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Germination niche of the endangered dragon tree *Dracaena draco* (L.) L. subsp. *draco* of the Macaronesian Islands

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ABSTRACT

The Canary Islands dragon tree (*Dracaena draco* (L.) L. subsp. *draco*) is an endangered Tertiary relict species endemic to the Canary and Madeira archipelagos. Based on an *ex-situ* experiment under controlled conditions, we investigated its germination response to both constant and alternating temperatures, moisture levels (water potential), exposure to light, and desiccation. We found that suitable temperatures for germination (> 5 % of germinated seeds) range from 12.1 °C to 32.8 °C (thermal germination niche limits) and optimal temperatures (> 95 % of germinated seeds) range from 16.6 °C to 28.3 °C. Light exposure and water potential below 0 MPa drastically decreased germination performance while seed desiccation pre-treatments and alternating temperatures had slightly negative effects. Comparing the spatial projection of the thermal germination niche with actual occurrences of *D. draco* subsp. *draco* revealed that native populations are mainly distributed in areas where temperatures are colder than the optimum for germination. For native populations, germination rate is predicted to reach 78 % on average based on temperature requirements. Our results suggest that niche conservatism and adaptation are involved in shaping the germination requirements of the dragon tree.

1. Introduction

Plant regeneration niche, i.e., the requirements adult plants have for successful reproduction, dispersal, germination, and seedling establishment, is key to explain species persistence in their environment (Grubb, 1977; Saatkamp et al., 2019). A number of environmental conditions are needed jointly to ensure successful germination in the field, the sum of which are referred to as the germination niche (Grubb, 1977), of which temperature, moisture and light have outstanding importance (Baskin and Baskin, 2014). Environmental requirements for regeneration can significantly differ from mean environmental conditions experienced by living wild individuals and more importantly those maximizing vital rates of other life history steps (Pironon et al., 2018). Given the importance of germination for plant population dynamics (Giménez-Benavides et al., 2008; Graae et al., 2011), it is critical to analyse environmental factors for threatened plants that might limit their regeneration by seed under field conditions.

Numerous plant species are threatened by future climate warming

because they are predicted to experience temperatures exceeding suitable temperature ranges for germination (Cochrane, 2020; Sentinella et al., 2020). Moreover, future projections of species distributions based on their germination niche showed that rare and range restricted species might be even more vulnerable to climate change (Catelotti et al., 2020). Thus, a detailed knowledge of temperature and moisture conditions that determine germination niche appears essential to anticipate species response to climate change and guide relevant conservation planning.

The genus *Dracaena* Vand. ex L. (Asparagaceae) includes 195 taxa, which are mostly herbaceous or shrubby species distributed throughout the tropics (POWO, 2023). A few remarkable *Dracaena* species show an arborescent habit and adaptation to xeric environments, and are commonly called “dragon trees” (Madêra et al., 2020). The geographic distribution of this group follows a West-East split pattern across the Sahara Desert with two species in the Macaronesian Islands and Morocco, and three others in Eastern Africa, Socotra, and the Arabian Peninsula. This pattern, along with the Oligocene and Miocene fossil records of dragon trees in Southern Europe, suggests that dragon trees

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are Tertiary relict species (Marrero et al., 1998; Denk et al., 2014). Amongst them, *Dracaena draco* (L.) L. consists of three subspecies: subsp. *draco* occurring in the Canary Islands and Madeira Archipelago, subsp. *caboverdeana* Marrero Rodr. and R.S. Almeida endemic to the Cabo Verde Archipelago (Marrero and Almeida Pérez, 2012), and subsp. *ajgal* Benabid & Cuzin in the Anti-Atlas Mountains (SW Morocco) (Benabid and Cuzin, 1997). Along with *Dracaena tamaranae* Marrero Rodr., R.S. Almeida & M. González-Martín, endemic to Gran Canaria, phylogenetic evidence showed that Macaronesian dragon trees form a monophyletic group which diversified throughout the Pleistocene (Durán et al., 2020). Current wild populations of the Canary Islands dragon tree, *Dracaena draco* (L.) L. subsp. *draco*, are restricted to Tenerife with the addition of a few isolated individuals in Gran Canaria and Madeira Islands, growing on rocky slopes within the thermo-sclerophyllous vegetation belt (Almeida Pérez, 2004). Some old and isolated individuals in La Palma and La Gomera might be wild as well (Santos Guerra pers. com.). However, historical records indicate that the dragon tree geographic extent was wider in the past, mentioning its presence in Porto Santo Island and some of its satellite islets, and other places on the Southern coast of Madeira as well as other islands from the Canary Archipelago such as El Hierro, La Palma and La Gomera (Byström, 1960; Knoche, 1923; Torriani, 1959). Indeed, palaeoecological and archaeological records suggest that the original vegetation in the Canary Islands has been extensively impacted by human activities (e.g., fire, over-exploitation, clearings, introduction of herbivores) since the arrival of humans, i.e., the Guanches, c. 3000–2000 years before present, and after the phase of European colonization from the 15th century (del Arco et al., 1997; Fernandez-Palacios et al., 2008a). The Canary Islands dragon tree has been widely exploited by both the Guanches for various usages (del Arco, 1993; Vidal-Matutano et al., 2021a, 2021b), and the Europeans mainly for medicinal use (Sánchez-Pinto and Zárata, 2009–2010). Due to its rarity, i.e., less than 700 individuals in the wild, and the rarefaction and fragmentation of its habitat, *D. draco* subsp. *draco* has been stated as “Endangered” (EN) following the IUCN conservation status assessment methodology (Almeida Pérez, 2004). Moreover, it has been acknowledged that many dragon tree populations suffer from low recruitment (Madèra et al., 2020). Although gut treatment by the White-tailed Laurel-pigeon (*Columba junoniae* Hartert, 1916), a putative disperser of *D. draco*, does not increase germination rate of *D. draco* seeds, it has been shown that its zoochorous dispersal system may be partially eroded nowadays due to the decline of large fruit dispersers endemic to the Canary Islands (*Gallotia* spp., *Columba* spp.) (González-Castro et al., 2019). Thus, a detailed knowledge of its germination niche would help conservation planning (Madèra et al., 2020). Also, *ex situ* germplasm maintenance outside original habitats in seed banks constitutes an important tool for the conservation of endangered plant species. Seed storage behaviour, i.e., orthodox (desiccation tolerant) versus recalcitrant (desiccation nontolerant) (Roberts, 1973), must be known for successful preservation of seeds because only desiccation tolerant seeds can be maintained in seed banks on the long term (Hong et al., 1996). Seed lots can serve as a source for species recovery in the wild, including population reinforcement, reintroduction, or conservation introduction. Germination requirements must be known to implement efficient propagation protocols from seeds (Abeli et al., 2019).

However, very little is known on the post-dispersal abiotic germination requirements of *D. draco* subsp. *draco*, and only one study was published, testing solely the effects of pre-soaking, substrate, and light availability treatments on seed germination (Kheloufi et al., 2020). To fill this gap, we conducted series of *ex-situ* experiments under controlled conditions to describe the response of germination to gradients of constant and alternating temperatures and to a gradient of moisture, exposure to light, and to test for desiccation tolerance. Also, we aimed at identifying favourable conditions for germination throughout the native range of *D. draco* subsp. *draco* using spatial projection of the germination niche. In the light of our results, we discuss the Canary Islands dragon tree ecology and conservation and provide recommendations on

propagation protocols to ensure its conservation facing climate change.

2. Materials and methods

We performed four germination experiments to study germination response of *Dracaena draco* subsp. *draco*. To do so, we performed four *ex-situ* experiments in growth chambers with conditions set to, (i) 13 levels of constant and one level of alternating temperatures, (ii) six levels of moisture (i.e., water potential Ψ), (iii) light exposure, and (iv) seed desiccation pre-treatments. Fig. 1 summarises the experimental conditions of the treatments implemented for each experiment. Ripe fruits were collected from four individuals grown at Rayol-Canadel-sur-Mer, South Eastern France in April 2021 and April 2022. Study of González-Castro et al. (2019) showed that pulp removal enhances seed germination of *Dracaena draco* subsp. *draco* and that the seeds are non-dormant. Consequently, the pulp was removed by hand and seeds were washed using running water and no dormancy breaking was performed. A total number of 2,160 seeds were used in the experiments.

2.1. Experimental design

All experiments were carried out under controlled conditions in growth chambers using Petri dishes with 10 seeds inside of each. For each treatment, 3 to 10 replicate Petri dishes were used (depending on the treatment, see below). Also, for each treatment we watered the Petri dishes for the first time (i.e., onset of the experiment duration in which seeds can potentially germinate) at different dates (e.g., for treatments with 10 Petri dishes, the first watering was done for two of them each day for five days), while we surveyed the Petri dishes twice a week (same date for all dishes) during 80 days (except for desiccation treatments: 50 days). In this way, we increased tenfold the number of survey time by Petri dish combinations compared to watering all replicates at the same day. At each survey date, newly germinated seeds were counted and removed from the Petri dish.

2.1.1. Temperature conditions

We carried out thirteen constant temperature treatments varying from 10 °C to 34 °C with a 2 °C increment (i.e., 10 °C, 12 °C, 14 °C, 16 °C, 18 °C, 20 °C, 22 °C, 24 °C, 26 °C, 28 °C, 30 °C, 32 °C and 34 °C). Also, we tested response to day-night alternating temperatures with a treatment set to 12 h at 16 °C during the night and 12 h at 24 °C during the day. The experiment was performed with ten replicate Petri dishes per treatment, resulting in 140 Petri dishes and 1400 seeds in total. We used quartz sand (≈ 1 mm grains, $\text{pH} \approx 7$) as a germination substrate. Petri dishes were placed in the dark and watered two times a week with distilled water ensuring constant free water at the substrate surface ($\Psi \approx 0$ MPa). Treatments at 18 °C, 20 °C, 22 °C, 26 °C, 30 °C, 32 °C and 34 °C were performed using the seeds sampled in April 2021 while seeds sampled in April 2022 were used for the remaining temperature treatments.

2.1.2. Moisture conditions

We used artificially fixed water potentials to study the effect of moisture on germination of *Dracaena draco* subsp. *draco*. Water potential varied from $\Psi = -1.5$ MPa to $\Psi = 0$ MPa (i.e., free water) with six treatments: $\Psi = -1.5$ MPa, -1.2 MPa, -0.9 MPa, -0.6 MPa, -0.3 MPa and 0 MPa. The experiment was performed with ten replicate Petri dishes per treatment, resulting in 60 Petri dishes and 600 seeds in total. We simulated different water potentials using Polyethylene glycol solution (PEG8000), following the equations provided by Michel (1983). Then, Petri dishes were filled with 10 mL of PEG8000 solutions, seeds were added, and the dishes were sealed with Parafilm© and placed in the dark at 26 °C constant temperature.

2.1.3. Light exposure experiment

Two treatments were implemented: darkness (same Petri dishes as for the $\Psi = 0$ MPa treatment in the water potential experiment) and a

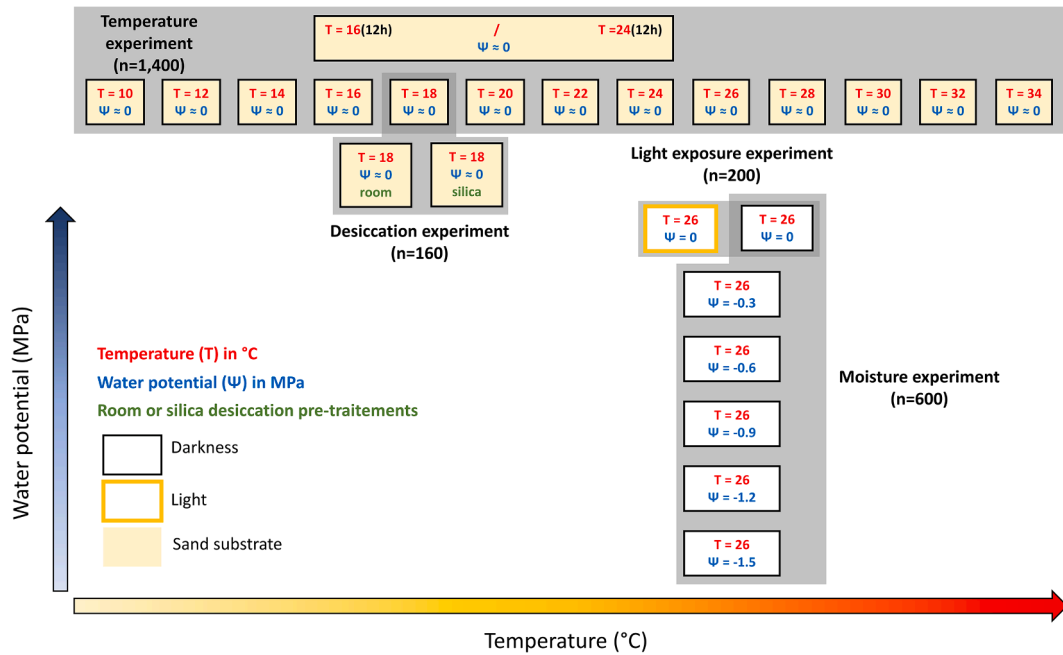


Fig. 1. Graphical outline of the experimental design to study the germination niche of *Dracaena draco* subsp. *draco*. Treatments (boxes) are plotted along the temperature and water potential gradients. Grey shaded boxes indicate the four experiments to investigate germination response to temperature and moisture (water potential) variations, light exposure, and seed desiccation. The total number of seeds used in each experiment is mentioned (n).

daily photoperiod of 12 h at a 26 °C constant temperature. Light source was 4.5 W LED lights (4,000 K, 400 lumen). The experiment was performed with ten replicate Petri dishes per treatment, resulting in 20 Petri dishes and 200 seeds in total. Petri dishes were filled with 10 mL of distilled water, seeds were added, and the dishes were sealed with Parafilm®.

2.1.4. Seed desiccation tolerance experiment

To test for seed desiccation tolerance, we followed the methods suggested by Pritchard et al. (2004): (i) no desiccation (fresh seeds, same Petri dishes as for the 20 °C constant temperature treatment); (ii) desiccation using silica gel at 26 °C for 55 days (“silica” treatment), and (iii) spontaneous air desiccation at room temperature (≈ 20 °C) for 55 days (“room” treatment). Three replicate Petri dishes per desiccation treatment (i.e., “silica” and “room”) were implemented. To control the amount of water loss by the seed lots after desiccation, we estimated the moisture content of fresh seeds as following: we weighted three 10 seeds lots (other than those we used for the germination essay as our method is likely to be destructive) when they were fresh (mean \pm sd: 4,377 \pm 170 mg), and after seven days (when constant weight was reached) in the oven at 103 °C (mean \pm sd: 2,927 \pm 65 mg), resulting in a moisture content of 33 \pm 2% for fresh seeds (no desiccation). By weighting 10 seeds lots when they were fresh and after desiccation pre-treatments, we estimated that desiccated seeds reached a moisture content close to 0% (we could not calculate the accurate moisture content as the dry mass varies amongst seeds). Then, petri dishes were placed at 20 °C constant temperature in the dark, on quartz sand as germination substrate and watered two times a week with distilled water ensuring constant free water at the substrate surface ($\Psi \approx 0$ MPa).

2.2. Data analysis

Germination courses were modelled to extract estimates of germination performance metrics to investigate the effects of moisture, light exposure, desiccation (no desiccation versus “room” and “silica” treatments) and alternating temperatures (16/24 °C versus 16 °C, 24 °C and 20 °C, i.e., the mean between 16 °C and 24 °C treatments). As we implemented 13 constant temperature treatments with a constant 2 °C

increment, we modelled germination probability along constant temperatures regarded as a continuous gradient.

2.2.1. Germination course modelling

To estimate germination performance metrics, we modelled for each treatment the germination course with four parameters log-logistic models using the *drm* function from the *drc* R package (Ritz et al., 2015):

$$f(x) = c + \frac{d - c}{1 + \exp(b(\log(x) - \log(e)))}$$

where $f(x)$ corresponds to the proportion of germinated seeds at time x , b is the slope, c and d the lower and upper response limits respectively, and e the value of x where the response is halfway between c and d . As we modelled cumulative germination proportions from day = 0, we fixed the lower limit to $c = 0$ and constrained the upper limit to $0 \leq d \leq 1$. The parameters b and e were estimated from the data without constraints. We compared estimates of e and d parameters to assess the effects of the studied factors on germination performance using the *compParm* function from the *drc* R package. The d parameter corresponds to the final germination percentage. The e parameter corresponds to the T_{50} , i.e., the number of days needed to reach 50 % of the final germination percentage, which is a proxy for germination speed (high T_{50} indicates slow germination while low T_{50} indicates fast germination). We also recorded for each treatment the observed final germination percentage, i.e., the percentage of germinated seeds at the end the experiment.

2.2.2. Thermal germination niche modelling

We modelled germination probability along the temperature gradient following Sentinella et al. (2020), allowing us to delineate the thermal germination niche of *D. draco* subsp. *draco*. To do so, we used a generalized linear mixed model (GLMM) with a quadratic term for temperature and we added the year of sampling, the mother tree, and the Petri dish as nested random effects. A logit link function was chosen because the response variable was binary (each seed either germinated or did not germinate at the end of the experiment, i.e., day=80). Then, we extracted four metrics from the model’s predictions: T_{min} and T_{max}

correspond respectively to the lower and upper ends of the model fit where germination probability is inferior or equal to 0.05 (i.e., 5 % of a seed lot); while $T_{opt-min}$ and $T_{opt-max}$ correspond respectively to the lower and upper ends of the model fit where germination probability is predicted to reach 0.95 (i.e., 95 % of a seed lot). Thus, the temperature range between T_{min} and $T_{opt-min}$ is qualified as “sub-optimal”, the range between $T_{opt-min}$ and $T_{opt-max}$ as “optimal”, and the range between $T_{opt-max}$ and T_{max} as “supra-optimal”. All temperatures below T_{min} or above T_{max} are considered as unsuitable for *D. draco* subsp. *draco* germination.

2.2.3. Identifying favourable conditions for germination throughout the native range

To map areas where temperatures are suitable for *D. draco* subsp. *draco* germination in its native range (i.e., Madeira and Canary archipelagos) we projected germination probability and sub-optimal, optimal, and supra-optimal temperature ranges predicted by our GLMM on the map of the mean temperature of the wettest quarter of the year at soil surface (0–5 cm, hereafter referred as “SBIO08”) (i.e., we calculated germination probability based on SBIO08 values). This map was obtained from a global raster layers dataset of soil bioclimatic variables at 30 arc seconds resolution (Lembrechts et al., 2022; van den Hoogen et al., 2022). We chose this variable because temperatures are

averaged over the wettest quarter of the year, i.e., i) corresponding roughly to the experiment duration, and ii) when moisture is less susceptible to be a limiting factor. In order to calculate the area of unsuitable, sub-optimal, optimal and supra-optimal areas for germination, we computed raster cells area (km²) using the *area* function from the *raster* R package (Hijmans, 2021), to account for the latitudinal gradient. Finally, we extracted the germination percentages predicted for the known native localities of *D. draco* subsp. *draco* from the spatial projection of the thermal germination niche. To do so, we retrieved georeferenced records of *D. draco* subsp. *draco* from the IUCN Red List (Global Tree Assessment, 2021), the Global Biodiversity Facility (GBIF, 2022) and from A. Santos-Guerra and F. Médail field and literature surveys. We only kept reliable records by filtering for records georeferenced at less than 1 km uncertainty (for GBIF data) and spontaneous populations in natural habitats throughout the native range of Macaronesian dragon trees (see introduction section) using Google Street View imagery for planted individuals in urban areas, and expert knowledge (A. Santos-Guerra). Occurrence points were aggregated on a 30 arc seconds spatial grid to match the SBIO08 raster layers resolution resulting in $n = 45$ grid cells with presence of *D. draco* subsp. *draco*.

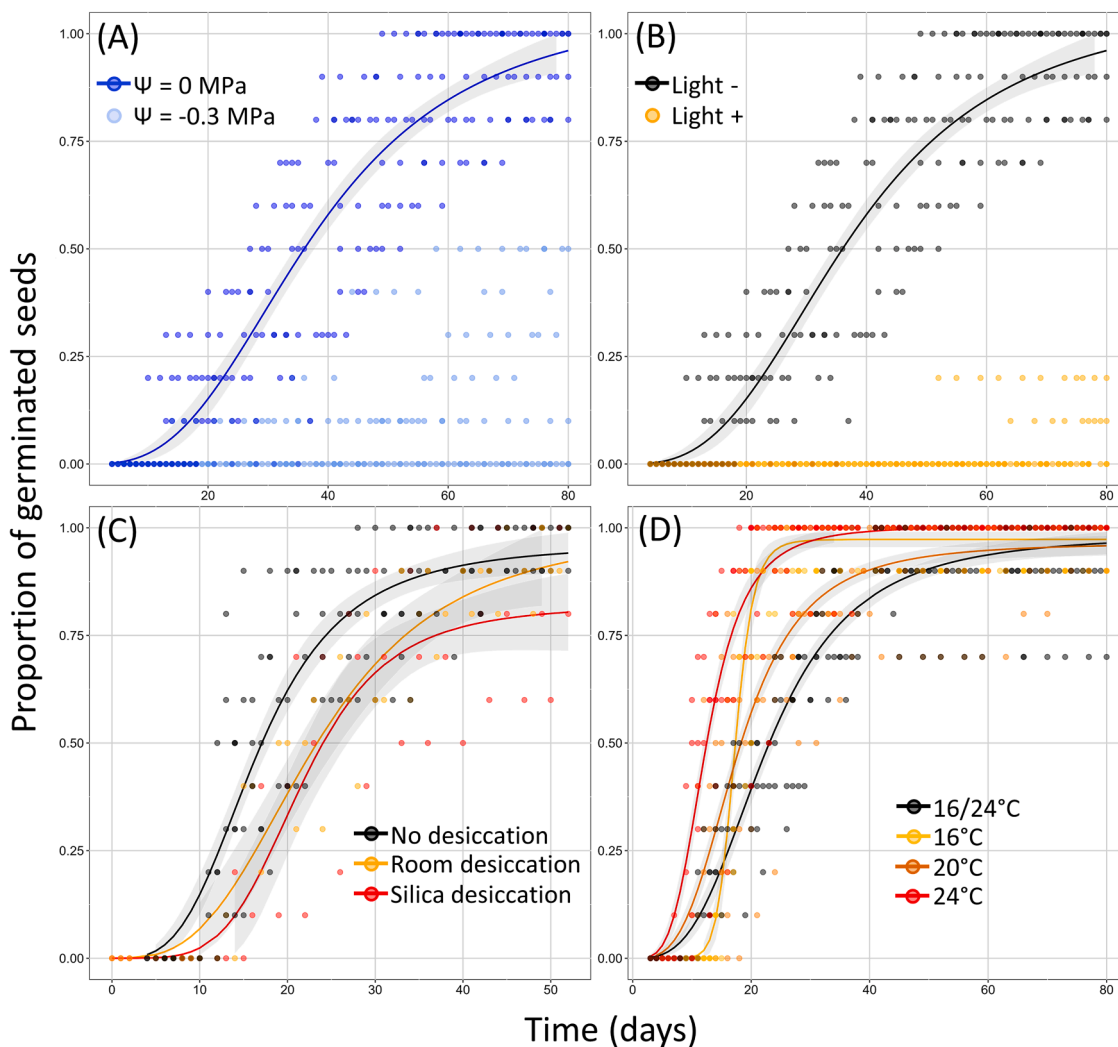


Fig. 2. Effects of moisture (A), light exposure (B), seed desiccation (C) and alternating temperatures (D) on the germination course of *Dracaena draco* subsp. *draco*. Solid lines correspond to the log-logistic models’ predictions of the proportion of germinated seeds (y-axis) through time (days, x-axis); the grey shaded areas represent the 95 % confidence intervals. Dots denote observed proportions of germinated seeds in each Petri dish at each survey time. No log-logistic models were fit to germinations in the treatments “ $\Psi = -0.3$ MPa” (A) and “Light +” (B).

3. Results

3.1. Moisture, light exposure and seed desiccation effects on germination

The six water potential treatments revealed a strong effect of moisture limitation on seed germination of *Dracaena draco* subsp. *draco*: seeds germinated only at $\Psi = -0.3$ MPa and $\Psi = 0$ MPa. Germination percentage was much higher at $\Psi = 0$ MPa (94 %) than at $\Psi = -0.3$ MPa (18 %) (Fig. 2A). Light exposure also had a strong effect since the observed final germination percentage was much higher in full darkness (94 %) compared to 12 h of light (7 %) (Fig. 2B). Very low germination percentages and slow germination courses in the $\Psi = -0.3$ MPa and light exposed treatments did not allow reliable estimation of germination time courses.

Regarding seed desiccation tolerance, the observed final germination percentages were high in each of the three treatments (“no desiccation”: 98 %, “room”: 93 %, “silica”: 80 %). The modelled final germination percentages were not significantly different: 96 ± 3 % for the “no desiccation” treatment, 100 ± 11 % for the “room” treatment and 82 ± 6 % for the “silica” treatment ($p > 0.06$ in all three comparisons). While “room” and “silica” treatments had germination speeds not significantly different ($T_{50} = 23.4d \pm 2.5$ and $T_{50} = 21.8d \pm 1.5$ respectively, $p = 0.558$), they were significantly slower than for the “no desiccation” treatment ($T_{50} = 16.7d \pm 0.7$, $p < 0.001$ in both comparisons), although the differences in T_{50} are tenuous (Fig. 2C).

3.2. Alternating temperatures effect on germination

Alternating temperatures did not significantly impact the final germination percentage: 98 ± 2 % (observed: 94 %) for the 16/24 °C treatment versus 97 ± 1 % (observed: 98 %), 96 ± 1 % (observed: 97 %) and 100 ± 1 % (observed: 100 %) for the 16 °C, 20 °C and 24 °C treatments respectively ($p > 0.300$ for all three comparisons). However, germination speed in the 16/24 °C treatment ($T_{50} = 22.8d \pm 0.6$) was significantly lower than for the 16 °C ($T_{50} = 17.2d \pm 0.2$), 20 °C ($T_{50} = 17.9d \pm 0.4$) and 24 °C treatments ($T_{50} = 12.5d \pm 0.3$, $p < 0.001$ in all three comparisons) (Fig. 2D).

3.3. Thermal germination niche

The GLMM (pseudo- R^2 of fixed effects = 0.67) allowed us to describe the thermal germination niche of *D. draco* subsp. *draco* (Fig. 3). The

suitable temperatures for germination range from $T_{min} = (11.7) 12.1$ (12.5) °C to $T_{max} = (32.4) 32.8$ (33.2) °C, and germination percentage reaches ≥ 95 % from $T_{opt-min} = (16.0) 16.1$ (17.4) °C to $T_{opt-max} = (27.5) 28.3$ (29.0) °C (number in brackets correspond to the lower and upper bounds of the 95 % confidence interval).

Across the 45 current locations hosting native populations of *D. draco* subsp. *draco* in the Canary and Madeira archipelagos, the germination percentage predicted by our model is on average 78 ± 25 % (\pm standard deviation); 30 locations (i.e., 67 %) are under sub-optimal conditions, 14 (i.e., 31 %) are under optimal conditions, and only one (i.e., 2 %) is in temperature ranges modelled as unsuitable for germination (Fig. 3).

Areas predicted as suitable for germination (i.e., mean temperature of the wettest quarter of the year ranging from T_{min} to T_{max}) occupy 6,476 km² throughout the native range of *D. draco* subsp. *draco*, mainly distributed in the Canary Islands (94 % of the suitable area surface). A surface of 5,074 km² is predicted as optimal (98 % of this surface occur in the Canary Islands) and 1,402 km² are predicted as sub-optimal (80 % of this surface occur in the Canary Islands). SBIO08 do not exceed $T_{opt-max}$ in the Canary and Madeira archipelagos, thus the distribution of *D. draco* subsp. *draco* is not limited by temperatures too warm for seed germination. In contrast, high-altitude areas have SBIO08 values below T_{min} . Therefore, *D. draco* subsp. *draco* is absent from those areas because temperatures are too cold for seed germination (Figs. 3&4).

4. Discussion

This is the first comprehensive study on *Dracaena draco* subsp. *draco* considering germination response to temperature, moisture variations and seed desiccation tolerance. Based on series of *ex-situ* experiments under controlled conditions, we found that its germination requirements include constant temperatures ranging from 16.6 °C to 28.3 °C (optimal range), dark and moist environments ($\Psi \geq -0.3$ MPa) with highest germination rates in free water ($\Psi = 0$ MPa). Also, germination speed was reduced by alternating temperatures. Moreover, we highlighted germination tolerance to seed desiccation pre-treatments, indicating an orthodox storage behaviour and tolerance to temporary drought conditions.

4.1. Ecological significance of *D. draco* subsp. *draco* germination requirements

Native Canary Islands dragon tree populations occur in semi-arid to

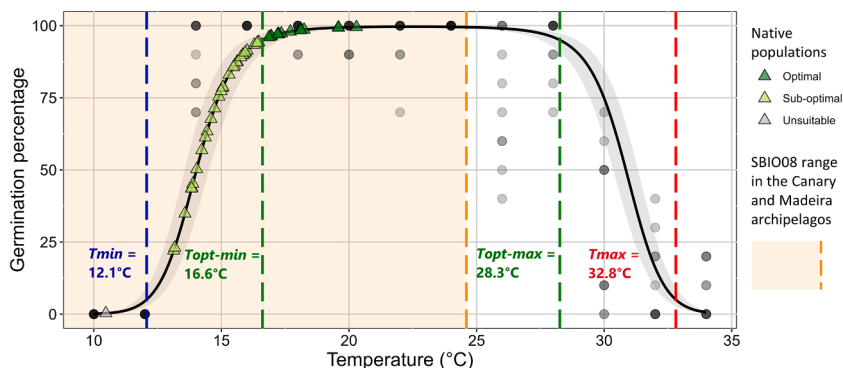


Fig. 3. The thermal germination niche of *D. draco* subsp. *draco*. The solid line corresponds to the GLMM predictions of germination percentage (i.e., germination probability $\times 100$, y-axis) along the temperature gradient (x-axis) and the grey shaded area represents the 95 % confidence interval. The blue and red dashed lines correspond respectively to the lower and upper ends of the model fit where the germination percentage is predicted to reach 5 % (T_{min} and T_{max} respectively) and the green dashed lines to the lower and upper ends of the model fit where the germination percentage is predicted to reach 95 % ($T_{opt-min}$ and $T_{opt-max}$). The dots display germination percentage at the end of the experiment (day=80) of each of the 130 Petri dishes ($n = 1300$ seeds in total). The orange shaded area along with the dashed orange line (upper limit) denote the range of mean temperature of the wettest quarter of the year at soil surface (SBIO08) occurring throughout the distribution area of *D. draco* subsp. *draco* in Canary and Madeira archipelagos; the lower limit, -2 °C, is not displayed. Triangles represent the germination percentage predictions by the GLMM for the 45 locations where native *D. draco* subsp. *draco* occur (their colour denote suitability ranges, i.e., unsuitable, sub-optimal or optimal).

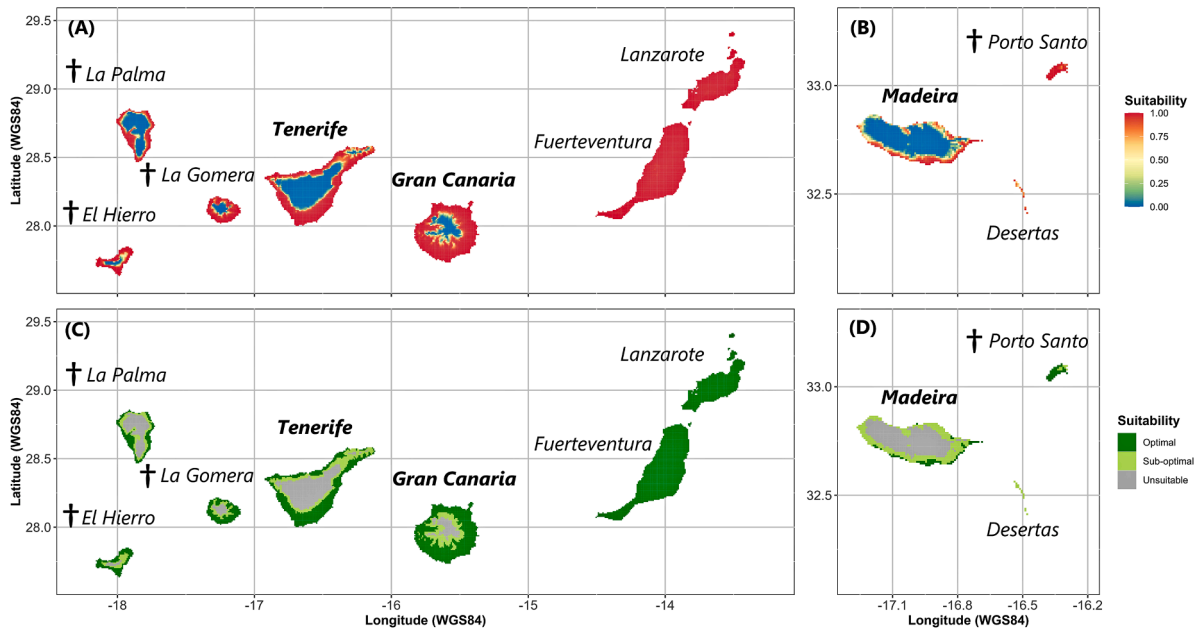


Fig. 4. Spatial projection of *D. draco* subsp. *draco* thermal germination niche in the Canary (A, C) and Madeira (B, D) archipelagos. Panels A and B display continuous suitability (i.e., germination probability) and C and D optimal, sub-optimal and unsuitable temperature ranges. Supra-optimal temperatures do not occur in the Canary and Madeira archipelagos. Locality names in bold letters host extant native dragon tree populations while names marked with a cross denote localities where it is extinct in the wild.

arid warm climates (Trabucco and Zomer, 2018; Cartereau et al., 2022). Unsurprisingly, *D. draco* subsp. *draco* germinates at relatively high temperatures with optimal temperatures between 16 and 28 °C. This is also the case for *Dracaena cinnabari* Balf.f., the dragon tree from Socotra Island, germinating at up to 30 °C (Bauerová et al., 2020). Phylogenetic conservatism of temperature requirements for germination has been shown across angiosperms (Arène et al., 2017), indicating that closely related taxa tend to share similar temperature requirements for germination.

Surprisingly, we found that *D. draco* subsp. *draco* seeds do not tolerate low levels of moisture to germinate although it occurs today in notoriously arid areas (Cartereau et al., 2022). Indeed, the current habitat of *D. draco* subsp. *draco* is characterized by climatically dry conditions, with annual precipitations ranging from 50 to 500 mm and relatively low precipitation and temperature seasonality (del Arco Aguilar and Rodríguez Delgado, 2018). Amongst the few studies on moisture requirements for germination of wild plants, some tree species inhabiting dryland ecosystems, such as *Ceratonia siliqua* L. (Cavallaro et al., 2016), *Pinus* spp. (Thanos and Skordilis, 1987), *Colophospermum mopane* (J.Kirk ex Benth.) J.Léonard, or *Combretum apiculatum* Sond. (Choinski and Tuohy, 1991), or inhabiting deserts such as *Welwitschia mirabilis* Hook.f. (Di Salvatore et al., 2016), can germinate under strong water stress, i.e., $\Psi \leq -1$ MPa, even at high temperatures. Wilman et al. (2014) found that some woody species in South African xeric subtropical thickets have high moisture germination requirements, mismatching the xeric conditions in which they occur. They hypothesized that this pattern could be the consequence of niche conservatism since lineages of these taxa arose during past wetter climates. The same process could explain why *D. draco* subsp. *draco* has such high moisture requirements for germination while inhabiting current arid and semi-arid environments. Indeed, *Dracaena* species are mostly distributed in wet tropical forests (POWO, 2023) and based on the analysis of depositional settings and associated plant taxa of fossil dragon tree records, modern dragon trees have been hypothesized to arise from a western Eurasian, more mesic lineage occurring under warm temperate climate (Denk et al., 2014; 2022). Also, if the current climate where *D. draco* subsp. *draco* occurs is characterized by low and irregular precipitations (del Arco

Aguilar and Rodríguez Delgado, 2018), Macaronesian islands experienced wetter periods before the onset of the Mediterranean-type climate in the late Pliocene (Fernández-Palacios et al., 2011).

In this context, given the high moisture requirements of *D. draco* subsp. *draco* for germination, it is key for its seeds to detect favourable conditions to ensure successful germination and seedlings establishment. Regarding the effect of light exposure, our results agree with Kheloufi et al. (2020), showing that *D. draco* subsp. *draco* seeds germinate better when sown at 2 cm depth in the germination substrate, which means darkness, rather than at its surface (i.e., exposed to light). In rocky habitats and thermo-sclerophyllous open vegetation belt, where the Canary Islands dragon tree occurs (Almeida Pérez, 2004), such conditions could be met under the ground surface or in microsites maintaining high moisture such as under the canopy of chamaephytes (i.e., nurse effect, particularly important for plants recruitment in drylands, see Swanson et al., 2021) or inside crevices in cliff systems forming microrefugia (Danin, 1999). This kind of microsites can be detected by seeds via i) shade and ii) reduced diurnal temperature fluctuations (Franco and Nobel, 1989; Ren et al., 2008; Saatkamp et al., 2011; García et al., 2020). Regarding shade, light photoinhibition on germination is particularly frequent in monocots and is strongly associated with open and dry habitats (Carta et al., 2017), optimising germination when seeds are moved to these microsites fixing the plant before they can be moved to less favourable ones. This mechanism, when occurring in drylands, has been interpreted as a physiological adaptation to avoid germination on the soil surface where solar radiations can reach the seed, i.e., where conditions are unsuitable for germination due to low moisture (Carta et al., 2017). Regarding diurnal temperature fluctuations, it has been shown that in drylands, seed germination of perennial ornithochorous species is inhibited by alternating temperature regimes like those found in open sites (Kos and Poschlod, 2007). This type of seeds rather germinates under more constant temperature regimes, such as in shaded sites under the canopy of sparsely distributed trees to which they are associated because these latter maintain reasonable moisture conditions under their canopy (Kos and Poschlod, 2007). Therefore, our results suggest that the negative responses to light and alternating temperatures of *D. draco* subsp. *draco*

seed germination constitute an adaptation to detect such favourable conditions.

4.2. Geographic distribution of temperature requirements for germination of *D. draco* subsp. *draco*

By combining our model of temperature requirements for germination of *D. draco* subsp. *draco* with a map of soil temperatures during the wet season in the Canary and Madeira archipelagos, we were able to project suitable areas for its germination throughout its native range. Of the 45 known native populations of *D. draco* subsp. *draco*, 44 are predicted by our model to occur in favourable conditions for germination, most occurrences tend to be in slightly colder site conditions compared to the warmer optimum temperature requirements for germination found in our study.

Since the congruence of our projection with known occurrences suggests that our model correctly predicts favourable temperature conditions for germination, we identified suitable areas for germination throughout the entire range of *D. draco* subsp. *draco*. Most of them are situated in the Canary Islands, since only few individuals remain in the southern coast of Madeira. Moreover, we also identified suitable areas on several islands where the species is nowadays extinct in the wild, i.e., the islands of El Hierro, La Gomera, La Palma and Porto Santo. Our map highlights that suitable temperature conditions for germination are widespread at low altitudes, and that the Canary Islands dragon tree germination is limited by low temperatures in higher altitudes. The Canary Islands dragon tree is absent and has probably never occurred in the low altitude islands Lanzarote and Fuerteventura, where thermophilous woodlands, i.e., the main habitat of the dragon tree, are very scarce (with the exception of restricted areas, e.g., Famara and Jandia mountains, in Lanzarote and Fuerteventura respectively, [Fernández-Palacios et al., 2008b](#)). However, our suitability map for *D. draco* subsp. *draco* germination reveals that those islands offer almost exclusively optimal conditions. This is because we predicted germination probability only based on temperatures. Thus, even though we used the mean temperature of the wettest quarter of the year, those two islands, the most arid of the archipelago ([Betchel, 2016](#)), might still not offer habitats sufficiently moist given the seeds high moisture requirement for germination. We underline that soil water potential depends not only on climatic parameters, but also on various edaphic characteristics which are highly heterogeneous at small spatial scales ([Ma et al., 2022](#)). Therefore, modelling soil water potential variations over large spatial scales is still very difficult, if not impossible, and this constitutes a challenge for the mapping of germination niche based on moisture requirements.

4.3. Implications for conservation

Global climate is predicted to become warmer and drier in the future due to human-induced greenhouses gas emissions ([IPCC, 2018](#)). Based on environmental niche modelling, two studies suggest that other dragon tree species, i.e., *D. cinnabari* in Socotra ([Attorre et al., 2007](#)) and *D. draco* subsp. *caboverdeana* in the Cabo Verde ([Varela et al., 2022](#)), are highly threatened by future climate change. In this study, we found that *D. draco* subsp. *draco* native populations are located in areas where temperatures are sub-optimal to optimal and that the dragon tree distribution is not limited by temperatures above the warm limit of the germination niche in the Canary and Madeira archipelagos. Under future climate warming, the mean temperature of the wettest quarter of the year where *D. draco* subsp. *draco* occurs would have to increase of 12.5 °C and of 17.0 °C on average to reach the supra-optimal and warm unsuitable temperature limits for germination, respectively. Therefore, it is unlikely that populations regeneration will be negatively impacted by temperature changes in the near future based on temperature requirements alone, or even inversely, more sites could become favourable. However, an increase of evapotranspiration with increasing

temperatures, or decreasing precipitations, could lead to reduced soil moisture, limiting the regeneration by seed of *D. draco* subsp. *draco*. This situation calls for a detailed field study on microsites and soil moisture for regeneration by seed, and further experimental studies might reveal the optimal sowing depth for germination and seedling survival of this species.

Given the very low number (< 700) of *D. draco* subsp. *draco* individuals remaining in the wild ([Almeida Pérez, 2004](#)) and the uncertainties regarding its response to future climate change, and since our results showed that the seeds have an orthodox storage behaviour, germplasm maintenance in seed banks could be a relevant tool for its *ex-situ* conservation ([Abeli et al., 2019](#)). Also, propagation protocols for possible *in-situ* species recovery actions should take into account the favourable germination conditions revealed in this study, i.e., seeds should be sown in moist substrate, in the dark and at constant temperatures between 16.6 °C and 28.3 °C. Finally, population reinforcement or reintroductions should consider to bury seeds at sufficient depth to increase the probability of germination and seedling establishment of *D. draco* subsp. *draco*.

CRediT authorship contribution statement

Manuel Cartereau: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Alex Baumel:** Supervision, Writing – review & editing. **Agathe Leriche:** Supervision, Writing – review & editing. **Frédéric Médail:** Data curation, Supervision, Writing – review & editing. **Arnoldo Santos Guerra:** Data curation, Writing – review & editing. **Arne Saatkamp:** Conceptualization, Investigation, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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