sherwood et al. 2017). Nevertheless, at elevations above 2000 m asl, temperature below frost resistance of fully developed tissues of plants can still occur throughout the whole growing season (Körner 2003).

During winter, snow cover insulates alpine plants from freezing temperature (Körner 2003), so that the timing of snowmelt in spring determines when plant tissues are exposed to atmospheric air temperature and potentially with freezing temperatures. Freezing resistance of common plant species from the European Central Alps inducing 100% of mortality in the plant tissues was reported to range from -4 to -16 °C, with an average freezing resistance of -9 °C for most species (Ladinig et al. 2013; Taschler and Neuner 2004).

Species growing at sites with little snow protection, such as ridges, are typically more freezing resistant than species growing under snowbed conditions (Nagy and Grabherr 2009). The high interannual variability of the time of snowmelt shown in Klein et al. (2016) might also alter the freezing resistance of alpine and subalpine plants, which has been linked to the fluctuations of the snow depth during the onset of spring (Palacio et al. 2015).

Warming air temperatures since the 1970s have considerably advanced the spring onset of growth below the treeline in Western and Central Europe (Ahas et al. 2002; Menzel et al. 2006; Vitasse et al. 2018b), but little is known concerning alpine plants in the Alps, as, to the best of our knowledge, no long-term series of phenological observations are available for plants above the treeline in these regions. Besides, only a few studies describe the climatic conditions shortly after the snowmelt in alpine and subalpine regions (Inouye 2008; Inouye et al. 2002; Jonas et al. 2008; Wheeler et al. 2014), likely due to the difficulty to obtain accurate meteorological data at such elevations.

In a warmer climate, three different scenarios for the risk of frost exposure for alpine plants could be expected (Vitasse et al. 2018a): (i) an increase of the risk of frost exposure due to a faster advance of the phenology compared to the frost-free period, (ii) a decrease of the risk of frost exposure because of a faster advance of the frost-free period compared to phenology, (iii) no change in the risk of frost exposure due to a similar advance of both phenology and frost-free period. With a slower warming of minimum air temperatures compared to maximum air temperatures during spring above 800 m in the

Swiss Alps over the last five decades (Vitasse et al. 2018a) and an earlier time of snowmelt (Klein et al. 2016), the risk of frost exposure for subalpine and alpine plants may not necessarily decrease during their growth period in spring in a warmer climate. Below the treeline in the Swiss Alps, the risk of frost exposure and potential damage for some tree species has already increased during their leaf-out and flowering period at elevations higher than 800 m over the period 1975–2016, despite climate warming (Vitasse et al. 2018a). Hence, increasing frequency of potentially damaging freezing events might increase frost injuries (Wheeler et al. 2014), reduce growth (Wipf et al. 2009), or increase the mortality of sensitive frost plant species, such as shown for several species in the Rocky Mountains (Inouye 2008).

Here, we examined long-term air temperature and snow depth measurements in the Swiss Alps at six weather stations during the period 1970–2016, together with data from another meteorological network of 77 weather stations covering the period 1998–2016, both located at elevations ranging from 1418 to 2950 m asl. We focused our analysis on events with daily freezing temperatures below –4 °C during a period of 3 weeks enclosing the GDD 100, i.e., the most vulnerable period for subalpine and alpine plants when growth begins. Specifically, we aimed at (i) examining how the risk of frost exposure for plants is related to the time of snowmelt, both in its frequency and intensity, and (ii) testing whether the intensity and the occurrence of frost events have changed over the last five decades, when temperatures and the time of snowmelt have significantly increased and advanced.

Materials and methods

Study sites

We analyzed air temperature and snow data from two independent weather networks both located in Switzerland. One of them was the IMIS network (Intercantonal Measurement and Information System), which consists of high-elevation automatic weather stations set up by the Swiss Federal Institute for Snow and Avalanche Research (SLF). This network was started in the beginning of the 1990s with a few stations and has been steadily developed until reaching 103 stations in 2016. We selected 77 stations, ranging from 1630 to 2950 m asl (Fig. 1), that covered a temporal period from 1998 to 2016 and provided accurate daily snow depth and temperature data for at least 80% of the years during this period.

From the second and long-term weather network used in this study, we selected 11 weather stations from the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss) providing more than 45 years of daily snow data and described in Klein et al. (2016). From these 11 weather stations, we selected six stations covering the period 1970—



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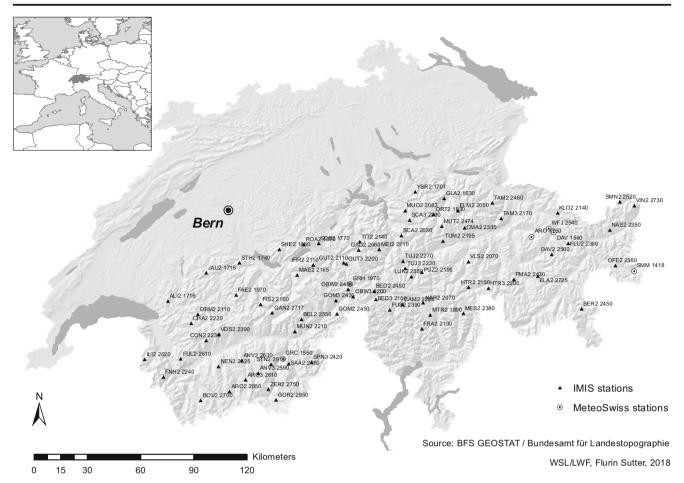


Fig. 1 Map of Switzerland showing the location and elevation of the 83 weather stations of both IMIS and MeteoSwiss networks used in the analyses

2016 that provided daily temperature data in at least 90% of the years and that were situated at approximately the same altitude range than the IMIS weather stations, i.e., ranging from 1418 to 2540 m asl (Fig. 1).

Temperature and snow data

All climatic parameters analyzed during the vulnerable period for subalpine and alpine plants were calculated for all stations and years that provide at least 80% of available data during that period. For the MeteoSwiss stations, daily snow depth was manually recorded every morning, whereas daily minimum and maximum air temperatures were automatically measured. For the IMIS stations, snow depth was automatically monitored every half hour through an ultrasonic sensor situated 6 m above the ground (SR50, Campbell Scientific, USA). Daily morning snow depth values were then extracted for a better comparison with the MeteoSwiss stations. Temperature and snow data for both networks were manually checked and tested for outliers and missing data.

Each year was considered as the period ranging from 1 September until 31 August of the following year. For each year, the time of snowmelt was defined as the first snow-free

day after an at least 40-day snow-covered period (~6 weeks) from 1 September until 31 August, following the methodology used by Klein et al. (2016).

Data analysis and statistics

In this study, we analyzed the risk of frost exposure for plant species growing through the altitudinal range of both IMIS and MeteoSwiss selected stations, i.e., from 1418 to 2950 m asl, which includes both subalpine and alpine plant species.

We defined the vulnerable period for alpine plants as the weeks enclosing the time when an accumulation of 100 degree days was reached since the time of snowmelt (GDD 100), corresponding roughly to the onset of growth at plant community scale (Vitasse et al. 2017). Specifically, we considered the duration of this vulnerable period as the time ranging from 7 days before the GDD 100 to 14 days following this GDD 100, corresponding to a total duration of 21 days. Choosing a shorter or a longer period (7 or 14 days before and after the GDD 100) for defining the duration of this period did not change the final results.

Among the two networks, non-relevant vulnerable periods for plants were found for 4 stations-years, because the GDD



100 was not reached before 1 September that defines the beginning of the following year and were thus discarded from the analysis (for the IMIS network: station GAN2 at 2717 m asl in 1999 and 2004 and for the MeteoSwiss network: station WFJ at 2540 m asl in 1978 and 1980).

For calculating the day of the year (abbreviated DOY hereafter) of the GDD 100 from the time of snowmelt, we first computed the daily mean temperature for both networks, based on the mean of the daily minimum and maximum air temperature. We then accumulated all daily mean temperature values >0 °C from the time of snowmelt, until reaching 100 °C.

Yearly snowmelt date anomalies of each IMIS and MeteoSwiss weather station were determined by calculating the difference between the yearly time of snowmelt and the mean time of snowmelt of each station over the period 1998–2016, if at least 50% of the snowmelt dates were available.

In our analysis, we considered frost events below -4 °C during the vulnerable period for plants, as this threshold corresponds to the lowest freezing resistance of numerous common plant species from the European Central Alps, typically growing in snowbed conditions where the IMIS stations are located (Ladinig et al. 2013; Taschler and Neuner 2004). The intensity of frost was calculated by extracting the absolute minimum air temperature occurring during this vulnerable period. The last frost day of the season was defined as the last occurrence of frost below -4 °C for each year (1 September–31 August).

General spatial and temporal patterns analyzed in this study were tested across all stations within each IMIS and/or MeteoSwiss network, by using mixed effect models with stations or elevation as a random effect. Different model types were tested for each analysis (linear and non-linear models, such as polynomial or exponential models). The best model for each relationship was then selected based on the lowest Akaike information criterion (AIC). Comparisons between each model (mixed or fixed effect models) were conducted using ANOVA to test whether they significantly differ. Detailed statistics of each selected mixed effect model are presented in Supplementary Material (Online Resource 1).

All individual temporal analyses reported in this study were performed for each MeteoSwiss station, by applying the non-parametric Theil-Sen estimator slope, combined with a Mann-Kendall significance test over the common temporal period for all six stations (1970–2016), as most of the analyzed parameters were not following a normal distribution (verified using Shapiro tests). No consistent breakpoints were detected (tested by step-wise regressions) in the temporal trends for all parameters and stations over the study period.

All analyses, tables and figures were performed using R 3.3 (R Core Team 2016) and the following R-packages: EnvStats, Kendall, Hmisc, nlme, and plotrix.



Results

Temporal trends of the monthly minimum and maximum air temperatures

A global increase of the monthly mean minimum air temperatures was detected over the study period at the six MeteoSwiss stations in the Swiss Alps, but with strong disparities across seasons (Online Resource 2). While only slight warming was detected during winter, minimum air temperatures increased considerably during spring and summer, especially during the snowmelt period from April to June, with rates ranging on average from $+0.42\pm0.05$ °C decade⁻¹ to $+0.72\pm0.06$ °C decade⁻¹ in May and April, respectively (Fig. 2). Similar results were found for the warming rate of mean maximum air temperatures, with slightly higher values than for minimum air temperatures in spring, ranging from $+0.52\pm0.13$ °C decade⁻¹ in May to $+0.78\pm0.11$ °C decade⁻¹ in April, and with lower values from September to December (Fig. 2).

Relationships between snowmelt and frost frequency and intensity within stations

The mixed effect models, both with stations or elevation as a random effect, showed significant exponential and linear relationships across all stations for both IMIS and MeteoSwiss networks (P < 0.001), between snowmelt anomalies and frost frequency or

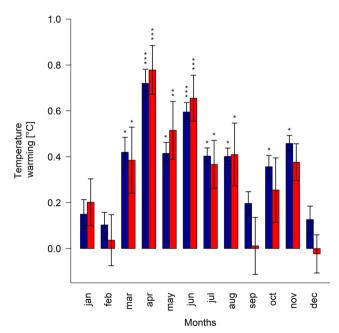


Fig. 2 Estimated trends (slope per decade) with associated standard errors for the monthly mean minimum (blue bars) and maximum air temperatures (red bars), averaged from the six MeteoSwiss stations over the period 1970–2016 and calculated from the Theil-Sen tests. The significance level of the Theil-Sen slopes was calculated with Mann-Kendall tests and is indicated with stars (*P<0.05, **P<0.01, and ***P<0.001)

frost intensity during the vulnerable period for subalpine and alpine plants across the study years (Fig. 3). The earlier the time of snowmelt, the more frequent and intense the frost events during the vulnerable period for plants in the Swiss Alps, irrespective of elevation, the temporal period analyzed (1998–2016 or 1970–2016), or the network used (IMIS or MeteoSwiss).

Temporal trends of the frost day frequencies and intensities

The date corresponding to the GDD 100 after the time of snowmelt has advanced significantly across all six available MeteoSwiss stations during the period 1970–2016, when using both stations or elevation as a random effect (P < 0.001) (Fig. 4a). Individual rates per station ranged from – 4.3 ± 0.1 to -7.0 ± 0.1 days decade⁻¹ (Online Resource 3). However, no significant general patterns were found for the temporal variations of the frequency or intensity of frost during the vulnerable period for plants over the period 1970–2016 (respective p values of 0.45 and 0.13) (Fig. 4b, c).

Occurrence of the last frost day of the season

The last frost day of the season (1 September-31 August) advanced significantly during the period 1970–2016 across all six

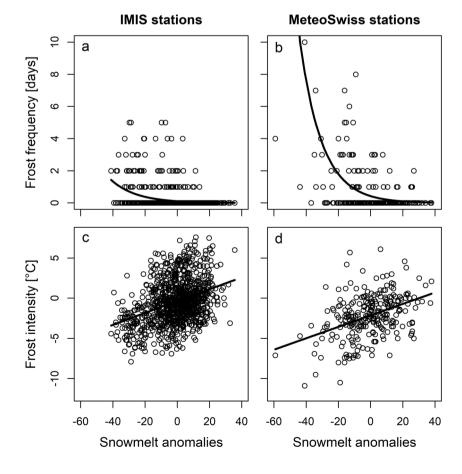
Fig. 3 Relationships within stations between snowmelt anomalies and frost frequency (a, b) or frost intensity (c, d) during the vulnerable period for plants, separated for each IMIS and MeteoSwiss networks over the periods 1998–2016 and 1970–2016, respectively. The black line corresponds to the predicted values from the best mixed effect model (with stations as a random effect), plotted when significant at P < 0.05

MeteoSwiss stations, when using both stations or elevation as a random effect (P < 0.001) (Fig. 5a). These trends ranged from -1.0 ± 0.2 to -10.0 ± 0.4 days decade⁻¹ depending on stations (Online Resource 3). As both the time of snowmelt (see Klein et al. 2016) and the occurrence of the last frost day of the season advanced over the last five decades at similar rates, we did not find any general pattern across all six MeteoSwiss stations for the duration of the period between the time of snowmelt and the occurrence of the last frost day of the season (P value 0.32) (Fig. 5b).

Discussion

Relationship between snowmelt and frost exposure for plants

Through the analysis of two independent high-elevation weather networks in the Swiss Alps over the period 1970–2016, our study demonstrates the strong connection between the time of snowmelt and the spatial and temporal distribution of the risk of frost events during the early growing season for subalpine and alpine plants. Specifically, our analysis focused on the most vulnerable period for plants to freezing events, i.e., the time shortly after snowmelt occurring generally between spring and early summer in subalpine and alpine regions.





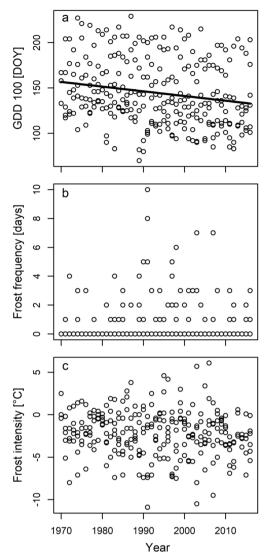
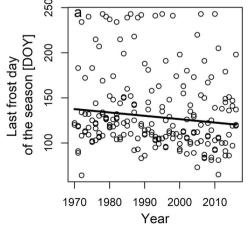


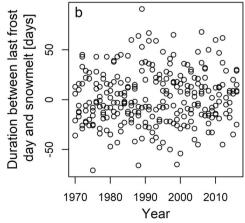
Fig. 4 Temporal variations of the yearly **a** GDD 100 calculated from the time of snowmelt and frost **b** frequencies, and **c** intensities calculated during the vulnerable period for plants across the six MeteoSwiss stations over the period 1970–2016. The black line corresponds to the predicted values from the best mixed effect model (with stations as a random effect), plotted when significant at P < 0.05

On average, we found that in years with early snowmelt, the frequency and intensity of frost were higher, regardless of elevation. This finding is in agreement with results of previous studies conducted in the Rocky Mountains (Inouye 2008; Inouye et al. 2002) or in the Swiss Alps (Wipf et al. 2009). Our results were consistent across both IMIS and MeteoSwiss networks and showed a consistent relationship between snowmelt and frost risk, whether we looked at numerous stations over a short period of time or at only a few stations over 46 years. Our results were also consistent for stations located in dryer or more humid regions (data not shown), according to the yearly mean precipitations map in Switzerland over the 1981–2010 period (MeteoSwiss website, unpublished work).

Despite a very high interannual variability of both plant phenology and snowmelt timing, our methodology for analyzing the risk of frost exposure for subalpine and alpine plants provided robust results, as findings were very similar when testing different durations for the vulnerable period around the GDD 100. This approach may thus be mainly valid for alpine species inhabiting snowbed conditions, where plants are generally more sensitive to frost, but also for species which are able to start their growth before the time of snowmelt, such as Crocus albiflorus, one of the first species to start growing and flowering when the snow cover becomes very thin (Rixen et al. 2008). It may, however, be less valid for species inhabiting ridge habitats (e.g., Loiseleuria procumbens), which are generally more freezing resistant than snowbed species. Our findings suggest that early snowmelt and a long growing season are not necessarily beneficial for plants, as during such years, plants are more exposed to freezing temperatures during the vulnerable period of initial growth. Furthermore, earlier phenology was found to be a costly strategy for certain alpine plants when their habitat faces temperature warming (Scheepens and Stöcklin 2013).

Fig. 5 Temporal trends of the yearly **a** last frost day of the season and **b** duration between this last frost day and the time of snowmelt across all six MeteoSwiss stations over the period 1970–2016. The black line corresponds to the predicted values from the best mixed effect model (with stations as a random effect), plotted when significant at P < 0.05







Trends in temperatures, timing of snowmelt, and frost exposure

We found that both minimum and maximum air temperatures have increased over the period 1970-2016 for all six MeteoSwiss stations used in this study, and particularly during the period where snowmelt generally occurs at these elevations (April-June), with average rates exceeding 0.5 °C decade⁻¹ for the maximum air temperatures. This result is consistent with previous studies, showing similar temperature trends during spring and summer (Rebetez and Reinhard 2008). The high consistency observed among the six MeteoSwiss stations indicates a general warming that may not be related to local climate conditions only. The stronger temperature increase observed in spring, corresponding to the mean snowmelt period, could be partly explained by the snow-albedo positive feedback loop described by Scherrer et al. (2012). This aforementioned study showed that around the snow line in the Swiss Alps, a spring day without snow cover is on average 0.4 °C warmer than a spring day with snow cover at the same location (Scherrer et al. 2012).

Despite the strong relationships found between snowmelt anomalies and the frequency or intensity of frost events during the vulnerable period for subalpine and alpine plants, no consistent temporal trends were found for the frequency or intensity of frost over the period 1970–2016. The stable frost exposure risk for plants found in this study may be explained by the compensatory effect of a similar increase in minimum and maximum air temperatures observed over the period 1970–2016. Increasing maximum air temperatures have contributed to the advance of both snowmelt and spring phenology, while increasing minimum temperatures have delayed the last potentially damaging frost, resulting in an overall unchanged risk of frost damage.

A faster worldwide increase of maximum air temperatures than minimum air temperatures in spring in high-elevation regions (Rangwala et al. 2013), as well as a reduction of the snow cover thickness and duration at all elevations in the Swiss Alps, strongly connected to temperature warming (Schmucki et al. 2015; Steger et al. 2013) are expected over the next decades. This prediction, following the general trends of temperature warming and snowmelt observed since 1970 in the Swiss Alps, suggests that the risk of frost exposure for subalpine and alpine plants might not be reduced and may even increase in the near future. Longer growing seasons with unchanged risk of frost damage may help plants adapted to such harsh environment to persist longer when more competitive lowland species migrate upslope (Matteodo et al. 2013; Steinbauer et al. 2018), as plants have generally a stronger freezing resistance at higher elevation (Sierra-Almeida et al. 2009). An increase in plant height and biomass production is also expected by the end of the century in the Swiss Alps, in connection with an earlier time of snowmelt and onset of growth for plants, but without taking into account the risk of frost exposure for plants (Rammig et al. 2010; Carlson et al. 2017).

However, with the predicted reduction in snow cover duration over the next decades, we may expect that the snow cover will become too thin, removing the snow insulation effect against late frost events, eventually resulting in an increase of the frost exposure for plants. Warming air temperatures was also shown to increase the freezing sensitivity of plants during the beginning of their growing season (Martin et al. 2010). With future climate warming and a weaker protecting effect of the snow cover against frost, the risk of exposure to frost damage for subalpine and alpine plants may increase over the next decades.

Conclusions

The time of snowmelt is a major factor determining the exposure of subalpine and alpine plants to late frost events, as plants become coupled with surrounding air temperature. By using long-term series of snow and temperature parameters at high-elevation in the Swiss Alps, we showed that an early time of snowmelt generally leads to an increasing frequency and intensity of frost during the vulnerable period for plants, irrespective of elevation or the temporal period analyzed (1998– 2016 or 1970-2016). However, despite climate warming and the general decline of both snowmelt timing and last frost day of the season in the Swiss Alps, our study suggests that the frequency and intensity of frost during the vulnerable period for plants have remained unchanged over the period 1970-2016. This absence of trends may be explained by the similar increase of minimum and maximum air temperatures found over the same period, which has shifted spring phenology and the last occurrence of potentially damaging frost to a same extent. Longer growing season with unchanged risk of frost damage may help plants adapted to such harsh environment to persist longer, whereas new thermophile species colonizing from lowlands areas could experience severe frost slowing down their upward shift. It remains a future research challenge if our results also hold in a global context of different alpine climates. In oceanic regions with unpredictable climate, frost can occur at any time of the year and hence, the freezing resistance of plants can be higher than in regions with predictable snow cover (Bannister 2007; Bannister et al. 2005; Venn et al. 2013). Understanding the role of frost events in different climates will considerably improve our predictions of vegetation changes under ongoing climate.

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References

- Ahas R, Aasa A, Menzel A, Fedotova V, Scheifinger H (2002) Changes in European spring phenology. Int J Climatol 22:1727–1738
- Bannister P (2007) Godley review: a touch of frost? Cold hardiness of plants in the southern hemisphere. N Z J Bot 45:1–33
- Bannister P, Maegli T, Dickinson KJ, Halloy SR, Knight A, Lord JM, Mark AF, Spencer KL (2005) Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? Oecologia 144:245–256
- Carlson BZ, Corona MC, Dentant C, Bonet R, Thuiller W, Choler P (2017) Observed long-term greening of alpine vegetation—a case study in the French Alps. Environ Res Lett 12:114006
- Gerdol R, Siffi C, Iacumin P, Gualmini M, Tomaselli M (2013) Advanced snowmelt affects vegetative growth and sexual reproduction of Vaccinium myrtillus in a sub-alpine heath. J Veg Sci 24:569–579
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362
- Inouye DW, Morales MA, Dodge GJ (2002) Variation in timing and abundance of flowering by Delphinium barbeyi Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. Oecologia 130:543–550
- Jonas T, Rixen C, Sturm M, Stoeckli V (2008) How alpine plant growth is linked to snow cover and climate variability. J Geophys Res 113(G03013):10. https://doi.org/10.1029/2007JG000680
- Klein G, Vitasse Y, Rixen C, Marty C, Rebetez M (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. Clim Chang 139:637–649
- Körner C (2003) Alpine plant life: functional plant ecology of high mountain ecosystems. 2nd ed. Springer, Berlin Heidelberg
- Ladinig U, Hacker J, Neuner G, Wagner J (2013) How endangered is sexual reproduction of high-mountain plants by summer frosts? Frost resistance, frequency of frost events and risk assessment. Oecologia 171:743–760
- Martin M, Gavazov K, Körner C, Hättenschwiler S, Rixen C (2010) Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO2. Glob Chang Biol 16:1057–1070
- Marty C (2008) Regime shift of snow days in Switzerland. Geophys Res Lett 35(L12501):5. https://doi.org/10.1029/2008GL033998
- Matteodo M, Wipf S, Stöckli V, Rixen C, Vittoz P (2013) Elevation gradient of successful plant traits for colonizing alpine summits under climate change. Environ Res Lett 8:024043
- Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, ALM-KÜBLER K, Bissolli P, Braslavská O, Briede A (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976
- Nagy L, Grabherr G (2009) The biology of alpine habitats. Oxford University Press, Oxford
- Palacio S, Lenz A, Wipf S, Hoch G, Rixen C (2015) Bud freezing resistance in alpine shrubs across snow depth gradients. Environ Exp Bot 118:95–101
- Park S-H, Lee M-J, Jung H-S (2012) Analysis on the snow cover variations at Mt. Kilimanjaro using Landsat satellite images. Korean J Remote Sens 28:409–420
- Pederson GT, Betancourt JL, McCabe GJ (2013) Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains, US. Geophys Res Lett 40:1811–1816
- Rammig A, Jonas T, Zimmermann N, Rixen C (2010) Changes in alpine plant growth under future climate conditions. Biogeosciences 7:2013–2024
- Rangwala I, Sinsky E, Miller JR (2013) Amplified warming projections for high altitude regions of the northern hemisphere mid-latitudes from CMIP5 models. Environ Res Lett 8:024040
- Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. Theor Appl Climatol 91: 27–34

- Rixen C, Freppaz M, Stoeckli V, Huovinen C, Huovinen K, Wipf S (2008) Altered snow density and chemistry change soil nitrogen mineralization and plant growth. Arct Antarct Alp Res 40:568–575
- Rixen C, Dawes MA, Wipf S, Hagedorn F (2012) Evidence of enhanced freezing damage in treeline plants during six years of CO2 enrichment and soil warming. Oikos 121:1532–1543
- Scheepens J, Stöcklin J (2013) Flowering phenology and reproductive fitness along a mountain slope: maladaptive responses to transplantation to a warmer climate in Campanula thyrsoides. Oecologia 171: 679–691
- Scherrer S, Ceppi P, Croci-Maspoli M, Appenzeller C (2012) Snowalbedo feedback and Swiss spring temperature trends. Theor Appl Climatol 110:509–516
- Schmucki E, Marty C, Fierz C, Lehning M (2015) Simulations of 21st century snow response to climate change in Switzerland from a set of RCMs. Int J Climatol 35:3262–3273
- Serquet G, Marty C, Rebetez M (2013) Monthly trends and the corresponding altitudinal shift in the snowfall/precipitation day ratio. Theor Appl Climatol 114:437–444
- Sherwood J, Debinski D, Caragea P, Germino M (2017) Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources. Ecosphere 8(3): e01745. https://doi.org/10.1002/ecs2.1745
- Sierra-Almeida A, Cavieres LA, Bravo LA (2009) Freezing resistance varies within the growing season and with elevation in high-Andean species of central Chile. New Phytol 182:461–469
- Steger C, Kotlarski S, Jonas T, Schär C (2013) Alpine snow cover in a changing climate: a regional climate model perspective. Clim Dyn 41:735–754
- Steinbauer MJ, Grytnes J-A, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556:231–234
- Taschler D, Neuner G (2004) Summer frost resistance and freezing patterns measured in situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. Plant Cell Environ 27:737–746
- R Core Team (2016) R: A Language and Environment for Statistical Computing. Vienna, Austria
- Valt M, Cianfarra P (2010) Recent snow cover variability in the Italian Alps. Cold Reg Sci Technol 64:146–157
- Venn SE, Morgan JW, Lord JM (2013) Foliar freezing resistance of Australian alpine plants over the growing season. Austral Ecol 38: 152–161
- Vitasse Y, Rebetez M, Filippa G, Cremonese E, Klein G, Rixen C (2017) 'Hearing' alpine plants growing after snowmelt: ultrasonic snow sensors provide long-term series of alpine plant phenology. Int J Biometeorol 61:349–361
- Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018a) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. Agric For Meteorol 248:60–69
- Vitasse Y, Signarbieux C, Fu YH (2018b) Global warming leads to more uniform spring phenology across elevations. Proc Natl Acad Sci 115:1004–1008
- Wheeler J, Hoch G, Cortés AJ, Sedlacek J, Wipf S, Rixen C (2014) Increased spring freezing vulnerability for alpine shrubs under early snowmelt. Oecologia 175:219–229
- Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Clim Chang 94:105–121
- Xu Y, Ramanathan V, Washington W (2016) Observed high-altitude warming and snow cover retreat over Tibet and the Himalayas enhanced by black carbon aerosols. Atmos Chem Phys 16:1303–1315

