PRIMARY RESEARCH ARTICLE

WILEY | Global Change Biology

Thermal buffering capacity of the germination phenotype across the environmental envelope of the Cactaceae

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Abstract

Recruitment from seeds is among the most vulnerable stage for plants as global temperatures change. While germination is the means by which the vast majority of the world's flora regenerate naturally, a framework for accurately predicting which species are at greatest risk of germination failure during environmental perturbation is lacking. Taking a physiological approach, we assess how one family, the Cactaceae, may respond to global temperature change based on the thermal buffering capacity of the germination phenotype. We selected 55 cactus species from the Americas, all geo-referenced seed collections, reflecting the broad environmental envelope of the family across 70° of latitude and 3700 m of altitude. We then generated empirical data of the thermal germination response from which we estimated the minimum (T_b), optimum (T_o) and ceiling (T_c) temperature for germination and the thermal time (θ_{50}) for each species based on the linearity of germination rate with temperature. Species with the highest T_b and lowest T_c germinated fastest, and the interspecific sensitivity of the germination rate to temperature, as assessed through θ_{50}, varied tenfold. A left-skewed asymmetry in the germination rate with temperature was relatively common but the unimodal pattern typical of crop species failed for nearly half of the species due to insensitivity to temperature change at T_o. For 32 fully characterized species, seed thermal parameters correlated strongly with the

mean temperature of the wettest quarter of the seed collection sites. By projecting the mean temperature of the wettest quarter under two climate change scenarios, we predict under the least conservative scenario ($+3.7°C$) that 25% of cactus species will have reduced germination performance, whilst the remainder will have an efficiency gain, by the end of the 21st century.

1 | INTRODUCTION

With the urgent need to understand the impact of climate change on species biodiversity, mechanistic approaches, which relate the environment with physiological responses and functional limitations, are critical in assessing how well species cope with environmental perturbation (Buckley et al., 2010; Pacifici et al., 2015; Tomlinson et al., 2014). Fitness traits which rely on temperature as an environmental cue or are thermal dependent, such as seed germination, are particularly at risk of being negatively impacted from global temperature change (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). The vast majority of the world's flora relies on seed germination for natural regeneration, and variation in seed germination rate has important downstream consequences on seedling performance, such as emergence timing, and on later stages of the plant life cycle, such as seed yield (Finch-Savage, 1995). Yet surprisingly, the sensitivity of germination to global temperature change has been quantified for only about 0.1% of species (Dürr, Dickie, Yang, & Pritchard, 2015), including crop species such as pearl millet (Garcia-Huidobro, Monteith, & Squire, 1982) and chickpea (Ellis, Covell, Roberts, & Summerfield, 1986), and wild species from Europe (alpine species, Mondoni, Rossi, Orsenigo, & Probert, 2012; *Vitis vinifera*, Orrù, Mattana, Pritchard, & Bacchetta, 2012; *Carex diandra*, Fernández-Pascual, Seal, & Pritchard, 2015), Australia (40 species of *Banksia*, Cochrane, 2015), Africa (*Colophospermum mopane*, Stevens, Seal, Archibald, & Bond, 2014) and Mexico (*Polaskia chende* and *P. chichipe*, Ordoñez-Salanueva et al., 2015).

The thermal germination range can be quantified through the proportion of seeds within a seed population which germinate, usually spanning a wide temperature range with a curvilinear response to temperature (Garcia-Huidobro et al., 1982). In contrast, the germination rate, a measure of seed vigour, has a linear relationship to temperature which can be exploited to define cardinal temperatures for germination (minimum or base temperature, T_b; optimum temperature, T_o; and maximum or ceiling temperature, T_c) for the nondormant seed fraction under conditions of unlimited water availability (Covell, Ellis, Roberts, & Summerfield, 1986; Ellis et al., 1986; Garcia-Huidobro et al., 1982), reflecting germination capability during the rainy season. The reciprocal of the linear regressions at temperatures between $T_o–T_b$ and $T_c–T_o$ characterizes the thermal times (degree-days or –hours; θ) for germination in the suboptimal and supraoptimal range, respectively (Covell et al., 1986; Ellis et al., 1986; Garcia-Huidobro et al., 1982), and are measures of how sensitive or responsive germination is to environmental temperature change. Thermal time modelling of germination was initially developed on crop species (Covell et al., 1986; Ellis et al., 1986; Garcia-Huidobro et al., 1982), and subsequently extended to wild species. Through both intra- and interspecific comparisons of species' responses to ex situ and in situ environments, insights have been gained of the spatial and temporal components of emergence, with apparent universal applicability across habitats and lifeforms (Dürr et al., 2015; Orrù et al., 2012; Porceddu, Mattana, Pritchard, & Bacchetta, 2013; Pritchard, Steadman, Nash, & Jones, 1999; Steadman & Pritchard, 2004). Recently, thermal time modelling has been applied to a limited number of species to predict and validate germination performance under various climate change scenarios (Fernández-Pascual et al., 2015; Ordoñez-Salanueva et al., 2015; Orrù et al., 2012).

With the development of global data repositories, meta-analysis has revealed that up to 98% of plant trait variance at a global scale occurs at the interspecific level (Kattge et al., 2011). Yet there is still a lack of interspecific comparisons using common germination descriptors that are mechanistic, linking function to environment and providing a framework for assessing the impact of climate change. Critically, such studies appear to be lacking for species considered at high risk of extinction. Here, we provide the first assessment of how one taxonomic plant family, the Cactaceae, may cope with changes in global temperature at the germination stage. We chose the Cactaceae as they are key components of diverse habitats, ranging from arid deserts, to occasionally, tropical rainforests (Hunt, Taylor, & Charles, 2006; Ortega-Baes et al., 2010), and are of high socioeconomic interest for food, medicine, building materials and ornaments (Anderson, 2001). Small changes in climate are predicted to dramatically restrict the distribution of cactus plants (Téllez-Valdés & Dávila-Aranda, 2003) and impact on key processes such as flowering phenology (Bustamante & Búrquez, 2008). Many cactus species are already of high conservation concern (IUCN, 2016) and more are predicted to face extinction in the near future (Goettsch et al., 2015). While the temperature dependency of the maximum germination potential is known for many cacti (for review see Rojas-Aréchiga & Vázquez-Yanes, 2000), germination rate and thermal time investigations are limited to c. 10 species (Dürr et al., 2015; Ortega-Baes

et al., 2011; Simão, Takaki, & Cardoso, 2010) and rarely address future germination performance (Ordoñez-Salanueva et al., 2015). Moreover, these species occupy narrow environmental niches compared with the totality of environmental envelopes across the family.

To assess the thermal buffering capacity and consequent risk of cactus seed germination to climate change, we first generated empirical data of the thermal germination response of 55 cactus species (Table S1) across latitudinal (spanning 70°) and altitudinal (spanning 3700 m) gradients, covering the full distributional range of the family in the Americas. We used a thermal time model approach to quantify the cardinal temperatures and sub- and supraoptimal thermal time, evaluating the extent of plasticity in the germination phenotype to reveal broad trends in performance across the family. We then considered associations between the phenotype and the environment of the seed collection site. These thermal descriptors enabled a projection of the impact of global warming on cactus seed germination, predicting the proportion of cactus species that will have germination that is negatively affected during the 21st Century.

2 | MATERIALS AND METHODS

2.1 | Seed material

Mature seeds of 55 cactus species, from 36 genera, were collected from sites in Argentina, Chile, Dominican Republic, Mexico, Peru and USA, spanning an area of 38.49° to −31.93° latitude and 10 to 3710 m a.s.l. (Table S1). Seeds of *Echinopsis atacamensis* were collected from sites in both Argentina (lot 1; Species 17a) and Chile (lot 2; Species 17b). Three subspecies of *Echinopsis chiloensis* (ssp. *chiloensis* [Species 18a], ssp. *litoralis* [Species 18b] and ssp. *skottsbergii* [Species 18c]) were also collected. Thus in total, there were 58 seed lots or 55 species. After arrival at the Royal Botanic Gardens, Kew, UK, seeds were stored at 15% RH and at 15°C for up to four weeks, or longer term dry at −20°C (in hermetically sealed screw cap vials) to maintain seed quality.

2.2 | Germination protocol

For each seed lot, three replicates of 25 seeds were sown onto the surface of 1% agar-water in Petri dishes. Seeds were germinated at 14 constant temperatures using a thermal gradient plate (Grant Instruments, Cambridge, UK) which established a temperature gradient of *c.* 10–45°C at *c.* 2.5°C intervals. A 12 hr photoperiod was used (white light with photon flux density of 50 W/m^2). For *Espostoa melanostele* (Species 25), *Haageocereus acranthus* (Species 31) and *Mila caespitosa* (Species 41), seed numbers were limited and so germination was performed at seven constant temperatures between 10–40°C. The temperature of each Petri dish was calculated using five temperature probes placed at each corner and in the centre of the thermal gradient plate, set to record every 10 min for the duration of each study. Germination was scored every 24 hr for at least four weeks until no further germination was observed. Germination was defined as radicle emergence by 2 mm.

### 2.3 | Germination data modelling

Cumulative germination curves were plotted for each temperature regime (777 curves in total) and the time (*t*) taken to reach 50% of the final proportion of germinated seeds at each temperature was estimated (t_{50}) (Grundy, Phelps, Reader, & Burston, 2000). The reciprocal ($1/t_{50}$) was plotted against the temperature which gives a unimodal response with a linear rise and fall (Figure 1a) (Garcia-Huidobro et al., 1982). The sub- and supraoptimal germination temperature ranges were identified by visual inspection of the germination rate plots. A linear regression was performed (Origin 6.1; OriginLab Corporation, MA, USA) to calculate the x-intercept of both the sub- and supraoptimal temperature ranges, giving estimates of the base temperature (T_b), at which $1/t_{50}$ is estimated to be zero, and the ceiling temperature (T_c), above which $1/t_{50}$ is equal to zero (Garcia-Huidobro et al., 1982). The intercept of the sub- and supraoptimal temperatures linear regression lines was used to estimate the optimum temperature (T_o). Where the maximum germination rate was represented by more than one but similar data points (to 2 decimal places), the points corresponding to the lowest and highest temperature were included in the sub- and supraoptimal temperature regressions respectively, and all data points for the maximal rate were used to estimate the optimal temperature range (Figure 1b). The thermal time to achieve 50% germination (degree days; θ_{50}) was taken from the reciprocal of the slope of the suboptimal and supraoptimal temperature regression lines (Garcia-Huidobro et al., 1982; Ortega-Baes et al., 2011; Pritchard & Manger, 1990).

2.4 | Relating the environment to the germination response

Climate data were obtained from WORLDCLIM 1.4 (release 3) based on the GIS coordinates of the seed collection site, at a resolution of 30 arc-seconds for the period 1950–2000 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). The climate data were analysed according to the 19 bioclimatic (BioClim) parameter definitions which represent annual parameters (e.g. mean annual temperature), seasonality (e.g. annual range of temperature) and extreme events (e.g. mean temperature of the wettest quarter) (Hijmans et al., 2005).

A stepwise multiple regression was performed on the germination cardinal temperatures and suboptimal θ_{50}, and latitude, altitude and the 19 Bioclim parameters related to temperature and precipitation (Hijmans et al., 2005). Alternating forward selection and backwards elimination steps of term selection were used in SAS for Windows V8 (SAS institute, Cary, NC, USA) and models were considered significant at the level of $p < .05$.

We then estimated the germination performance of 32 species (or 33 seed lots, where significant cardinal temperatures could be estimated) under two theoretical global climate change scenarios, RCP2.6 (+1.0°C) and the more likely scenario RCP8.5 (+3.7°C) (IPCC, 2014), using the mean temperature of the wettest quarter of the year which the stepwise multiple regression revealed as being most closely associated with the germination behaviour (see Results).
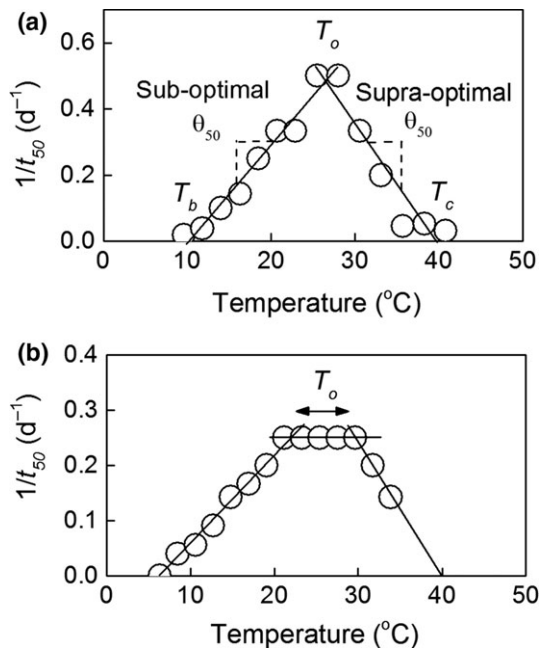
FIGURE 1 Cardinal temperatures were estimated using the reciprocal of the time taken to reach 50% of the maximum germination ($1/t_{50}$). (a) Following the principles of a thermal time model approach, $1/t_{50}$ was plotted against the germination temperature to produce a linear model identifying the base temperature (T_b), ceiling temperature (T_c) and one temperature as the optimum temperature (T_o). The thermal time for 50% germination to occur (degree days; θ_{50}) was estimated from the reciprocal of the slope of the suboptimal and supraoptimal temperature regression lines. Data points are shown for *Echinopsis chiloensis* ssp. *litoralis* (Species 18b). (b) For some species, plotting $1/t_{50}$ against the germination temperature gave a model with multiple values of T_o. Data points are shown for *Echinopsis chiloensis* ssp. *chiloensis* (Species 18a)

Current and future environmental temperatures were calculated by taking the mean temperature of the wettest quarter projected from the global mean surface temperature changes of the RCP2.6 (+1.0°C) and RCP8.5 (+3.7°C) climate change scenarios (IPCC, 2014). For each species, these values were compared with estimates of T_o, or the upper limit of the T_o temperature range where applicable, to evaluate whether the environmental temperature will exceed T_o and more widely if the environmental temperature falls within the sub- or supraoptimal temperature range. We also predicted how germination timing (i.e. the number of days to achieve 50% germination) might change under the two climate change scenarios using estimated values of both sub- and supraoptimal θ_{50}.

2.5 | Additional statistics

Seed quality was assessed by performing a linear regression between the temperature range to achieve 50% of maximal germination plotted against maximal germination. A two-sampled *t* test was used to evaluate differences in the T_o-singular and T_o-multiple groupings with regard to the cardinal temperatures and the environmental

explanatory variables (19 BioClim parameters, altitude and latitude). These analyses were performed in Origin 9.0 (OriginLab Corporation, MA, USA).

3 | RESULTS

3.1 | Seed quality

The majority of the 55 species (58 seed lots), of which 26 species are recognized as a conservation risk (Table S1), were of high viability with the median maximal germination of 89.3%, and a 25–75 percentile of 63.4 to 97.3%. There was no significant correlation between the temperature range to achieve 50% of maximal germination and the maximal germination ($r = .26$; $p = .07$).

3.2 | Thermal germination traits

The thermal time approach provided significant ($p < .05$) estimates of T_b for all species, except *Cylindropuntia imbricata* (Species 10), and explained over 80% of the variation in the germination rate for 55 seed lots (representing 52 species; Table S2). The median T_b was 10.6°C and the 25–75 percentile was between 8.4°C and 12.1°C (Figure 2). The supraoptimal range was more difficult to model, with only two data points available for six species and no data points for *Obregonia denegri* (Species 45) which was projected to germinate well above the maximum temperature limits of the thermal gradient plate. In 29 of the 33 seed lots (representing 28 out of 32 species) with significant models ($p < .05$) and more than two data points (Table S2), over 80% of the variation in the germination rate was accounted for. Estimates of T_c were found to have a median of 41.8°C and a 25–75 percentile value of 39.6°C to 44.9°C (Figure 2). Significant estimates of T_o (33 seed lots, representing 32 species), calculated from the intercept of the sub- and supraoptimal
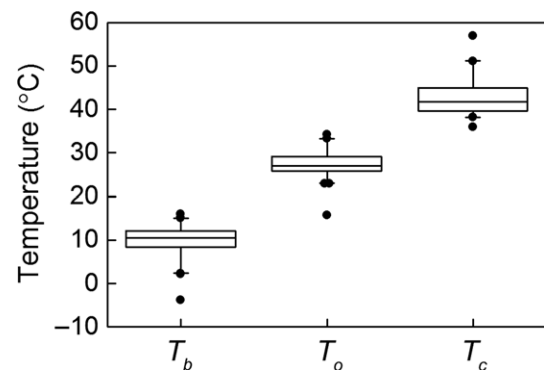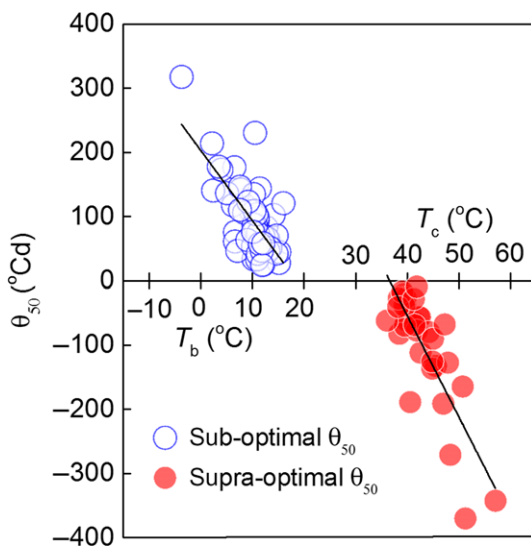

FIGURE 2 Estimated cardinal temperatures for the seed germination of 55 cactus species. Significant values of T_b (n = 57 seed lots, representing 54 species), T_o (n = 33 seed lots, representing 32 species) and T_c (n = 33 seed lots, representing 32 species) are shown. Boxes represent the 25th to 75th percentiles (median shown as the solid line), with the 5th and 95th percentiles represented by the whiskers and outliers as closed circles

temperature linear regression lines, were found to have a median value of 26.9°C and a 25–75 percentile range of 25.8°C to 29.0°C (Figure 2).

We made several observations from these analyses. Firstly, the graphs of $1/t_{50}$ plotted against temperature were not always symmetrical. For 32 species (33 seed lots) where both sub- and supraoptimal θ_{50} could be significantly estimated, 19 species (20 seed lots) had a longer suboptimal θ_{50} than supraoptimal θ_{50}, 11 species had a shorter suboptimal θ_{50} than supraoptimal θ_{50} and only two species were symmetrical (Fig. S1). Secondly, we observed that for 54 species the suboptimal θ_{50} was negatively correlated with T_b and for 32 species the supraoptimal θ_{50} was negatively correlated with T_c (Figure 3).

The most striking difference in germination behaviour among species related to T_o. For 30 species (including *Echinopsis chiloensis* ssp. *litoralis* [Species 18b]), T_o was identified at only one temperature as the germination rate was responsive to all temperature changes and decreased at temperatures above T_o ("T_o-singular"; Figure 1a; Table S2). However, for 26 species (including *Echinopsis chiloensis* ssp. *chiloensis* [Species 18a] and ssp. *skottsbergii* [Species 18c]), the maximal germination rate extended over a range of temperatures up to 8°C ('T_o-multiple'; Figure 1b; Table S2). We found that T_o-singular species had a lower T_b, higher T_c and therefore a wider T_c–T_b differential than T_o-multiple species, but T_o was not significantly different between the two groups (Table 1). As all seed collections had accompanying GIS coordinates, we accessed climate data from WORLDCLIM 1.4 and tested the 19 BioClim parameter definitions (Hijmans et al., 2005) along with altitude and latitude as explanatory

TABLE 1 Comparison of cardinal temperatures between the T_o-multiple and T_o-singular species

Cardinal temperature	T_o-multiple	T_o-singular	Two-sample *t* test		
			p value	*t* value	*n*
T_b	11.1 ± 2.6	9.1 ± 4.3	0.045	2.050	57
T_o	27.8 ± 1.8	26.8 ± 4.0	0.413	0.831	33
T_c	39.9 ± 1.3	44.6 ± 4.8	0.002	−3.302	33
T_c–T_b range	28.9 ± 1.9	35.0 ± 8.9	0.025	−2.353	33

Cardinal temperature values are means (± SD). *n*, Number of data points.

variables for the two groupings. A two-sampled *t* test revealed there were no significant differences in any of the parameters between the two groups ($p > .05$).

3.3 | Germination phenotype and the environment

To position germination sensitivity to temperature into context under both current and future environments, we performed a stepwise multiple regression to examine any association between the germination parameters (T_b, T_o, T_c and suboptimal θ_{50}) and the environment of the seed collection site [BioClim parameters (Hijmans et al., 2005), latitude and altitude] (Tables 2, S1, S2). The mean temperature of the wettest quarter of the year explained significant variation in germination performance in the suboptimal temperature range, including T_o ($p < .01$). At the macro-environmental scale, we found no effect ($p > .05$) of seed germination response altering systematically along altitudinal gradients and only a weak association with latitude.

We then estimated the germination performance of 32 species under current and two theoretical global climate change scenarios using the mean temperature of the wettest quarter (Figure 4). At current values, the mean temperature of the wettest quarter is within the suboptimal temperature range for all but three species (*Copiapoa cinerea* [Species 6], *Echinocereus stramineus* [Species 14] and *Ferocactus cylindraceus* [Species 26]; Figure 4a). We identified five species (*Consolea moniliformis* [Species 5], *Copiapoa cinerea* [Species 6], *Echinocereus stramineus* [Species 14], *Ferocactus cylindraceus* [Species 26] and *Hylocereus undatus* [Species 34]) where an increase of 1.0°C will have a negative impact on germination rate as the environmental temperature will exceed T_o (Figure 4a). With an increase of 3.7°C, eight species (*Consolea moniliformis* [Species 5], *Copiapoa cinerea* [Species 6], *Echinocereus stramineus* [Species 14], *Ferocactus cylindraceus* [Species 26], *Harrisia gracilis* [Species 33], *Hylocereus undatus* [Species 34], *Leptocereus paniculatus* [Species 35] and *Stenocereus fimbriatus* [Species 53]) were identified to have reduced germination performance (Figure 4a). Using the estimated values of sub- and supraoptimal θ_{50} to see how germination timing might change, 27 and 24 species will have faster germination under +1.0°C and +3.7°C climate change scenarios, respectively (Figure 4b). For most species, an increase of 3.7°C shortens the time to achieve 50% germination by a few days but for three species germination is estimated to occur over 30 days faster (*Corryocactus brevistylus* [Species

FIGURE 3 Linear relationship between the suboptimal thermal time (θ_{50}) and T_b, and the supraoptimal θ_{50} and T_c. The respective equations of the linear regressions are y = 203.157−10.955x (r = −0.715, P < 0.0001, n = 57 seed lots (representing 54 species)), and y = 577.399−15.799x (r = −0.814, P < 0.0001, n = 33 seed lots (representing 32 species)). Estimates of T_b, T_c and θ_{50} were calculated from plotting $1/t_{50}$ against the germination temperature as described in Figure 1

TABLE 2 Standardized regression coefficients to predict germination from environmental parameters using stepwise multiple regression. Variables contributing to each significant model are shown with standardized regression coefficients and the coefficient of partial determination in parentheses

Environmental parameters[a]	T_b (°C)	T_o (°C)	T_c (°C)	Suboptimal θ_{50} (°Cd)
Latitude (°)			0.457** (0.209)	
Mean temperature of wettest quarter	0.495***(0.371)	−0.386** (0.249)		
Precipitation of wettest quarter		−0.335* (0.099)		−0.349** (0.122)
Precipitation of warmest quarter	0.269* (0.059)			
Intercept	2.685	49.935	26.953	122.396
R^2 of total model	0.431***	0.348**	0.209**	0.122**
Coefficient of variation	36.358	10.552	12.202	60.628

[a]Latitude, altitude and 19 BioClim parameters (annual mean temperature, mean monthly temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, precipitation of the coldest quarter) as described by Hijmans et al. (2005) were considered in the analysis.

*p < .05, **p < .01, ***p < .0001.
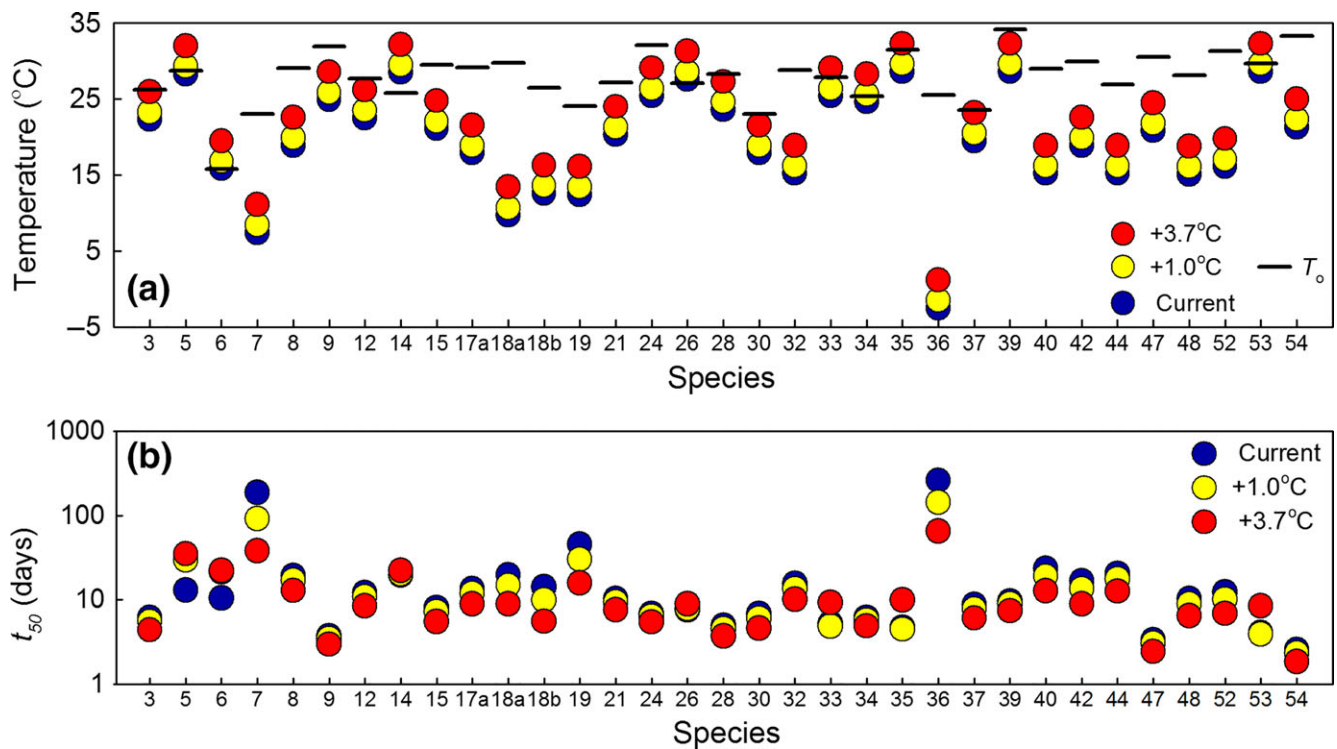
FIGURE 4 Germination performance under current and future climates. Environmental temperature, taken as the mean temperature of the wettest quarter, was projected according to the RCP2.6 (+1.0 °C) and RCP8.5 (+3.7 °C) scenarios. (a) Predictions were made by comparing T_o (line) with projected environmental temperature values at the collection site (significant estimates of T_o only, n = 33 seed lots (representing 32 species)). Where the environmental temperature exceeds T_o, a negative impact on germination rate is predicted. (b) The period (logarithmic scale) required to achieve 50% germination for the species in (a) under the different environmental temperature projections. Species are numbered as described in Table S1

7], *Echinopsis schickendantzii* [Species 19] and *Maihueniopsis glomerata* [Species 36]). *Consolea moniliformis* [Species 5] will see the largest predicted increase in germination time from 12.9 days to 34.9 days under the +3.7°C scenario.

4 | DISCUSSION

Interspecies comparisons of seed germination from across the environmental envelope of cacti in the Americas have revealed several

common thermal descriptors of germination that relate to the environment of the seed collection site, enabling an overview of the risk that cactus seed germination may face as global temperature changes. T_o is a critical threshold for germination, defining the temperature of the maximum germination rate, above and below which the germination rate is negatively affected. Exceptional thermal germination resilience was identified in 26 species by the extension of the maximal germination rate (T_o) up to an 8°C range. Broad similarities in the T_o range of 2–8°C are to the 3–12°C plateau estimated for two cultivars of ryegrass (Zhang, McGill, Irving, Kemp, & Zhou, 2013). Moreover, a curvature of the T_o–T_c response, rather than a strict plateau at T_o, was observed but not quantified in 28 crops/weeds and two wild species (Watt & Bloomberg, 2012) and quantified over a 5°C range for tomato (Labouriau & Osborn, 1984). The remaining 30 cactus species (T_o-singular) follow classical threshold modelling that typically describes a germination rate that is responsive to temperature change at T_o (e.g. Ellis et al., 1986; Garcia-Huidobro et al., 1982). To our knowledge, two distinct groupings based on the T_o of wild species have not been described within a taxonomic family.

The buffering effect of the T_o plateau on germination rate change represents a form of ecological resilience to environmental temperature perturbation for all T_o-multiple species. However, T_o-singular species are not necessarily more at risk as these species were able to germinate over a wider temperature range than the T_o-multiple species (Table 1). The widest range of 61°C was achieved by a T_o-singular species (*Maihueniopsis glomerata* [Species 36]), in contrast to the widest range of the T_o-multiple species of 33°C (*Echinopsis chiloensis* ssp. *chiloensis* [Species 18a]; Table S2). We found no environmental parameter that explains the grouping of the species by responsiveness to temperature at T_o. Any underlying taxonomic basis is unlikely as the T_o-multiple group included the genera *Mammillaria*, *Coryphantha* and *Ferocactus*, all of which have undergone a major diversification event (Vázquez-Sánchez, Terrazas, Arias, & Ochoterena, 2013). Unpredictability in this thermal resilience trait highlights the necessity to identify where environmental temperatures fall within the thermal germination range in order to fully assess the germination risk.

The mean temperature of the wettest quarter of the year was identified as the most significant climatic variable associated with the thermal germination descriptors, consistent with intra- and interspecific studies which have also correlated mean climatic variables to the developmental responses of seeds and plants (Daws, Garwood, & Pritchard, 2006; Daws et al., 2004; Moles et al., 2014). By comparing T_o with the mean temperature of the wettest quarter, we identified 29 species as currently germinating within their suboptimal temperature ranges (Figure 4a). Of these, 17 species have a longer suboptimal θ_{50} than supraoptimal θ_{50} (Fig. S1), the same left-skewed, asymmetrical response of thermal fitness traits to body temperature typical of many nonplant ectotherms (Martin & Huey, 2008). For these species, a germination rate which is less responsive to temperature change below T_o than above it, mitigates any immediate threat from environmental temperature change. The strategy in *Consolea*

moniliformis [Species 5] appears to be different, such that the current environmental temperature is buffered within the extended T_o range (Figure 4a).

Inevitably, continuing environmental temperature increase will force germination above T_o into the supraoptimal temperature range, with a progressive negative impact of slowed germination due to thermal stress. This is demonstrated for *Echinocereus stramineus* [Species 14] and *Ferocactus cylindraceus* [Species 26], which as T_o-singular species do not have an extension of T_o and as a consequence, are presumed to currently operate within the supraoptimal temperature range. Under the two climate change scenarios (IPCC, 2014), an additional six species will follow. Nonetheless, it is a positive finding of our research that Cactaceae species overall are predicted to germinate to some extent under the two climate scenarios as T_c was not exceeded by the environmental temperature of the seed collecting sites.

The remaining 24 cactus species are predicted to germinate faster throughout the 21st Century as the temperature of the wettest quarter will remain within the suboptimal temperature range (Figure 4b). For an exceptional few, this efficiency gain could be large (e.g. *Maihueniopsis glomerata* [Species 36]) which may change significantly the seasonality of germination, but for the vast majority, germination will be up to 10 days faster than currently. Critically, if rainfall is not continuously present, fewer seeds will germinate and the germination response of the seed population will become increasingly spread over time. Changes to the timing of germination will impact upon germination synchronization, seedling establishment and niche competitiveness, with ramifications at the population and community level (Yang & Rudolf, 2010).

Other important descriptors of germination behaviour were observed through the tight coupling of T_b and suboptimal θ_{50}. Ecologically, this is an effective strategy to increase the odds of seedling survival, inferring slower germination in cold environments (Table 2) that might counteract the risk of late frosts or chilling excursions, and faster germination in hot environments (Table 2) that could ameliorate the risk of drought. With a decrease in θ_{50} by 11.0°C d for every 1°C increase in T_b, perennial cacti are more similar in thermal responsiveness to the seeds of tropical trees (c. 17°C d; Dürr et al., 2015) than crops and herbs (c. 3.0°C d; Trudgill, Squire, & Thompson, 2000; Dürr et al., 2015). For the first time, we also suggest that the tight coupling of T_c and supraoptimal θ_{50} may reduce the risk of cumulative heat stress. These strategies complement the habitat preferences of many cacti which rely on the buffering of environmental extremes by nurse plants or seed location in rock cavities to provide a microclimate of stable temperature, reducing direct sunlight and improving water availability for successful seedling establishment (Flores & Jurado, 2003).

With cacti identified as the fifth most threatened major taxonomic group (Goettsch et al., 2015), there is an urgency to adopt mechanistic frameworks to predict which species are at greatest risk of germination failure during environmental perturbation. Here, we provide the first overview of interspecific plasticity of the germination phenotype across a family's environmental envelope. As regional

differences in environmental temperature change become clearer (IPCC, 2014) and regional climate models are refined (Giorgi & Gutowski, 2015), the modelling approach described here should be extended to other families and greater attention given to intraspecific plasticity within the germination phenotype. Such models should also account for germination rate dependency on precipitation loss and gain (e.g. hydro-time; Stevens et al., 2014), and the effect of environmental temperatures that alternate and transgress thermal thresholds to reveal whether temperature shifts per se have an effect on germination (Fernández-Pascual et al., 2015; Galindez et al., 2017; Murdoch, Roberts, & Goedert, 1989). Identifying species which will be overall winners and losers of climate change throughout their entire life cycle is complex. For the early life-history stages, our study reveals the majority of cacti have sufficient thermal buffering capacity of the germination phenotype to cope with the anticipated global temperature change.

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