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Small-scale drivers: the importance of nutrient availability and snowmelt timing on performance of the alpine shrub *Salix herbacea*

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Abstract Alpine plant communities are predicted to face range shifts and possibly extinctions with climate change. Fine-scale environmental variation such as nutrient availability or snowmelt timing may contribute to the ability of plant species to persist locally; however, variation in nutrient availability in alpine landscapes is largely unmeasured. On three mountains around Davos, Switzerland, we deployed Plant Root Simulator probes around 58 *Salix herbacea* plants along an elevational and microhabitat gradient to measure nutrient availability during the first 5 weeks of the summer growing season, and used in situ temperature loggers and observational data to determine date of spring snowmelt. We also visited the plants weekly to assess performance, as measured by stem number, fruiting, and herbivory damage. We found a wide snowmelt gradient which determined growing season length, as well as variations of an order of magnitude or more in the accumulation of 12 nutrients between different microhabitats. Higher nutrient availability had negative effects on most shrub performance metrics, for instance decreasing stem number and the proportion of stems producing fruits. High nutrient availability was associated with increased herbivory damage in early-melting microhabitats, but among late-emerging plants this pattern was reversed. We demonstrate that nutrient availability is highly variable in alpine settings, and that it strongly influences performance in an alpine dwarf shrub, sometimes modifying the response of shrubs to snowmelt timing. As the climate warms and human-induced nitrogen deposition continues in the Alps, these factors may contribute to patterns of local plants persistence.

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This study examines how fine-scale variation in the interactions among nutrient availability, snowmelt timing, soil moisture, and other abiotic factors aredistributed throughout a Swiss alpine landscape. Unlike many previous studies that have used single-factor approaches to assess spatial variation in nutrient availability, we used a multivariate, integrative technique that includes the effects of soil moisture on nutrient uptake. Using this approach, we show that microhabitats can vary as much over 30 to 40 meters as they do from the top to bottom of kilometer-long elevational transects.

Keywords Global change · Herbivory · Microhabitat · Spring warming · Reproduction

Introduction

Climate change influences summer growing season temperatures, growing season length, timing of snowfall and

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snowmelt, and quantity of both summer and winter precipitation (IPCC 2013). Alpine regions are projected to experience faster warming than many other ecosystems, leading to substantial habitat change. Biodiversity loss is predicted for many alpine plant communities (Guisan and Theurillat 2000), through range shifts or extinction of plant species leading to high species turnover rates in alpine communities (Bakkenes et al. 2002; Thuiller et al. 2005). As a response to warming and accelerated snowmelt, alpine plants may alter their phenological patterns, growth and reproduction (Galen and Stanton 1993; Inouye 2008; Wipf et al. 2009), further altering alpine communities.

In alpine systems, environmental variation on a fine spatial scale can represent an important driver of plant fitness and persistence. For instance, one study of snowmelt timing and temperature in the Swiss Alps found "remarkable variation" in surface temperatures and suggested that, even though warming in some areas may exceed IPCC predictions, the vast majority of plant species would be able to escape climate warming by moving very short distances (Scherrer and Körner 2011). Rather than modeling temperature in these landscapes, the related metric of snowmelt timing may be a more relevant factor in determining species richness (Choler 2005), as well as phenology, plant traits and fitness within individual populations (Walker et al. 1995; Kudo and Hirao 2005; Wheeler et al. 2014). Snowmelt time has important implications not only for early phenological events like budbreak and flowering but also for the presence and timing of pollinators and herbivores (Roy et al. 2004) and the period available for fruits to mature (Kudo 1993). These complex effects on multiple growth and reproductive responses could potentially accelerate the differences in shrub performance between microhabitat types.

Although temperature and the timing of spring snowmelt are often the primary climatic drivers of plant distribution and performance (Inouye 2008; Wipf 2010; Gerdol et al. 2013), other biotic and abiotic factors also have important effects. Nutrient availability may be of particular importance, as experimental manipulations have found that nitrogen and phosphorus are either limiting or co-limiting nutrients in many alpine systems, affecting vegetative growth and flowering of both communities and species (Bowman et al. 1993; Seastedt and Vaccaro 2001; Petraglia et al. 2013). In addition, nutrient availability can influence phenological timing, complicating the response to snowmelt timing (Smith et al. 2012), and may even determine plant traits and life-history strategies (Körner 1989; Reich et al. 2003). Furthermore, nutrient availability can interact with snowmelt and snowpack characteristics to determine individual species performance (Seastedt and Vaccaro 2001). While prior research has examined nutrient effects under climate change by performing factorial manipulations, few studies have assessed existing in situ variation in nutrient availability across a specific alpine landscape (but see Scott and Billings 1964; Bliss 1966; nitrogen and phosphorus, Stanton et al. 1994; nitrogen only, Fisk et al. 1998). Those studies have often found highly variable supply rates of the primary macronutrients nitrogen, phosphorus, and potassium, depending on substrate type (Michalet et al. 2002) or across the alpine ecotone (Jacobs et al. 2014), sometimes with variation spanning one or two orders of magnitude (Bowman et al. 2003).

To our knowledge, few if any detailed studies have surveyed nutrient availability in the Swiss Alps. Meanwhile, in the past decade, the possibility has arisen to study nutrient availability in entirely new ways, assessing not only the total pool of a few nutrients such as nitrogen and phosphorus using chemical extractions but also by measuring the plant-available pools of both macro- and micro-nutrients simultaneously using ion exchange membranes (for example, Bengtson et al. 2007). By simulating plant root uptake, these new methods allow for a different understanding of in situ nutrient supply rates, with accumulation being sensitive to soil moisture and availability, taking up labile sources first and more recalcitrant sources as the season continues (Johnson et al. 2005). This method also integrates nutrient availability over time instead of giving a snapshot of availability at one particular time point, which might be important, since nitrogen availability, for example, is often highest in an early-season flush in alpine environments (Chapin 1980; Edwards et al. 2007). However, the ion exchange technique is used primarily in agricultural and forest systems, and rarely in the alpine zone (but see Kusbach and Van Miegroet 2013; Wheeler et al. 2011; Jacobs et al. 2014).

Local models and those which incorporate spatial relationships can mean the difference between predicting extinction and predicting persistence of alpine plant species (Randin et al. 2009; Crase et al. 2014). This is likely an effect of fine-scale temporal and spatial variability in temperature, precipitation, microtopography and geology, which affect both plant abundance and diversity (Moser et al. 2005; Stein et al. 2014). However, while elevational gradients, for example, have been built into prior climate change studies, natural variation in nutrient availability has rarely been measured in field experiments or included in species distribution models. Given experimental results showing that nutrients strongly affect plant distributions and productivity, it is not unreasonable to expect that this fine-scale variation in nutrient availability across microhabitats may also determine plant responses to climate change. Furthermore, the extent to which nutrient availability covaries or interacts with other climate-based drivers of plant performance, such as temperature and snowmelt timing, is still poorly understood.

To examine the concurrent and interactive effects of snowmelt timing and soil nutrient availability on a common and widespread alpine plant, we selected *Salix herbacea*, a prostrate dwarf shrub currently distributed throughout alpine habitats in Europe, Greenland, and North America. The range of *S. herbacea* is predicted to substantially contract in the European Alps by 2080 due to the effects of climate change on its habitat (Alsos et al. 2009). Previous work in the same area of the Swiss Alps has shown that earlier snowmelt reduces *S. herbacea* fruit set and clonal stem production (Wheeler et al., in revision). However, we hypothesized that local-scale environmental characteristics may further influence *S. herbacea* performance. We measured both snowmelt timing and bioavailable soil nutrients surrounding 58 *S. herbacea* shrubs to determine whether nutrient availability significantly influences growth and reproductive patterns and/or modifies the effect of snowmelt timing. Specifically, we ask:

1. Does soil nutrient availability vary on a fine spatial scale across an alpine landscape, and is this variation associated with snowmelt timing, an important factor in alpine plant distributions which is predicted to change with climate?
2. Does observed nutrient availability modify the effect of snowmelt timing on shrub performance?

Describing and understanding how snowmelt and nutrient availability, two fine-scale potential drivers of shrub growth and reproduction, interact to influence shrub productivity, would fill a significant gap in our knowledge of how alpine communities function under current conditions, as well as provide better information for predicting community response to future climate change.

Materials and methods

Study sites and microtopography

We established elevational transects on three mountains near Davos, Switzerland: Jakobshorn (46°46′N, 09°50′E, 2100–2600 m asl), Schwarzhorn (46°44′N; 09°57′E, 2380–2780 m asl), and Chörbschhorn (46°48′N, 09°46′E, 2280–2640 m asl). All three mountains have bedrock primarily of gneiss, amphibolite, and mica schists. Precipitation is relatively consistent between the mountains, as long-term climate records (1975–2013) from just below the Jakobshorn transect indicate mean annual precipitation of 1150 mm, and across the valley near the Wannengrat transect, the Weissfluhjoch weather station received on average 1160 mm.

We selected 58 focal patches containing *Salix herbacea* L., a clonal, diploid ($2n = 38$), dioecious, prostrate dwarf shrub. Patches were distributed in elevational bands (11 on Jakobshorn, 10 on Chörbschhorn, and 9 on Schwarzhorn) along the transects with one patch in each band located in an early-exposure ridge microhabitat and one patch in a later-melting snowbed microhabitat, and microhabitat patches separated by between 10 and 50 m (Supplementary material Appendix 1, Figure A1). The number of patches included in the analysis was later reduced to 53 due to marmot destruction of some nutrient probes mid-season (see below). The site selection corresponded to an elevational range from 2109 to 2778 m asl., and 2013 snowmelt dates from April 15 to August 2. The center of each patch was marked with a nail and an aluminum tag, and all the stems within a 10-m-diameter circle around this center nail were considered as the "patch". *S. herbacea* are clonal and individuals cannot be identified by eye; however, previous genetic analysis of shrubs in the study area showed that 38 % of clones on ridges and 49 % of clones in snowbeds were smaller than 10 cm in diameter (Häggberg 2013). Thus, our "focal patch" identification was intended to sample, ideally, a single clone, and to avoid sampling the same clone multiple times. The 10-cm-diameter patches comprised between 3 and 120 stems, depending on the patch. Ridges in our study area were typically dominated by the shrubs *Loiseleuria procumbens* and *Vaccinium uliginosum*, in addition to herbaceous *Phyteuma hemisphaericum*; snowbeds were generally characterized by herbaceous *Gnaphalium supinum* and the moss *Polytrichastrum sexangulare* (Sedlacek et al. 2015). These patches were mapped using a differential GPS, with data later overlaid on a 2-m digital surface model to extract the elevation, aspect, slope, and curvature of the surface at each patch. For analysis, we scaled and centered the distribution of aspect measurements to measure distance from a northerly orientation.

Nutrient and snowmelt data collection

Nutrient availability was measured for a 5-week period using plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, Canada). Probes use 17.5-cm^2 ion-exchange membranes to accumulate bioavailable ions [NH_4^+, NO_3^-, total nitrogen (sum of previous two types of nitrogen), $H_2PO_4^-$, K^+, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Mn^{2+}, Zn^{2+}, Fe^{3+}, Cu^{2+}, Pb^{2+}, Cd^{2+}, and B^{3+}] from the soil over the course of the burial period, simulating plant root uptake by taking up labile ions and moving on to more recalcitrant sources once those are depleted. Nutrient availability measurements (taken as μg/10 cm^2/burial period) estimate plant-available nutrients over the burial period. At each patch, four pairs of probes (four anion and four cation) were deployed together between 0.5 and 1 m of the edge of the

Table 1 Correlation of microenvironmental variables derived from differential GIS, temperature loggers, and soil moisture probes to snowmelt timing and accumulation of macronutrients at 58 *Salix herbacea* patches in the Rhaetian Alps outside of Davos, Switzerland

	Snowmelt timing	Nutrient accumulation (log-transformed)						
		Ammonium (NH_4^+)	Nitrate (NO_3^-)	Total nitrogen (N)	Phosphorus (P)	Potassium (K)	Calcium (Ca)	Magnesium (Mg)
Elevation	0.26	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Aspect	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Slope	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Curvature	−0.36	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Post-snowmelt soil moisture	0.28	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
May mean temperature	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
June mean temperature	−0.52	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
July mean temperature	−0.52	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
August mean temperature	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
June–August mean temperature	−0.43	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Growing season growing degree days	−0.77	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Only r^2 of significant ($p < 0.05$) correlations are listed

Non-significant correlations are marked with *n.s.*

focal patch. In some cases, the probe's position relative to the *S. herbacea* patch was determined by where it was possible to dig a 10-cm-deep × 3-cm-wide hole and insert the probe without having the ion exchange membrane damaged or torn by rocks. Taking that into consideration, probes were deployed as close as possible to the edge of the *S. herbacea* shrub's foliage. Probes were deployed within 1 week after snowmelt in the spring of 2013 and removed 5 weeks after the initial burial, with nutrient uptake values for all four sets of probes from a patch pooled in subsequent reporting. Despite being covered with rocks to shield them from animal activity, probes at five patches were destroyed by marmots. Copper, lead, and cadmium were below detection limits at almost all of the patches, so were left out of subsequent analyses.

In-situ soil temperature loggers (iButton; Maxim Integrated, San Jose, CA, USA) were previously buried in autumn 2012 within 1 m of each *S. herbacea* patch's center but outside the shrub canopy, at a depth of approximately 5 cm. Some variability in the location and distance of the temperature logger burial from the focal patches was necessary since, in some locations, large rocks prevented digging/burial, although as the iButtons were small this was not as much of a challenge as for the nutrient probes. Soil temperature was recorded at 2-h intervals for the duration of the burial period. Snowmelt date for each site was considered to be the day that soil temperature rose a few degrees above 0 °C, the characteristic stable temperature for soil that is under snow cover. Site visits were used to confirm estimates of snowmelt date for each patch, and adjust the date if there seemed to be an inaccurate measurement by the temperature logger. The growing season temperature data collected from these probes was not correlated to nutrient accumulation, nor were either topographic variables or soil moisture, which was also measured using an HH2 Moisture Meter (Delta-T Devices, Cambridge, UK) within 1 m of each focal patch on three different occasions during the course of the growing season (Table 1). These factors were included in initial model testing on shrub performance, but did not have significant main effects on shrub performance and so were left out of subsequent analyses.

Salix herbacea measurements

S. herbacea focal patches of 10 cm diameter were monitored from the time they emerged from the snow until leaf senescence, usually in late August. Each patch was visited weekly, where we counted the number of inflorescenses and, for female shrubs, fruits within the 10-cm-diameter patch, Because there was a variable number of stems within a patch (with the smallest shrubs having just 3 or 4 stems, and the largest up to 120), flowering and fruiting were treated as a proportion of the total number of stems for all statistical analyses. In the middle of the growing season when all stems had experienced budbreak, we counted the number of stems within each patch; this was used as both a response variable in and of itself and as the basis for the proportional responses of other variables.

At each visit, we also performed a visual estimation of herbivory damage by estimating the proportion of total leaves within the 10-cm-diameter patch that had experienced at least some herbivory damage, that is, which were missing part of their leaf area or where entire leaves were missing. As a response variable, we used the greatest proportion of herbivory damage estimated over the season.

Data analysis

All statistical analyses were performed by R (v.3.1.0; R Development Core Team 2014). Accumulation of the 11 nutrients above detection limit on the cation and anion exchange surfaces was explored using principal components analysis of the log-transformed values. The importance of principal components was explored using eigenvalues and Horn's parallel analysis to account for finite sample size (v.1.5.1; Dinno 2012). The "ridge" and "snowbed" microhabitats were mapped onto the principal components analysis to determine whether patterns of nutrient availability were related to categorical microhabitat designations. Then, associations between nutrient availability, as estimated by the first two principal components, and specific continuous environmental variables were examined using correlation tests. The first and second principal components of nutrient accumulation were tested for correlation to the snowmelt date of focal patches, and both snowmelt timing and the principal components were also tested for their correlation to the elevational gradient built into the study design.

To assess environmental effects on shrub performance, we used linear and generalized linear models including snowmelt date and the first principal component of nutrient variation as fixed effects. For the response variable stem number, we used a generalized linear model with quasi-Poisson error structure due to overdispersion of a simpler Poisson error structure model. We analyzed female fruiting likelihood using a binomial error structure. For the proportion of stems fruiting (among those plants which did produce fruits) and the proportion of stems damaged by herbivory, we used generalized linear models with quasi-binomial distribution to overcome overdispersion. We did not include transect as a random factor, because it did not explain any significant variation in the response variables when used in initial mixed-effects models with the R package nlme (Pinheiro et al. 2013).

After model analysis, in order to visually present significant interaction effects, nutrient availability was categorized as "high" (PC1 > 0) or "low" (PC1 < 0) for visual representation only (all statistics and conclusions are based on the models, which used the continuous values of the principal component). Because all the loadings of individual nutrients onto PC1 were positive, this corresponded to higher versus lower accumulation of each nutrient.

Results

Nutrient availability

Availability of all measured nutrients varied across patches by at least one if not several orders of magnitude (Supplementary material Appendix 1, Figure A2). Snowbed and ridge microhabitats, despite a snowmelt day range spanning 3 months, did not show predictable patterns of nutrient availability according to exploratory principal components analysis (Fig. 1a). The first principal component of nutrient accumulation, which explained 47 % of total variance in the dataset, was not correlated to snowmelt timing ($r^2 = 0.16$, $p = 0.26$; Fig. 1b). The second principal component, which explained an additional 30 % of total variance, showed a strong positive association with snowmelt timing ($r^2 = 0.47$, $p < 0.001$; Fig. 1c). Phosphorus made the strongest contribution to each of the first two principal components, with strong positive loadings on each; other macronutrients such as potassium, calcium, and magnesium also showed strong positive loadings on the first principal component, while the second had strong negative loadings of those as well as of zinc and manganese (Supplementary material Appendix 1, Table A1). The accumulation of these strongly-loaded nutrients (phosphorus, calcium, and magnesium) were all strongly correlated to snowmelt timing (all $p < 0.05$), while accumulation of the other nutrients was not (all $p > 0.05$). We chose to include only the first principal component in our models of shrub performance. This was based on both egenvalues produced by the PCA itself (PC1: eigenvalue $= 1.25$; PC2: eigenvalue $= 0.80$) and by parallel analysis, which indicated that only the first principal component should be retained (adjusted eigenvalue $= 4.41$ with an estimated bias of 0.81). Neither snowmelt timing ($r^2 = 0.25$, $p = 0.06$) nor the first ($r^2 = 0.06$, $p = 0.69$) or second ($r^2 = 0.24$, $p = 0.08$) principal components of nutrient availability were significantly correlated to elevation, nor were accumulations of any of the nutrients.

Growth, reproduction and damage probability

Stem number showed a significant positive response to later snowmelt ($F_{1,52} = 9.67$, $p = 0.003$; Fig. 2a) and a significant

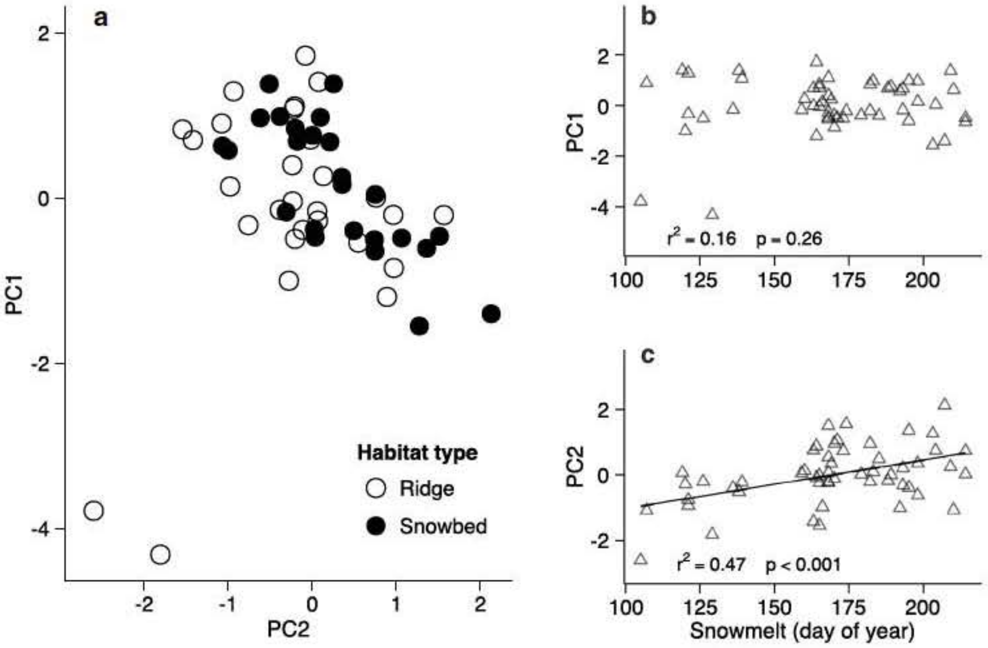
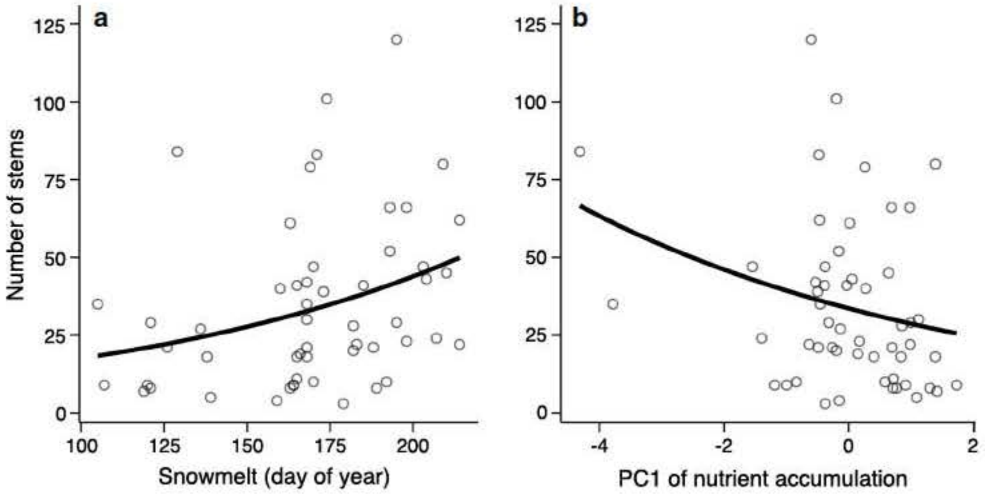


Fig. 1 **a** Distribution of "snowbed" and "ridge" microhabitat patches of *Salix herbacea* (as indicated by *closed* and *open circles*, respectively) in a PCA of 11 nutrients over a 5-week summer growing period. Correlation tests of **b** the first principal component of nutrient availability, and **c** second principal component of nutrient availability to snowmelt timing. The two apparent outliers in the *bottom right* corner of plot (a) characterize the amount of variation in nutrient availability across the landscape; omitting them from the analyses does not change our findings significantly

Fig. 2 Association between the number of *Salix herbacea* stems in a 10-cm-diameter circle and **a** snowmelt timing, and **b** nutrient availability, as indicated by the first principal component of nutrient availability



negative response to nutrient availability ($F_{1,52} = 7.19$, $p = 0.01$; Fig. 2b); however, there was no interaction between the two factors. Fruiting likelihood was not associated with either snowmelt timing or nutrient availability. However, when plants did produce fruit, the proportion of fruiting stems showed a significant negative response to nutrient availability ($F_{1,25} = 7.13$, $p = 0.01$; Fig. 3), but no response to snowmelt timing. Finally, the proportion of leaf material damaged by herbivory was influenced by a significant interaction between snowmelt timing and nutrient availability ($F_{1,51} = 6.58$, $p = 0.01$). Among early-emerging plants, high nutrient availability was associated with increased herbivory damage, but among late-emerging plants this pattern was reversed (Fig. 4). This pattern was partially driven by two plants with particularly low nutrient availability (also visible in Fig. 1); however, when these points were removed from the dataset, the conclusions themselves did not change. Furthermore, there is no reason to believe that the measurements of these two points were compromised in any way, so their low-nutrient status represents valuable ecological information.

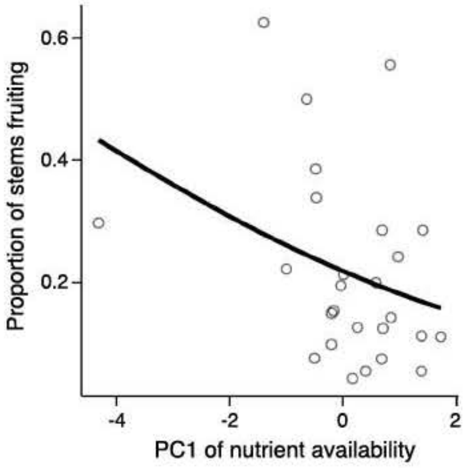


Fig. 3 Association between nutrient availability and the proportion of *Salix herbacea* stems within a 10-cm-diameter patch which produced fruits during the 2013 growing season

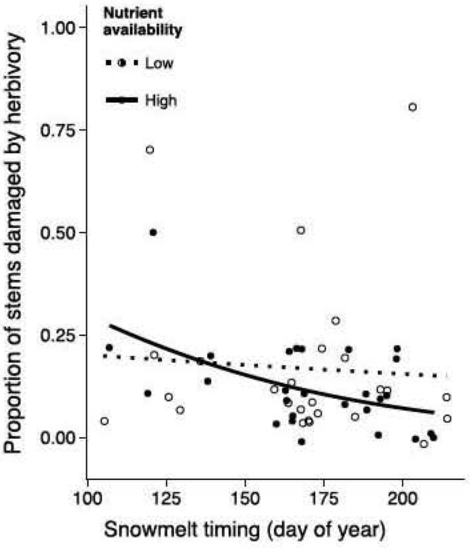


Fig. 4 The proportion *Salix herbacea* stems within a 10-cm-diameter patch damaged by herbivory during the 2013 growing season in relation to snowmelt timing and nutrient availability. Nutrient availability is here designated by *low*, a negative value for the first principal component of the accumulation of 11 nutrients, or *high*, a positive value for this principal component; this categorization was done for visual representation purposes only, and all statistics and conclusions are based on models which used the continuous values of the principal component

Discussion

In this study, we found that soil nutrient availability, as summarized by its principal components, varied widely at the microsite scale and along the snowmelt gradient. The availability of individual nutrients such as nitrogen and phosphorus varied by an order of magnitude or higher across the elevation and microhabitat gradient. This corresponds to previous studies finding widespread variation in nitrogen, phosphorus, and other nutrient supply rates in heterogeneous alpine landscapes (Bowman et al. 2003; Jacobs et al. 2014).

The date of first snowmelt spanned a range of over 3 months across the 58 *S. herbacea* patches. However, the bulk of this variation in ecologically-important nutrient availability was not strongly correlated to this variation in snowmelt timing. Furthermore, in terms of both nutrient availability and snowmelt timing, variation was highly spatially localized and not associated with elevation. The first principal component of nutrient availability, which explained almost half of the total variation in nutrient availability, was not associated with snowmelt. We also found evidence that some aspects of nutrient availability, albeit not necessarily the most ecologically important ones, may be associated with other environmental gradients: the second principal component of nutrient accumulation showed a strong positive correlation with snowmelt timing. However, this was based largely on patterns of phosphorus accumulation which seems unlikely to have strong effects on vegetation, as phosphorus only limits productivity of some alpine plant species and is not a good predictor of aboveground biomass (Seastedt and Vaccaro 2001; Litaor et al. 2005). Nevertheless, it is important to recognize that snowmelt timing may influence micro-environmental conditions.

The lack of strong association between ecologically important nutrient availability and either elevation or microhabitat snowmelt timing may be a result of differences between community productivity, litter accumulation and microbial activity, among other biotic influences, all of which may be more important drivers of nutrient availability (Choler et al. 2001). These factors were largely unmeasured in our study. Snowmelt timing, meanwhile, is correlated to other microtopographic variables such as curvature (Supplementary material Appendix 1, Table A1). It has been noted that local topographic variability is one reason why local fine-scale models predict species persistence in alpine regions where regional models predict that all suitable habitat will disappear with global change (Randin et al. 2009). Our results emphasize the "micro" in microhabitat and suggest that there is widespread environmental heterogeneity in the alpine zone. This is particularly true because soil nutrient availability cannot be predicted from snowmelt timing or elevation—two of the more easily assessed drivers of shrub distribution and performance—as we showed that nutrient accumulation is only partially related to snowmelt timing and has no correlation to elevation.

In our study, earlier snowmelt timing had a generally negative effect on shrub performance, with *S. herbacea* plants in earlier snowmelt sites producing fewer stems.

This is consistent with the results of a larger space-for-time substitution study examining *S. herbacea* performance in the Swiss Alps (Wheeler et al., in revision), as well as more generally to similar studies looking at community responses (Carbognani et al. 2012). However, our finding that higher nutrient availability also had primarily negative effects on shrub performance adds considerable nuance to this previously understood role of snowmelt microhabitat. One possible mechanism driving this effect is that nutrient availability may mediate the strength of competitive interactions by increasing community productivity. When shrubs produced fruits, higher nutrient availability was associated with a lower proportion of stems fruiting. This is counterintuitive. as experimentally increasing nutrient availability often has bottom–up effects of improving reproductive output in alpine shrubs (Campbell and Halama 1993; Wookey et al. 1993; Muñoz et al. 2005; Petraglia et al. 2013). However, *S. herbacea* does not always conform to this pattern. In subarctic alpine Sweden, *S. herbacea x arctica* hybrids showed few aboveground effects of fertilizer addition, instead shifting resources to root allocation and morphology (Clemmensen and Michelsen 2006). Since many alpine species, particularly graminoids, do respond positively to increased nutrient supply in terms of biomass and increased growth (Bowman et al. 1993; Petraglia et al. 2013), this may add to the competitive pressure on *S. herbacea* in more fertile microhabitats. This is particularly relevant in a global change context as nitrogen deposition in the western Alps is currently above estimated critical loads (Rogora et al. 2006) and has not decreased despite legislated controls on emissions. In addition, warmer temperatures can increase N mineralization in the soil (Rustad et al. 2001). Besides warmer temperatures and earlier snowmelt, *S. herbacea* may face increasing stress from increased competition due to nutrient enrichment.

The probability of herbivory damage showed the most complex response to micro-environmental factors, with snowmelt timing and nutrient availability showing strong and sometimes conflicting effects on shrub damage. Timing is key in this system because moth caterpillars (primarily *Zygaena exulans*) emerging early in the growing season were the main herbivores of the shrubs (Wheeler et al. 2015), as has been found in other *S. herbacea* snowbed communities (Schöb et al. 2010). Like many alpine plants, *S. herbacea* pre-forms leaf tissue in terminal buds at the end of the previous growing season, which break soon after snowmelt and likely provide higher-quality forage compared to later in the season when leaves are mature and more hardened. Further, leaf nitrogen content decreases over the course of the growing season (Hansen et al. 2006), which may also make the shrub less attractive to herbivores as the season progresses. Thus, the concurrent timing of young leaf emergence in early-melting patches and the caterpillar hatching likely explains a large part of the snowmelt timing effect on herbivory damage. While snowmelt timing had a strong and predictable effect on herbivory levels, the slope of this relationship depended to some extent on nutrient availability, as we observed greater herbivory on higher-nutrient relative to lower-nutrient patches early in the season. These early-exposure patches are also characterized by higher species richness and taller vegetation (Nussbaumer 2012); higher community productivity can attract herbivores (Huntly 1991), whereas low-productivity sites generally support fewer herbivores (Hairston et al. 1960). The pattern may be particularly pronounced in the early spring in this system because this is when the moth caterpillars emerge. Furthermore, nutrient availability likely determines community productivity, providing the link between the two patterns. These effects have important implications for shrub fitness as herbivory damage was previously shown to decrease flowering probability (a fitness proxy) in the following summer (Wheeler et al. 2015). Further, herbivory pressure, like competitive interactions, may increase under climate warming (Roy et al. 2004). Thus, changes in not just environmental conditions themselves but also their effects on biotic interactions may influence species performance and distribution in the future under climate change.

Conclusions

Across mountain transects, we observed substantial variation in micro-environmental conditions. Our observations of *S. herbacea* shrub performance indicate that nutrient availability, which was previously largely unmeasured in terms of naturally-occurring variation across alpine landscapes, may have important effects on vegetation and should be considered in predictions of future vegetation change in response to climate. For instance, *S. herbacea* vegetative growth as measured by stem number appeared to depend both on snowmelt timing, with later snowmelt timing having a positive effect, and on nutrient availability, with higher nutrient availability having a negative effect through biotic interactions. Additionally, the level of herbivory experienced by *S. herbacea* showed a strong response to snowmelt timing, and was also modified by nutrient availability. Thus, only considering temperature or snowmelt timing in predictive models may omit essential information which helps to determine shrub performance. Furthermore, both snowmelt timing and nutrient availability varied at a fine scale, meaning that coarse-grained models may overlook factors that could lead to local persistence of alpine plant populations.

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Author contribution statement CR, JAW, JS, and AJC conceived and designed the experiment. CJL, JS and JAW performed the fieldwork. AJC, JAW, CJL and JS carried out data extraction. CJL performed labwork and statistical analysis. CJL wrote the manuscript. JAW, CR, JS and AJC reviewed and commented on the manuscript. The authors declare they have no conflict of interest and that all experiments comply with the current laws of Switzerland.

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