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RESEARCH PAPER

Differential effects of increasing temperature on the germination of five wild species with varying range sizes in a Carrara marble quarry

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Abstract

Assessing the performance of spontaneous plants in abandoned quarries under future environmental scenarios is important for successful restoration practises. Air warming is one of the most relevant ongoing climatic changes in the Mediterranean. We tested the effects of increasing temperature on the germination of five species spontaneously colonising the abandoned sectors of a Carrara marble quarry (Tuscany, central Italy). We selected five plant species with different widths of their distribution range, from local endemic to invasive alien: *Santolina pinnata, Globularia incanescens, Hypericum coris, Helichrysum italicum,* and *Buddleja davidii*. Seeds were collected in situ and their germination was tested in laboratory conditions at 10, 15, 20, 25, and 30 °C. The effects of temperature and species on germination percentage (GP) and mean germination time (MGT) were tested through two-way ANOVA. Increasing temperatures negatively affected the GP of *S. pinnata* and *H. coris*. *G. incanescens* performed better at intermediate temperatures, whilst *H. italicum* benefited from increasing temperatures. *B. davidii* showed a similar high GP under all the treatments. MGT decreased with increasing temperature for all the species, except for *S. pinnata*, which showed an increase of MGT with increasing temperature. We highlighted that, under future warmer climatic conditions, the two endemic species will be disadvantaged with respect to the species with a wider distribution range and the non-native species in the studied quarry. This evidence is relevant for restoration planning since seeding the two endemic species could be unsuccessful under future environmental scenarios, when *H. italicum* and *B. davidii* will be more competitive in the colonisation of the quarry.

Keywords Biodiversity · Global change · Non-native plant · Threatened species · Seed

1 Introduction

Quarries are harsh environments for plant life, hosting extreme ecosystems where human support for spontaneous vegetation succession may be needed (Khater et al. 2003). In fact, despite natural recolonisation may sometimes be more effective (Martínez-Ruiz et al. 2007), the difficult environmental conditions of quarries can hamper the re-establishment of pre-existing vegetation types (Pitz et al. 2019). In this context, ecological restoration is the practise of assisting the recovery of an ecosystem trying to replicate its original fauna and flora, until flows of natural goods and the provision of cultural values are restored (Lima et al. 2016). Selecting plant species for restoration needs to take into account the biology and ecology of each taxon, to assess their suitability (Bonari et al. 2021). Thus, planting species that spontaneously colonise abandoned quarries may be a good option to accelerate soil stabilisation and vegetation dynamics (Porqueddu et al. 2016; Fois et al. 2023), e.g. through hydroseeding (Oliveira et al. 2012). To guarantee the successfulness of restoration interventions, using native seed material from reference sites is more effective than

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introducing native plants from non-local populations (Bischoff et al. 2006; Gann et al. 2019).

Climate change in the Mediterranean basin is having relevant impacts on biodiversity, particularly in mountain ecosystems (Giorgi 2006; Ballester et al. 2010). Such areas are amongst the most sensitive to species loss and turnover (Thuiller et al. 2005). This is due to rising temperatures, lower precipitation especially in spring and summer, and an increasing frequency of extreme events (Giménez-Benavides et al. 2018). Such extremization of climatic patterns can thwart the beneficial effects of restoration practises in Mediterranean mountain ecosystems and in other ecosystem types (Maccherini et al. 2018; Zabin et al. 2022). Thus, understanding the biological and ecological performance of the species used for restoration under future climatic conditions is essential to plan correct and successful interventions (Harris et al. 2006).

Mediterranean mountains are often biodiversity hotspots that harbour notable levels of taxonomic richness and uniqueness (Stanisci et al. 2016). They can be rich in endemic species and offer refugia for populations of northern plants being at the southern limit of their distribution range (Stanisci et al. 2011; Gentili et al. 2015). At such latitudes, the latter are particularly threatened by current climate warming since they only survive in refuge sites at higher elevations (Medail and Diadema 2009; Abeli et al. 2014). The upper belts of Mediterranean mountains are hotspots of plant endemicity and conservation value (Di Musciano et al. 2021). In degraded sites of Mediterranean mountains, such as quarries, restoration procedures may be highly needed for native plant diversity and ecosystems to recover after human exploitation. In this context, understanding the specific germination requirements of native plants can provide valuable information for their successful propagation and use for restoration practises (Acharya 1989; Fenu et al. 2020), besides guaranteeing the effectiveness of in situ and ex situ conservation of threatened species (Bacchetta et al. 2008; Cursach and Rita 2012).

Like many sites being severely modified by human activities, quarries offer an ideal environment for the spread of invasive alien plants (Alston and Richardson 2006). Once established, such species can permanently alter original ecosystems by outcompeting native plants (Prach et al. 2016). In European limestone quarries, species like *Buddleja davidii* and *Senecio inaequidens* are amongst the most common and abundant non-native plants (Pitz et al. 2019). Such species are effective pioneers that can modify ecological succession and ecosystem properties, though not necessarily with negative impacts (Bellingham et al. 2005; Van De Walle et al. 2022). However, in areas characterised by high levels of endemism, the invasion by alien species can be a major threat to the survival of endemic species (Pyšek et al. 2017). In this context, understanding the different responses of native and non-native species to environmental conditions is of crucial importance to plan an effective ecosystem restoration, which favours native plants over non-native ones (Pitz et al. 2019).

Seeds are essential for plant-based ecological restoration (Pedrini et al. 2020). For instance, sowing seed material from local populations of native species boosts ecological succession in quarries, improving the effectiveness of restoration practises in such harsh environments (Ballesteros et al. 2012; Figueiredo et al. 2021). In areas that are predicted to experience relevant climatic changes, testing the performance of native species under future conditions appears necessary to guarantee the successfulness of restoration interventions (Lewandrowski et al. 2021). Species with a restricted distribution range may have a lot of differences in their biological features with respect to species with wider distribution ranges (Kunin and Gaston 1997). In particular, previous studies showed that species with a narrower distribution range have a worse germination performance under increasing temperatures than widely distributed species (Luna et al. 2012). Moreover, non-native, invasive species are known to germinate earlier, faster, and more abundantly in their introduction than in their original distribution range (Gioria and Pyšek 2017), and to show quicker and more successful germination than native species (Chrobock et al. 2011). The spontaneous invasion by non-native plants could thus hamper the establishment of native species introduced for restoration. To contrast this process, a good option is to sow high densities of competitive native species (Csákvári et al. 2023).

In quarries, natural vegetation succession after the ceasing of extraction activities can be very slow, so that restoration may be needed (Porqueddu et al. 2016; Pitz et al. 2019; Fois et al. 2023). In this context, a preliminary assessment of the germination performance of the plant species selected for restoration could be important, especially under future climatic conditions (Gentili et al. 2011; Bhatt et al. 2023). Thus, in this work, we collected local plant material of five species with different widths of their distribution range from the abandoned sectors of an active Carrara marble quarry. Despite their undeniable cultural and economic value, quarries from the area represent one of the biggest extraction complexes on Earth, and became a symbol of the huge environmental impacts of human activities in the Anthropocene (Quagliati 2022). We carried out germination tests at increasing temperatures to assess the response of differently distributed native species and on the invasive alien *B. davidii* to climate warming. Based on previous evidence from other study areas (Luna et al. 2012), we hypothesised that narrowly distributed species are more sensitive to warming than widely distributed and invasive alien species.

2 Methods

2.1 Study area

We studied a Carrara marble quarry located on the southwestern slope of the Apuan Alps, in northwestern Tuscany (central Italy). The Apuan Alps are a mountain chain running from NW to SE parallel to the Tyrrhenian coastline, from which they are separated by a narrow coastal plain. They extend over an area of about 650 km^2 and include some of the highest peaks in the region, culminating at 1,946 m a.s.l. with Mount Pisanino (Di Musciano et al. 2021). These mountains are a hotspot of plant diversity, hosting over 2,000 native plant species, which represent about 25% of the Italian native flora (Bartolucci et al. 2018; Carta et al. 2018, 2019). Many of such species are of conservation interest, including 104 taxa being threatened at different levels, 30% of which are endemic (Vaira et al. 2004). Due to its high natural value, the mountain chain has been protected by a regional park since 1985 (EUAP code EUAP0229, IUCN category VI, WDPA code 14636—Tuscany Region 1985). Quarrying for marble extraction is one of the main economic activities of the area, carried out since ancient Roman times (Fig. 1).

Across centuries, massive marble quarrying had a deep impact on the landscape and biodiversity of the Apuan Alps, favouring the spread of alien/ruderal species like *B. davidii* at the expense of endemic plants (Gentili et al. 2011). In particular, it produced huge amounts of gravel wastes that are locally known as "ravaneti" (Fig. 2). Such landforms are so widespread in the area that they became a characterising element of the Apuan landscape (Bruschi et al. 2004).

The bioclimate is classified as temperate sub-Mediterranean at low elevations and as temperate at higher elevations. Such climatic types are characterised by mild or absent aridity during summer. Thermotypes range from lower mesotemperate to lower orotemperate, and ombrotypes vary from lower humid to ultrahyperhumid (Pesaresi et al. 2017). The Apuan Alps are one of the rainiest areas in the

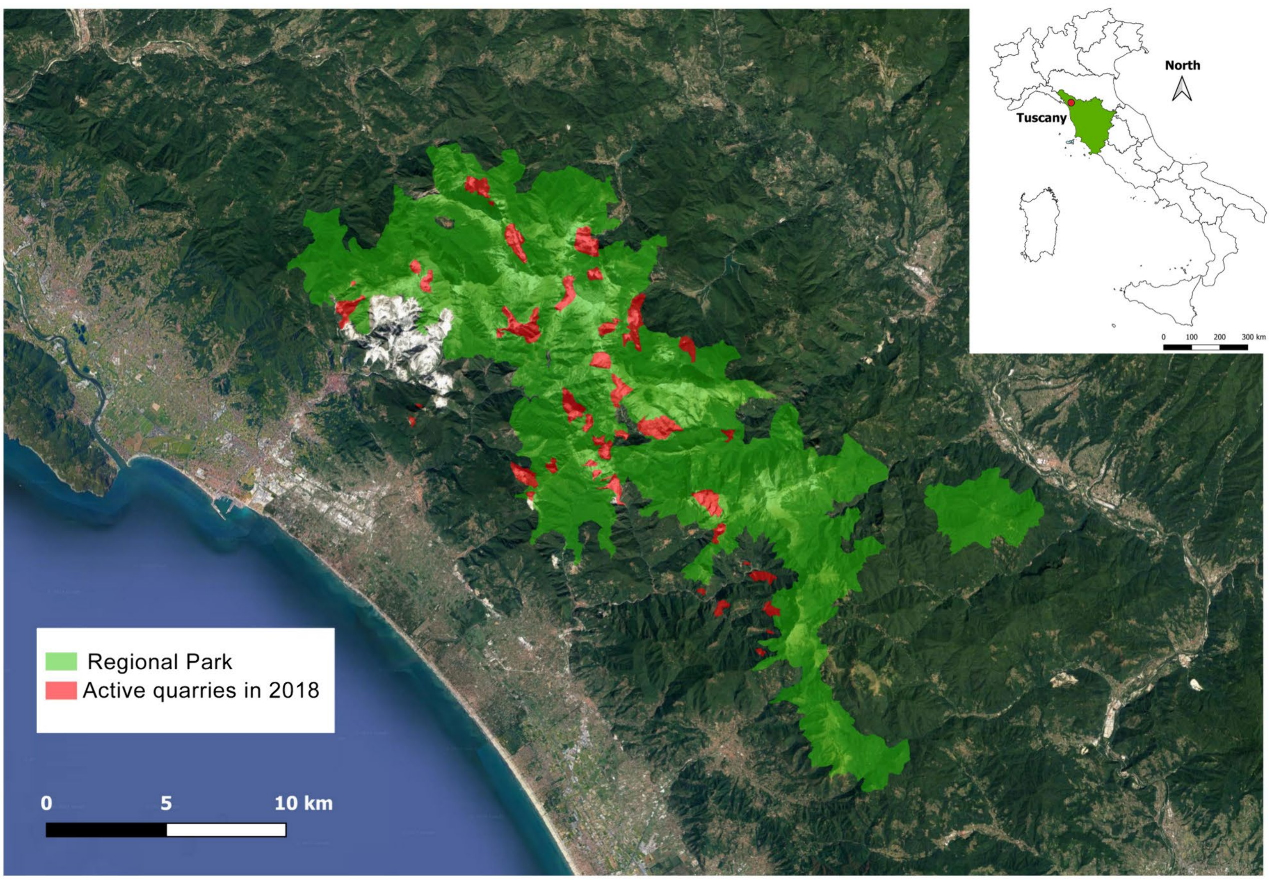

Fig. 1 Territory of the Apuan Alps and (upper right) its location in Tuscany (red dot) and Italy. The area under protection by the regional park is highlighted in green; active quarries in 2018 are highlighted in red (Parco Regionale delle Alpi Apuane 2019). Satellite image from Google (2024)

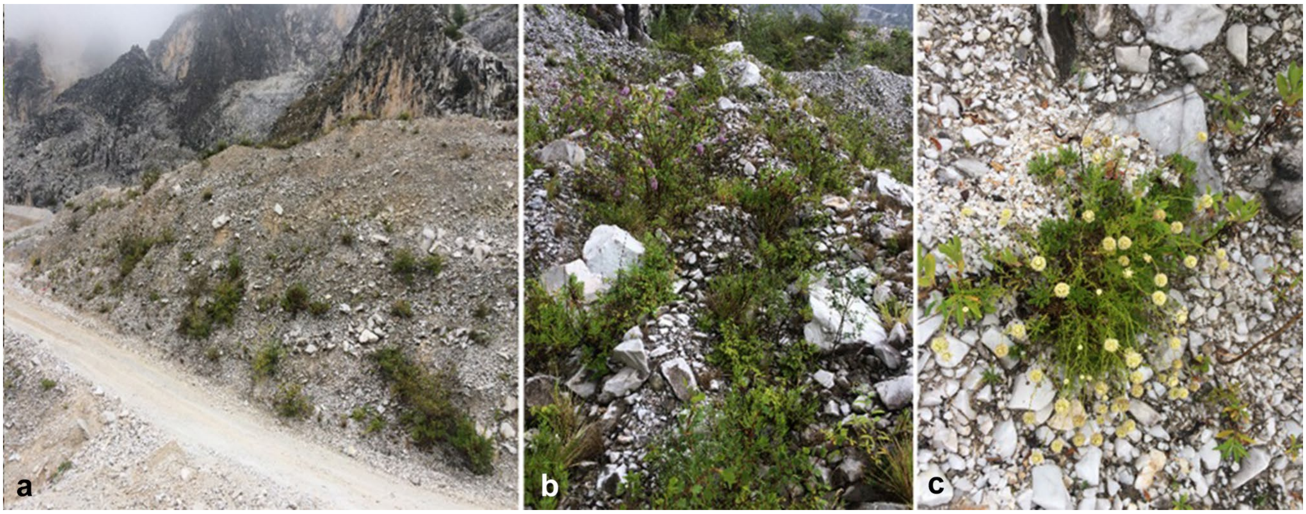

Fig. 2 **a**, **b** Inactive sectors of the studied marble quarry with spontaneous vegetation colonising "ravaneti" wastes; **c** individuals of the Apuan endemic *Santolina pinnata* growing on marble wastes

Italian Peninsula and the whole Mediterranean basin, with mean annual precipitation of up to 2500 mm/year (Doveri et al. 2019). The peak of precipitation is in autumn, whilst summer is the driest season (Bartolini et al. 2018). A warming trend of about 0.1–0.2 °C per decade was detected in the area, and temperatures are predicted to further rise of 1–1.3 °C by 2060 (Bartolini et al. 2008; D'Oria et al. 2017), in line with the general warming trend observed in the Mediterranean basin (Brunetti et al. 2006). In the Apuan Alps, climate warming is particularly threatening endemic flora, since the distribution of most endemic species is limited to higher elevations (Tomaselli and Agostini 1994; Di Musciano et al. 2021).

2.2 Study species

As a preliminary investigation, local plant communities were surveyed in the quarry through 21 square plots of 4 m^2 (total surface of the quarry: 223,043 m^2). In each plot, we recorded species presence and abundance, the latter expressed using the Braun-Blanquet scale (Braun-Blanquet 1964—Table S1). We selected five species amongst those spontaneously growing in the quarry and colonisers of "ravaneti" in the area. The selection was made based on the width of species' distribution range, from narrow endemic to invasive alien. Native species were amongst the ones suggested to be sown for the ecological restoration of Carrara marble quarries (Gentili et al. 2011). *B. davidii* was selected as one of the most abundant invasive alien species in the quarries of the Apuan Alps, as well as in many limestone quarries worldwide (Gentili et al. 2011; Thompson and Abbott 2013; Pitz et al. 2019). We selected the following five species (nomenclature according to the Portal to the flora of Italy v.2023.1—Portal to the flora of Italy 2023):

1. *Santolina pinnata* Viv. (Asteraceae); it is endemic to the Apuan Alps (Pignatti et al. 2017–2019; Giacò et al. 2022). It is a nanophanerophyte, flowering from May to August (Pignatti et al. 2017–2019). It grows on cliffs and sunny rocks on calcareous substrates, at elevations between 500 and 1500 m a.s.l. (Barbero and Bono 1973; Ferrarini 1973; Varaldo et al. 2021). The dispersal unit is a trigone cypsela without pappus (Acta Plantarum 2007). Climate warming is considered a major threat to the conservation of this species, which is predicted to lose much of the extent of its suitable habitat (Varaldo et al. 2021).
2. *Globularia incanescens* Viv. (Plantaginaceae) is an Italian endemic, with a range limited to the Apuan Alps, the Tuscan-Emilian Apennines, and the eastern Ligurian coast (Ferrarini et al. 1997; Baldini et al. 2010; Ansaldi and Bedini 2013). It is considered a paleoendemic species given its systematic and ecological isolation and due to its low dispersal ability (Corsi and Garbari 1971). It is a scapose hemicryptophyte, flowering between May and June (Pignatti et al. 2017–2019). It mainly grows on southern cliffs and slopes, on limestone, marble, schist, and sandstone, from 0 to 1600 m a.s.l. (Alessandrini et al. 2003; Di Fazio et al. 2004). The dispersal unit is a diclesium containing an ellipsoid achene about 1–1.3 mm long, enclosed in a hairy calyx (Acta Plantarum 2007).
3. *Hypericum coris* L. (Hypericaceae) is a Southern-European orophyte distributed from eastern France to Tuscany, with populations also occurring in Switzerland and

Austria (Marhold 2011; GBIF 2022). It is a suffruticose chamaephyte, flowering from May to July (Pignatti et al. 2017–2019). It grows on cliffs and sunny rocks, on calcareous substrates, from 0 to 2000 m a.s.l. (Pignatti et al. 2017–2019). The dispersal unit is a septicidal capsule with numerous cylindrical seeds, about 1.5–2 mm long (Acta Plantarum 2007).

4. *Helichrysum italicum* (Roth) G.Don (Asteraceae) is a southern European species. It is a suffruticose chamaephyte, flowering from May to September (Pignatti et al. 2017–2019). It grows in garrigues and dry grasslands on rocky and poorly developed soils, from 0 to 1400 m a.s.l. (Acta Plantarum 2007; Pignatti et al. 2017–2019). The dispersal unit is a cypsela with a 0.6–1.2 mm long achene and a pappus made of 3 mm long hairs (Acta Plantarum 2007; Pignatti et al. 2017–2019).
5. *Buddleja davidii* Franch. (Scrophulariaceae) is a phanerophyte native to central and south-western China, where it grows on mountain slopes between 800 and 3000 m a.s.l. (Zheng-yi and Raven 1996; Ebeling et al. 2008). It flowers from June to September (Pignatti et al. 2017–2019). Outside its native range, it grows in cliffs, wastelands, floodplains, rivers and lake banks, forest clearings, and railway embankments, from 0 to over 1300 m a.s.l. It is able to grow on all soils, preferring calcareous substrates. The dispersal unit is a bilocular septicidal capsule with numerous 3.5–4.5 × 0.2–0.3 mm long, obovoid seeds prolonged at the base and apex into a membranous wing (Acta Plantarum 2007). *B. davidii* is quickly spreading in many countries outside its native range (Tallent-Halsell and Watt 2009; Kriticos et al. 2011). The abundant production of very small, wind-dispersed diaspores makes this pioneer species highly invasive in different habitats in the study area (Gasperini et al. 2020).

2.3 Germination experiment

The diaspores of the selected species were collected in the studied quarry, at elevations between approximately 500 and 600 m a.s.l. Seeds or fruits were collected from the plant populations present in the mid part of the quarry between early summer and late autumn 2020, depending on each species' phenology.

Germination tests of the five species were carried out at the Tuscia Germplasm Bank (Tuscia University, Viterbo, Italy). Seeds were surface sterilised for 5 min in a solution of sodium hypochlorite with 5% available chlorine, supplemented with a drop of Tween 20 to improve the efficiency of sterilisation. They were then rinsed three times with sterile distilled water for 3 min. For each species, five replicates of 20 seeds for each temperature were sown on the surface of 1% water agar as a solid, sterile medium for germination, in 90 mm plastic Petri dishes. Seeds of each species were incubated in five refrigerated incubators with a 12/12 h photoperiod, at five constant temperatures (10, 15, 20, 25, and 30 °C). Germination was defined as visible radicle emergence and scored every day under a stereomicroscope (Nikon SMZ1000). Experiments lasted for a maximum of 30 days, at which time no further germination was observed. At the end of the germination tests, a cut test was carried out to determine the viability of the remaining seeds (soft or firm).

2.4 Calculation of germination parameters and statistical analysis

Per each Petri dish, we calculated the final germination percentage (GP) as the percentage of germinated seeds over the total number of firm seeds at the end of the experiment. The mean of the five replicates ± standard deviation was calculated for each temperature. Moreover, we calculated mean germination time (MGT) according to the following formula (1):

$$\mathrm{MGT} = \sum (n \times d) / N \qquad (1)$$

where: n = the number of seeds that germinated on each day; d = the number of days from the beginning of the experiment; N = the total number of seeds that germinated at the end of the experiment (Ellis and Roberts 1981).

Since some response variables had a non-normal distribution (Shapiro test; *shapiro.test* function in the package *stats*—R Core Team 2023), we log ($x + 1$) transformed GP data and square-root transformed MGT data before the analyses, to improve normality. Nevertheless, in the results, original values are shown. The responses of GP and MGT to the factors "temperature", "species", and their interaction were tested through two-way ANOVAs, using the function *aov* in the package *stats*. When the interaction temperature × species showed a statistically significant effect of the predictive variables, we carried out pairwise post-hoc Tukey tests using the function *TukeyHSD* in the package *stats*. We set α at 0.05. All the analyses were performed in R version 4.3.2 (R Core Team 2023).

3 Results

The factors "temperature", "species", and their interaction significantly affected both GP and MGT (Tab. 1).

Temperature affected the GP of all the studied species, except for *B. davidii*, which showed high mean GP (90–98%) at all the tested temperatures (Fig. 3). In *S. pinnata*, GP gradually increased from 54% at 10 °C to 64% at 20 °C, and decreased at higher temperatures, down to 6% at 30 °C. In

Table 1 Results of two-way ANOVA showing the effect of temperature on the germination percentage (GP) and mean germination time (MGT) of the five selected species

Source of variation	GP				MGT		
	Df	SS	MS	*F*	SS	MS	*F*
Temperature	4	3.94	0.99	17.44***	1645.40	413.60	26.65***
Species	4	17.04	4.26	75.39***	914.50	228.60	14.73***
Temperature × species	16	8.59	0.54	9.51***	1667.10	104.20	6.71***
Residuals	100	5.65	0.06		1551.70	15.50	

***$p < 0.001$

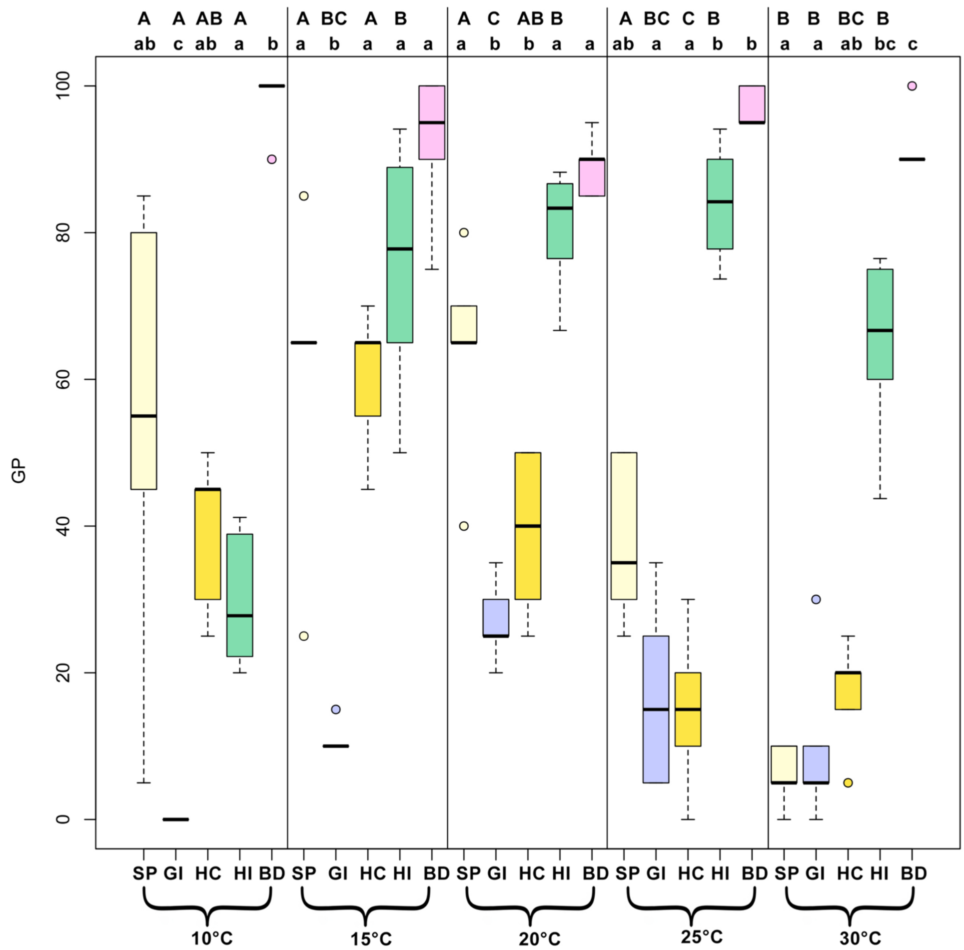

Fig. 3 Boxplots showing the germination percentage (GP) of the seeds of the studied species under different temperature treatments. SP, *Santolina pinnata*; GI, *Globularia incanescens*; HC, *Hypericum coris*; HI, *Helichrysum italicum*; BD, *Buddleja davidii*. Different letters indicate statistically significant differences at $p < 0.05$. Capital letters indicate statistically significant differences in GP of the same species at different temperatures. Lowercase letters indicate statistically significant differences in GP between different species at the same temperature

G. incanescens, GP had a maximum at 20 °C, though with a low value (27%), lower values (10–17%) for the other temperatures, and no germination at 10 °C. In *H. coris*, there was a peak of GP with 60% at 15 °C, and then a decrease to 15–17% at increasing temperatures (25–30 °C). In *H. italicum*, GP increased from a minimum of 26% at 10 °C to 64–68% at 15–20 °C, with a maximum of 78% at 25 °C. At 30 °C, *S. pinnata* and *G. incanescens* had the lowest mean GP (6% and 10%, respectively).

MGT was affected by temperature in all the studied species. Namely, MGT decreased with increasing temperature for all the species except *S. pinnata*, for which it increased with increasing temperature. The quicker and slowest germination, respectively, were at 15 °C and 30 °C for *S. pinnata,* at 30 °C and 10 °C for *G. incanescens* and *H. coris*, and at 10 °C and 25 °C for *H. italicum* and *B. davidii*. *Santolina pinnata* was the best performing species at 10 °C, where *Globularia incanescens* was the worst performing one. Conversely, at 30 °C, *Globularia incanescens* was the best performing species and *Santolina pinnata* was the worst performing one (Fig. 4).

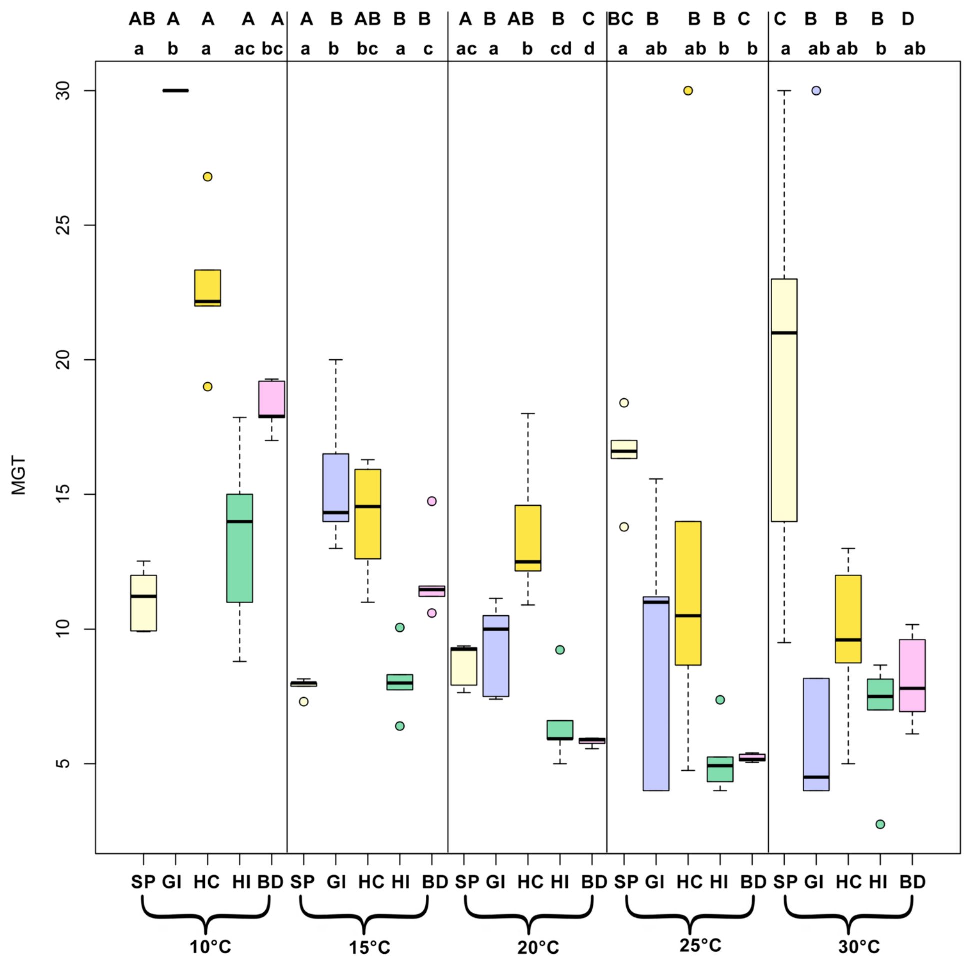

Fig. 4 Boxplots showing the mean germination time (MGT, expressed in days) of the seeds of the studied species under different temperature treatments. SP, *Santolina pinnata*; GI, *Globularia incanescens*; HC, *Hypericum coris*; HI, *Helichrysum italicum*; BD, *Buddleja davidii*. Different letters indicate statistically significant differences at $p < 0.05$. Capital letters indicate statistically significant differences in MGT of the same species at different temperatures. Lowercase letters indicate statistically significant differences in MGT between different species at the same temperature

4 Discussion

Our study highlighted differential responses in GP and MGT of the studied species to the temperature treatments, confirming our hypothesis that narrowly distributed species are more sensitive to warming. Species with a narrower distribution range, and especially the local endemic *S. pinnata*, were the most negatively affected by increasing temperature. Conversely, the non-native invasive species *B. davidii* was the only one not to be affected by the treatment as regards GP, benefited from increasing temperatures in terms of MGT, and showed the highest GP at all temperatures. Such findings highlight that, under future climatic conditions characterised by higher temperatures, *B. davidii* could be favoured over native species either in the spontaneous revegetation of the studied quarry or after restoration practises. Consistently, the selected species have different temperature requirements, with the two endemics being the most adapted to cool conditions and *H. italicum* and *B. davidii* being the most adapted to warm conditions (FloraVeg.EU 2024). Successful restoration planning of the quarry should consider such issues when selecting the plant species to be sown since the use of *S. pinnata, G. incanescens,* and *H. coris* might be less successful in a warmer climate scenario.

Our findings are supported by previous evidence. In terms of GP, narrowly distributed species, and especially endemic ones, are known to be more sensitive to climate warming than species with a wide distribution range (Luna et al. 2012). *S. pinnata* is predicted to lose a relevant extent of its habitat under warmer conditions in the Apuan Alps, due to its sensitivity to temperature increase (Varaldo et al. 2021). The other species showed intermediate responses. The northern Apennine endemic *G. incanescens* benefited from increasing temperatures up to 20 °C as regards GP. However, higher temperatures inhibited its germination. By contrast, its MGT was reduced by increasing temperature. Previous evidence suggests that the extent of the distribution range of *G. incanescens* is being negatively affected by climate warming, consistent with our results (Casazza et al. 2014). Besides, *G. incanescens* showed the lowest germination rates, with a maximum of 27%. Although no germination data are available for this species, similarly low germination values were observed for other *Globularia* species, like *G. punctata* and *G. alypum* (Bertsouklis and

Papafotiou 2010; Brînză et al. 2019). The orophyte *H. coris* showed reduced germination at temperatures higher than 15 °C, consistent with the species' preference for mountain ecosystems (Pignatti et al. 2017–2019). However, germination speed benefited from warmer conditions, with a reduction of MGT. *H. italicum* was overall positively affected by increasing temperature. This species has a high ecological plasticity, which allows it to adapt to a wide range of temperatures across its distribution range (Ninčević et al. 2021). The non-native species *B. davidii* showed the best performance with increasing temperatures. *B. davidii* is known to be more vigorous in its introduction than in its native range, though not relative to germination parameters (Ebeling et al. 2008). Consistently with our results, its optimal germination temperature is around 25 °C, whilst seeds stop germinating only at 35 °C (Tallent-Halsell and Watt 2009). In particular, we observed that the species seeds germinated with high abundance at all the tested temperatures, and that higher temperatures sped up its germination. This is in line with the fact that climate warming will benefit *B. davidii* worldwide, with a predicted range expansion under warmer conditions (Kriticos et al. 2011). Moreover, the good germination performance of the species is consistent with recent evidence that showed how neophytes germinate better than native and archaeophyte species under simulated increasing temperatures (Trotta et al. 2023).

A higher sensitivity to increasing temperatures and heat-shocks of narrowly distributed species compared to widely distributed ones was previously highlighted also elsewhere (Thompson 1970; Luna et al. 2007). Endemic species were also found to be more sensitive to other environmental factors related to climate change in the Mediterranean, like increasing light (Luna and Moreno 2009). Previous studies showed that narrow endemic species of the Apuan Alps can only grow in a restricted range of ecological conditions (Vaira et al. 2010), in accordance with our findings. This may lead to an improved ability of widely distributed and non-native species to colonise new environments at the expense of endemic species (Luna et al. 2012). In our case, this would imply a better performance of *H. italicum* and *B. davidii* in the studied quarry under climate warming conditions. This calls for the need to appropriately plan restoration interventions in Carrara marble quarries, for instance using *S. pinnata, G. incanescens,* and *H. coris* only for restoration activities at higher elevations. Moreover, strategies to control the invasion by *B. davidii* should be planned. For this purpose, promoting the earlier establishment of competitive native plants could help contain the invasion by non-native species after restoration (Csákvári et al. 2023). In the case of our study site, *H. italicum* could be a suitable species to counteract the spread of *B. davidii*. In the future, it will be useful to test the effect of increasing temperature on the germination of other native pioneer species spontaneously growing in the quarry, like *Chamaenerion dodonaei* (Vill.) Schur ex Fuss, *Satureja montana* L., and *Teucrium montanum* L.

The worst germination performance of Mediterranean species at higher temperatures could be related to their higher specialisation, which leads them to germinate in the colder months. The germination of Mediterranean plants is set to avoid drought periods, which coincide with summer and the hottest months of the year (Pesaresi et al. 2017). On the contrary, widely distributed species seem less dependent on temperature. From this perspective, Mediterranean plants are well-adapted to their environment, characterised by hot and dry summers that are not a good moment to germinate due to a reduction of seedling survival (Luna et al. 2012).

With this work, we had further evidence of the importance of testing the germination performance of the plant species used for restoration under future climatic conditions to guarantee the success of interventions. Despite our findings were consistent with previous evidence and provide useful knowledge for local restoration interventions, we only assessed the germination response to increasing temperature of one species per range size. To have more generalizable results, in the future it will be useful to repeat similar tests using more species per range size. Thus, in the marble quarries of the study area, more studies are needed to better detect the most suitable species to restore the "ravaneti", other quarry sectors that are no longer used for marble extraction, or inactive quarries. Quarrying activities should be carefully planned in space and time, in order not to accelerate the invasion process by *B. davidii*, which could threaten the conservation of the endemic species *S. pinnata* and *G. incanescens* after extreme anthropogenic disturbance and climate warming.

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Author contributions EF, TF, SiM, SaM, GZ, CA conceived and designed the research; EF, IB, PC, TF, GZ, CA performed the field survey, seed collection and preparation; SaM performed the germination tests; EF, SiM analysed the data; EF wrote the manuscript; all authors reviewed and edited the manuscript.

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Availability of data and material The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability Codes will be made available on request.

Declarations

Conflicts of interest The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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