



# Alpine plant communities differ in their seed germination requirements along a snowmelt gradient in the Caucasus

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## Abstract

Mesoscale heterogeneity of alpine landscapes generates snowmelt gradients resulting in a distinct vegetation zonation from almost snow-free fellfields to long-lasting snowbeds. Although the vegetative trait variation along such gradients has been intensively studied, little is known about whether and how seed germination is adapted to the variable snowpack duration. Here, we compare the seed germination niches of 18 characteristic plant species occurring in four distinct plant communities (alpine lichen heath—*Festuca varia* grassland—*Geranium-Hedysarum* meadow—snowbed) along an alpine snowmelt gradient in the North Caucasus (Russia). In a fully factorial experiment, we tested seed germination responses to temperature (10/2, 14/6, 18/10, 22/14, 26/18 and 30/22 °C) and water potential (0, −0.2, −0.4, −0.6 and −0.8 MPa) gradients, reflecting the full spectrum of seedling establishment conditions in the study system. Community-specific germination niches were identified by generalised mixed model with Bayesian estimation. Our study revealed that the species from the four focal communities significantly differed in their temperature requirements for germination, whereas soil moisture was found to be a limiting factor for seedling establishment along the entire gradient. The snowbed germination was constrained to comparatively high temperatures above 10 °C, whereas seed germination in alpine lichen heaths occurred under a wide range of experimental conditions. The seed germination patterns of species from *Festuca varia* grasslands and *Geranium-Hedysarum* meadows reflected their intermediate position along the snowmelt gradient. We conclude that seed germination niche is affected by the environmental filtering along the snowmelt gradient thus departing from the general alpine germination syndrome.

**Keywords** Water potential · Fellfield · Germination niche · Mountain regeneration · Snowbed · Water stress

## Introduction

Alpine habitats occur worldwide above the natural treeline (Körner and Paulsen 2004; Körner et al. 2011; Testolin et al. 2020) and are characterized by low temperatures, unstable

substrates and short growing seasons (Körner 2021). Their dependence on extreme and strict climatic conditions (Körner and Paulsen 2004), coupled with the relatively small terrestrial area they occupy (Testolin et al. 2020), could make alpine environments disproportionately vulnerable to climate change (Pickering et al. 2014; Huss et al. 2017). Climate change has caused some upwards shifts of alpine plant species (Rumpf et al. 2019) and these shifts could ultimately lead to extinction if plant species were to find themselves in a position where they have nowhere higher to retreat. Nonetheless, the complex alpine topography creates a mosaic of microhabitats varying greatly in microclimatic conditions (Scherrer and Körner 2009). This high topographical variation could help alpine vegetation to cope with climate change by providing local micro-refugia (Körner and Hiltbrunner 2021).

Mesoscale habitat heterogeneity in combination with wind and solar radiation generates snowmelt gradients in the alpine belt, driving the distinct vegetation zonation

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from almost snow-free windswept crests to long-lasting snowbeds (Onipchenko 1994; Stanton et al. 1994; Choler 2005). Snow depth and snowmelt patterns strongly influence surface-level temperature, moisture and light, three key abiotic factors determining plant growth and reproduction in the corresponding communities (Winkler et al. 2018; Körner 2021). The sparse, thin snowpack on steep, leeward slopes (fellfields) melts early resulting in freezing soil in winter, frost damage in spring and drought stress during summer. Contrastingly, thick, long-lasting snowpack in flat, wind-protected snowbeds protects plants from freezing temperatures in winter and spring and supplies them water during the early summer. At the same time, delayed snowmelt in the snowbeds restricts photosynthetic carbon gain, depletes carbohydrate reserves, stimulates growth of pathogenic fungi or encourages winter herbivory by small mammals (Stanton et al. 1994; Kudo et al. 1999; Shimono and Kudo 2005).

Although alpine plants usually are capable of clonal reproduction (Körner 2021), sexual reproduction via diaspores (i.e. seeds, fruits, or fruits with extra-ovarian structures attached; hereafter ‘seeds’) is essential to maintain genetic diversity and to migrate to suitable new sites in response to climatic changes (Fernández-Pascual et al. 2019). However, the short alpine growing seasons limit the timespan for flowering, pollination, seed development and seed dispersal. For successful regeneration, seeds must germinate in the most appropriate period to ensure seedling survival (Bell and Bliss 1980; Forbis 2003). The physiological process of seed germination is therefore an essential life stage that must be timed to occur when the environment is favourable for subsequent seedling survival and growth (Poschlod et al. 2013). This has led to a widespread alpine seed germination strategy characterized primarily by physiological seed dormancy, a strong need for cold stratification to break dormancy and warm-cued germination (Fernández-Pascual et al. 2021; Carta et al. 2022). However, this common strategy most likely hides important variability among species. For example, alpine species show higher optimal temperature for germination than either subalpine species (i.e. species that live close to the treeline; Fernández-Pascual et al. 2017) or their congeneric counterparts from below the treeline (Walder and Erschbamer 2015). Differences in germination traits have been attributed also to species’ successional niche and habitat preferences, with pioneer species germinating better at colder temperatures than later successional species (Schwienbacher et al. 2012), while species from calcareous and siliceous alpine grasslands respectively show a slow overwinter germination or high germination under all conditions (Tudela-Isanta et al. 2018a, b). Surprisingly, not enough attention has been paid to germination strategies along the snowmelt and growing-season-length gradient determined by mesotopographical variations, despite their high importance for alpine

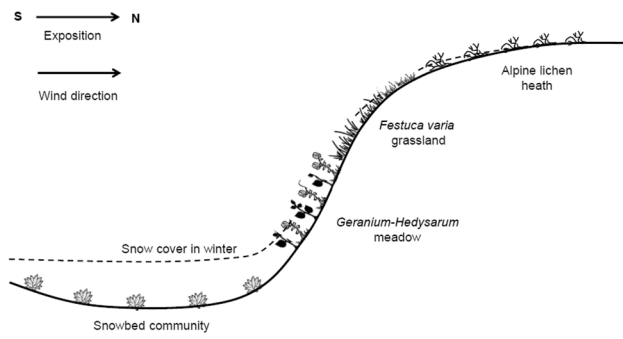
vegetation responses to climate change (Körner and Hiltbrunner 2021). To our knowledge, this question has only been tackled directly by Shimono and Kudo (2005), who found no habitat-related germination differences when comparing fellfield and snowbed habitats in Japan. The remaining published evidence on seed germination behaviour along the snowmelt gradient is limited to experiments [e.g. Bell and Bliss (1980)] or field observations of a very few snowbed species; [Shimono and Kudo (2001)].

The importance of micro- and mesotopographic variation for alpine plant ecology makes it necessary to study it in more detail, in other mountain regions, and with updated methodologies. In this study, we compare the seed germination niches of characteristic plant species of four distinct plant communities (alpine lichen heath—*Festuca varia* grasslands—*Geranium-Hedysarum* meadows—snowbeds) occurring along a snowmelt gradient in the alpine belt of the North Caucasus. Using experimental data on 18 species, we tested the hypothesis that species responses to germination temperature and water potential will depend on their optimal position in the topographic gradient. Specifically, we expected the snowbed germination to be confined to comparatively high temperatures and high water supply, conditions typical for subnivean soils shortly after snowmelt in this habitat (Björk and Molau 2007). In alpine lichen heaths, communities occurring at the snow-poor end of the gradient, we expected seeds to be able to germinate at comparatively low soil water contents, due to the low water supply from the melting snowpack and the fast drying skeletal soils (Onipchenko 2004). Likewise, we expected them to have broader temperature requirements for germination, thus displaying an opportunistic germination phenology whenever soils become relatively moist. The seed germination pattern in *Festuca varia* grasslands and *Geranium-Hedysarum* meadows, two communities occupying the middle parts of the toposequence, were expected to display intermediate seed germination responses to temperature and water with tendencies towards their snow-poor and snow-rich neighbors, respectively.

## Materials and methods

### Study area

This study was conducted in the Teberda National Park (Karachaevo-Cherkessian Republic, the Northwestern Caucasus, Russia), in the alpine belt of the Malaya Khatipara mountain (N43.4398, E41.6749). The local climate is typically temperate-zone montane with mean annual temperature of  $-1.2\text{ }^{\circ}\text{C}$  and annual precipitation of 1400 mm. The warmest month is August with a mean monthly temperature of  $+8.3\text{ }^{\circ}\text{C}$ , but frost can occur throughout summer



**Fig. 1** Location of study communities along the snowmelt gradient

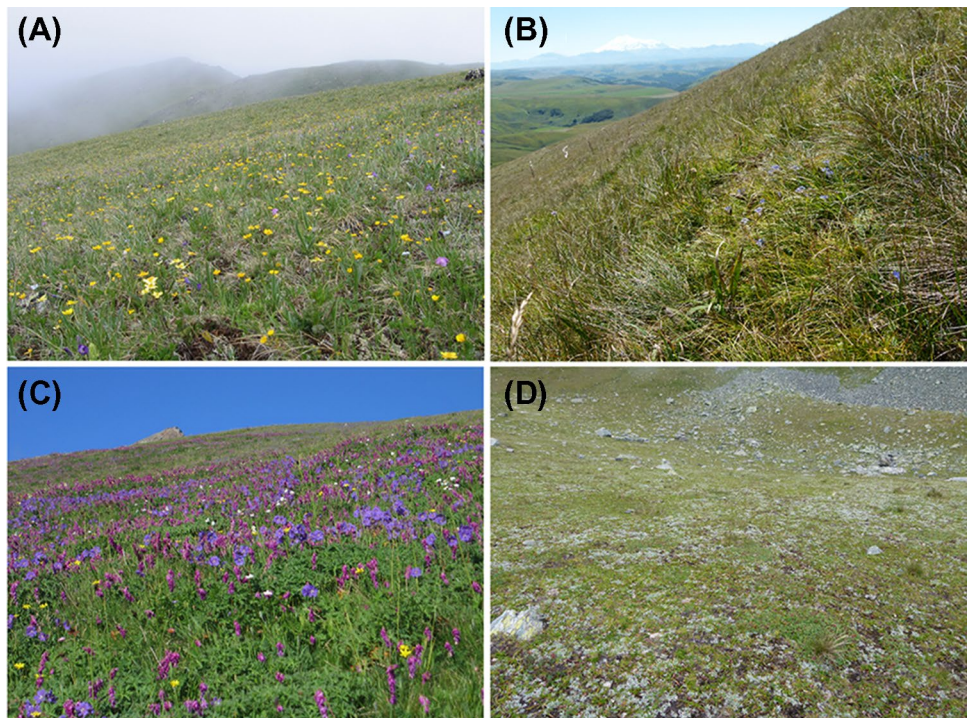
(Onipchenko 2004). Siliceous parent rocks predominate in the study area and soils are Umbric Leptosols (Malysheva et al. 2004).

Snow accumulation is the main factor determining the composition and structure of alpine plant communities in the Reserve (Onipchenko 1994). Depth and duration of snow cover is in turn controlled by landscape position (slope orientation and tilt). Northwestern Caucasian alpine plant communities can be arranged along a zonation of snowmelt gradient as shown in Fig. 1 and described in the next section (see also Table 1 and Fig. 2).

**Table 1** Characteristics of the studied communities based on Onipchenko (2004)

Community	<i>Alpine lichen heath</i> (ALH)	<i>Festuca varia</i> grasslands (FVG)	<i>Geranium-Hedysarum</i> meadow (GHM)	Snowbed (SBC)
Typical relief forms	Crests, ridges, windward slopes	Steep slopes	Leeward slopes, small depressions	Deep depressions
Max snowpack depth, m	0–0.3	0.5–1.5	1.5–3	> 4
Growth period duration, months	4.5–5.5	3.5–4.5	2.5–3.5	1.5–2.5
Growing season	May–September	June–September	July–September	August–September
Exposition	S	SSW	SW	SW
Max tilt, °	15	10	5	1
Productivity, g/m <sup>2</sup>	150	400	550	200

**Fig. 2** Study communities at the peak of growing season: **A** alpine lichen heath, **B** *Festuca varia* grassland, **C** *Geranium-Hedysarum* meadow and **D** snowbeds. Photographs by V. Onipchenko



## Study plant communities

Alpine lichen heaths (ALH; Fig. 2A) occupy windward crests and steep slopes with no or little snow accumulation (up to 30 cm snow depth) that results in a comparatively long growing season of about 5 months. The low-productive ALH communities develop on shallow, skeletal soils with comparatively low microbial activity, low water holding capacity and low nutrient content (Vertelina et al. 1996). Deep freezing (down to 200 cm) is typical for the ALH soils. The ALHs are mainly dominated by fruticose lichens (e.g. *Cetraria islandica*, *Cladonia gracilis*, *Flavocetraria cucullata* and *Thamnolia vermicularis*), dwarf shrub *Vaccinium vitis-idea* and to a smaller extent by graminoids (e.g. *Festuca ovina*, *Carex sempervirens*, *C. umbrosa*) and herbs (*Anemone speciosa*, *Antennaria dioica*, *Campanula tridentata*).

*Festuca varia* grasslands (FVG; Fig. 2B) occur on dry, moderate to steep, mainly southern slopes with little snow accumulation (about 0.5–1 m), and the growing season lasts about 4 months. Soils under these communities are thick, well developed and with comparatively low soil skeleton content (10% by volume in the upper 10 cm; (Grishina et al. 1993). Dense tussock narrow-leaved grasses *Festuca varia* and *Nardus stricta* strongly dominate these communities. Due to high litter accumulation in the community (Leinsoo et al. 1991), the co-occurring xeromorphic herbs (e.g. *Ajuga orientalis*, *Campanula collina*, *Galium verum*, *Sempervivum caucasicum*, *Viola altaica*) are confined to more or less open gaps between the dense cover of grasses.

*Geranium-Hedysarum* meadows (GHM; Fig. 2C) occupy lower parts of leeward, gentle slopes and shallow depressions with maximal snow depth in winter of 2–3 m and the growing seasons of 2.5–3.5 months. The soils in the GHM communities are thick, have comparatively high water holding capacity and contain the largest amount of soil nutrients among the four study communities. Soil properties in combination with the favourable snow regime explain the fact the GHMs are the most productive communities among the studied vegetation types in the alpine belt of the National Park (Onipchenko 2004). GHMs are mainly dominated by two herbs, *Geranium gymnocaulon* and *Hedysarum caucasicum*, with a few other herbs (e.g. *Carum meifolium*, *Pedicularis condensata* and *Pulsatilla aurea*) being the constant constituents in these meadows. Some bunch grasses, such as *Festuca brunnescens*, *F. varia* and *Nardus stricta*, are frequent associates, though they are usually not abundant in the community (Onipchenko 2004). One peculiar characteristic of the GHM communities is the high activity of pine voles (*Microtus majori*) that maintain soil water and air permeability, as they intensify soil biological processes by burrowing (Onipchenko 2004).

Snow bed communities (SBC; Fig. 2D) occur in deep depressions and lower, flat parts of leeward northern and

eastern slopes with heavy winter snow accumulation (5 m and even more). Snow melting ends in late July or the first half of August, thus SBCs have the shortest vegetation season among the alpine communities (1.5–2.5 months). As compared to other study communities, soils under the SBCs are rich in nitrogen, have high water content and the lowest skeleton content. Nonetheless, the short growing period leads to low productivity of these potentially productive communities. The SBCs are composed of low-stature (2–3 cm), short-rosette or creeping plants (e.g. *Sibbaldia procumbens*, *Minuartia aizoides* and *Taraxacum stevenii*), forming a dense herbaceous cover without pronounced layers.

## Soil temperature measurements

Soil temperatures were measured in each of the study communities from September 2008 to September 2009 with the help of temperature loggers (Thermochron iButtons DS1921G#F5; Maxim Integrated Products, Inc., Sunnyvale, CA, United States) every 4 h. To reduce the effects of frost heaving on the temperature measurements, loggers were buried at the depth of 10 cm. Our preliminary data analysis (results are not shown) indicates that the soil temperatures at this depth correlate well with the soil surface temperatures. We used the soil temperature logs to calculate the number of days of snow cover in each plant community, estimated as days with no diurnal temperature variations between the night and the day (Zhang 2005). We used these values as a predictor variable in the seed germination model (see below).

## Seed germination experiment

Fully ripened seeds and fruits (thereafter ‘seeds’) of 18 species typical for each of the focal communities were collected in the end of growing season in 2017 (Online Appendix 1). The focal species were selected based on their community fidelity (i.e. clear ecological preferences for one of the study communities) and standing biomass contribution to the communities (i.e. species with comparatively high abundance). A large dataset of vegetation surveys conducted in the region was used as a basis for the species selection (Onipchenko V., unpublished data).

Seeds of each species were collected in the community the species represents. The seeds were collected from at least 20 randomly selected individuals growing at least 2 m apart from each other. After collection, seeds were air-dried for several days, cleaned manually, and allowed to after-ripen in a paper bag at room conditions for 3 months followed by dry storage in a cold room at +4 °C until the beginning of the germination experiments.

To reveal the requirements for optimal germination as an adaptation to environmental conditions in the study communities, we used a five-level full factorial experiment to test seed germination responses to temperature and water, two major environmental drivers of the physiological process of seed germination (Bewley et al. 2013). To compare the temperature and water threshold for germination across species, we conducted the experiments with non-dormant seeds. Seeds of *Arenaria lychnoides* and *Nardus stricta* were cold-wet stratified at +4 °C for 3 months to break physiological dormancy. Physical seed dormancy in *Anthyllus vulneraria* and *Trifolium polyphyllum* was broken by keeping the seeds in boiling water for 10 s (Rosbakh et al. 2020a). Seeds of the remaining species did not require any dormancy-breaking pre-treatment as they readily germinated with high percentages (> 80%) in a preliminary experiment.

In each experimental treatment and species, three replicates of 20 seeds were placed in a Petri dish on two layers of filter paper moistened with 5 ml of either distilled water or a polyethylene glycol 6000 solution (PEG; see below). Due to low seed filling rates the number of seeds in Poaceae was increased to 30. Seeds were incubated in RUMED 1301 climatic chambers (Rubarth Apparate GmbH, Laatzen, Germany) at diurnal fluctuating temperatures with 14 h of light supplied by white fluorescent tubes and 10 h of darkness. Germination (cotyledon appearance) was monitored weekly for 6 weeks; germinated seeds were removed during the checks. After the experiments were terminated, the viability of non-germinated seeds was checked by inspection of embryos. Seeds with white and firm embryos were considered viable (Baskin and Baskin 2014).

Seeds were germinated along two gradients of temperature and water potential representing the germination conditions that seeds may encounter along the snowmelt gradient. To test temperature requirements for germination, we selected six temperatures (10/2, 14/6, 18/10, 22/14, 26/18 and 30/22 °C; 14/10 h day/night photoperiod). The effect of water potential on seed germination was studied by incubating the seeds at five water potentials (0, -0.2, -0.4, -0.6 and -0.8 MPa) of PEG solutions prepared according to Michel and Kaufmann (1973). Petri dishes were sealed with Parafilm to maintain relatively constant water potential during the entire experiment; filter paper remained moist for the entire duration of the experiment.

## Data analysis

To test the hypothesis that community-specific responses of seed germination to temperature and water varied along the snowmelt gradient, we fitted a generalised mixed model with Bayesian estimation (Markov Chain Monte Carlo generalised linear Mixed model, MCMCglmm) using the package ‘MCMCglmm’ in R (Hadfield 2010). MCMCglmm allows

to model seed germination as a binomial response variable, take into account the lack of independence caused by the shared phylogenetic history of the study species, and consider more than one sample (i.e. Petri dish) per species.

The response variable in the model was the final seed germination proportion. The fixed predictors were as follows: (1) snow cover length (i.e. number of days of snow cover estimated with the soil temperature logs), (2) germination temperature, (3) water potential, plus (4) the interactions snow length × germination temperature and (5) snow length × water potential. We did not include the interaction temperature × water potential nor the three-way interaction because they fall outside the questions of the experiment, and further we checked that they were non-significant in a separate model.

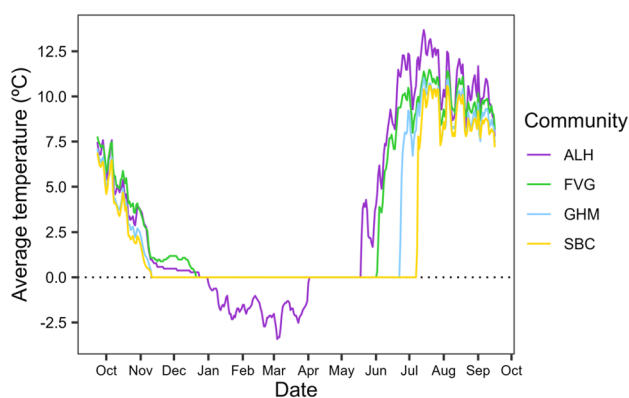
To account for non-independence in the data caused by the existence of different study species which are linked by a shared phylogeny, the model included as random factors species identity and a reconstructed phylogenetic tree of the study species. To create the phylogeny, we used the R package *V.PhyloMaker* (Jin and Qian 2019) that contains an updated mega-tree of the seed plants based on Smith and Brown (2018). We placed taxa absent from the mega-tree at the genus-level basal node.

We used weakly informative priors for the model, with parameter-expanded priors for the random effects. Each model was run for 500,000 MCMC steps, with an initial burn-in phase of 50,000 and a thinning interval of 50 (Villemeireuil and Nakagawa 2014) resulting, on average, in 9000 posterior distributions. From the resulting posterior distributions, we calculated mean parameter estimates and 95% highest posterior density and credible intervals (CI). We estimated the significance of model parameters by examining CIs, considering parameters with CIs overlapping with zero as non-significant. The R script to fit the model is included as a supplementary material (Online Appendix 2).

## Results

### Soil temperatures in the study communities

Soil temperatures (Fig. 3) measured from September 2008 to September 2009 varied along the snowmelt gradient. The soil of the alpine lichen heath community showed thermal variation below zero between January and April, indicating that snow cover was little or non-existent, and therefore the soil was not insulated from the air. Conversely, the other three communities showed a flat temperature of zero during winter, suggesting that they were under the cover of snow and insulated from external air variation. Time of snowmelt also varied along the gradient as follows: from mid-May in the alpine lichen heath, to early June in the *Festuca varia*



**Fig. 3** Soil temperatures of four study communities located along the snowmelt gradient. The measurements were carried out at 10 cm depth in 2008–2009 with the help of temperature loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, USA)

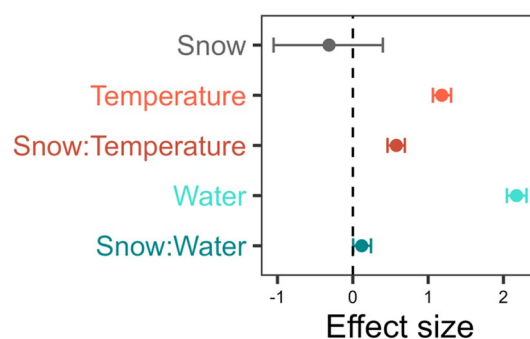
grassland, late June in the *Geranium-Hedysarum* meadow and early July in the snowbed community.

### Seed germination patterns in the study species

Study species differed considerably in their seed germination response to the experimental gradients of temperature and water varying from narrow to broad germination niche (Online Appendix 3). As for the former, seeds of *Festuca varia*, *Hedysarum caucasicum*, *Phleum alpinum* and *Trifolium polyphyllum* germinate over a broad range of temperatures and water potentials, except for the  $-0.8$  MPa. As for the latter, seed germination in *Anthoxantum odoratum*, *Potentilla verna* and *Taraxacum stevenii* was limited to comparatively high temperatures ( $> 15$  °C) and moderate water potentials (from  $-0.4$  to  $-0.6$  MPa). The germination patterns of the remaining species varied between these two extremes.

### Community-specific seed germination patterns

The MCMCglmm (Fig. 4) indicated that snow length per se did not have a significant main effect on germination: the average germination proportion across germination treatments was not different between the four communities. Germination temperature and water potential had significant and positive main effects: overall, germination was higher at higher temperatures and at comparatively higher water potentials. Germination temperature and snow depth had a significant positive interaction: species from communities with higher snow depth (e.g. the snowbeds) had their germination more limited to the



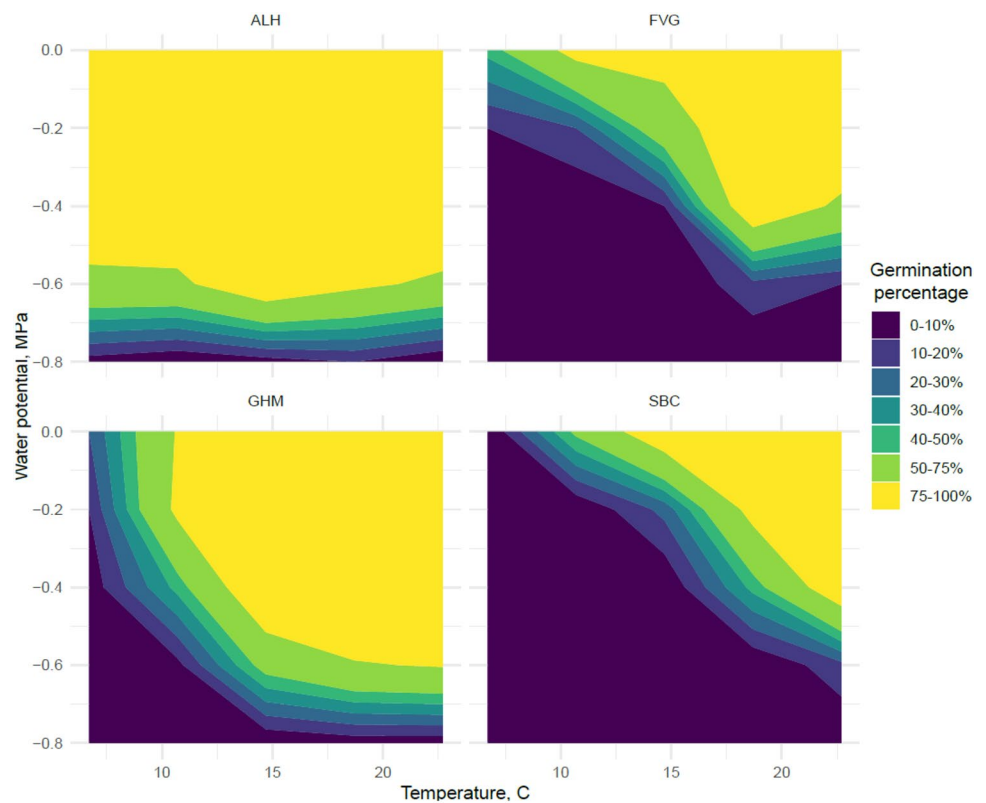
**Fig. 4** Effect of the germination environment on final germination proportions according to the MCMC model. Dots indicate the posterior mean of the effect size, and whiskers its 95% credible interval. The line of zero effect is shown. When the credible intervals overlap with the zero-effect line, the effect is not significant. Some effects that overlapped with zero (i.e. had no effect) and whose credible intervals were excessively wide are not shown for clarity's sake

warmer end of germination temperatures (Fig. 5). The interaction between water potential and snow depth was not significant, indicating that the different communities did not differ in their response to water potential (Fig. 5). The community-specific germination patterns at the most optimal for germination conditions (water potential of 0 MPa (pure water) or incubation temperature of 22/14 °C), are shown in Fig. 6.

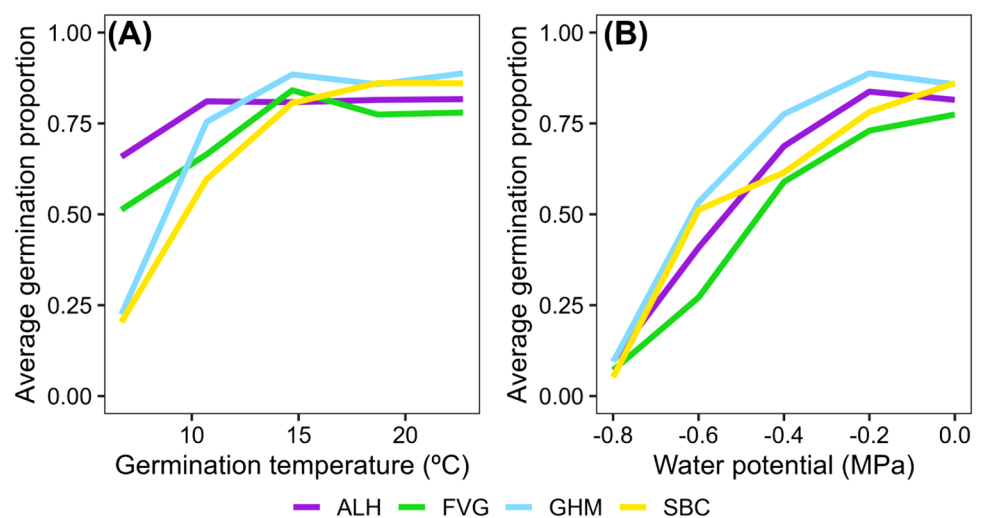
### Discussion

Alpine seed germination has been suggested to follow a common strategy aimed at increasing seedling establishment chances under harsh environmental conditions (Fernández-Pascual et al. 2021; Carta et al. 2022). The general tendency to a warm-cued germination detected for the study species suggests that North Caucasian alpine plants employ the same strategy to postpone seed germination to warmer summer months characterised by a comparatively low probability of severe frost events negatively affecting seedling of alpine plants (Rosbakh and Poschlod 2015; Rosbakh et al. 2020b). In its turn, the overall positive effects of low osmotic potentials on the germination of the focal species confirms the evidence that seedling establishment in terrestrial habitats with seasonal climates, including arctic and alpine environments (Bell and Bliss 1980; Oberbauer and Miller 1982; Tudela-Isanta et al. 2018b), is water-limited (Orsenigo et al. 2015; Walder and Erschbamer 2015). From the ecological point of view, it implies that alpine seed germination is triggered by comparatively high soil moisture levels (e.g. after a snowmelt or summer rainfalls), a key adaptation to avoid seedling emergence on commonly desiccated surfaces of summer alpine soils (Körner 2021) known to be one of the

**Fig. 5** Community-specific final germination percentage of four study communities along temperature and water potential gradients



**Fig. 6** Community-specific seed germination requirements for **A** temperature at water potential of 0 MPa (pure water) and **B** water potential at 22/14 °C incubation temperature



main reasons for seedling mortality in alpine regions (Welling and Laine 2000; Forbis 2003). High soil moisture is necessary for germination and seedling establishment because small seeds do not contain sufficient carbohydrate reserves for rapid production of deep roots in a drying environment (Oberbauer and Miller 1982).

Analysing the community-specific germination patterns, we revealed a clear separation of the germination niches along the snowmelt gradient regarding temperature only (Figs. 4 and 5). As expected, the main germination

in snowbed species was constrained to comparatively high temperatures above 10 °C (Figs. 5 and 6) corresponding well with the in situ soil temperature conditions after the snowmelt (Fig. 3). This temperature range corroborates seed germination experiments in the lab and field observations on Italian (Bernareggi et al. 2016) and Japanese snowbed species (Shimono and Kudo 2001, 2005) suggesting a broader occurrence of snowbed germination syndrome in alpine ecosystems. Such high temperature requirements for snowbed germination seem to be adaptive

in preventing germination under the snow cover, in years with smaller snow accumulation, or unexpectedly earlier onset of snowmelt. At the same time, emergence of seedlings in the middle of the growing season exposes them to favorable environmental conditions as soil and air temperatures are close to their maxima, meltwater protects from soil desiccation and daylight period is long [reviewed in Björk and Molau (2007)]. In other words, the late start of the growing season is compensated by favorable growth and development conditions that allow juvenile plants to quickly attain a critical size and develop adaptations required to winter survival (Shimono and Kudo 2001, 2005).

In contrast to our hypothesis, snowbed species did not differ in their germination requirements for water from the species occurring on the other three communities and were able to germinate under moderate levels of water availability (ca.  $-0.5$  MPa; Figs. 5 and 6). This finding suggests that snowbed species might not depend entirely on habitat-specific ample meltwater supply during germination and can tolerate short-term summer droughts common in years with low precipitation.

In accordance with our hypothesis, seed germination in alpine lichen heaths (ALH) was found to occur under a wide range of experimental conditions including lower temperatures (Fig. 5), thus departing from the general alpine germination syndrome (Fernández-Pascual et al. 2021). Such opportunistic strategy for non-dormant seeds to germinate equally under conditions of frost damage in spring (Fig. 2) and drought stress in summer (Onipchenko 2004) can be explained by biotic interactions of the seedlings and surrounding vegetation. First, lichens have been shown to facilitate seedling recruitment in alpine heaths by buffering extreme soil temperatures and soil drying under droughts (Nystuen et al. 2019). Second, the vascular plants occurring in these communities could also protect germinated seeds from, e.g. frost damage (Rosbakh et al. 2021), thereby additionally enhancing seedling establishment (Margreiter et al. 2021). As a result, seeds of alpine lichen heath plants may germinate with equal success throughout the growing season. Finally, the broad seed germination niche could be explained by the high relative energy investment into offspring by the ALH species and their short-term persistence in soil seed banks (Onipchenko et al. 1998): once produced, seeds should germinate or die.

Finally, our experimental results confirmed our expectation that the intermediate position of the *Festuca varia* grassland and *Geranium-Hedysarum* meadow communities along the snowmelt gradient was reflected in their community-specific germination patterns. Although the species from these two communities did not differ in their requirements for water, they tended to have similar temperature requirements of their neighboring communities.

The tendency for higher germination temperatures in the communities with intermediate snow length could be attributed to the vegetation structure in the *Festuca varia* grasslands and *Geranium-Hedysarum* meadows. Most likely, seedling establishment in such productive communities with tall and dense vegetation is possible only in gaps caused by animal activities (Onipchenko et al. 1998) with reduced levels of competition (Fenner et al. 2005). Early germination in such gaps is linked with high probability of frost injury of maladapted alpine seedlings (Rosbakh et al. 2020b), particularly during the night radiation frost events (Körner 2021). The onset of comparatively high temperatures in later summer months with reduced frost probability triggers then the seed germination in the corresponding communities.

## Conclusions and implications

Our study reveals that, in addition to vegetative traits (Choler 2005; Pickering et al. 2014; Körner 2021), seed germination niche is also affected by environmental filtering along the snowmelt gradient. We clearly demonstrate that species from four focal communities differencing in snowmelt patterns significantly differ in their temperature requirements for germination, whereas soil moisture was found to be a limiting factor for seedling establishment along the entire gradient. These findings provide further support to the recent argument that vegetation ecology research should consider traits related to germination, as they represent different ecological niche axes (Jiménez-Alfaro et al. 2016; Rosbakh et al. 2021).

The revealed community-specific germination responses to temperature have important implications not only for alpine ecological research in general, but also for climate change research and conservation/restoration ecology. The recent climate warming in the North Caucasus has already affected the timing of snowmelt leading to detectable/considerable changes in the alpine vegetation, with those at the extreme end of the snowmelt gradient (snowbeds and *Geranium-Hedysarum* meadow) experiencing the most fundamental change (Elumeeva et al. 2013). With even greater reductions in winter precipitation and continuous rising temperatures predicted for the study region, the altered snowpack thickness and duration will inevitably affect regeneration from seeds in the study communities. Particularly, earlier snowmelt in snowbeds may relax this environmental filter allowing species with less demanding requirements for germination from the other communities to colonize and establish in this unique habitat (Hülber et al. 2011; Elumeeva et al. 2013; Pickering et al. 2014).



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## Declarations

**Conflict of interest** The authors declare no competing interests.

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## References

- Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination. Elsevier, Academic Press, San Diego
- Bell KL, Bliss LC (1980) Plant reproduction in a high Arctic environment. *Arct Alp Res* 12:1–10. <https://doi.org/10.1080/00040851.1980.12004158>
- Bernareggi G, Carbognani M, Mondoni A, Petraglia A (2016) Seed dormancy and germination changes of snowbed species under climate warming: the role of pre- and post-dispersal temperatures. *Ann Bot* 118:529–539. <https://doi.org/10.1093/aob/mcw125>
- Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) Germination. In: Bewley B et al (eds) *Seeds: physiology of development*. Springer, pp 133–181
- Björk RG, Molau U (2007) Ecology of alpine snowbeds and the impact of global change. *Arct Antarct Alp Res* 39:34–43. [https://doi.org/10.1657/1523-0430\(2007\)39\[34:EOASAT\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[34:EOASAT]2.0.CO;2)
- Carta A, Fernández-Pascual E, Gioria M, Müller JV, Rivière S, Rosbakh S, Saatkamp A, Vandelook F, Mattana E (2022) Climate shapes the seed germination niche of temperate flowering plants: a meta-analysis of European seed conservation data. *Ann Bot*. <https://doi.org/10.1093/aob/mcac037>
- Choler P (2005) Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arct Antarct Alp Res* 37:444–453. [https://doi.org/10.1657/1523-0430\(2005\)037\[0444:CSIAPT\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0444:CSIAPT]2.0.CO;2)
- Elumeeva TG, Onipchenko VG, Egorov AV, Khubiev AB, Tekeev DK, Soudzilovskaia NA, Cornelissen JHC (2013) Long-term vegetation dynamic in the Northwestern Caucasus: which communities are more affected by upward shifts of plant species? *Alp Bot* 123:77–85. <https://doi.org/10.1007/s00035-013-0122-7>
- Fenner MK, Fenner M, Thompson K (2005) *The ecology of seeds*. Cambridge University Press, Cambridge
- Fernández-Pascual E, Jiménez-Alfaro B, Bueno Á (2017) Comparative seed germination traits in alpine and subalpine grasslands: higher elevations are associated with warmer germination temperatures. *Plant Biol J* 19:32–40. <https://doi.org/10.1111/plb.12472>
- Fernández-Pascual E, Mattana E, Pritchard HW (2019) Seeds of future past: climate change and the thermal memory of plant reproductive traits. *Biol Rev* 94:439–456. <https://doi.org/10.1111/brv.12461>
- Fernández-Pascual E, Carta A, Mondoni A, Cavieres LA, Rosbakh S, Venn S, Satyanti A, Guja L, Briceño VF, Vandelook F, Mattana E, Saatkamp A, Bu H, Sommerville K, Poschlod P, Liu K, Nicotra A, Jiménez-Alfaro B (2021) The seed germination spectrum of alpine plants: a global meta-analysis. *New Phytol* 229:3573–3586. <https://doi.org/10.1111/nph.17086>
- Forbis TA (2003) Seedling demography in an alpine ecosystem. *Am J Bot* 90:1197–1206. <https://doi.org/10.3732/ajb.90.8.1197>
- Grishina LA, Onipchenko VG, Makarov MI, Vanyasin VA (1993) Changes in properties of mountain-meadow alpine soils of the northwestern Caucasus under different ecological conditions. *Eurasian Soil Sci* 25:1–12
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmmR package. *J Stat Softw* 33:1–22. <https://doi.org/10.18637/jss.v033.i02>
- Hülber K, Bardy K, Dullinger S (2011) Effects of snowmelt timing and competition on the performance of alpine snowbed plants. *Perspect Plant Ecol Evol Syst* 13:15–26. <https://doi.org/10.1016/j.ppees.2011.01.001>
- Huss M, Bookhagen B, Huggel C, Jacobsen D, Bradley RS, Clague JJ, Vuille M, Buytaert W, Cayan DR, Greenwood G, Mark BG, Milner AM, Weingartner R, Winder M (2017) Toward mountains without permanent snow and ice. *Earth's Future* 5:418–435. <https://doi.org/10.1002/2016EF000514>
- Jiménez-Alfaro B, Silveira FA, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. *J Veg Sci* 27:637–645. <https://doi.org/10.1111/jvs.12375>
- Jin Y, Qian H (2019) V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* 42:1353–1359. <https://doi.org/10.1111/ecog.04434>
- Körner C (2021) *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer Nature
- Körner C, Hiltbrunner E (2021) Why Is the alpine flora comparatively robust against climatic warming? *Diversity* 13:383. <https://doi.org/10.3390/d13080383>
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31:713–732. <https://doi.org/10.1111/j.1365-2699.2003.01043.x>
- Körner C, Paulsen J, Spehn EM (2011) A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alp Bot* 121:73. <https://doi.org/10.1007/s00035-011-0094-4>
- Kudo G, Nordenhäll U, Molau U (1999) Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. *Écoscience* 6:439–450. <https://doi.org/10.1080/11956860.1999.11682543>
- Leinsoo TN, Onipchenko VG, Leinsoo TA, Velikanov LL (1991) Biomass variation of soil micromycetes in the alpine communities in the Northwest Caucasus. *Mikol Fitopatol* 25:206–212
- Malysheva TI, Makarov MI, Onipchenko VG, Volkov AV, Bulatnikova IV (2004) Soils and nutrient turnover. In: Onipchenko VG (ed)

- Alpine ecosystems in the Northwest Caucasus. Springer Netherlands, Dordrecht, pp 9–23
- Margreiter V, Walde J, Erschbamer B (2021) Competition-free gaps are essential for the germination and recruitment of alpine species along an elevation gradient in the European Alps. *Alp Bot* 131:135–150. <https://doi.org/10.1007/s00035-021-00264-9>
- Michel BE, Kaufmann MR (1973) The osmotic potential of polyethylene glycol 6000. *Plant Physiol* 51:914–916. <https://doi.org/10.1104/pp.51.5.914>
- Nystuen KO, Sundsdal K, Opedal ØH, Holien H, Strimbeck GR, Graae BJ (2019) Lichens facilitate seedling recruitment in alpine heath. *J Veg Sci* 30:868–880. <https://doi.org/10.1111/jvs.12773>
- Oberbauer S, Miller PC (1982) Effect of water potential on seed germination. *Ecography* 5:218–220. <https://doi.org/10.1111/j.1600-0587.1982.tb01040.x>
- Onipchenko VG (1994) The structure and dynamics of alpine plant communities in the Teberda Reserve, the Northwestern Caucasus. *Oecol Mont* 3:40–50
- Onipchenko VG (2004) Alpine ecosystems in the Northwest Caucasus. Springer Science & Business Media
- Onipchenko VG, Semenova GV, van der Maarel E (1998) Population strategies in severe environments: alpine plants in the northwestern Caucasus. *J Veg Sci* 9:27–40. <https://doi.org/10.2307/3237220>
- Orsenigo S, Abeli T, Rossi G, Bonasoni P, Pasquaretta C, Gandini M, Mondoni A (2015) Effects of autumn and spring heat waves on seed germination of high mountain plants. *PLoS ONE* 10:e0133626. <https://doi.org/10.1371/journal.pone.0133626>
- Pickering C, Green K, Barros AA, Venn S (2014) A resurvey of late-lying snowpatches reveals changes in both species and functional composition across snowmelt zones. *Alp Bot* 124:93–103. <https://doi.org/10.1007/s00035-014-0140-0>
- Poschlod P, Abedi M, Bartelheimer M, Drobnik J, Rosbakh S, Saatkamp A (eds) (2013) Seed ecology and assembly rules in plant communities. Wiley Online Books
- Rosbakh S, Poschlod P (2015) Initial temperature of seed germination as related to species occurrence along a temperature gradient. *Funct Ecol* 29:5–14. <https://doi.org/10.1111/1365-2435.12304>
- Rosbakh S, Baskin CC, Baskin JM (2020a) Nikolaeva et al.'s reference book on seed dormancy and germination. *Ecology* 101:e03049. <https://doi.org/10.1002/ecy.3049>
- Rosbakh S, Margreiter V, Jelcic B (2020b) Seedlings of alpine species do not have better frost-tolerance than their lowland counterparts. *Alp Bot* 130:179–185. <https://doi.org/10.1007/s00035-020-00237-4>
- Rosbakh S, Chalmandrier L, Phartyal S, Poschlod P (2021) Inferring community assembly processes from functional seed trait variation along temperature gradient. *bioRxiv*. <https://doi.org/10.1101/2021.12.17.473108>
- Rumpf SB, Hülber K, Zimmermann NE, Dullinger S (2019) Elevational rear edges shifted at least as much as leading edges over the last century. *Glob Ecol Biogeogr* 28:533–543. <https://doi.org/10.1111/geb.12865>
- Scherrer D, Körner C (2009) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob Change Biol* 16:1. <https://doi.org/10.1111/j.1365-2486.2009.02122.x>
- Schwienbacher E, Navarro-Cano JA, Neuner G, Erschbamer B (2012) Correspondence of seed traits with niche position in glacier foreland succession. *Plant Ecol* 213:371–382
- Shimono Y, Kudo G (2001) Pattern of seedling emergence of alpine plants: comparisons between fellfield and snowbed habitats (scientific note). *Mem Natl Inst Polar Res* 54:467–478
- Shimono Y, Kudo G (2005) Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. *Ecol Res* 20:189–197. <https://doi.org/10.1007/s11284-004-0031-8>
- Smith SA, Brown JW (2018) Constructing a broadly inclusive seed plant phylogeny. *Am J Bot* 105:302–314. <https://doi.org/10.1002/ajb2.1019>
- Stanton ML, Rejmánek M, Galen C (1994) Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U. S. A. *Arct Alp Res* 26:364–374. <https://doi.org/10.1080/00040851.1994.12003081>
- Testolin R, Attorre F, Jiménez-Alfaro B (2020) Global distribution and bioclimatic characterization of alpine biomes. *Ecography* 43:779–788. <https://doi.org/10.1111/ecog.05012>
- Tudela-Isanta M, Fernández-Pascual E, Wijayasinghe M, Orsenigo S, Rossi G, Pritchard HW, Mondoni A (2018a) Habitat-related seed germination traits in alpine habitats. *Ecol Evol* 8:150–161. <https://doi.org/10.1002/ece3.3539>
- Tudela-Isanta M, Ladouceur E, Wijayasinghe M, Pritchard HW, Mondoni A (2018b) The seed germination niche limits the distribution of some plant species in calcareous or siliceous alpine bedrocks. *Alp Bot* 128:83–95. <https://doi.org/10.1007/s00035-018-0199-0>
- Vertelina OV, Onipchenko VG, Makarov MI (1996) Primary minerals and processes of weathering in high-mountain soils of the Teberda Reserve. *Vestnik Moskovskogo Universiteta, seria 17. Pochvovedenie* 51:1–8
- Villemereuil de P, Nakagawa S (2014) General quantitative genetic methods for comparative biology. In: Garamszegi LZ (ed) *Modern phylogenetic comparative methods and their application in evolutionary biology*. Springer, pp 287–303
- Walder T, Erschbamer B (2015) Temperature and drought drive differences in germination responses between congeneric species along altitudinal gradients. *Plant Ecol* 216:1297–1309. <https://doi.org/10.1007/s11258-015-0509-1>
- Welling P, Laine K (2000) Characteristics of the seedling flora in alpine vegetation, subarctic Finland, I. Seedling densities in 15 plant communities. *Ann Bot Fenn* 37:69–76
- Winkler DE, Butz RJ, Germino MJ, Reinhardt K, Kueppers LM (2018) Snowmelt timing regulates community composition, phenology, and physiological performance of alpine plants. *Front Plant Sci* 9:1140. <https://doi.org/10.3389/fpls.2018.01140>
- Zhang T (2005) Influence of the seasonal snow cover on the ground thermal regime: an overview. *Rev Geophys* 43:R4002. <https://doi.org/10.1029/2004RG000157>

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