

# Soil seed bank potential of Himalayan alpine meadows – A case study of anthropogenically disturbed Tungnath treeline

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**Abstract:** Many alpine plants disperse dormant seeds at maturity towards the end of the growing season, characterised by cooler temperatures preventing immediate seed germination. The seeds then accumulate in the soil and germinate in the next growing season, or remain buried until favourable conditions occur. Since soil seed bank potential depends on species-specific (intrinsic) and site-specific (extrinsic) characteristics, it is worth to ask: can anthropogenically disturbed Himalayan alpine meadows form a soil seed bank? Two hundred and sixty soil cores were sampled down to 10 cm depth in two layers from alpine meadows parallel to the Tungnath treeline in Uttarakhand State of India. Sampling was carried out in autumn (after seed dispersal) and spring (before seed germination) and incubated under *ex situ* (net house) and *in situ* (on-site field) conditions for seedling emergence. Overall, 2,141 seeds/m<sup>2</sup> of 13 species were recorded from *in situ* incubated samples. Seed density and species number substantially decreased with increasing soil depth. The upper layer (0-5 cm) had a mean density of 3,586 seeds/m<sup>2</sup>, while the lower layer (5-10 cm) had 697 seeds/m<sup>2</sup>, respectively. The study revealed that anthropogenically disturbed Himalayan alpine meadows have low soil seed bank potential compared to alpine meadows of other mountain systems. High disturbance pressure like grazing and high human footfalls probably damaged the reproductive phase of plant life and led to low seed production, hence the low seed inputs in the soil. Some methodological issues in studying soil seed banks of alpine plants were also discussed.

**Keywords:** alpine meadow; Bugyal; Garhwal Himalaya; grassland; seed ecology; soil seed bank; treeline.

**Nomenclature:** The nomenclature of the vascular plants follows Rai et al. (2017).

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## Introduction

The soil seed bank is the natural reservoir of viable seed, present within the soil of most ecosystems, often in the dormant stage (Roberts 1981). It consists of new seeds shed only recently and older seeds that have persisted in the soil for several years (Zobel et al. 2007). The persistence of the seed bank plays a crucial role in population dynamics since it enables the plant to spread germination over time by remaining viable and avoiding germination under unfavourable environmental conditions (Bakker et al. 1996; Saatkamp et al. 2011; Ooi 2012; Long et al. 2015; Mašková et al. 2022). The capacity of seeds to retain their viability in the soil allows species to survive episodes of disturbance and destruction (Thompson 2000).

In an ecosystem, soil seed banks often have high temporal and spatial variability, with conspicuous changes in seed density and species composition (Perera 2005; Ma et al. 2010; Konsam et al. 2020). Temporal variability is represented by the longevity of seed buried in the soil as transient, short-term persistent, and long-term persistent seed bank

(Thompson & Fenner 1992). In contrast, spatial variability is represented by the distribution of viable seeds horizontally and vertically in the soil. The horizontal distribution shows how far the seed has been dispersed from its parents, while the vertical distribution shows how deep the seed is buried within the soil profile. The temporal and spatial variability of a soil seed bank largely depends on several species-specific biotic characteristics. Such as seed production per ramet, seed morphology, seed dispersal syndrome, seed longevity, degree of seed dormancy and germination niche width. It also depends upon post-dispersal site-specific abiotic environmental factors, for example, soil substrate type, soil compaction, soil moisture, soil nutrient status, the amplitude of light and temperature fluctuation at or below the soil surface (Poschlod et al. 2013; Abedi et al. 2014; Baskin & Baskin 2014; Saatkamp et al. 2014; Long et al. 2015; Mašková et al. 2022). Additionally, other habitat-specific characteristics such as surrounding vegetation or canopy cover (Rice 1989; Godefroid et al. 2006), level of disturbance such as grazing (Ma et al. 2010; Erfanzadeh et al.

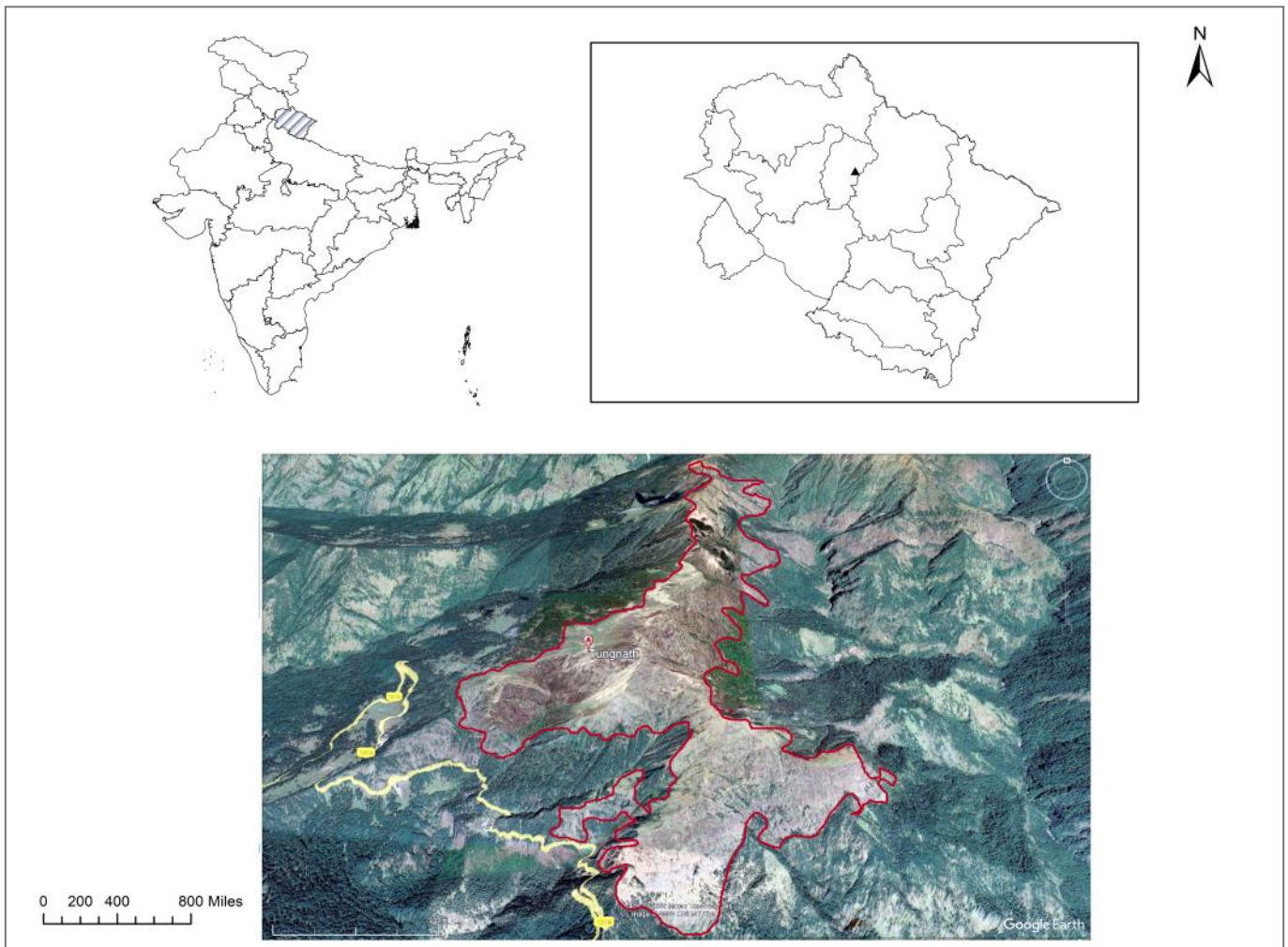
2016), fire (Konsam et al. 2020), flooding (Hölzel & Otte 2004), etc. also influence the seed persistence potential.

Seeds of many alpine plant species are dormant at maturity. They do not germinate immediately after dispersal (Baskin & Baskin 2014) but instead require frequent cold stratification to break dormancy followed by warm temperature to germinate (Fernández-Pascual et al. 2021). As a result, they remain viable in a transient soil seed bank and release their dormancy through winter chilling and begin to germinate in the following growing season or enter deep in persistent soil seed bank if they fail to germinate during the first growing season, where they can remain dormant and viable for years (Molau & Larsson 2000; Baskin & Baskin 2014).

Four major transition stages in the sexual regeneration pathway of plant species influence their life-history. These stages are seed production, seed accumulation in the seed bank, seed germination, and the survival and growth of seedlings into adult plants (Welling et al. 2004). During favourable years, seed production from alpine vegetation is usually high, but its accumulation in the seed bank generally remains low (Molau & Larson 2000). Additionally, alpine plant seed germination and seedling survival are constrained by several other factors, such as competition with established vegetation, seed predation, low temperatures,

frost, and soil drought (Chambers 1995; Kiviniemi 1999). The dispersal of seeds through zoochory is supposed to contribute to the spatial distribution of alpine plants (Rosbakh et al. 2022), which can also contribute to forming soil seed banks along ecological gradients.

Several studies conducted in recent years in different mountainous habitats around the world have revealed the presence of a considerable number of seeds in the soil seed banks of alpine vegetation (Ma et al. 2010; Venn & Morgan 2010; Li et al. 2012; Loydi et al. 2012; Hoyle et al. 2013; Wang et al. 2013). However, the recruitment of plant individuals through seed germination is often almost negligible in the alpine zones (Thompson 1978; Bell & Bliss 1980; Archibald 1981) as cold and unsuitable environments constrain biomass and seed production with the short growing season (Onipchenko et al. 1998; An et al. 2020). The alpine soil seed bank is often neglected because of the general view that sexual reproduction becomes less important with increasing latitude or altitude (Thompson 1978; but see Bliss 1958). Instead, vegetative means of propagation appear to be a better survival strategy and a dominant mode of reproduction to sustain alpine plant populations under harsh *in situ* conditions (Grime 1979; Onipchenko et al. 1998; An et al. 2020). Furthermore, alpine soil seed bank studies have to



**Fig. 1.** Location map of Tungnath treeline area.

address some key methodological issues. Such as when (autumn vs. spring) soil samples should be collected and where (*in situ* vs. *ex situ*) these samples should be incubated to meet the most appropriate environments for alpine seed germination and seedling establishment since they have a particular seed germination niche (Mondoni et al. 2011; Baskin & Baskin 2014; Satyanti 2017; Fernandez-Pascual et al. 2021).

Considering the mentioned challenges, that the alpine soil seed banks face and knowing that the Tungnath treeline zone is one of the highly disturbed Himalayan landscapes, particularly stressed by the high pressure of human influx (Singh et al. 2018) and extensive grazing (Nautiyal et al. 2004), we hypothesized that the local alpine meadow plants have low potential to form a viable soil seed bank. Moreover, we believe that such disturbance factors prevent plants from reaching the complete regenerative stage required to produce enough seeds, which eventually limits seed input to the soil. Although it is well known that the alpine meadows of the Indian Himalayan Region represent diverse ecological plant communities, we know little about their natural regeneration from seeds. In this study, the specific question we asked was: Do anthropogenically disturbed Himalayan alpine meadows have the potential to form a soil seed bank?

### Study Area

Tungnath treeline (30°29'22" N, 79°12'47" E) is located in Kedarnath Wildlife Sanctuary, Uttarakhand (India) and covers a large area of upper catchments of river Alaknanda (Fig. 1). Like other substantially depressed western Himalayan treelines with a long history of anthropogenic pressure (Singh et al. 2019), the Tungnath treeline has one of the worst disturbed alpine meadows due to the high pressure of the religious, eco, and adventure tourism (Singh et al. 2018). Anthropogenic activities also attract high movement of domestic grazing animals, causing habitat destruction and changes in vegetation composition (Nautiyal et al. 2004). Around the Tungnath treeline, the monthly minimum and maximum temperatures of the coldest and warmest months range from -2.0°C to 20.3°C. The mean annual temperature is 10.7°C and the mean annual precipitation 1,932 mm (extracted from The Global Vegetation Project, Fleri et al. 2021) (Fig. 2). A floristic inventory of the study area (Rai et al. 2017), revealed that about 226 species belonging to 54 families and 158 genera grow there. Among them, the most dominating functional group was forbs (190 species), followed by shrubs (22 species), grasses (5 species, *Danthonia cachemyriana*, *D. schneideri*, *Festuca rubra*, *F. valesiaca*, *Poa alpina*), sedges (4 species), trees (3 species, *Abies spectabilis*, *Quercus semecarpifolia*, *Rhododendron campanulatum*), and climbers (2 species). Closer scrutiny of the phenological stage revealed that the most prominent flowering season in the study area was summer (58.7% flowering species), followed by the monsoon period (33.7%), with the monsoon (79.4%) as the peak fruiting season, followed by autumn (15.7%).

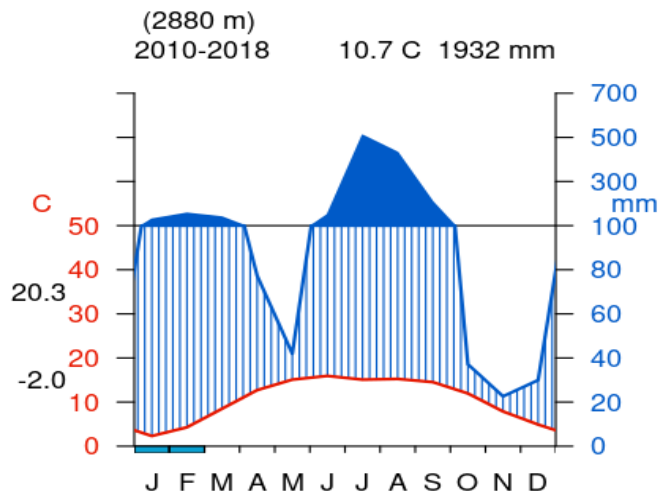


Fig. 2. The Walter and Leith Climate Diagram (2010 to 2018) of the Tungnath treeline retrieved from the Global Vegetation Project (Fleri et al. 2021).



Fig. 3. A tracking route trespassing Tungnath treeline located at around 3,000-3,300 m a.s.l. *Abies spectabilis* trees are seen in the background with the krummholz formation of *Rhododendron campanulatum* in the foreground. Photo: S.S. Phartyal.



Fig. 4. Soil cores exhumed for soil seed bank experimentation from the 2 m x 2 m plots located along treeline around 3,000-3,300 m a.s.l. The trees seen in the background are *Abies spectabilis* and *Rhododendron campanulatum*. Photo: S.S. Phartyal.

## Methods

### Soil sampling, incubation, and seedling emergence

Thirteen 2 m × 2 m plots were selected on grassy slopes just above the treeline (Figs. 3, 4) extending from one end to another (near the Tungnath temple; Fig. 5). These 13 plots were marked permanently using iron nails for repeated soil sampling. In autumn 2017, soil samples were collected from each of 13 plots both horizontally and vertically using ten separate cores of 5 cm diameter and 10 cm depth (Fig. 4). After that, each core was sub-divided into two layers of 0-5 cm and 5-10 cm and stored separately into two zip lock bags. However, ten cores of each soil layer were mixed for every plot to make a bulk sample of 0-5 cm and 5-10 cm for each plot. In general, we collected 260 soil cores representing 26 soil samples with two soil layers from 13 plots as replications covering a total of 0.255 m<sup>2</sup> of soil surface.

All soil samples were transported to the Department of Forestry and Natural Resources, HNB Garhwal University, Srinagar (520 m a.s.l.), and allowed to air dry for 48-72 hours under a ceiling fan at room temperature before processing for further experimentation. After drying, soil samples were sieved initially through a 1.0 cm mesh screen to remove rocks, twigs, and leaves, after that, through a fine sieve (0.21 mm mesh size) to concentrate soil samples by reducing the excess amount of sand and clay as per universally adopted methodology for soil seed bank studies (Ter Heerdt et al. 1996). Finally, the concentrated soil samples were spread over a sterile potting medium in plastic trays and placed in net-house benches for seedling emergence (Fig. 6). Four control trays filled with only sterilized potting soil were also placed randomly on the benches to assess contamination from local seed rain. However, no alpine plant species have emerged from this autumn sample even after six months of incubation.

Soil samples were collected again in the spring of 2018 and transported to the Pothibasa Experimental Station (2,200 m a.s.l.) of the High-Altitude Plant Physiology Research Centre



**Fig. 5.** Tungnath Temple, located (3,680 m a.s.l.) just above the treeline on a slopy alpine meadow, is one of the highest Lord Shiva temples in the world and is visited by thousands of devotees every day for pilgrimage during the growing season. Flowers from nearby alpine plants are an offering to Lord Shiva. Photo: S.S. Phartyal.



**Fig. 6.** Incubation of soil samples for seedling emergence under *ex situ* (net house) conditions at low altitude (520 m a.s.l.) climate in Srinagar-Garhwal.



**Fig. 7.** Incubation of soil samples for seedling emergence under *in situ* (open field) conditions at high altitude (3,600 m a.s.l.) climate at Tungnath treeline experimental station.

(HAPPRC) of the University after initial processing as described above. Again, no alpine plant species emerged from spring samples. Finally, soil samples were collected again in the fall of 2018 and overwintered under *in situ* outdoor alpine environments in Tungnath at HAPPRC Experimental Station (3,600 m a.s.l.) to facilitate the dormancy release of the buried seeds. For this round of soil sampling, the same process was adopted to collect and prepare samples for incubation, except concentrating them through a fine mesh of 0.21 mm size as suggested by Ter Heerdt et al. (1996). All the trays were placed on an elevated platform and covered by a fine net to minimize seed inputs from neighbouring plants. After the snow melted in spring, the trays were watered as and when necessary, and the number of emerging seedlings was counted and classified as dicot and monocot plants (Fig. 7). Since the majority of the emerged plants failed to survive until flowering, the identification to the genus and species level was problematic.

**Statistical analysis**

The mean and standard deviations for the seed density and the number of species were calculated based on the seedlings that emerged from the soil samples. Since the data did not meet the assumption of normality and homogeneity, a non-parametric Mann-Whitney U test was used for comparison. All statistical analyses were carried out using SPSS 21.

**Results**

**Soil seed bank density and species life-form composition**

A total of 1,093 alpine plant seedlings emerged from the soil samples collected in autumn 2018 and were kept for seedling emergence under *in situ* environmental conditions at HAPPRC Experimental Station, Tungnath. These 1,093 seedlings emerged corresponded to an overall mean seed density of 2,141 seeds/m<sup>2</sup> at 10 cm of soil depth. Altogether, 13 species were recorded in the soil seed bank from both soil

layers, of which 10 were dicot and three were monocot plants (Table 1).

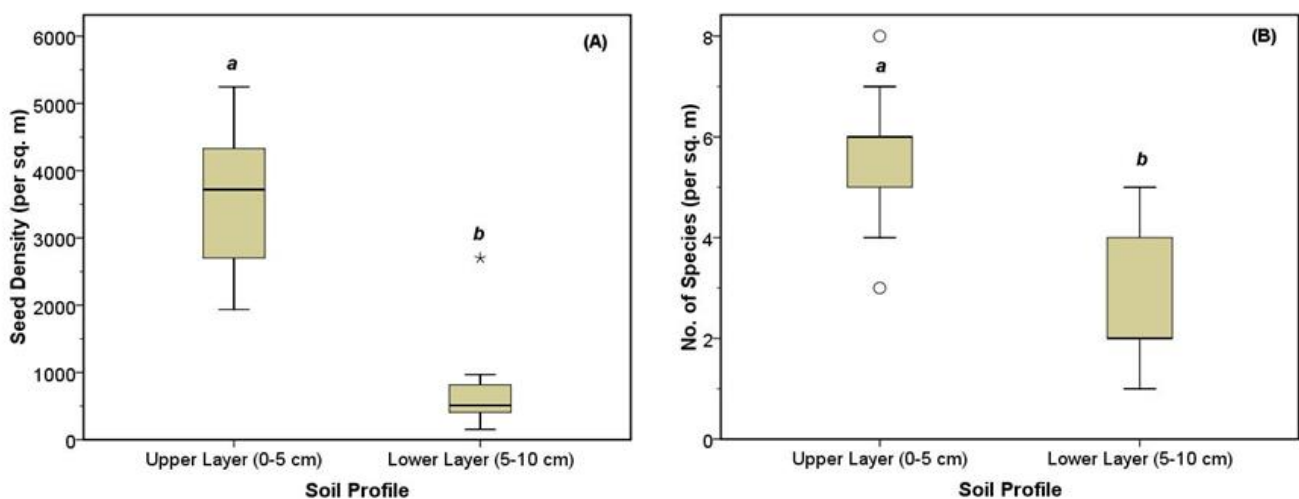
**Table 1. Overview of the soil seed banks of the alpine plants of Tungnath treeline.**

Parameters	Seed Density (m <sup>2</sup> )	Number of species
Overall	2,141	13
Dicot Plant	1,581	10
Monocot Plant	560	03

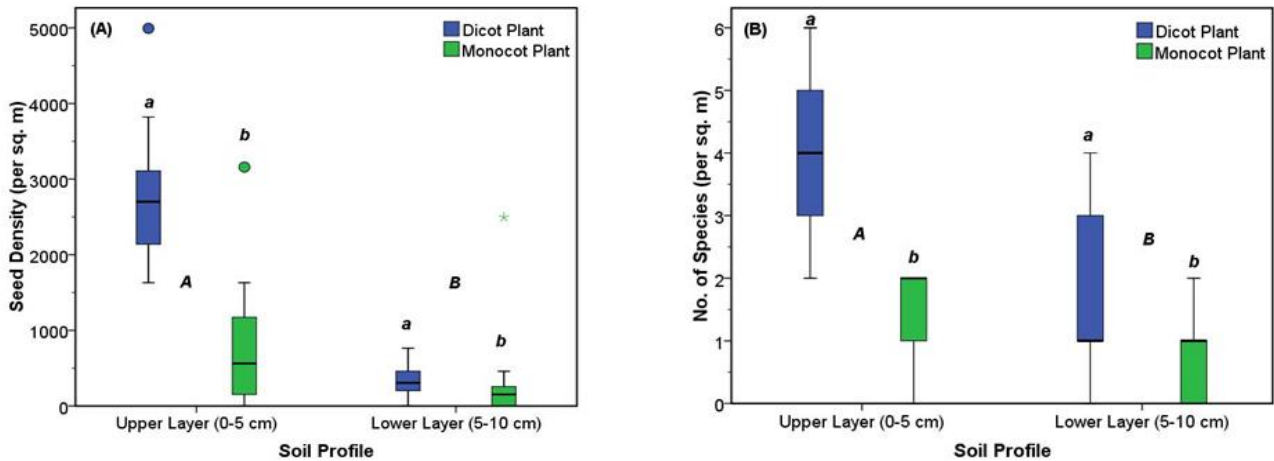
**Spatial distribution of the soil seed banks**

Depth distribution of soil seed bank density showed spatial variations as emerged seedling number decreased with increasing soil depth. There was a distinct variation in the depth distribution of the dicot and monocot species between the soil layers (Fig. 8). The upper soil layer of 0-5 cm had a mean seed density of 3,586 ± 1,056 with a median density of 3,719, while the lower soil layer of 5-10 cm had a mean seed density of 697 ± 655 with a median density of 509. Similarly, a high number of species (5 ± 1) was recorded from the upper layer compared to the lower layer of soil (2 ± 1). The above-decreasing trends in seed density and species numbers were also found to differ significantly (p < 0.001) between the upper and lower layer (Fig. 8).

Furthermore, a layer-wise comparison of the soil seed bank density and species numbers was significantly (p < 0.001) higher in the upper layer compared to the lower layer for dicot plants (Fig. 9). The upper soil layer retained 2,806 ± 869 seeds of dicot and 779 ± 884 seeds of monocot plants. Contrary to this, the lower layer retained only 356 ± 243 seeds of dicot and 340 ± 664 seeds of monocot plants, respectively.



**Fig. 8. Box plots showing the median, quartiles, outliers (o), and extremes (\*) of (A) soil seed bank density and (B) the number of species per unit area of soil surface of Tungnath treeline. Different letters above box plots refer to statistically significant (U = 3.00, n = 13, p < 0.001) differences regarding the soil depth.**



**Fig. 9.** Box plots showing median, quartiles, outliers (o), and extremes (\*) of (A) soil seed bank density, and (B) species of dicot and monocot plants per unit area of soil surface of Tungnath treeline. The letters in 'lowercase' represent subsets of dicot and monocot plants in the corresponding soil layers, while the letters in 'uppercase' represent subsets between soil layers ( $p < 0.001$ ).

## Discussion

The present study showed that the anthropogenically disturbed alpine meadow of the Tungnath treeline has considerably low soil seed bank potential, as only 1,093 viable seeds were found, representing 13 plant species. In general, the mean density of 2,141 seeds/m<sup>2</sup> is very low compared to the density of the worldwide seed bank for alpine vegetation. For example, Ma et al. (2010) and Klug-Pümpel & Scharfetter-Lehrl (2008) reported a density of 3,069-6,105 and 6,000-34,000 seeds/m<sup>2</sup> in their respective research. However, studies from other parts of the world also reported low soil seed bank density of alpine plants, as in the present study. For example, Welling et al. (2004), McGraw & Vavrek (1989), and Molau & Larsson (2000) reported seed bank densities of 99-1,109, 0-3,367, and 0-4,080 seeds/m<sup>2</sup>, respectively. Several factors could be responsible for the low number of seeds at such sites. In many alpine species, the evolution of highly-specific germination requirements (cold stratification, light, and warm regimes) delays the germination of autumn-dispersed seeds until spring (Hoyle et al. 2015; Jaganathan et al. 2015). Thus, the interplay of factors, including dormancy, specific alternating temperature requirement to germinate, and light or dark requirements for seedling emergence, offers triple safety measures against the harsh alpine climate; without these controls, seeds are more likely to have asynchronous germination, thereby posing a severe risk of seedling mortality (Billings & Bliss 1959; Fenner & Thompson 2005; Rosbakh & Poschold 2015). In close agreement with this, Hoyle et al. (2015) reported three germination strategies adopted by Australian alpine seeds as an immediate, staggered and postponed germinator. Species with nondormant seeds germinate immediately after natural dispersal in autumn, dormant seeds postpone germination until spring to overcome harsh winter temperatures, while species with a staggered strategy have seeds that germinate both before and after winter (Hoyle et al. 2015; Satyanti 2017).

In addition to a complex suite of responses to varying environmental cues, it has been suggested that not all the seeds of a particular species may respond uniformly to germination cues stimulated by seasonal temperature cycles in alpine environments; thus, carry-over of a proportion of seeds to next year is expected to maximize species fitness (Meyer & Kitchen 1994; Meyer et al. 1995). Carry-over mechanisms are common in unpredictable conditions because the risk of germination is spread to different years (Jaganathan et al. 2015), like in *Carex frigida*, an alpine species in which low germination in the growing season tends to favour carry-over mechanisms (Schütz 2002). In the present study, the incubation of soil samples of autumn 2017 and spring 2018 under *ex situ* conditions failed to initiate seedling emergence, meaning it is unfavourable to fit the specific germination strategies of buried seeds. It may be that these soil samples contain a majority of dormant seeds which follow a postponed germination strategy and required a long period of cold winter temperature to overcome dormancy, similar to several Australian alpine species (Hoyle et al. 2015; Satyanti 2017). So, it seems that incubating them directly under *ex situ* net house conditions at a relatively warmer and constant temperature without overwintering was a wrong methodological approach. The soil samples might need to be kept under the dark condition at a low temperature (~ 4°C) in the refrigerator to cold, moist stratified for 3-4 months and then moved to a sequence of warmer temperatures of spring and summer. This approach can simulate the *in situ* natural climate as done by Godefroid et al. (2011) to evaluate the soil seed bank potential of western European temperate species from the city forest of Brussels, Belgium. The emergence of seedlings from autumn 2018 samples continuously exposed to the natural climate under *in situ* field conditions supports the above argument.

The majority (~80%) of the alpine plants at our study site dispersed seeds during the monsoon rather than in the fall. Therefore, there is a possibility that seeds buried in the soil

samples collected in fall 2017 and spring 2018 may already have lost viability before being kept for incubation under *ex situ* environmental conditions. Mondoni et al. (2011) reported that the seeds of Italian alpine plants are short-lived in storage compared with those of lowland populations/related taxa. They argued that alpine regions are characterised by a short growing season and cool temperatures. There is a possibility that the late maturation (or desiccation) seed development phase remains short, so seed immaturity and short longevity become inevitable. Since the Tungnath treeline also experiences a short growing season, there may be a possibility that the seeds of alpine plants that grow there may be short-lived. However, this does not seem to be entirely correct; we explored the seed desiccation information of 27 species from our study site in the Kew Seed Information Database, which reveals that the majority (22) of them disperse desiccation-tolerant seeds (Royal Botanic Gardens Kew 2020). The production of desiccation-tolerant seeds further suggested that rather than seed dormancy or short seed longevity, seed production (seed inputs in soil) may be the leading cause of low soil seed bank density in our study site. The possibly immense pressure of grazing and human intervention in this highly disturbed treeline may hardly allow alpine plants to reach full reproductive age, disperse and accumulate seeds in the soil. During the field visit, we observed very few individual plants with fruiting bodies as we failed to harvest enough mature seeds for other experiments. It is a general notation that in stressful alpine ecosystems, clonality provides plants with a reproductive insurance and to some extent, clonality is one of the essential features of plants adapted to cold environments (Klimešová & Doležal 2011; Wu et al. 2011). Since the Tungnath treeline is under high anthropic pressure (Figs. 10, 11), species that grow there (Fig. 12) may have developed clonal means of regeneration as an alternative survival strategy. Therefore, more in-depth studies are needed to disentangle the impact of disturbances on the regeneration (asexual vs. sexual) ecology of alpine meadow plants.

Our results show that a low soil seed bank density in a deeper soil depth indicates the inability of seeds to penetrate downward with increasing soil depth. This finding is consistent with what has already been found in other studies (e.g. Bossuyt et al. 2002; Olano et al. 2002). Furthermore, in the present study, a layer-wise comparison revealed a significant spatial variation in soil seed bank composition as in various other studies on soil seed bank reserve in alpine or high-subalpine grasslands (Archibold 1981; Roach 1983; Morin & Payette 1988; McGraw & Vavrek 1989; Chambers 1993; Ingersoll & Wilson 1993; Semenova & Onipchenko 1994).

### Conclusion

Our study concludes that Tungnath, a highly disturbed treeline, has low soil seed bank potential, as most plant species growing there may not be able to reach their reproductive age to produce enough seeds to rejuvenate the soil



**Fig. 10. Heavy grazing pressure of domestic herbivores in the meadow of Tungnath treeline at 3,330 m a.s.l. Photo: S.S. Phartyal.**



**Fig. 11. Daily upward and downward migration (2,998 m a.s.l.) of domestic herbivores from the Tungnath treeline. Photo: S.S. Phartyal.**

seed bank. This study also reveals, that to investigate the seed persistence potential of alpine vegetation, soil samples should be collected from undisturbed sites and incubated in *situ* to meet the near-natural conditions or under *ex situ* conditions where the seasonal sequence of the alpine environment must be maintained.

### Author contributions

S.S.P. planned the research, S.C. and S.S.P. conducted the field sampling and experiments. S.S.P. performed the statistical analyses and led the writing, while all authors helped with manuscript revision and gave final approval for publication.

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Fig. 12. Some of the typical plants of Tungnath treeline (a) *Primula denticulata*, (b) *P. nana*, (c) *Oxygraphis polypetala* and (d) *Bistorta milletii*. Photos: S.S. Phartyal.



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