The seed germination spectrum of 528 plant species: a global meta-regression in relation to temperature and water potential

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1 **The seed germination spectrum of 528 plant species: a global meta-regression in**
2 **relation to temperature and water potential**

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11
12 **Abstract**

13 The germination niche of plant species depends primarily on the seeds' responsiveness to temperature and
14 water potential. However, to appreciate future climate risks to natural regeneration through germination, a
15 global level synthesis across species is needed. We performed a meta-regression of primary data from 377
16 studies on 528 species, including trees, grasses, crops and wild species, to determine patterns and co-correlants
17 in the cardinal values that define species' germination niche. A negative correlation was found between thermal
18 time and base temperature, and positive correlations between other cardinal temperatures and base
19 temperature. Mean values of thermal time indicate that annual crops germinate more rapidly compared to wild
20 species, potentially as a consequence of domestication, and tropical tree seeds the slowest. Dryland species
21 (Cactaceae and Agavaceae) have the widest upper thermal and lower moisture niche, indicative of an ability to
22 grow under harsh conditions, while forages have the narrowest thermal and moisture niche, suggesting higher
23 sensitivity to frost or drought. We propose a new conceptual framework for understanding germination niche as
24 shaped by thermal and moisture traits. Our database represents a unique source of information to further
25 determine the vegetation boundaries of wild or cultivated species, including within simulation studies on plant
26 species adaptations under changing land-use and climate.
27

28 **Keywords;** Adaptive traits, climate change, ecological niche, land-use change, seed functional traits, seed
29 germination niche, threshold-type models.

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Introduction

34 Germination is a critical growth stage both for domesticated and wild plants and, as such, it plays a vital role in
35 their reproduction and regeneration. As the main environmental drivers, temperature and water potential
36 modulate the germination response of all species (Baskin & Baskin, 2014). Water potential is the most
37 important factor required for successful seed germination, influencing the vigour and final germination
38 level/percentage. The soil is the main source of water for seeds from the environment (Bewley *et al.*, 2012;
39 Zhang *et al.*, 2020). Temperature-regulated seed germination may act either by regulating dormancy status or
40 by controlling the capacity and rates of germination (Bewley *et al.*, 2012; Baskin & Baskin, 2014; Soltani *et al.*,
41 2017a,b). In the presence of adequate moisture, the germination process is limited to a permissible range of
42 temperatures that can be defined by 'cardinal' values; beyond these metabolic activities are impacted and
43 germination does not progress (Bewley *et al.*, 2012). A comprehensive understanding of seed germination
44 behavior and description of intra- and inter-variabilities between groups of species (perennials and annuals,
45 trees, grasses, crops and wild species etc.) to these two main environmental drivers of temperature and water
46 potential is thus informative for two key reasons. First, in defining where seed-producing species are currently
47 able to regenerate on the planet, and second, in predicting how these species will respond to unpredictable
48 environments in the future (Fenner & Thompson, 2005; Baskin & Baskin, 2014; Gremer *et al.*, 2020a,b).
49 Moreover, environmental cues, as an indication of climatic factors, shape the germination niche of plant species
50 that are responsive to specific germination requirements, including dormancy loss under warm and dry
51 conditions, contributing to the timing of germination (Carta *et al.*, 2022).

52 Identification of threshold-type responses to temperature and water potential values help characterize each
53 species' potential for regeneration via seed germination. Germination takes place between a minimum
54 (hereafter referred to as base temperature; T_b) and a maximum (T_{max}) threshold temperature (also known as the
55 ceiling temperature, T_c), with the highest germination speed used to define the optimal temperature (T_{opt})
56 (Bewley *et al.*, 2012; Baskin & Baskin, 2014). T_b is defined as the predicted minimum temperature to be
57 exceeded for germination to progress. It follows that germination will not progress at or below this temperature
58 (Garcia-Huidobro *et al.*, 1982a; Dahal & Bradford, 1994). Estimates of T_b are also valuable in calculating thermal
59 times for the completion of germination in the sub-optimal range between the T_{opt} and T_b. As thermal time
60 varies with sub-populations/percentiles, such estimates represent a powerful means for predicting germination
61 efficiency amongst a seed population under any, including changing, environmental conditions (Gummerson,
62 1986; Dahal & Bradford, 1994; Finch-Savage *et al.*, 2005; Maleki *et al.*, 2021). This concept of the thermal
63 parameters of germination can be expanded by incorporating different water potentials, leading to hydrotime
64 and hydrothermal time models describing the seed response above a base water potential for germination (b)
65 and its interaction with temperature, respectively (Gummerson, 1986; Dahal & Bradford, 1994; Finch-Savage *et*
66 *al.*, 2005; Donohue *et al.*, 2010; Bewley *et al.*, 2012)

67 Estimates of thermal times, cardinal temperatures (i. e. T_b, T_{opt} and T_{max}) and $_b$ have been quantified for many
68 species, allowing an interpretation of seed germination within different environments (Trudgill *et al.*, 2005;
69 Orrù *et al.*, 2012; Dürr *et al.*, 2015; Seal *et al.*, 2017; Zhang *et al.*, 2020; Maleki *et al.*, 2021) as well as intra- and
70 inter-species comparisons facilitating prediction of their spatial distribution (Dürr *et al.*, 2015). How crop and
71 weed establishment occur under current and future climates (Forcella *et al.*, 2000; Dürr *et al.*, 2001; Gardarin *et*
72 *al.*, 2012; Lamichhane *et al.*, 2020, 2022) and how plants synchronize germination and subsequent seedling
73 growth with favorable conditions can be interpreted quantitatively (Dürr *et al.*, 2015; Gremer *et al.*, 2020a;

74   Maleki *et al.*, 2021). Application of these approaches for agricultural and ecological purposes has proven to be
75   useful for an increased understanding of crop diversification in space (intercropping, relay cropping) and time
76   (e.g. introduction of cover crops between two cash crops, double cropping). Designing innovative cropping
77   systems as well as improving environmental sustainability (e.g. restoration of forests, dunes, arid lowlands) also
78   benefit from thermal modelling (Waha *et al.*, 2020; Fernández-Pascual *et al.*, 2021; Beillouin *et al.*, 2021).

79   A comprehensive review of cardinal temperatures for germination indicated that species originating from
80   different geographical origins may show variable cardinal temperatures (Dürr *et al.*, 2015), and this response
81   may result from evolutionary adaptations (Donohue *et al.*, 2010; Baskin & Baskin, 2014). How trait–
82   environment interactions can shape the germination response through the thermal niche has been
83   comprehensively modelled in the laboratory (Thompson & Ceriani, 2003; Catelotti *et al.*, 2020) and *in situ*
84   (Porceddu *et al.*, 2013; Blandino *et al.*, 2022). Thermal time models in combination with relevant
85   environmental parameters have been widely used to investigate thermal niche and germination responses to
86   accumulated temperature in agricultural and more natural settings (Garcia-Huidobro *et al.*, 1982b; Covell *et al.*,
87   1986; Pritchard & KR., 1990; Hardegree, 2006; Porceddu *et al.*, 2013; Dantas *et al.*, 2020; Maleki *et al.*, 2021).
88   Previous studies have shown that variation in threshold-type responses to ongoing environmental conditions
89   among species may reflect the seeds' thermal memory of the maternal environment (Fernández-Pascual *et al.*,
90   2019), as evidenced by the cumulative thermal effects on seed development (Daws *et al.*, 2004; Baskin &
91   Baskin, 2014) and varying levels of seed dormancy (Pritchard *et al.*, 1999; Porceddu *et al.*, 2013).

92   The concept of ecological niche has been used to define the breadth of thermal and moisture ranges in which
93   seeds should be able to germinate under current or future climatic conditions (Porceddu *et al.*, 2013; Sultan,
94   2015; Catelotti *et al.*, 2020; Ordoñez-Salanueva *et al.*, 2021). While the thermal time approach has been used
95   to predict the consequences of climate change (Orrù *et al.*, 2012; Seal *et al.*, 2017; Dantas *et al.*, 2020), hydro
96   time and hydrothermal time quantification should better enable predictions of the impact of global
97   environmental change on species' emergence and habitat patterns. Such insight can then contribute to the
98   design of amelioration and adaptation strategies for environmental management based on seed fitness. A
99   previous study proposed a qualitative conceptual framework to define the temperature tolerance ranges of
100   plant species (Walck *et al.*, 2011) while more recent studies have shown that tropical plants will face the
101   greatest risk from climate warming as they experience temperatures closer to their upper germination limits
102   (Seal et al., 2017; Sentinella *et al.*, 2020). However, no large scale study has yet quantified the germination
103   sensitivity to temperature and moisture that is useful to predict the potential impacts of shifts in environmental
104   conditions on germination.

105   Meta-analysis, meta-regression and systematic review have been widely used to analyze and synthesize data
106   from published and unpublished sources (Borenstein *et al.*, 2021). By employing a simple regression analysis
107   for synthesizing results from multiple studies, meta-regression seeks consensus on significant scientific issues
108   (Borenstein *et al.*, 2021). To this aim, we built on the framework used by Dürr et al. (2015) for a global analysis
109   of >200 species' seed germination response, but with two major differences. First, we updated their database,
110   which included 223 articles previously published on plant species with worldwide distribution, by including
111   data from an additional 154 studies published in the last decade on threshold-type responses to both
112   temperature and water potential conditions. Second, while Durr et al. (2015) used a simple literature mining
113   method, we applied a meta-regression approach and employed a new statistical method to interpret changes in
114   threshold-type responses to temperature and water potential values and the relationships among the tested

3

115   traits. To this aim, we first took seven classes of variables into account, including the variation in ranges of
116   critical temperature and water potential values among species. We then assessed how each species has variable
117   threshold-type values, and what the relationship among traits would be. The information we collated provides
118   new insight into the relevant ecologically-meaningful traits required for plant recruitment and reproduction that
119   must be considered in studies within a quantitative framework for spatial distribution of habitats, and species
120   dispersal.

121   **Materials and method**

122   Data collection

123   We updated a previous database from Dürr et al. (2015) that was based on 223 articles published before
124   December 2011. We integrated additional data that were extracted from 154 articles published between
125   December 2011 and April 2021. We used ISI-Web of Science database to retrieve these articles by using the
126   keywords "thermal requirements + germination" (199 publications), "cardinal temperature + germination"
127   (194 publications), "germination + hydrotime" (94 publications), "germination + hydrothermal time" (275
128   publications), and "thermal ranges + germination" (429 publications) for a total of 377 publications. The
129   original dataset can be accessed at https://doi.org/10.15454/XP3XHW (see Data Availability statement). We
130   used Microsoft Excel (version 2016) to collate data on traits related to hydro-thermal times and germination
131   thresholds from the published papers (Garcia-Huidobro *et al.*, 1982b; Gummerson, 1986; Dahal & Bradford,
132   1994). The traits considered in this study included cardinal temperatures (T_b, T_{opt} and T_{max}, which are estimated
133   through regression procedure), thermal time required for germination (θ_{50}, which is calculated via $\theta_{sub}(g) = (T - $
134    $T_b) \, t_g$ and $\theta_{sup}(g) = (T_c - T) \, t_g$), and base water potential (ψ_b which is quantified by $\theta_H = (\psi - \psi_{b(g)}) \, tg$ and $probit(g)=[$
135    $\psi(\theta_H/tg) - \psi_{b(50)}]/\sigma_{\psi b}$). For further information, see Garcia-Huidobro *et al.*, (1982), Gummerson (1986), Dahal &
136   Bradford (1994) and Maleki et al. (2021), and references therein. For literature mining, seven categories of
137   plant species were defined as previously (Dürr *et al.*, 2015): crops, horticultural species (vegetables, leafy
138   vegetables, ornamentals and medicinal plants), forage and rangeland species, Cactaceae and Agavaceae, wild
139   species (invasive, endangered, wild potential medicinal plants), tropical trees and other trees. All perennial
140   plants (trees and shrubs) were put into the trees category. To collect data on forage species, crops, and
141   vegetables, only species that are important for agricultural purposes, were taken into account. Our study was
142   premeditatedly limited to species with non-dormant seeds, or to seed lots where a pretreatment was applied to
143   release dormancy to avoid the influence of differing patterns of dormancy on germination and on their
144   interrelationships. Furthermore, weeds were excluded because of considerable variations in dormancy level as
145   dormancy status can change cardinal temperatures (Baskin & Baskin, 2014).

146   Determination of germination niche

147   We proposed a new conceptual framework based on the assumption that species construct their germination
148   niche in response to environmental conditions they have experienced (Sultan, 2015; Fernández-Pascual *et al.*,
149   2019). In considering germination niche, we took into account both thermal and moisture dependency. Then,
150   we collected all available data on threshold-type responses to ψ_b and cardinal temperatures. We then used a well-
151   established framework for explaining the seed thermal niche. Based on the framework, thermal niche falls into
152   two distinct categories, namely, the sub-optimal temperature range and the supra-optimal temperature range.

4

153 The sub-optimal temperature range, from T_b to T_{opt}, in which the germination rate increases as the prevailing
154 temperature rises up to T_{opt}. The supra-optimal temperature range, from T_{opt} to T_{max}, in which the germination
155 rate becomes progressively slower with temperature increase. To determine differences in moisture niche
156 shaped by $_b$ values among plant categories, we set a range varying from 0 to negative values assigned to each
157 plant category, suggesting a range in which seeds are able to germinate rapidly compared to the niche range
158 occupied. To calculate both dimensions of niche, we computed the average potential and cardinal temperature
159 values for each plant category, and then plotted the computed values on separate graphs to illustrate how the
160 ecological niche might be distinct among species and plant category.

161 Meta-regression analysis

162 Meta-regression is conceptually similar to simple linear regression, in which explanatory variables predict
163 response variables. Here, the slopes of meta-regression are the effect size predicted by a regression line. Meta-
164 regression coefficients explain how the response variable changes with an increase in the explanatory variable.
165 The effect estimate denotes log risk ratio. Explanatory variables define aspects of studies that have considerable
166 impact on the effect size (also called co-variates). A meta-regression method differs from linear regression in two
167 ways: in a meta-regression, larger studies are more influential than smaller ones; and the residual
168 heterogeneity can be modelled by explanatory variables, giving rise to random-effects meta-regression. The
169 correlation between the tested traits is indicated by positive regression slopes with significant P-values.

170 To perform meta-regression analysis, the following standard regression model was used;

$$Y = {}_0 + X + $$

171
172 Where $_0$ is intercept showing the overall effect size, Y denotes outcome variable that estimates the changes in
173 traits of interest. X is matrix of explanatory variable. and indicate the vector of coefficients and the random error
174 that refers to the classical regression model, respectively.

175 Weighted least-squares estimators of and 0 were computed as follows (Hartung *et al.*, 2008);

$$= \frac{\sum (x_i - x)(Y_i - \hat{Y})}{\sum (x_i - x)2}$$

$$_0 = \hat{Y} - X$$

$$\hat{Y} = \frac{w_i}{\sum w_i}$$

176 $\hat{Y}$ denotes the estimates of the population effect size, w_i is weight of each study.

177 Residual sum of squares was calculated using following equation:

$$Q_{residual} = W_i ({}_0 + X +)^2$$

178

179 w_i is weight of each study.

180 We employed log risk ratio as dependent variable and threshold-type traits were used as co-variate variable;

$$\text{log risk ratio} = log\ (RRi)$$
$$Ln(R) = ln\ (X1)\text{-}ln(X2)$$

181　　X1 is T_b values regressed on X2 representing other traits, including T_{max}, $T_{oopt,\ b}$ and $_{50}$

182　　The variance of log risk ratio ($vlnR$) is calculated as follows;

$$vlnR = \left(\frac{1}{n1\,(X1)^2}\right) + \left(\frac{1}{n2(X2)^2}\right)$$

183

184　　Where n_1 and n_2 denotes number of studies incorporated into analysis; X_1 and X2 are T_b values regressed on X2
185　　representing other traits, including T_{max}, $T_{oopt,\ b}$ and $_{50}$

186　　The approximate standard error (SE) was computed as follows:

$$SE\ ln\ R = \sqrt{vlnR}$$

188　　We performed meta-regression on only one covariate (e.g. T_b vs. T_{max}), and, therefore, we suggested the
189　　possibility of the Z-test to examine its relationship with effect size. This meta-regression is thus based on the Z-
190　　distribution, which is a statistical approach to test the significance of the regression slopes. Therefore, we
191　　reported the Z-value with a corresponding p-value to indicate significant correlations, and, we also computed
192　　the magnitude of the relationship. The relationship of traits to effect size (defined as log risk ratio) is calculated
193　　as follows:

194　　　　　　　　　Ln (RR) = intercept – the slope of each covariate(X)

195　　Where X is the absolute value of traits.

196　　The 95% confidence interval for each covariate is estimated as follows:

197　　　　　　　　　LL= X-1.96×SE

198　　　　　　　　　UL=X+1.96×SE

199　　LL and UL refer to lower limit and upper limit, respectively. In the above-mentioned equations, 1.96 shows the
200　　Z-value corresponding to confidence limits of 95% (making space for 2.5% error at both end of the distribution).

201　　**Results**

202　　Intraspecific variation in traits among plant categories

203　　Values related to intraspecific variation in traits among plant categories are reported in **Table 1** while the
204　　number of species included in intraspecific variation in the analyzed traits among the plant categories is
205　　presented in **Figure 1**.

6

206 **Table 1.** Intraspecific variation in the analyzed traits among the plant categories. The estimates were separately computed using the
207 standard deviation of observed values for each category. T_b, T_{opt} and T_{max}, ΔT_{opt}-T_b, ΔT_{max}–T_{opt} indicate the base, optimum, maximum
208 sub- and supra optimal temperature values, respectively; θ_{50} indicates thermal time required to attain 50% germination while $_b$
209 indicates the base water potential values.

Plant category	T_b (C)	T_{opt} (C)	T_{max} (C)	ΔT_{opt}-T_b (C)	ΔT_{max}–T_{opt} (C)	θ_{50} (°Cd)	$_b$ (MPa)
Tropical trees	4.034	3.404	4.852	5.352	6.006	134.113	0.392
Other trees	4.993	9.732	8.199	9.012	11.794	44.567	1.018
Crops	4.589	5.160	5.722	5.071	7.595	12.791	0.578
Horticulture	4.106	5.679	5.616	3.809	4.185	23.200	0.266
Forage and rangeland	2.322	4.599	4.735	3.456	5.037	12.495	0.344
Cactaceae and Agavaceae	3.477	4.504	5.535	4.527	5.366	19.434	0.569
Wild species	4.657	7.438	6.046	6.386	4.200	43.880	0.448
Average	4.025	5.788	5.815	5.373	6.343	41.497	0.516

210

211 Much information was available on forage and rangeland (198 species) and wild species (107 species) followed
212 by tropical trees (85 species) and crops (45 species). In contrast, we found much less data on Cactaceae and
213 Agavaceae (10 species). The range of variation in T_b was similar among plant categories with the ranges varying
214 from 3°C for forage and rangeland to nearly 5°C for other trees. There was a considerable variation in $_{50}$ with a
215 window ranging from 12°Cd in forage and rangeland to 134°Cd in tropical trees. Variation in T_{opt}, T_{max} and ΔT_{opt}-
216 T_b was not important among plant categories. $_b$ values showed the lowest variation among the plant categories.
217 Among all traits considered, forage and rangeland species included higher number of species followed by wild
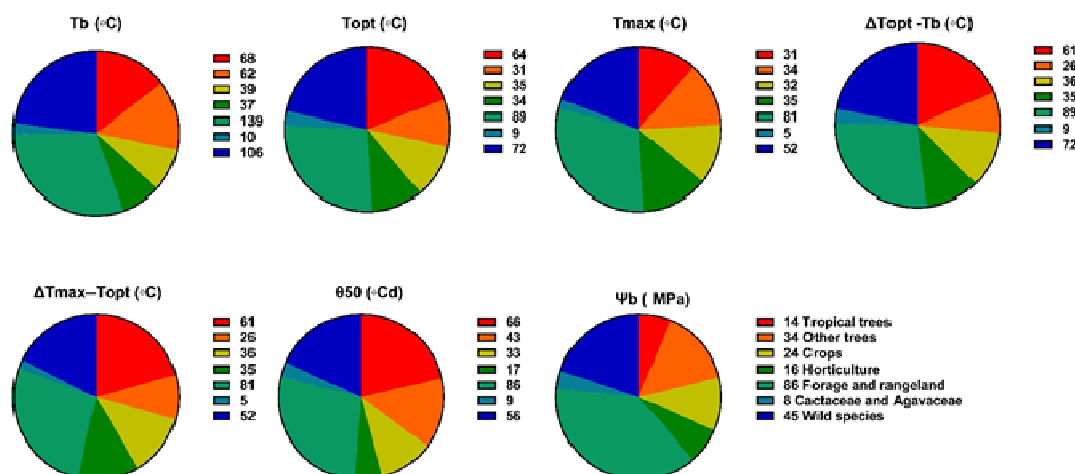218 species and tropical trees **(Figure 1)**.

219

220 **Figure 1.** Number of species included in intraspecific variation in the analyzed traits among the plant categories. The numbers
221 reported in the legend show the number of species in this set of analysis (the number of studies is provided in parenthesis of Figure
222 1). The number of species exceeds the number of studies as a given study may have reported data on different species. T_b, T_{opt} and T_{max},
223 ΔT_{opt}-T_b, ΔT_{max}–T_{opt} indicate the base, optimum, maximum sub- and supra optimal temperature values, respectively; θ_{50} indicates
224 thermal time required to attain 50% germination while $_b$ indicates the base water potential values.

225

7

226   Cardinal temperatures

227   While Ψ_b values were reported only for 226 species, temperature-based traits were the most studied with T_b and
228   T_{opt} values being reported for 461 and 334 species, respectively. T_b values varied greatly among plant groups,
229   ranging from -4.8°C for *Koeleria vurilochensis* (i.e. forage and rangeland category) to 21.9°C for *Terminalia*
230   *brassii* (Tropical trees category; **Figure 2a**). Succluent species (Cactaceae and Agavaceae families) showed less
231   extreme values with the same mean of 10 C while other species groupings in the analysis had wider variabilities
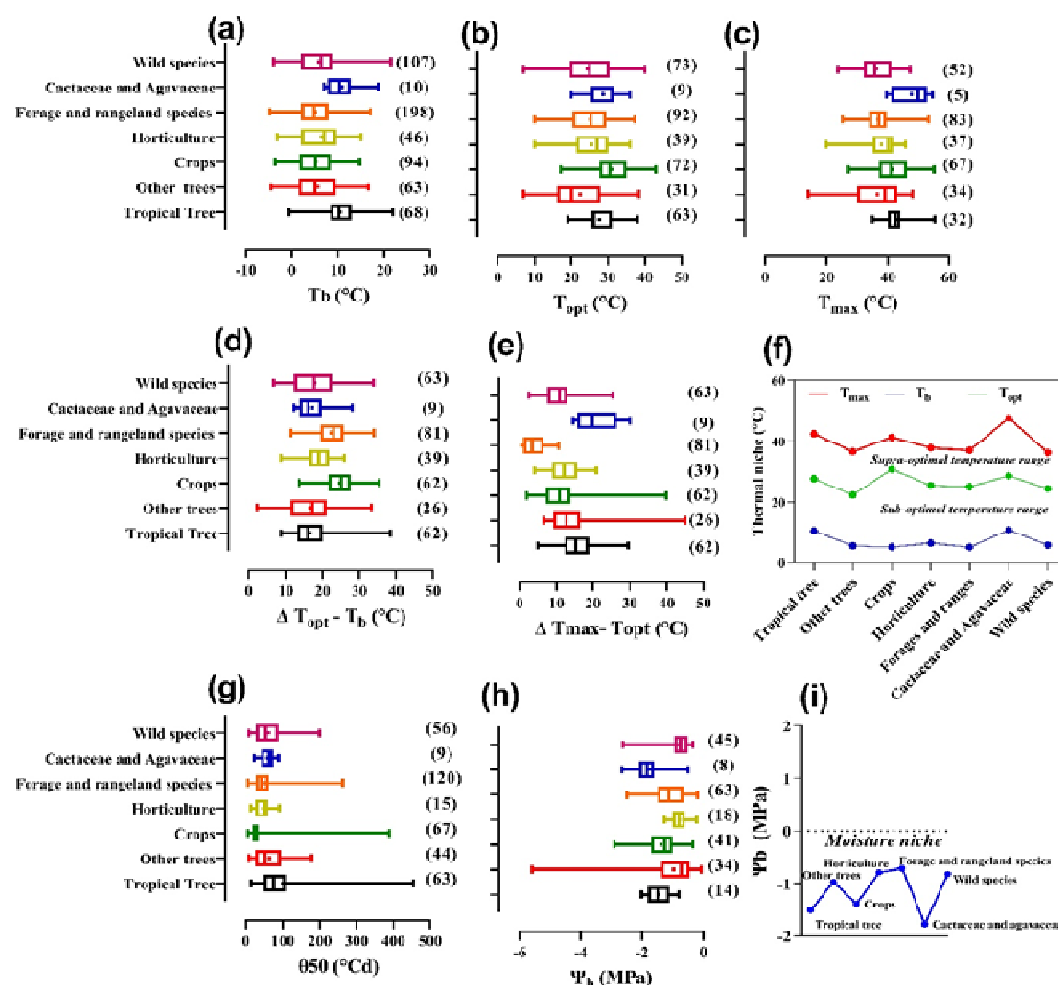232   in T_b values.

233

234   **Figure 2.** Ranges of base (T_b; **a**), optimum (T_{opt}; **b**), maximum (T_{max}; **c**) temperatures, sub-optimal (ΔT_{opt}-T_b; **d**), supra-optimal (ΔT_{max}-
235   T_{opt}; **e**), thermal niche (upper and lower; **f**), thermal time required to attain 50% germination ($_{50}$; **g**), base water potential ($_b$; **h**), and
236   moisture niche (**i**) values of different plant categories considered in this study. The numbers in the parenthesis represent the number
237   of studies found in the literature for each plant group. A frequency distribution was used to show the overview of all traits in some
238   plant categories. In this case, the approach used represents how frequencies are distributed over the observed values. Two-
239   dimensional visualization of the ecological niche of plant species indicating the mean thermal (**f**) and moisture niche (**i**) occupied by
240   each plant category. The breadth of sub-optimal temperature range characterizing the lower thermal niche was estimated by the
241   difference between minimum and optimum temperature while the of supra-optimal temperature range characterizing the upper
242   thermal niche was estimated by the differences between maximum and optimum temperature. Moisture niche was a dimension
243   estimated by taking the mean $_b$ values of each plant category from the database.

8

244 T_{opt} for germination of crops was limited to a window ranging from 17°C to 44°C, the latter being the highest
245 observed values **(Figure 2b)**. The widest range of T_{opt} for germination was found for wild species, from 7 C to 40
246 C, followed by the category "other trees" from 6°C to 38°C. In contrast, inter-species variation for T_{opt} for
247 Cactaceae and Agavaceae and tropical trees had the narrowest range, with values of 20 C to 39 C and 20°C to
248 40°C, respectively.

249 T_{max} also varied considerably among plant categories. The lowest T_{max} values were observed for non-tropical trees
250 (14C for *Acer saccharum*) and horticultural plants (20°C for *Muscari comosum*). In contrast, the highest T_{max}
251 values were around 55°C, in tropical trees (55.4°C for *Cenostigma microphyllum*), Cactaceae and Agavaceae
252 (54.5°C for *Polaskia chende*), forage and rangeland species (53.3°C for *Urochloa brizantha*) and crops (55°C for
253 *Cicer arietinum L.*) **(Figure 2c)**. Amongst species groupings, T_{max} varied the most for non-tropical trees (14°C for
254 *Acer saccharum* to 48°C for *Anadenanthera colubrine*; **Figure 2c**) and the least for Cactaceae and Agavaceae
255 (from 39.5°C to 54.5°C for *Manfreda brachystachya* and *Polaskia chende*, respectively).

256 Thermal niche for germination and $_{50}$

257 Values of sub- and supra-optimal temperature range varied markedly among plant species (**Figure 2d,e,f**).
258 Forage and rangeland species and crops, showed the widest sub-optimal temperature range, with the extreme
259 values of 20°C and 26°C, respectively. In contrast, non-tropical and tropical trees had the narrowest sub-optimal
260 temperature range, with an average value of 17C for both plant categories. In the supra-optimal temperature
261 range all species had a thermal niche spanning mean values of 12°C to 19°C, e.g. Cactaceae and Agavaceae
262 (19°C), tropical trees (15°C), non-tropical trees (14°C), crops (11°C) and wild species and horticulture species
263 (both 12°C) .

264 $_{50}$ values varied nearly two orders of magnitude among plant groups ranging from 6 °Cd to 500Cd **(Figure 2g)**.
265 Tropical tree species had the highest range of $_{50}$ values, ranging from 15.1°Cd for *Anadenanthera colubrina* to
266 477°Cd for *Araucaria angustifolia*. In crops, $_{50}$ ranged only about 10-fold, from 6.3°Cd for *Sesamum indicum* L.
267 to 59.4°Cd for *Vicia variabilis*. Wild species, forage and rangeland species, and non-tropical trees showed a
268 similar range in terms of thermal time required for germination, varying from 6°Cd to 263°Cd. Cactaceae and
269 Agavaceae all had relatively short $_{50}$ varying only two-fold from 39.3°Cd to 87.6°Cd.

270 Ψ_b and moisture niche for germination

271 Ranges of Ψ_b values are presented **Figure 2h**. Compared to the other traits mentioned above, we found fewer
272 data on Ψ_b values of tropical trees (14 papers) and horticultural plants (18 papers). In contrast, much more
273 information was available on Ψ_b values of forage and rangeland species (63 papers) and wild species (45
274 papers). Overall, Ψ_b values differed considerably among plant species, ranging from a lowest value of -6 MPa for
275 *Atriplex halimus* (a non-tropical tree species) to nearly -0.2 MPa observed for *Stipa grandis* (a forage and
276 rangeland species). Wild species, Cactaceae and Agavaceae, and crops showed similar Ψ_b values, with a range
277 varying from -3 MPa to nearly 0 MPa. In contrast, the narrowest range of Ψ_b values was for horticultural crops
278 (from -1.27 MPa for *Cucurbita pepo* to -0.21 MPa for *Trachyspermum ammi*) followed by that for tropical trees
279 (from -2.02 MPa for *Apeiba tiborbou* to -0.81 MPa for *Peltophorum dubium*) and wild species (from -2.62 for
280 *Pectocarya heterocarpa* to -0.34 MPa for *Erodium cicutarium*). Forage and rangeland species showed the highest
281 Ψ_b values (near to zero as for example -0.21 MPa for *Stipa grandis*).

9

282 Values of moisture niche are presented in **Figure 2i**. Similar to the higher thermal niche, tropical trees (14
283 species and 13 papers), and Cactaceae and Agavaceae (12 species and 8 papers) were revealed to be the most
284 tolerant groups to drought, with a range varying from -2.64 MPa to -0.5 MPa . In contrast, non-tropical trees,
285 and forage and rangeland species showed higher (less negative) Ψ_b values, of -0.07 and -0.19 MPa,
286 respectively. Crops had the widest moisture niche, with a range varying from 0 MPa to -1.39 MPa. Forage and
287 rangeland, and horticulture species have the narrowest moisture niche, with the occupancy range varying from
288 0 to -0.71 MPa and from 0 to -0.79 MPa, respectively.

289 Correlations between traits

290 A positive correlation was found between T_b and T_{opt} values for all plant categories (**Figure 3a)**. The steepness of
291 regression slopes was the highest for forage and rangeland species (0.07; P=0.02; **Table 2**) and lowest for
292 Cactaceae and Agavaceae and tropical tree species (0.02 and P=0.00 for both species; **Table 2**).

293 **Table 2.** Meta-Regression reporting T_{opt}, T_{max}, ΔT_{opt}-T_b, ΔT_{max} –T_{opt}, 50 and $_b$, values for different categories of plant species as a function
294 of T_b for germination. The coefficients were obtained using linear regression. Residual heterogeneity indicates variation around the
295 true regression line. Tau-squared shows the variance of the effect size across studies included in the analysis. T_b, T_{opt} and T_{max}, ΔT_{opt}-T_b,
296 ΔT_{max}–T_{opt} indicate the base, optimum, maximum sub- and supra optimal temperature values, respectively; θ_{50} indicates thermal time
297 required to attain 50% germination while $_b$ indicates the base water potential values.

298

Plant group	Coefficient		SE	P-value	Residual heterogeneity	Tau-squared
	Intercept	Slope				
T_{opt}						
Tropical trees	-0.71	0.02	0.00	0.00	86.44	0.00
Other trees	-0.87	0.04	0.01	0.03	22.41	0.00
Crops	-1.05	0.05	0.00	0.00	89.24	0.00
Horticulture	-0.84	0.03	0.00	0.03	52.40	0.00
Forage and rangeland	-1.17	0.07	0.00	0.02	74.14	0.00
Cactaceae and Agavaceae	-0.71	0.02	0.0	0.00	6.38	0.00
Wild species	-0.95	0.05	0.00	0.01	10.02	0.01
Average	-1.08	0.05	0.00	0.014	53.04	0.01
T_{max}						
Tropical trees	-1.20	0.06	0.00	0.01	14.30	0.00
Other trees	-1.07	0.04	0.00	0.01	18.68	0.00
Crops	-1.16	0.05	0.00	0.00	74.76	0.00
Horticulture	-1.06	0.04	0.00	0.04	45.38	0.00
Forage and rangeland	-1.26	0.07	0.00	0.02	83.64	0.00
Cactaceae and Agavaceae	-1.03	0.03	0.01	0.03	4.69	0.00
Wild species	-1.15	0.06	0.00	0.02	53.17	0.00
Average	-1.23	0.06	0.00	0.00	55.31	0.01
ΔT_{opt}-T_b						
Tropical trees	-0.84	0.06	0.00	0.04	51.12	0.00
Other trees	-0.69	0.04	0.00	0.00	17.58	0.00
Crops	-1.02	0.06	0.00	0.03	12.46	0.01
Horticulture	-0.87	0.05	0.00	0.01	52.93	0.00
Forage and rangeland	-1.19	0.09	0.00	0.00	62.39	0.00
Cactaceae and Agavaceae	-0.74	0.04	0.00	0.02	8.11	0.00

Wild species	-0.97	0.07	0.00	0.02	82.97	0.01
Average	-1.01	0.07	0.00	0.00	63.75	0.01
$\Delta T_{max} - T_{opt}$						
Tropical trees	-0.938	0.07	0.00	0.04	31.16	0.00
Other trees	-1.15	0.09	0.00	0.00	27.32	0.01
Crops	-0.79	0.06	0.00	0.03	17.46	0.01
Horticulture	-0.71	0.06	0.00	0.01	22.53	0.00
Forage and rangeland	-0.91	0.07	0.00	0.00	12.25	0.00
Cactaceae and Agavaceae	-1.03	0.07	0.00	0.02	18.56	0.01
Wild species	-0.79	0.08	0.00	0.02	62.67	0.01
Average	-0.65	0.05	0.00	0.00	52.25	0.00
50						
Tropical trees	1.25	-0.03	0.01	0.02	60.32	0.06
Other trees	1.02	-0.03	0.01	0.00	63.74	0.09
Crops	0.52	-0.04	0.03	0.01	30.18	1.18
Horticulture	1.61	-0.11	0.02	0.03	11.79	0.07
Forage and rangeland	0.82	-0.02	0.05	0.02	19.38	0.00
Cactaceae and Agavaceae	0.93	-0.02	0.02	0.00	8.48	0.00
Wild species	1.40	-0.07	0.00	0.00	63.02	0.01
Average	0.90	-0.02	0.00	0.01	21.50	0.12
b						
Tropical trees	0.08	0.40	0.41	0.03	0.33	0.00
Other trees	-1.38	-0.44	0.22	0.02	8.67	0.00
Crops	-1.30	-0.60	0.13	0.01	18.20	0.08
Horticulture	-1.12	-0.38	0.37	0.01	19.61	0.01
Forage and rangeland	-0.50	-0.09	0.04	0.01	55.63	0.03
Cactaceae and Agavaceae	-1.70	-0.54	0.30	0.02	1.60	0.00
Wild species	-1.27	-0.73	0.14	0.01	40.08	0.01
Average	-0.003	-0.26	0.05	0.00	30.29	0.05

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Values of T_b positively correlated with T_{max}, with a high proportion of variance corresponding to high T_b values (**Figure 3b**). The steepness of the regression slopes differed markedly among plant categories, from 0.07 for Forage and Rangeland species (P=0.02 and 0.01, respectively; **Table 2**), then wild species and tropical trees, (0.06 for both, P=0.02 and 0.00, respectively; **Table 2**). In contrast, a weaker correlation was observed between T_b and T_{max} in Cactaceae and Agavaceae, and horticulture species as shown by the regression slope values of 0.03 and 0.04, respectively (P=0.03 and 0.04, respectively; **Table 2**).

Different data inputs and variance are shown in **Figure 3** by varying size of bubbles such that inflated bubbles refer to higher variance. Despite differing levels of data coverage that may influence the slopes of meta-regression and subsequently the correlations obtained, the general trend indicates that there is a positive correlation between T_b and T_{max} (the slope of 0.060; **Table 2; Fig 3b**). Tropical trees, and forage and rangeland species showed steeper slopes than the general trend while all other plant categories were characterized by values lower than the general trend (**Table 2; Fig 3b**). Overall, variance inflated with increasing T_b, indicating that theres is considerable difference between species groups and data shortage (**Figure 3**). This trend may be reflected in other parameters as well.
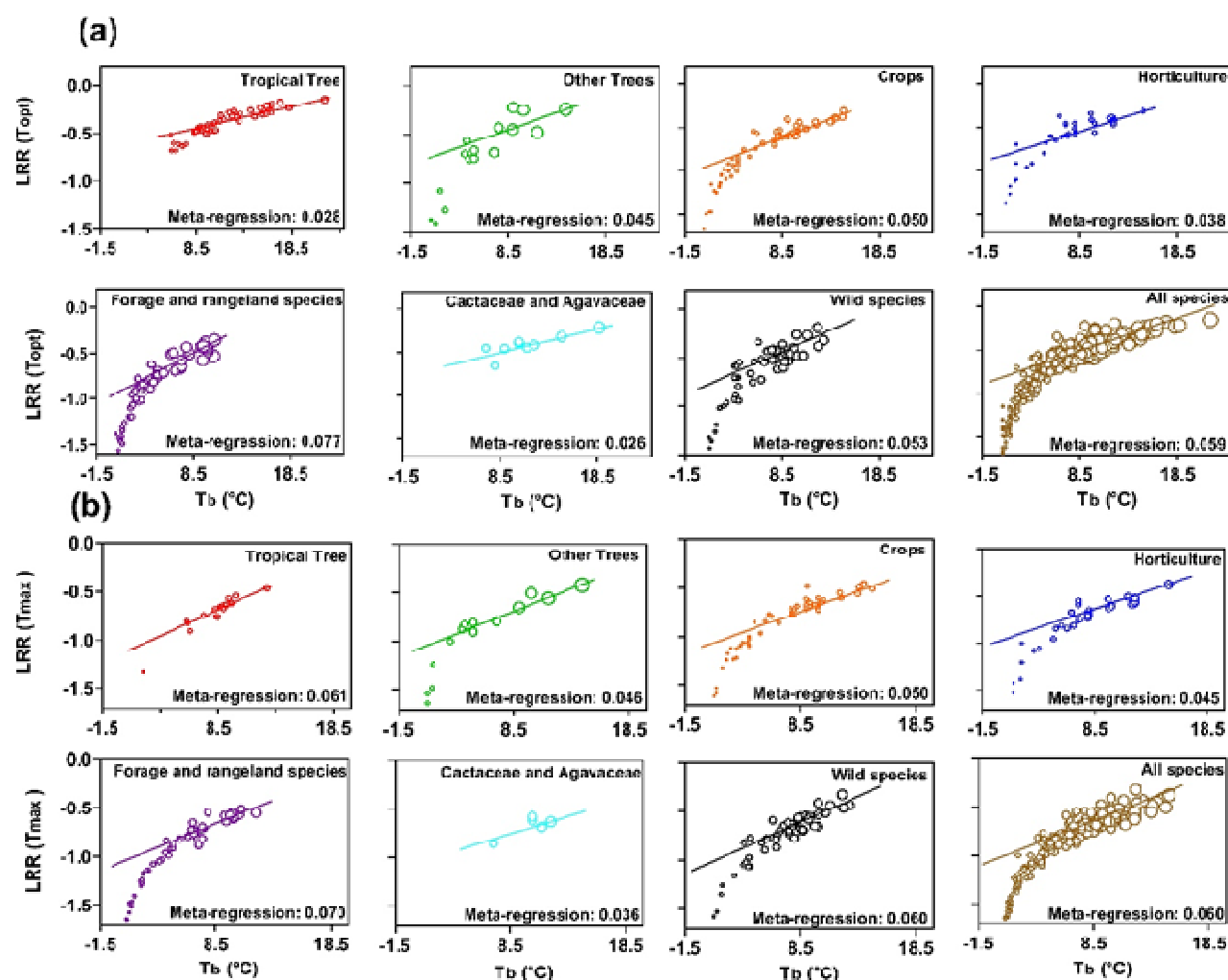
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Figure 3. Regression of log risk ratio (LRR) of optimum (a) and T_{max} (b) temperature on base temperature (T_b). The size of each bubble is inversely correlated with the variance of the log relative risk estimate with larger bubbles showing more inflated variance. LRR represents the probability of changes in the range of T_{opt} and T_{max} as a function of differing T_b ranges. Fitted lines were obtained through linear regression approach ($Y = _0 + X + $). Each plant category is indicated as a separate panel.

Correlation results between T_b and thermal niche are presented in **Figure 4**. We found a positive correlation between T_b and ΔT_{opt} -T_b values for all plant categories **(Fig 4a)**. The steepness of regression slopes was the highest for forage and rangeland species (0.095; P=0.00; **Table 2**), followed by that of wild (0.079; P=0.02; **Table 2**), crops (0.063; P=0.03; **Table 2**), tropical tree (0.061; P=0.04 Table 1), horticulture (0.0596; P=0.01 Table 1), Cactaceae and Agavaceae (0.048; P=0.02), and non-tropical tree (0.04; P=0.00; **Table 2**).
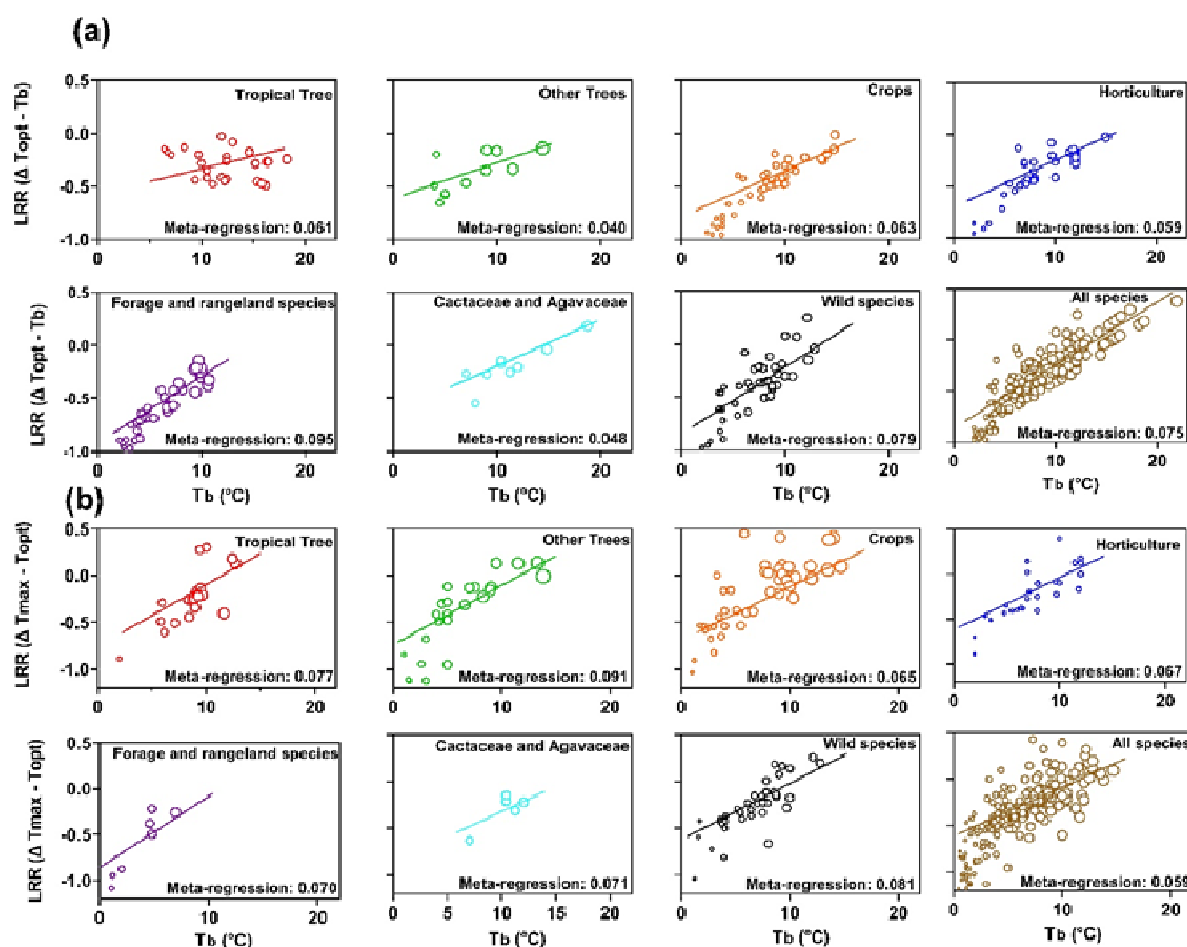
Figure 4. Regression of log risk ratio (LRR) of sub-optimal (ΔT_{opt}-T_b; **a**), supra-optimal (ΔT_{max}-T_{opt}; **b**), on base temperature (T_b). The size of each bubble is inversely correlated with the variance of the log relative risk estimate with larger bubbles showing more inflated variance. LRR represents the probability of changes in the range of Δ values of sub- and supra-optimal temperature as a function of changes in T_b. Fitted lines were obtained through linear regression approach ($Y = {}_0 + X + $). Each plant category is indicated as a separate panel.

There was also a positive correlation between T_b and ΔT_{max} –T_{opt} values for all plant categories (**Fig 4b**). Other trees and wild species showed the highest steepness of regression slopes, with the slope of 0.091 and 0.081(P=0.00; **Table 2**). Followed by other trees (0.091) and wild species (0.081), the highest slope was for tropical trees (0.077) and forage and rangeland species (0.070). In contrast, the steepness of regression slopes was the lowest for crops (0.065).
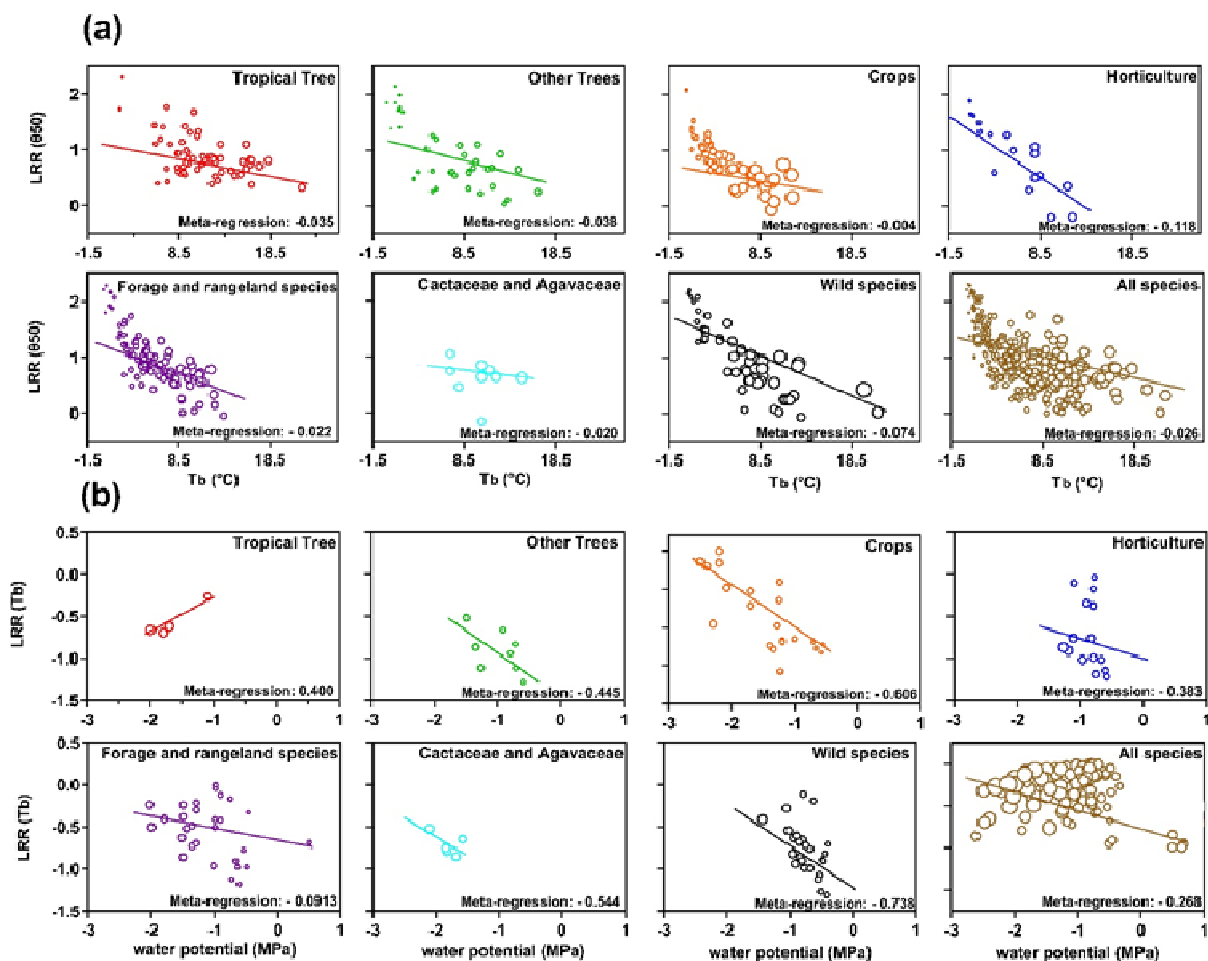
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Figure 5. Regression of log risk ratio (LRR) of thermal time required to attain 50% germination (θ50%) on base temperature (T_b; **a**) and LRR of base temperature (T_b) on base water potential ($_b$) values **(b)**. The size of each bubble is inversely correlated with the variance of the log relative risk estimate with larger bubbles showing more inflated variance. LRR represents the probability of changes in θ50% as a function of changes in T_b **(a)** values and in the range of T_b as a function of differing $_b$ values **(b)**. Fitted lines were obtained through linear regression approach ($Y=_0+X+$). Each plant category is indicated as a separate panel.

Correlation results between T_b and $_{50}$ are presented in **Figure 5a**. We observed a negative relationship between T_b and $_{50}$ with different meta-regression values among plant categories. The steepness of slope was the highest in horticultural species (i.e. -0.11; **Table 2**) followed by wild species (- 0.07) while the lowest slope was observed for crops (- 0.04). Horticultural species were followed by Cactaceae and Agavaceae, and forage and rangeland species showed a slight increase in $_{50}$ as a function of T_b, with the slope steepness of -0.020 and -0.022, respectively **(Table 2)**.

Overall, a negative relationship was found between T_b and Ψ_b values in all species included in this study, with the regression slope of -0.26 (-0.26 P=0.00; **Table 2**). A strong negative correlation between T_b and $_b$ values was observed for all but tropical tree species **(Figure 5b)**, with considerable difference in the steepness of regression slopes among plant categories **(**P=0.03; **Table 2)**. Wild species had the lowest values of the regression slopes (-0.73; P=0.01; Table 1), followed by those of crops (-0.60; P=0.01), Cactaceae and Agavaceae (-0.54; P=0.02; Table 1), non-tropical tress (-0.44; P=0.02; **Table 2**), and horticulture species (-0.38; P=0.01; **Table 2**). In

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355   contrast, a positive correlation between the T_b and $_b$ values was observed for tropical tree species with a slope of
356   0.40, although this plant category had few data (only 4 species).

4. Discussion

358   Sensitivity to environmental factors is a critical ecological process for plants occurring in unpredictable habitats
359   where successful germination is highly dependent on the spatio-temporal variability of temperature and rainfall
360   (Batlla & Benech-Arnold, 2015; Soltani *et al.*, 2017a,b; Maleki *et al.*, 2021). For 569 species of wild and
361   cultivated origin, we analysed the thermal and moisture germination niches through temperature and water
362   potential thresholds and thermal timing, and considered how these varied among different species and plant
363   categories.

364   Thermal germination niche was classified into two distinct ranges viz. sub- and supra- optimal ranges. Within
365   sub-optimal range, crops showed the widest thermal germination niche that could be a result of the selection
366   and domestication process. A wide sub-optimal temperature range increases the possibility of crop adaptations
367   across contrasted thermal environments, including fluctuating temperatures, which may allow the relative
368   synchronization of germination under known environmental and management conditions. The availability of fit-
369   for-purpose seed lots greatly reduces risks of germination failure, particularly at sub-optimal temperatures.
370   Predictable performance at low temperature means that spring crops can be sown early to escape late season
371   summer drought and winter crops sown to avoid early/late season frosts. In contrast to crops with the widest
372   thermal germination niche, species originating from warmer environments, such as tropical trees, had the
373   narrowest thermal niche within the sub-optimal temperature range. This could be due to a strong natural
374   selection and environmental drivers such that thermal niche is narrow when environmental filters are stronger
375   (Fernández-Pascual *et al.*, 2017). Consequently, when considering germination niche, habitat-specific strategies
376   should be taken into account as habitat-generalist and habitat-specialist plants can have broader and narrower
377   germination niches, respectively (Marques *et al.*, 2014). Although we did not focus on habitabt-specific
378   strategies, our results highlight the need for future research on the environmental and abiotic conditions (i.e.,
379   environmental and physico-chemical) which may limit the emergence of plant species (Tudela-Isanta *et al.*,
380   2018). We also show that crops relative to tropical trees have the steepest regression slope when considering
381   the relationship between T_b and T_{opt} and delta values, indicating that crops have higher sensitivity to sub-optimal
382   temperatures compared to tropical trees (**Figure 4a; 5a**). Such enhanced sensitivity effectively means that crop
383   seed germination is a more efficient over a range of conditions.

384   In contrast to sub-optimal temperature, the sensitivity pattern of supra-optimal temperature range was
385   considerably different, with Cactaceae and Agavaceae having the widest and crops showing the narrowest
386   supra-optimal temperature range (**Figure 2f**). This suggests that exposure of Cactaceae and Agavaceae to
387   extreme tropical dryland conditions may have facilitated population divergence through an adjustment in
388   germination behaviour as a consequence of parental environmental (Lampei *et al.*, 2017). Based on the concept
389   of parental environmental effects, offspring can take advantage of information about parental environment to
390   drive specific phenotypes for optimizing the match with the offspring environment (Lacey, 1988). This
391   ecological process requires a correlation between parental and offspring environments (Ezard *et al.*, 2014;
392   Burgess & Marshall, 2014; Leimar & McNamara, 2015). In contrast to Cactaceae and Agavaceae, crops, which
393   are often grown under optimal management conditions, have a lower capacity to tolerate warmer conditions,
394   and thus, could be subjected to higher mortality risks under climate change. An example is the reduced

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395   capabity of sunflower (*Helianthus annuus*) compared to its wild relatives to convert to normal seedlings at high

396   temperatures and low water potentials (Castillo-Lorenzo *et al.*, 2019a,b)

397   Our meta-regression results highlight a sensitivity pattern whereby, within both sub- and supra-optimal

398   temperature ranges, species (or gropus) with lower T_b might be the most sensitive to climate change because of

399   their smaller delta values (i.e., T_o-T_b; T_{max} – T_o). This means that increases in global average temperature could

400   impact such species germination performance as the supra-optimal temperature range would be relatively

401   easier to reach. Most likely, and if genotypic limits are not exceeded, natural selection for and evolution towards

402   higher T_b and wider delta values could enable continuing emergence. Such adaptation to a potentially new (but

403   still narrower) germination niche (Fernández-Pascual *et al.* (2017) might be more likely for annual species than

404   pererennials, such as trees, Cactaceae and Agavaceae.

405   The trend of supra-optimal temperature range also reflects the moisture niche dependency, with Cactaceae and

406   Agavaceae occupying broader moisture niche. Again, this may suggest that divergence in parental

407   environmental effects could have driven Cactaceae and Agavaceae toward wider moisture niche to be able to

408   capitalize on short periods of water availability under unpredictable conditions (Baskin & Baskin, 2014; Lampei

409   *et al.*, 2017) and the rapid initiation of the germination process as soil moisture increases. Overall, we show that

410   species with narrower moisture niche have a stronger relationship between T_b and Ψ_b explaining that species

411   with wider supra-optimal temperature range may have broader moisture niche, which results from a correlation

412   between parental and offspring environments (Ezard *et al.*, 2014; Burgess & Marshall, 2014; Leimar &

413   McNamara, 2015).

414   The sensitivity pattern reflected in sub- and supra-optima temperature range is also evidence in the Ψ_b values.

415   Species with higher T_b are potentially more tolerant to drought as shown by lower Ψ_b values. For instance,

416   tropical trees show a positive correlation between T_b and Ψ_b that is probably due to a high frequency of rainfall

417   in tropical areas. However, the ongoing variability in rainfall frequency and intensity due to climate change may

418   affect tropical trees through the germination phase of the life cycle (Pritchard *et al.*, 2022).

419   Variability in T_b values among plant categories

420   Cactaceae and Agavaceae are characterized by the lowest variabilities in terms of T_b extreme values, suggesting

421   their sensitivity to lower temperature range. A negative correlation was observed between T_b and $_{50}$ values.

422   Annual plant species of tropical origin (e.g. cotton and mungbean), have the highest T_b values, while tree

423   species from cooler regions (e.g. such as oak, betula and ash) show the lowest T_b values. Moreover, some crops

424   (e.g. winter pea) are projected to be able to germinate at sub-zero temperatures (T_b = -1.10 °C), which could be

425   due to selection through breeding (Stupnikova *et al.*, 2006) Overall, we found positive correlations between T_b

426   and other traits related to cardinal temperatures suggesting that plant species alter T_b values in harmony with

427   other thermal traits as a highly efficient adaptation strategy to coping with harsh conditions.

428   Based on the results of this study, T_b for some plant categories are below zero except for Cactaceae and

429   Agavaceae and tropical trees. Germination at subzero temperatures is likely because proteins and sugars in

430   plant cell that protect cell environment from damages caused by ice formation. A recent study (Jaganathan *et*

431   *al.*, 2020) proposed three main mechanisms for sustaining survival at subzero temperatures, including the

432   existence of water impermeable seed coats, the super-cooling of seed tissue and freezing tolerance triggered by

433 extracellular-freezing. Species included in our study might take advantage of these mechanisms to ensure their
434 survival at subzero temperatures.

435 Amplitude of T_{opt} and T_{max} values among plant categories

436 The range of T_{opt} was narrow compared to T_{max} range. The range of T_{max} ranged from 8C in forages and rangeland
437 species to 44C in crops, suggesting that crops seem to be a category that has higher T_{opt} (from 17.2C for
438 *Onobrychis subnitens* to 43C for *Sorghum bicolor*) due to domestication and selection events targeting rapid
439 germination across fluctuating environmental conditions.

440 Crops and horticultural species are likely to have higher T_{opt} and T_{max} values compared with other categories. This
441 could be driven by their selection aimed at adapting to wider environmental conditions, including hotter
442 regions of the world. For instance, horticultural species are high-value crops that are most often grown under
443 irrigated conditions that make it possible to grow them even across extremely hot conditions. Crops with
444 tropical origin, such as cotton and mungbean, have the highest T_{opt} and T_{max} values. For many species, the range
445 of T_{max} was 40-45 C, and it seems that seeds of these species are not able to progress towards completion of
446 germination above T_{max}. However, some crops are able to germinate at temperatures> 45°C (e.g. *Phaseolus*
447 *vugaris* L., *Glycine max* L., *Cicer arietinum* L. and *Sesamum indicum* L.). These values suggest that there may be
448 an upper temperature limit (T_{max}) to the germination process around 50-55°C. This limit could be imposed by
449 the onset of enzyme denaturation and activities at molecular level leading to cell death and failure of cell
450 growth. For example, lentil and pea seed amylase required for starch degradation in the early stages of
451 germination becomes inactive within minutes of exposure to 70°C and 80 °C, respectively (Tárrago & Nicolás,
452 1976; Adegbanke *et al.*, 2021).

453 This suggests that in addition to adaptation to environmental conditions within genetic limits, there might be
454 cell functional and signaling constraints that control the biological range within which seeds are able to
455 germinate. In contrast, the threshold-type response of wild species (other than Cactaceae and Agavaceae) to T_{max}
456 was weaker than that of crops and was restricted to 20-45°C. For instance, non-tropical trees such as sugar
457 maple (*Acer saccharum* M.) have the lowest T_{max} values (i.e. 14°C). Such a low T_{max} value may be confounded by
458 the presence of dormancy in this species. Species with such non-deep physiological dormancy have limited
459 cardinal temperatures at maturity, e.g. *Aesculus hippocastanum* (Pritchard et al., 1999), and seeds with this
460 'conditional dormancy' progressively gain the ability to germination over a broader temperature range (Baskin
461 & Baskin, 2014; Maleki *et al.*, 2021; Soltani *et al.*, 2022). As for T_{opt} values, they increased as a function of T_b, as
462 shown by the regression slope, which may suggest coevolution of threshold-type responses to temperature that
463 need to be explored by future research.

464 Range of $_{50}$ values among plant categories

465 Values of $_{50}$ provide a context for adaptive strategies optimizing the efficiency of germination in relation to
466 temperature and impacting timing (Donohue *et al.*, 2010; Maleki *et al.*, 2021). Higher thermal requirement is
467 mainly linked to dormancy status (Baskin & Baskin, 2014; Maleki *et al.*, 2021), although dormancy-breaking
468 treatment may be applied to overcome seed dormancy. Tropical trees, non-tropical trees and wild species are
469 shown to have longer $_{50}$ (i.e. larger thermal inputs for the same germination proportion). This could be a
470 valuable adaptation to cope with changing environments, such that germination is spread and the likelihood of
471 all seeds in a cohort dying due to unfavorable conditions is reduced. In contrast, crops showed the smallest $_{50}$

472 values, suggesting domestication has resulted in selection for fast germination and high vigour. This is also true
473 for horticultural species, particularly ornamental or medicinal species, that have been selected for a specific use
474 (provisioning, nutrients) and cropping cycle. A similar narrow range of short thermal requirements (i. e. lowest
475 $_{50}$ values) for germination found in horticultural species and crops is evident in Cactaceae and Agavaceae. Rather
476 than domestication and selection being important, for the latter groupings an adaptive germination strategy in
477 response to harsh environments is likely. In this way, Cactaceae and Agavaceae can take advantage of temporary
478 suitable conditions and rapidly complete this critical step (germination) in their life cycle. Such considerations
479 support the hypothesis of a bet-hedging strategy for germination that depends on specific environmental
480 conditions (Gremer *et al.*, 2016).

481 Extent of $_b$ values among plant categories

482 Unlike for traits related to T_b, $_{50}$ and cardinal temperatures, we found less literature on Ψ_b with only for 226
483 species compared to T_b and T_{opt} reported for 461 and 334 species, respectively. Nonetheless, studies published
484 in the last decade have focused more on seed Ψ_b compared with those published before 2011 (database of Dürr
485 *et al.*, 2015). Undoubtedly, with concerns growing about the wider impacts of climate change on drought, a
486 wider dataset on species' germination responses to water potential would be valuable.

487 Overall, the lowest values of Ψ_b were found for wild woody species, in particular -5.58 MPa for *Atriplex halimus.*
488 This shrub species is adapted to extreme environments, being highly drought resistant and tolerant of saline
489 conditions, and highlights one of the most important aspects of our new data: to identify model species at the
490 limits of environmental adaptability for further study.

491 Although we found 65 and 45 studies reporting Ψ_b values of forage and rangeland species, and wild species,
492 respectively, the dearth of information on tropical trees and horticultural plants (14 and papers, respectively)
493 calls for further research as germination response to water availability is one of the most important
494 environmental driver for adaptation of plant species.

495 Contrasted germination niches among plant categories

496 We found that sensitivity to environmental factors is a critical ecological process for plants occurring in
497 unpredictable habitats where successful germination is highly dependent on the spatio-temporal variability of
498 temperature. Therefore, germination niche, as a fundamental ecological indicator, should be included more in
499 future risk assessments to species survival. Environmental factors may determine germination niche through
500 regulating both seed dormancy and germination behaviour (Batlla & Benech-Arnold, 2015; Soltani *et al.*,
501 2017a,b; Maleki *et al.*, 2021). We found distinct thermal and moisture germination niche, which is defined as
502 limits characterizing species distribution, for various groups of species. Moreover, differential thermal times for
503 germination describes changes in the sensitivity of germination responses to randomly changing
504 environments, leading to various strategies adopted by plants in term of niche construction and regulation of
505 germination process. Maternal thermal environments may play a regulatory role in niche construction.
506 *Cactaceae* and *Agavaceae*, for example, have the widest Supra-optimal temperature range, suggesting that
507 species experiencing higher temperatures during their lifetime, or more precisely species having experience of
508 higher temperatures, should have wider thermal niche, which is consistent with the ecological concept of
509 germination niche, in which species construct their niche in response to environmental conditions they have
510 experienced (Sultan, 2015; Fernández-Pascual *et al.*, 2019). Although *Cactaceae* and *Agavaceae* have wider

511 upper thermal niche, a recent study showed that these plants are sensitive to increasing global temperatures as
512 the thermal environments in which they inhabit are close to their upper thermal limit (Sentinella *et al.*, 2020).
513 Similarly, species facing dry environments could be generally more tolerant to drought condition by having
514 wider moisture niche as seen in *Cactaceae* and *Agavaceae*. However, in some cases, species from wetter
515 environmental conditions may be better tolerant to drought as observed in *Brassica* sp. (Castillo-Lorenzo *et al.*,
516 2019a). Interestingly, plant groups manipulated to adapt to changing environmental conditions, such as crops
517 and horticultural species, are better suited to lower temperatures by showing wider lower thermal niche.
518 However, these plants are highly sensitive to higher temperatures as shown by a narrow upper thermal niche,
519 suggesting that genetic manipulation and agronomic practices applied to these plant species (e.g. irrigation)
520 may have led to these changes.

521 **5. Conclusion**

522 In this study, we extracted data from 377 studies conducted worldwide on 569 plant species including trees,
523 grasses, crops and wild species to determine ranges of threshold-type responses to temperature and water
524 potential, as two main environmental filters, to determine relationship among these traits. Despite all the
525 complexities in collecting and interpreting data, our results show a strong relationship among ecologically
526 meaningful traits quantifying ranges of threshold-type responses to temperature and water potential and the
527 results of our meta-regression provide insight into the adaptation of various categories of species distributed
528 worldwide to the environments in which they inhabit, factors constraining adaptation and the role of
529 domestication under current and future climate. We found that, under environmental disturbances, distinct
530 germination traits expressed among and within species can allow ecosystems to persist since such adaptive
531 traits are likely to determine threshold-type values for life-history transitions, particularly germination as an
532 important determinant of plant recruitment. Because climate change is expected to become increasingly severe
533 in the future, any changes in threshold-type responses to temperature and water potential may considerably
534 influence plant function and its performance. A better understanding of functional traits and precise field-based
535 validation underlying adaptation would be useful in providing detailed information on plant regeneration.

536 **Author contributions:** JRL conceived the original idea. ES collected and extracted the data from the literature.
537 KM assembled and managed the database, analyzed the data and drafted the manuscript. JRL and ES
538 supervised the work. KM, JRL, ES, CES and HWP commented on the data analyses and revised the manuscript.
539 All authors approved the final version.
540

545 **Conflicts of Interest:** The authors declare no conflict of interest

546
547 **Data availability**
548 The dataset has been deposited to a data repository of INRAE (Data identification number: XP3XHW_2022). A
549 version of record of the repository can be found at https://doi.org/10.15454/XP3XHW.
550
551

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