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ORIGINAL ARTICLE

Alpine plants with short-lived seeds have declined over the past two decades

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Abstract

The rate of temperature increase in alpine environments exceeds the global average, threatening alpine plant species. While some species benefit from changing conditions, others decline or risk extinction. Understanding the mechanisms that drive these divergent responses is crucial for biodiversity conservation. Although functional traits have been widely used to predict alpine plant responses to climate shifts, the role of seed traits remains largely overlooked. In this study, we tested the hypothesis that species decreasing in abundance produce shorter-lived seeds than those increasing. Seed longevity was estimated through accelerated ageing tests in 24 alpine and subalpine species from the Northern Apennines (Italy), estimating the time required for seed viability to decline to 50% (p_{50}) using probit analysis. The relationship between species-specific p_{50} value and 21-year population dynamics, quantified via the Cliff 'Delta' Index, was tested using a linear model. The results support the hypothesis, revealing a positive correlation between seed longevity (p_{50}) and species population trends, as measured by Cliff 'Delta' index. These findings highlight the potential role of seed longevity as a functional trait linked to plant population dynamics under environmental change. While vegetative traits have often been the focus of climate response studies, our results suggest that regenerative traits also warrant greater attention.

Keywords Climate change · Population dynamics · Seed longevity · Alpine species · GLORIA network

Introduction

Alpine environments are widely recognized as climate change hotspots, regions particularly vulnerable to warming and its ecological impacts (IPCC 2014), with warming rates exceeding the global average (IPCC et al. 2021; Pepin et al. 2022). Rising temperatures are altering the physiology and phenology of alpine species, affecting their performance and, consequently, their occurrence and abundance (e.g. Sandvik et al. 2004; Lenoir et al. 2008; Gottfried et al. 2012; Mondoni et al. 2015; Carbognani et al. 2016). These changes are reflected in altered population dynamics, with some taxa benefiting from climate change, whereas others are declining or even facing local extinction (Rumpf et al. 2019; Steinbauer et al. 2020; Porro et al. 2022; Lodetti et al. 2024).

In this context, understanding the mechanisms driving shifts in species occurrence and abundance is essential for the conservation of alpine plant biodiversity. Over recent decades, a functional trait approach has emerged as a powerful tool to assess plant vulnerability to alterations in climate (Angert et al. 2011; Gillison et al. 2019; Heilmeier et al. 2019). The underlying idea of this approach is to use functional traits (i.e. morphological, physiological, phenological, or behavioral characteristics that influence an individual's fitness by affecting its growth, reproduction,

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and survival; Violle et al. 2007), to provide a mechanistic understanding of why environmental change might favor or compromise certain groups of species (McGill et al. 2006; Pardee et al. 2022). To date, most of the trait-based studies that have examined the effects of climate change on alpine species have primarily focused on vegetative traits, such as canopy height or specific leaf area (Stanisci et al. 2020; Quan et al. 2024). However, regenerative traits, which are important for shaping population and community dynamics, remain comparatively unexplored (Jiménez-Alfaro et al. 2016; Poschlod et al. 2013; Saatkamp et al. 2014).

Seed traits linked to dispersal, persistence, and germination could play a fundamental role in how plants cope with climate change. For example, the presence of structures enhancing long-distance seed dispersal can promote the colonization of habitats previously unsuitable for growth (Vittoz et al. 2009; Matteodo et al. 2013). In addition, soil seed banks can mitigate the effects of extreme environmental fluctuations and enable rapid recovery following severe disturbances (Saatkamp et al. 2014), representing a key persistence strategy in variable environments. Climate warming has already been shown to affect seed persistence and germination-related processes in alpine plants, including seed bank dynamics, germination, and recruitment. Higher temperatures increase the number of species emerging from the seed bank but reduce the total number of germinants, suggesting a potential trade-off between diversity and establishment success (Hoyle et al. 2013). However, studies on seedling recruitment under warmer conditions have produced contrasting results: some report increased or unchanged recruitment in alpine species (e.g. Angers-Blondin et al. 2017; Klanderud et al. 2017), while others document declines (Shevtsova et al. 2009) or shifts in the timing of emergence (Mondoni et al. 2015). Despite the critical role of seeds and their strong link to climatic conditions, seed traits remain underexplored in the context of plant responses to climate change, especially in alpine regions that are among the most affected by global warming (but see Rosbakh et al. 2025).

Here, we focus on seed longevity, defined as the ability of seeds to retain germinability over time in a desiccated state (Rajjou and Debeaujon 2008). Estimates of seed longevity are typically derived from seed survival curves generated through accelerated ageing tests under controlled laboratory conditions (Ellis and Roberts 1980). A few studies have directly examined the relationship between seed longevity under controlled conditions and actual seed persistence in natural soil seed banks (Long et al. 2008; Guzzon et al. 2018), although the available evidence remains limited. Despite the limitations of this method, laboratory derived seed longevity measures provide a robust comparative estimate of a species' potential tolerance to ageing-related stress (Walters et al. 2005; Probert et al. 2009). Importantly, seed longevity has been shown to correlate with ecological and climatic gradients: seeds from warmer and drier environments generally exhibit greater longevity than those from colder and more humid regions (Probert et al. 2009; Mondoni et al. 2011). This pattern suggests that seed longevity may represent an adaptive strategy enhancing resilience to desiccation and temperature fluctuations, pressures that are expected to intensify under climate change (IPCC 2021). Furthermore, longevity has been shown to respond plastically to climatic factors over both short (Kochanek et al. 2011; Bernareggi et al. 2015) and long timescales (White et al. 2023). Together, these findings highlight the potential for adaptive responses that may influence species persistence through seed-mediated regeneration. However, the role of seed longevity in shaping plant population dynamics under climate change remains poorly understood, particularly in alpine ecosystems.

In this study, we aim to address this knowledge gap by investigating the role of seed longevity in shaping the response of alpine plants to climate change. Specifically, we compare the medium-term (21 year) population dynamics of 24 alpine and subalpine species from the Northern Apennines (Italy) with their seed longevity, estimated through accelerated ageing. We hypothesize that species with decreasing frequency and abundance produce shorter-lived seeds than those increasing, as shorter-lived seed may be more vulnerable to climate change, potentially reducing plant persistence and regeneration potential.

Materials and methods

Study area

The study area is located in the Northern Apennines of Italy, within the Tuscan-Emilian Apennine mountains, and includes two summits: Pian Cavallaro (44°12′09.7″N, 10°41′33.4″E; 1815 m a.s.l.) and Alpe di Mommio (44°16′31.0″N, 10°14′42.8″E; 1854 m a.s.l.). These summits are part of the Northern Apennines Target Region (IT-NAP) in the GLORIA network (Global Observation Research Initiative in Alpine environments; http://www.gloria.ac.at/home), a global consortium monitoring alpine plant diversity and microclimate. This Target Region was established in 2001, and is one of the oldest within the network, having been monitored every 7 years for 21 years. Summit vegetation in the study area consists of dwarf shrub heaths dominated by *Vaccinium* species, primarily on northern slopes, and secondary grasslands dominated by *Brachypodium genuense* (DC.) Roem. & Schult. or *Nardus stricta* L., which prevail on southern slopes (Ferrari and Piccoli 1997;

Gennai et al. 2014). The Target region is located at the borderline between continental and peninsular Italy, hosting many boreal and alpine species at the southernmost limit of their natural distribution (Tomaselli 1970; Gentili et al. 2006). Geologically, the summits are composed of thick-bedded turbiditic sandstones and marlstones, characteristic of the Macigno Formation (Nardi and Nardi 1974).

Due to its geographical position, the climate of the Northern Apennines exhibits both continental and temperate-subcontinental characteristics (Peel et al. 2007). The Pian Cavallaro site has a mean annual temperature of 9.0 °C and mean annual total precipitation of 1260 mm, while the Alpe di Mommio site has a mean annual temperature of 7.0 °C and receives an average of 1834 mm of precipitation annually. Climatic data were extrapolated from Eraclito61, an online climatic database provided by the Emilia-Romagna Region (https://dati.arpae.it/dataset/erg5-eraclito; Antolini et al. 2016). The database provides daily minimum and maximum temperatures, from which we calculated mean daily temperatures, and daily total precipitation. The data are based on a 5 km² grid resolution and therefore they are not specific to the summits but represents broader climatic patterns.

Using these data, we derived mean annual temperature and total annual precipitation for each site for the period 1961–2024 to visualize long-term climate trends. Since 1961, there has been a significant increase in the mean annual temperature for both areas (Fig. 1a), concretely 0.38 °C per decade (+2.4 °C over 63 years) at Pian Cavallaro and 0.45 °C per decade (+2.8 °C over 63 years) at Alpe di Mommio. Precipitation at both summits shows large inter-annual variability (833–1807 mm in Pian Cavallaro and 1126–2711 mm in Alpe di Mommio), with no significant trend observed (Fig. 1b).

Data collection

Vegetation data

Following the standardized GLORIA protocol (Pauli et al. 2015), vegetation structure and composition were surveyed every seven years over a 21-year period (2001–2022) within the uppermost 10 m of each summit. Each summit includes eight permanent plots, or Summit Area Sections (SAS), defined by dividing a polygon–traced 10 vertical meters below the peak and bounded by the four cardinal directions—into four sectors (NW, SW, NE, SE), each split into two elevation bands (0–5 m and 5–10 m).

In each SAS, all vascular plant species were recorded and their abundance classified into five categories: very rare (r!), rare (r), scattered (s), common (c), and dominant (d) (Pauli et al. 2015). Species nomenclature follows Tutin et al. (1964) as per GLORIA guidelines, and data were pre-processed according to Vittoz et al. (2010) and Pauli et al. (2012).

Species selection and seed collection

Species selection was initially based on the population dynamics evaluated up to 2015 by Lodetti et al. (2024), to include both species with increasing and decreasing frequency and abundance, as well as taxonomic representation. Further criteria for the final selection included seed availability and germinability.

Seeds of the selected species were collected at the time of natural dispersal (July-September) in 2017 and 2023 from populations located on the two summits. Once collected, the seeds were cleaned and tested within 3–4 weeks, except for *Luzula pedemontana* Boiss. & Reut., which underwent a 4-month cold stratification period at 0 °C to break dormancy. This treatment was applied based on previous findings indicating that the species exhibit deep physiological

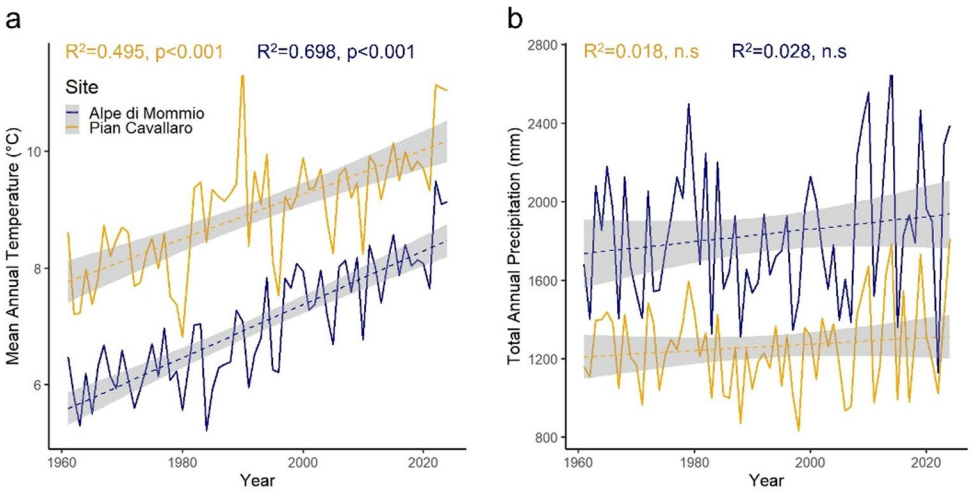


Fig. 1 Climatic trends at study sites from 1961 to 2024. The dashed lines represent the regression line, and the grey areas indicate the 95% confidence interval. **a** Mean annual temperature; **b** Total annual precipitation. Data extrapolated from the climate dataset of the Emilia-Romagna Region (https://dati.arpae.it/dataset/erg5-eraclito)

dormancy; conversely, the other species showed non-deep physiological dormancy *sensu* Baskin and Baskin (2014) (unpublished data).

Experimental ageing

Seed longevity was determined using an accelerated ageing experiment, following a protocol adapted from Davies et al. (2016).

To induce ageing, seeds were placed in a sealed electrical enclosure box (Ensto UK Ltd, Southampton, UK), above a non-saturated solution of LiCl (anhydrous, Laboratory Reagent Grade; Fisher Scientific UK Ltd, Leicester, UK) at 60% relative humidity (RH) and placed in a dark oven at 45 ± 2 °C (Binder FD53, Binder GmbH, Tuttlingen, Germany). The RH generated by the LiCl within the enclosure box was monitored using a data logger with an LCD display placed inside the box (Tinytag View 2 Temperature/Relative Humidity Logger, Gemini Data Logger, Chichester, UK). The bulk solution was adjusted as needed by adding distilled water, stirring, and allowing it to equilibrate (Hay et al. 2008; Newton et al. 2014). A sample of 350 seeds per species was used in the experiment, except in those species with limited seed availability (marked with an asterisk in Table 1), for which the sample size was reduced to 175 seeds. This adjustment was made based on prior evidence indicating that a seed count of 150 is sufficient for the protocol (Davies et al. 2016). A subsample of 50 seeds (25 for species with limited seed availability) for each species was removed after 0, 2, 5, 10, 15, 30 and 60 days for germination testing.

Germination test

Seeds were sown on 1% distilled water agar held in 50 mm diameter Petri dishes and placed in a temperature and light controlled incubator (LMS 250 A, LMS Ltd, Sevenoaks, UK) at conditions previously found to be optimal for germination (> 80% of seed germination; 20 °C constant with 250 mg L^{-1} GA3) and exposed to a 12 h daily photoperiod (photosynthetically active radiation 40–50 µmol m^{-2} s^{-1}). Plates were checked daily for germination during the first three weeks of the experiment and, subsequently, three times per week until the completion of each test (a

Table 1 Complete list of tested species (nomenclature follows Tutin et al. 1964), with classification to family level, population dynamics (Cliff 'Delta' index and 95% lower and upper confidence interval, CI), and time to 50% viability loss (p_{50} ± s.e.) at 45 °C, 60% RH

Species	Species code	Family	Cliff 'delta' index	CI low	CI up	p_{50} ± s.e. (d)
Achillea collina Becker ex Rchb.	Ac	Asteraceae	0.06	−0.24	0.35	28.5 ± 1.9
Armeria marginata (Levier) Bianchini	Am	Plumbaginaceae	−0.04	−0.29	0.22	12.3 ± 0.7
Brachypodium genuense (DC.) Roemer & Schultes	Bg	Poaceae	**0.31**	**0.07**	**0.52**	12.9 ± 1.6
Campanula scheuchzeri Vill.*	Cs	Campanulaceae	**−0.47**	**−0.69**	**−0.16**	1.7 ± 0.3
Centaurea uniflora subsp. *nervosa* (Willd.) Bonnier & Layens*	Cun	Asteraceae	0.00	−0.36	0.36	21.2 ± 2.7
Deschampsia flexuosa (L.) Trin.*	Df	Poaceae	0.19	−0.05	0.40	6.1 ± 0.7
Dianthus deltoides L. subsp. *deltoides**	Ddd	Caryophyllaceae	**0.42**	**0.19**	**0.60**	43.0 ± 4.1
Festuca riccerii Foggi & Graz. Rossi	Fr	Poaceae	0.19	−0.07	0.42	5.8 ± 1.3
Hypericum richeri Vill. subsp. *richeri*	Hrr	Hypericaceae	0.06	−0.14	0.26	17.6 ± 1.3
Leontodon pyrenaicus Gouan subsp. *helveticus* (Mérat) Finch & P.D.Sell	Lph	Asteraceae	−0.21	−0.50	0.13	8.2 ± 0.5
Lilium martagon L.*	Lm	Liliaceae	**0.46**	**0.22**	**0.64**	14.5 ± 1.8
Luzula pedemontana Boiss. & Reut.	Lp	Juncaceae	0.31	−0.08	0.62	8.7 ± 0.7
Pedicularis tuberosa L.	Pt	Orobanchaceae	**−0.25**	**−0.46**	**−0.02**	4.9 ± 0.3
Phyteuma hemisphaericum L.	Ph	Campanulaceae	**−0.44**	**−0.62**	**−0.22**	5.3 ± 0.5
Phyteuma orbiculare L.	Po	Campanulaceae	**−0.22**	**−0.41**	**−0.01**	1.7 ± 0.9
Plantago maritima subsp. *serpentina* (All.) Arcang.	Pms	Plantaginaceae	0.12	−0.05	0.30	17.6 ± 1.0
Scabiosa lucida Vill.*	Sl	Dipsacaceae	−0.08	−0.32	0.16	4.0 ± 0.7
Sedum alpestre Vill.	Sa	Crassulaceae	−0.08	−0.25	0.09	16.1 ± 1.8
Seseli libanotis (L.) W.D.J.Koch subsp. *libanotis*	Sll	Apiaceae	**0.31**	**0.04**	**0.54**	8.2 ± 0.6
Silene acaulis (L.) Jacq. subsp. *bryoides* (Jord.) Nyman	Sab	Caryophyllaceae	**−0.38**	**−0.65**	**−0.02**	13.7 ± 0.9
Silene nutans L. subsp. *nutans**	Snn	Caryophyllaceae	0.17	−0.07	0.39	25.8 ± 2.1
Vaccinium myrtillus L.	Vm	Ericaceae	0.12	−0.08	0.32	8.1 ± 0.7
Vaccinium uliginosum L. subsp. *microphyllum* Lange	Vum	Ericaceae	0.03	−0.20	0.26	23.4 ± 1.2
Vaccinium vitis-idaea L. subsp. *vitis-idaea*	Vvv	Ericaceae	−0.25	−0.52	0.07	31.5 ± 2.2

Species codes are the first letters of genus, species, and subspecies (if applicable). In bold, Cliff 'Delta' index values and their respective confidence intervals for significant species trends. Species marked with an asterisk were tested using a reduced sample size due to limited seed availability

minimum of 42 days, or until there were 14 consecutive days without germination, as suggested by Newton et al. 2014). Seeds were considered germinated when the radicle reached approximately 2 mm in length. At the conclusion of the germination test, a cut test was performed on non-germinated seeds to determine if the seed was empty. Non-germinated full seeds were assumed to have died during the ageing treatment, while empty seeds were excluded from the subsequent analyses.

Data analysis

Population dynamics

Species-specific changes in abundance and occurrence from 2001 to 2022 were quantified using the Cliff 'Delta' effect size index (Cohen 1988; Cliff 1996), providing an updated extension of the dataset analyzed by Lodetti et al. (2024), which encompassed data up until 2015. This index integrates both abundance and frequency data, providing a comprehensive measure of the magnitude and direction of species temporal changes. It also includes a confidence interval, allowing the statistical significance of these changes to be evaluated (Lodetti et al. 2024). Cliff 'Delta' values range from −1 to +1, with significantly positive values indicating increasing species, significantly negative values indicating decreasing species, and non-significant values representing stable species. We adopted this method because it jointly captures shifts in species abundance and occurrence while reducing sensitivity to sampling bias and extreme values, thus providing a robust and ecologically meaningful estimate of long-term population trajectories in alpine plant communities.

Seed longevity

Seed longevity was assessed by estimating the time required for seed viability to decline to 50% (p_{50}), which is used as a proxy for seed longevity (Probert et al. 2009; Mondoni et al. 2011; Merritt et al. 2014; White et al. 2023). Germination data were analyzed using probit analysis to estimate the p_{50} value of each species, as well as the intercept (K_i), and the slope ($1/\sigma$) of the seed survival curve. These estimates are based on the viability equation by Ellis and Roberts (1980):

$$v = K_i - (1/\sigma)\, p \quad (1)$$

where represents viability in probits after days in experimental storage. These parameters were then used to create seed survival curves. Probit analysis was performed using Genstat for Windows 20th edition (VSN International Ltd. 2019), and graphs were created in Origin Pro (v 2025).

Seed longevity–population dynamic relationship

To evaluate the potential correlation between species abundance changes over the last 21 years (Cliff 'Delta' Index) and their seed longevity (p_{50}), we employed a linear modeling approach. Specifically, we constructed a model using the Cliff 'Delta' Index as the dependent variable and the log-transformed p_{50} values as the independent variable, to improve normality of the residuals. The analysis was conducted in the R statistical environment version 4.3.1 (R Core Team 2023) using the *lme4* package (Bates et al. 2015) for model fitting. Model assumptions were assessed using the *DHARMa* package (Hartig 2024), and visualizations were created with the *ggplot2* package (Wickham 2016).

Results

Species selection resulted in a pool of 24 species (see Table 1), all occurring at the study sites throughout the entire monitoring period. The Cliff 'Delta' index values for the selected species ranged from −0.47 (*Campanula scheuchzeri* Vill.) to +0.46 (*Lilium martagon* L.). According to index confidence intervals, 16.7% of the species (4) were classified as increasing, 62.5% (15) as stable, and 20.8% (5) as decreasing.

Seed viability decreased over the duration of experimental ageing across all species (Fig. 2). However, there was significant variation among species in their p_{50} values (Table 1), with the shortest-lived seeds from *Phyteuma orbiculare* L. and *Campanula scheuzcheri* Vill. (p_{50} of 1.7 days), and the longest lived from *Dianthus deltoides* L. subsp. *deltoides* (p_{50} of 43.0 days). Across the full dataset, the mean p_{50} was 14.2 days, but this value differed among species groups: decreasing species showed a mean p_{50} of 5.5 days, stable species 15.7 days, and increasing species 19.6 days. This pattern suggests that species exhibiting population decline tend to have shorter seed longevity compared to stable or increasing species.

We found a significant positive relationship between seed longevity ($\log(p_{50})$) and species-specific abundance changes over time (Cliff 'Delta' index) (linear model: estimate = 0.133, SE = 0.060, t = 2.22, $p = 0.037$, $R^2 = 0.18$. Figure 3), with species decreasing in abundance having shorter-lived seeds.

Discussion

The analysis of population dynamics using the Cliff 'Delta' index indicates that most species in the study subset remained stable over the observation period, with 62.5%

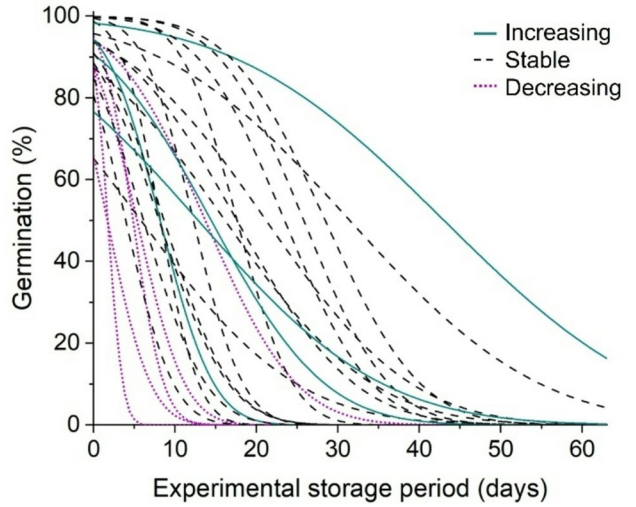


Fig. 2 Survival curves for all tested species, fitted using probit analysis (Eq. 1). Cyan solid lines represent increasing species, magenta dotted lines indicate decreasing species, and black dashed lines correspond to species with stable dynamics

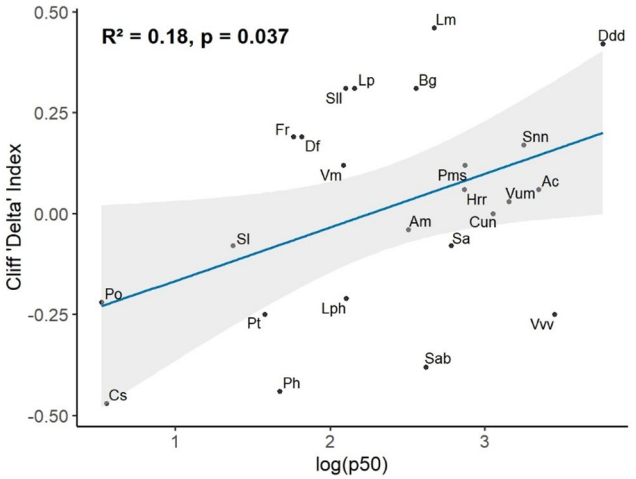


Fig. 3 Linear regression comparing seed longevity (log(p_{50})) and the species-specific abundance change (Cliff 'Delta' Index). Each point represents a species, labeled with its species code (first letters of genus, species, and subspecies, if applicable; see Table 1). The blue line indicates the fitted linear model, with the grey shaded area representing the 95% confidence interval

showing no significant changes. This pattern is consistent with previous observations over shorter time spans (Lodetti et al. 2024; Varricchione et al. 2022).

Probit analysis revealed considerable variation in p_{50} values among species (1.7–43 days). Although the limited number of representative species per most families precluded formal statistical testing of family effect, raw observations suggest that species within the same family can exhibit both low and high p_{50} values, as well as different population dynamics. The only exception is the Campanulaceae family (three species tested), which showed both low p_{50} values and significant decreasing trends (see Table 1).

We found that species-specific changes in occurrence and abundance over time, as measured by the Cliff 'Delta' index, were positively correlated with seed longevity (p_{50}). This supports our hypothesis that species decreasing in abundance tend to have shorter-lived seeds compared to those increasing. This finding highlights the potential role of seed longevity in shaping alpine plant communities under a warming climate and aligns with recent studies highlighting the importance of seeds in alpine plant populations' persistence (Rosbakh et al. 2025). Longer-lived seeds can contribute to the formation of a persistent soil seed bank (Long et al. 2008; Saatkamp et al. 2014), which is crucial for ensuring population persistence in the harsh conditions of alpine environments (Thompson and Grime 1979; Walck et al. 2005; Fenner and Thompson 2005). Existing research on the correlation between persistence in the natural soil seed bank and seed longevity estimated through accelerated ageing experiments is limited (e.g. Long et al. 2008; Guzzon et al. 2018) and remains subject to debate. As the p_{50} metric is laboratory-derived, it may not accurately capture the complexity of natural systems. Nevertheless, our study supports the possibility of a positive correlation between soil seed bank persistence and p_{50} suggesting that the latter could serve as a meaningful ecological indicator.

Our results suggest that p_{50} could be considered a promising trait for climate change research, improving predictions of how alpine ecosystems will respond to environmental change. For example, Satyanti et al. (2018) found that, among 57 alpine and subalpine Australian species, seven (12.3%) had a p_{50} value equal to or below 5.5 days, the average value observed for declining species in this study. Similarly, the seeds of 5% of the alpine species tested by Mondoni et al. (2011), exhibited p_{50} values below this threshold, which may indicate a potential risk of local extinction for such species. Nevertheless, it is important to note that alpine species also rely on alternative persistence strategies, such as clonal reproduction, to cope with adverse climate conditions (Körner 2003). Additionally, seed longevity is an adaptive trait, with plasticity observed over both short (Bernareggi et al. 2015; Kochanek et al. 2011) and long timescales (White et al. 2023). Alpine plants grown under warmer and drier conditions tend to produce longer-lived seeds (Mondoni et al. 2014; Bernareggi et al. 2015; Satyanti et al. 2018; White et al. 2023), suggesting that seed longevity could increase with climate change, partially compensating for this extirpation risk. However, the rate at which seed longevity can adapt to changing environmental conditions remains unclear, making it difficult to predict whether these adaptive responses will occur quickly enough to keep pace with the ongoing climate changes. The patterns observed in

alpine species could be evaluated more comprehensively and broadly through the development of comparable methodologies for other ecosystems that are particularly vulnerable to climate change, such as Arctic (Rantanen et al. 2022) or Mediterranean regions (MedECC 2020).

We have shown that, for seeds stored under identical artificial ageing conditions (60% RH, 45 °C), there is a significant variation in seed longevity amongst species from the same alpine habitat. Probert et al. (2009) estimated p_{50} values for seed lots from 195 taxonomically diverse species collected globally, with results ranging from 0.1 to 771 days, while Mondoni et al. (2011) found a variation between 4.7 and 95.4 days in 69 species from alpine and lowland sites. In comparison with these broader datasets, all the seed lots tested in this study were either short-lived (45.8% of species) or had medium longevity (54.2%). This classification is based on a logarithmic scale, where species are categorized as follows: very short ($p_{50} \leq 1$ day), short ($p_{50} > 1$ to ≤ 10 days), medium ($p_{50} > 10$ to ≤ 100 days), long ($p_{50} > 100$ to ≤ 1000 days), and very long ($p_{50} > 1000$ days) (Mondoni et al. 2011). The significant differences in seed longevity found here suggest that different species are also likely to have varying longevities under *ex situ* seed bank storage. The Global Strategy for Plant Conservation states that at least 75% of threatened plant species should be stored outside their natural habitat (Convention on Biological Diversity 2012). According to our results, short-lived seeds are a common characteristic of declining alpine species, which raises significant concerns for the *ex situ* conservation of those most threatened by climate change. Given their short-lived nature, regular recollection from natural populations is essential to maintain viable *ex situ* collections. This need is further supported by recent evidence showing that newly collected seed lots may exhibit improved tolerance to current climatic conditions compared to older accessions, suggesting short-term adaptive responses to ongoing environmental change (e.g. White et al. 2025). This highlights the importance of rethinking recollection and regeneration strategies for alpine species, one of the groups most sensitive to climate warming (Körner 2003).

Conclusion

Our findings highlight the potential role of seed longevity as a functional trait linked to plant population dynamics under climate change. By analyzing 24 alpine and subalpine species with contrasting abundance trends over a 21-year period, we observed a positive relationship between seed longevity (measured as p_{50}) and increasing species abundance and occurrence (measured as Cliff 'Delta' Index). Species producing shorter-lived seeds appeared to be more affected by climate change, being less capable of maintaining their presence in a warmer environment. These results underscore the importance of considering regenerative traits, such as seed longevity, alongside vegetative traits, to better understand and predict alpine plant responses to climate change. As climate change continues to alter the structure and composition of alpine and subalpine communities, integrating seed traits into trait-based ecological approaches can enhance vulnerability assessments and conservation planning. In particular, our results emphasize the need to safeguard species with short-lived seeds, which may be more prone to decline in rapidly changing environments, and to prioritize long-term seed storage for those at high risk. This study contributes to a growing body of evidence that seed longevity is a key, yet underappreciated, trait in shaping species resilience to environmental change.

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Author contributions MT, FP, and AM conceived and designed the study. Material preparation and data collection were performed by MT, VM, FP and AP. Data analysis was performed by MT, SR, and SL. GR obtained funding. The first draft of the manuscript was written by MT, FJW, and AM, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare no competing interests.

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