General

The influence of environmental conditions as drivers of these contrasting germination responses to temperature is gaining recognition. For example, alpine species show higher optimal temperatures for germination than either subalpine species (i.e. species that live close to the treeline, Fernández-Pascual *et al.* ([2017](#ref-RN2371))) or congeneric counterparts from below the treeline (Walder & Erschbamer, [2015](#ref-RN3266)). Differences in germination traits have been attributed also to species successional niche, with pioneer species germinating better at colder temperatures than later successional species (Schwienbacher *et al.*, [2012](#ref-RN3229)). Species from calcareous and siliceous alpine grasslands show a slow overwinter germination or high germination under all conditions, respectively (Tudela-Isanta *et al.*, [2018a](#ref-RN4727),[b](#ref-RN4726)). Other factors related to species germination characteristics include slope (Xu *et al.*, [2017](#ref-RN4733)) and biogeographical origin (Giménez-Benavides *et al.*, [2005](#ref-RN698)). Nevertheless, no habitat-related germination strategies were identified when comparing a major divide in alpine microhabitats, as is the one between fellfields and snowbeds (Shimono & Kudo, [2005](#ref-RN707)).

Discussion of FAMD ordination of regeneration traits

The factorial analysis of mixed data (FAMD) opposed alpine plants according to a fast-slow gradient across regeneration strategies in alpine species. This gradient opposes perennial, woody plants with slow germination (high MGT), with high temperature requirements, stratification or GA3, focussing on a single germination season (low UNC) against annual plants, with faster germination (low MGT), including a bet-hedging startegy (high UNC), with germination traits indicating possible fast germination after specific germination cues (PY, alternating temperatures). This gradient is interestingly linked to biogeographic patterns since the slow end is correlated with restricted distribution ranges.

The fast-slow gradient within regenerative strategies of alpine plants we found here is in parallel to prominent gradients of fast or slow population dynamics (Nobis and Schweingruber 2013; Silvertown et al. 1992), fast or slow developping leaf traits (Wright et al. 2004), or large sets of plant ecological features (Grime 1977). Fast regeneration can be understood as a strategy to cope with frequently disturbed alpine habitats such as avalanche ways, steep eroding slopes, regressing glaciers and riverbeds (Gentili et al. 2013; Pierce et al. 2007). These habitats link fast regeneration after disturbance, after snow-melt and before drying, with low need of GA3 or non dormant seeds, break of physical dormancy and effective cueing by factors indicating exposed bare soil such as alternating temperatures. Interestingly, fast germination seems to be linked to larger distributional areas, it has been suggested that short lived pioneer species tend to have larger distributional areas than late-successional species, because of their more far-ranging colonization capacity (Morin and Chuine 2006) and alpine pioneer species more rapidly move upwards during recent climate change (Pauli et al. 2007).

It is intriguing that strict alpine plants link longer life-spans with slower germination and germination at higher temperatures, as well as a higher need of GA3 or stratification. Alpine habitats with prominently long living plants and slow turnover include rocky alpine meadows, snow-beds, stable rocky outcrops and windblown sites at high altitudes (Forbis and Doak 2004; Nobis and Schweingruber 2013). These habitats have a continuous vegetation cover and if not evergreen, plants resprout and cover gaps rapidly after snowmelt (Choler 2005), probably with gaps later in the season at higher temperatures being more sensible for successful regeneration by seeds in these slow-turnover sites. Perennial plants may have stronger dormancy linked to avoidance of competition with mother-plants (Westoby and Rice 1982). Low UNC in our data also suggests that germination timing is more grouped for strict alpine species, contributing to the idea that regeneration windows are more specialized.

Other topics (perhaps discussed by others):

-Higher proportion of MPD and MD in alpine species, but this is not reflected in embryo:seed size ratio

- Larger seeds are less responsive to light

- Seeds with higher embryo:seed size germination faster (in agreement with Vandelook et al. 2012)

- Seeds with lower embryo:seed size are more responsive to stratification

Other facts to consider:

# Seeds with PD dormancy usually require one ‘cold-warm’ cycle, whereas in the case of M(P)D seeds there might be several of them.

# Although species with ND seeds do not contribute much to the spectra, they might reflect within-habitat heterogeneity of alpine landscapes (e.g. species with ruderal strategy occurring on rocky outcrops or screes with fast life-cycle).

Stratification and GA3

Our results clearly indicated that, in general, a stratification period where seeds experience cold and wet conditions over a period of months is important for promoting seed germination in species inhabiting alpine habitats. Cold stratification acts to decrease their time to germination and can increase their overall percent germination. These results concur with several studies that have shown that cold-stratification is important for seed germination of different alpine plant species (e.g. Cavieres & Arroyo, 2000; Schütz, 2002; Shimono and Kudo, 2005; Giménez-Benavides et al., 2005; Sommerville et al., 2013; García-Fernández et al., 2015; Hoyle et al., 2015; Fernández-Pascual et al., 2017; Cavieres & Sierra-Almeida 2018). Under natural conditions, a stable cold stratification treatment of the seeds occurs over winter when they are covered with snow. Hence, the role of cold stratification on the different germination parameters assessed suggests that this allows seeds to sense the snow season, and thereby promotes germination to occur in the spring and summer snow-free season, when conditions are more favourable for seedling survival and growth. Global climate change is causing large changes in the snow cover duration in several alpine areas around the world (Beniston, 2012; Gobiet al., 2014). In some areas, this is leading to shorter, or even the absence of, natural cold stratification periods under snow for some alpine species, and could suggest decreases in seed germination rates in the future, compromising their population viability and indirectly favoring species with no such requirement (Sommerville et al., 2013). Thus, our global assessment suggests that major impacts on the natural regeneration process of alpine species may be expected according to the current trends in climate change.

Seeds with the two most frequent dormancy classes (PD and MPD) require cold, wet stratification (one or several cycles) for after-ripening and dormancy break that usually occurs during winter and/or snowmelt in spring (Baskin and Baskin, 2014; Rosbakh et al. 2020). This corresponds well with the finding that laboratory approaches such as GA3 treatment and scarification stimulated seed germination in many alpine species. GA3 substitutes cold stratification by giving the embryo an hormonal 'push' and scarification removes either mechanical or chemical barriers in species with PD. PY is an alternative dormancy mechanism based on water-impermeable seed coat that is infrequent in alpine habitats but when it does occur can be broken by mechanical scarification via freezing-thawing cycles in spring and/or high diurnal temperature fluctuations in summer.