



## OPEN Using the optimal seed germination temperature approach to determine the potential distribution of *Inga jinicuil* in Mexico under climate change scenarios

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*Inga jinicuil* is used extensively in shade coffee farms in Mexico, a diversified agroforestry system providing important environmental goods and services. However, its recalcitrant seeds represent an important barrier to its propagation. Given the climate change scenarios, it will be necessary to generate information on the effect of temperature on germination, a key stage for the establishment and conservation of the species. The objective of the study was to determine the optimal germination temperatures for *I. jinicuil* using linear and non-linear models, as well as the species' potential distribution under contrasting climate change scenarios using the GISS-E2-1-G model. Seeds were placed in germination chambers at constant temperatures of  $5 \pm 0.5$  to  $40 \pm 0.5$  °C, and their thermal responses were then modelled using a thermal timing approach. Results indicated a good fit of models of *I. jinicuil* germination in response to temperature. Seeds germinated across a wide temperature range; the base temperature for germination was in the range of 4.8 to 9.45 °C (average  $T_b$ :  $6.21 \pm 2.23$  °C) and the ceiling temperature in the range of 44.51 to 49.20 °C (average  $T_c$ :  $47.6 \pm 2.73$  °C). While the optimal temperature was found in the range of 29.58 to 33.02 °C (average  $T_o$ :  $31.52 \pm 1.43$  °C). The suboptimal thermal time ( $\theta_{-1}(50)$ ) for germination of 50% of the seed lot was  $117.164 \pm 0.636$  °Cd, which under current climatic conditions is reached in 6.6 days. According to climate modeling, the distribution of *I. jinicuil* populations will decrease by up to 23% in the future relative to the current distribution. Results indicate that high temperatures have a negative effect on germination, which may be related to seed physiology. More research on seed germination and growth is needed to improve the management and conservation of this species and its continued use as a shade tree in coffee agroforestry systems.

**Keywords** Thermal time, Sensitive to desiccation, Viability, Thermal niche models, Temperature thresholds

Trees of the *Inga* genus belong to Fabaceae family, are native to the American tropics with a distribution extending from Mexico to Brazil<sup>1</sup>. In Mexico, *Inga jinicuil* Schltdl. & Cham. ex G. Don (common Spanish name: jinicuil) is distributed throughout the Gulf of Mexico, from Veracruz to Tabasco. In central México, this species is found in

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Puebla, Tlaxcala, Hidalgo, and Mexico State; and from Jalisco to Chiapas along the Pacific<sup>2</sup>. *I. jinicuil* forms part of the flora of deciduous tropical forest, gallery forests, and more commonly tropical montane cloud forest<sup>3,4</sup>. According to INEGI<sup>5</sup>, this latter forest occupies less than 1% of the country's terrestrial area, with remaining remnants isolated in agricultural matrices<sup>6</sup> including zones of shade-grown Arabic coffee farms (*Coffea arabica* L.)<sup>7</sup>.

*I. jinicuil* is mainly used as a shade tree in agroforestry systems with coffee (*C. arabica*), cocoa (*Theobroma cacao* L.), and citrus (*Citrus spp.* L.), which function as a refuge for the conservation of the species<sup>2</sup>. *I. jinicuil* is a multipurpose species of great importance for community development<sup>8</sup>, providing wood, food, fodder, and environmental services. Its seeds are edible and used for medicinal purposes<sup>9</sup>. Its pods are appreciated for their arils (cotton-like pulp), which are sweet<sup>10</sup>. It is a fast-growing species that can capture significant amounts of carbon<sup>11</sup> and fix nitrogen that can increase soil fertility<sup>2</sup>. It is a species that can reach up to 30 m in height, and its wood is used for rural construction<sup>12</sup>. It is therefore considered a promising tree for restoring degraded areas and counteracting global warming<sup>13</sup>.

Seeds of *I. jinicuil* are dispersed by gravity in May and are sensitive to desiccation, rapidly losing their viability under standard seed banking conditions<sup>14</sup>. The species presents a precocious germination, so it can germinate 100% between 20 and 25 °C and they are also capable of germinating at low temperatures between 10 and 15 °C<sup>15–17</sup>. Germination at low temperatures depends on the environmental conditions (water and temperature) during maturation and seed dispersal<sup>18</sup>. However, information is limited on germination of the species under the higher temperatures expected with global climate change.

Most plants, including *Inga spp.*, require seed production, emergence of seedlings to regenerate after germination<sup>19–21</sup>, a process that is sensitive to humidity and temperature signals and is therefore expected to be affected by climate change<sup>22</sup>. Increases in temperature and changes in rainfall patterns are predicted in various scenarios, threatening the diversity and functioning of ecosystems in coffee-growing regions of Mexico<sup>23</sup>. After humidity, the most important bioclimatic element is temperature, which shapes the speed and percentages of germination, thereby regulating plant growth<sup>24,25</sup>. Hence, the importance of conducting studies to estimate the cardinal germination temperatures using linear and non-linear functions that best describe the germination models for each species<sup>26</sup>. Each species has a thermal niche for germination, which can vary depending on its ecological niche, which is defined by its geographic origin. The corresponding model should better explain the effect of temperature on germination and be species-specific<sup>27</sup>.

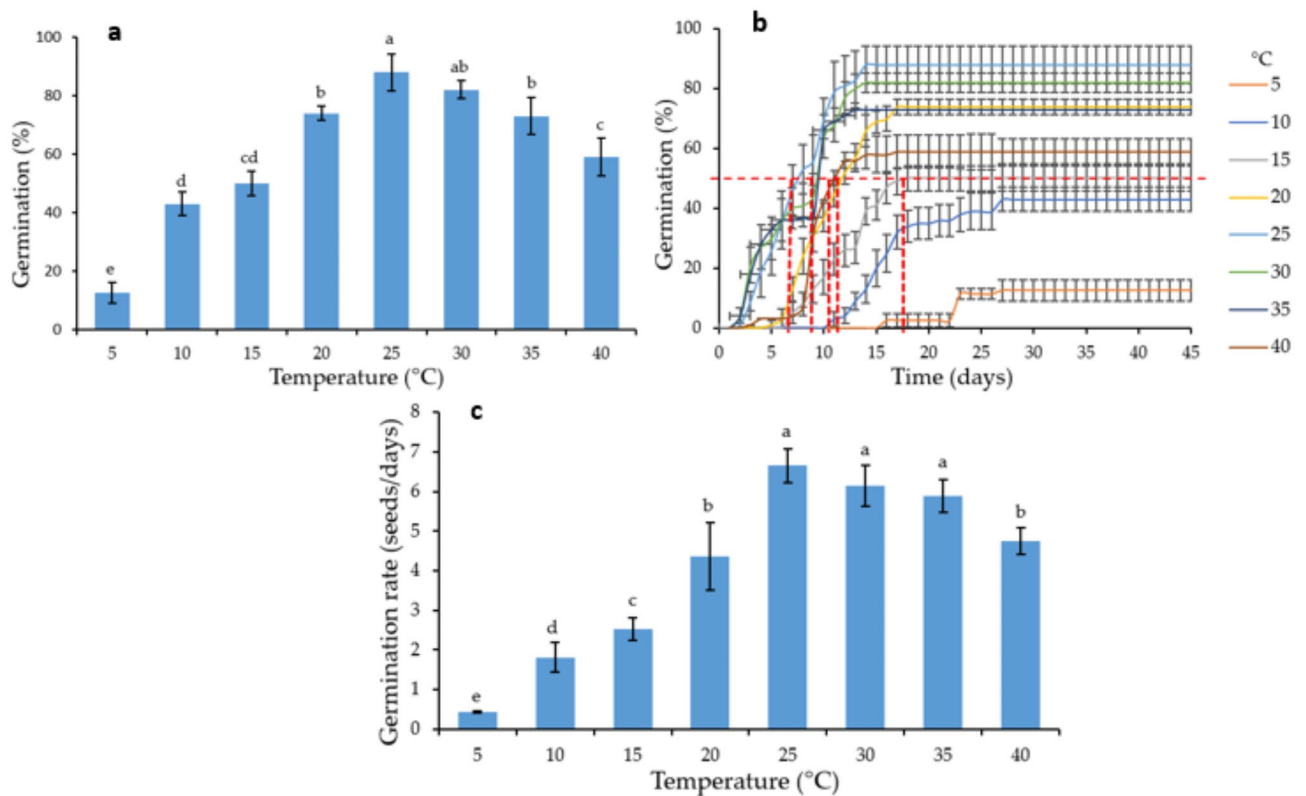
Climate change scenarios predict temperature increases, which are altering weather patterns in various regions of the planet, affecting plant phenology, modifying their structure, distribution and ecosystem functioning<sup>28</sup>. Faced with this threat, successful reproduction by seed is the mechanism that will allow plants to survive climate change<sup>29</sup>. Therefore, they will have to adapt or migrate to new areas with optimal conditions for their distribution, which will limit the thermal niche for germination, whose rates are a function of temperature, which will determine the regeneration site, potentially affecting the assembly of plant communities<sup>25</sup>. Therefore, studies of the effect of temperature on germination physiology will be necessary<sup>30</sup>. The study of cardinal temperatures and thermal time will be useful to find the optimal temperature where the greatest germination occurs in the shortest time as a criterion for the distribution of the species. For the potential distribution of *I. jinicuil*, the 19 climatic variables of WordClim were used, in addition to the soil type and altitude layers. To improve the accuracy of the distribution model, the optimal temperature range for germination was included as a physiological variable that increases the probability of the species presence. Therefore, a novel approach is presented that could improve accuracy of the predictions of potential distribution models under climate change scenarios. Germination is essential for individuals that are susceptible to desiccation tolerance, such as *I. jinicuil*, which has recalcitrant seeds that rapidly lose viability<sup>25</sup>. Changes in rainfall patterns and temperature increases may be particularly important for species with fragmented distributions, small and dispersed populations, perhaps even making them vulnerable to extinction<sup>13</sup>. There are no studies on thermal time or cardinal temperatures for germination of *I. jinicuil* despite the expected increase in temperatures due to climate change, and how this may affect its distribution and population size in the future. The aims of this study were (1) to evaluate the effect of temperature on the germination of *I. jinicuil* seeds (2); to calculate cardinal temperatures using linear and nonlinear models; (3) to determine the thermal niche for germination of *I. jinicuil* using a thermal time approach; and (4) Evaluate the effect of temperature on germination and develop distribution models under climate change scenarios using the GISS-E2-1-G model.

## Results

### Germination

The initial moisture content of the seeds was  $59.6 \pm 4.3\%$ , and 96% of them germinated. The use of a wide thermal gradient allowed us to observe the effect of temperature on germination. Germination was favoured with increasing temperature; then, at 25 °C, it reached its highest germination rate. However, if the temperature continued to increase, germination decreased with a well-defined trend. An average of 60% germination (with a range of 12–90%) was obtained in the temperature treatments, with significant differences between treatments ( $F_{7,79} 36.48$ ;  $p < 0.001$ ). The lowest germination was 12.5% at the lowest temperature (5 °C). As the temperature increases, germination shows a positive rate up to 25 °C; however, as the temperature continues to increase, germination decreases. Therefore, it is said that there is a direct relationship between suboptimal temperatures and germination; however, for supraoptimal temperatures and germination, an inverse relationship is presented (Fig. 1a).

The time at which germination of *I. jinicuil* began was determined for each temperature tested. The temperatures that presented the highest germination rates are those that first initiated germination and, in less time, reached 50% of germinated seeds ( $T_{50}$ ). After 2 days, the seeds started to germinate at 25 to  $35 \pm 0.5$  °C. Germination started at 40 °C after 3 days, and at 15 and  $10 \pm 0.5$  °C, it started at 7 and 11 days, respectively.



**Fig. 1.** Effect of temperature on the germination of *I. jinicuil* in Petri dishes with agar in germination chambers, according to a thermal gradient. **(a)** Germination percentages as an effect of temperature in a thermal gradient. **(b)** Cumulative germination percentages since the start of germination in Petri dishes with agar. In addition, the time needed for germination was 50% of germination for each temperature evaluated. **(c)** Rate of germination per day for every temperature setting. Error bars show the standard deviation. Significant differences between treatments are marked with lowercase letters.

However, at  $5 \pm 0.5$  °C germination slowed considerably, taking up to 16 days. There were significant differences between the temperature ranges in the amount of time that must pass before 50% of the seeds germinate ( $T_{50}$ ) ( $F_{7,79}$  13.08;  $p < 0.001$ ). After 7 days, at  $25 \pm 0.5$  °C, the  $T_{50}$  germination occurred at the fastest rate. Soon after, the  $T_{50}$  happened at 9 days, with temperatures between 30 and  $35 \pm 0.5$  °C. At  $40 \pm 0.5$  °C, 50% germination ( $T_{50}$ ) occurred after 11 days, but at  $15 \pm 0.5$  °C, it took more than 17 days. While at lower temperatures (10 and 5 °C), germination did not reach 50% of the total seeds (Fig. 1b).

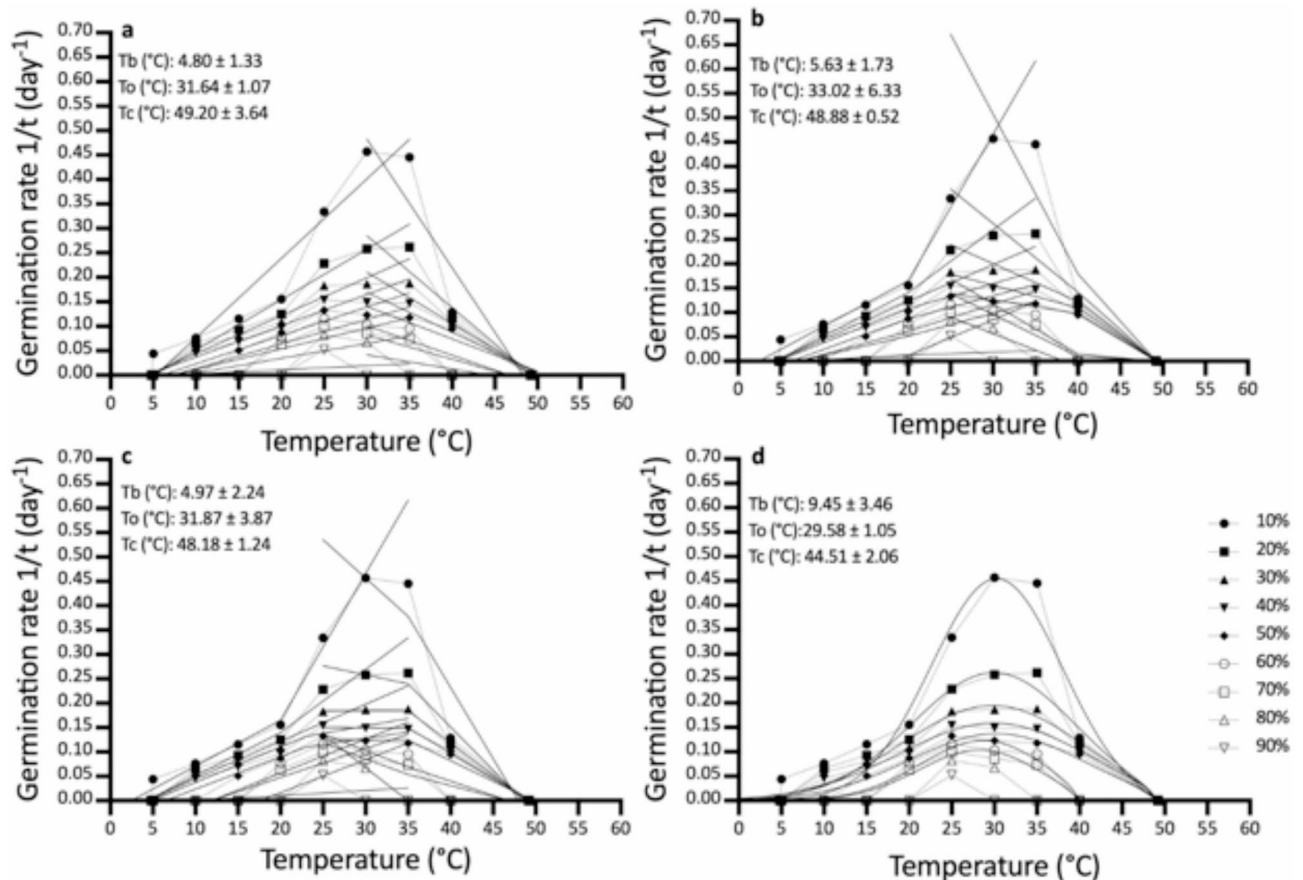
Germination rates were significantly different between treatments ( $F_{7,79}$  21.37;  $p < 0.001$ ). At temperatures ranging from 25 to  $35 \pm 0.5$  °C, seven seeds germinated on average every day. On average, five seeds were observed to germinate in a single day at temperatures of 20 and  $40 \pm 0.5$  °C. Two seeds per day germinated at lower temperatures (10 and  $15 \pm 0.5$  °C). However, a single seed took more than two days to germinate at the lowest temperature ( $5 \pm 0.5$  °C) (Fig. 1c).

### Cardinal temperatures

Analysis of the models for estimating cardinal temperatures revealed significant variation in germination along the thermal gradient, which impacted the fit of the regression models. For the linear model ( $X^2 = 0.58$ ,  $df = 35$ ,  $P < 0.001$ ), the segmented model 1 ( $X^2 = 0.89$ ,  $df = 35$ ,  $P < 0.001$ ), the segmented model 2 ( $X^2 = 0.63$ ,  $df = 35$ ,  $P < 0.001$ ), and for the beta 1 or curvilinear model ( $X^2 = 1.36$ ,  $df = 35$ ,  $P < 0.001$ ). Both linear and nonlinear models had a well-fitted fit in determining cardinal temperatures. The cardinal temperatures defining the limits of the thermal niche for germination of *I. jinicuil* varied widely from 4.8 to 49.2 °C. The suboptimal and supraoptimal temperatures were explained in 76 and 92% for the models, respectively. According to the models, the  $T_b$  for germination was in the range 4.8 to 9.45 °C (average of  $6.21 \pm 2.23$  °C) (Table 1). The germination rate rose with temperature until it reached its maximum rate at the  $T_o$  in the range of 29.58 to 33.02 °C (average of  $31.52 \pm 1.43$  °C). The germination rate drops as the temperature rises above  $T_o$ , reaching the  $T_c$  in the range of 44.51 to 49.20 °C (average of  $47.6 \pm 2.73$  °C). The linear (Fig. 2a) and segmented model 1 (Fig. 2b) and 2 (Fig. 2c) most closely approximated the average value of the cardinal temperatures. However, the Beta 1 or curvilinear (Fig. 2d) and linear models had the best fittings according to the parameter analysis where low RMSE and better model estimation is indicated by  $R^2$  values near 1.

Model	$T_b$ (°C)	$T_o$ (°C)	$T_c$ (°C)	RMSE	$R^2$	Adjusted $R^2$
Linear	4.80 ± 1.33	31.64 ± 1.07	49.20 ± 3.64	0.00212897	0.9500	0.9200
Segmented 1	5.63 ± 1.73	33.02 ± 6.33	48.88 ± 0.52	0.00259518	0.9225	0.7675
Segmented 2	4.97 ± 2.24	31.87 ± 3.87	48.18 ± 1.24	0.00259517	0.9225	0.7675
Beta 1	9.45 ± 3.46	29.58 ± 1.05	44.51 ± 2.06	0.00213562	0.9600	0.9200

**Table 1.** Cardinal temperature values for *I. jinicuil*, base temperatures, optimum temperatures and ceiling temperatures. Determined using linear and non-linear regression models, in addition to the regression parameters.  $T_b$  Base temperature,  $T_o$  Optimum temperature,  $T_c$  Ceiling temperature,  $RMSE$  Root mean square of errors standard,  $R^2$  regression coefficient,  $Adjusted R^2$  adjusted regression coefficient.



**Fig. 2.** The range of cardinal temperatures is described by the germination rate for each percentile (the inverse of the germination rate) for each temperature. The solid lines correspond to the values predicted by the model functions and the symbols represent the experimental data: (a) linear model with 92% fit, (b) segmented model 1 with 76% fit, (c) segmented model 2 with 76% fit, (d) beta model 1 or curvilinear model with 96% fit.

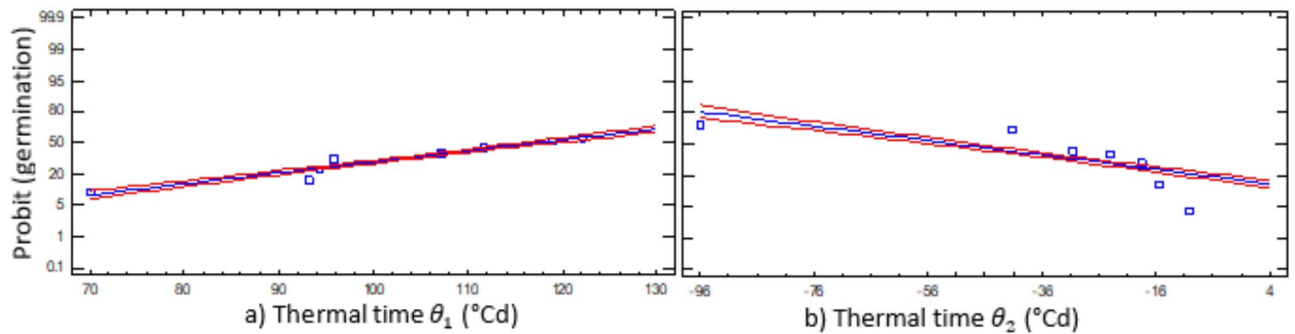
### Thermal time

The thermal time for germination of *I. jinicuil* could be determined with a good fit of the Probit model. The suboptimal temperature ( $\theta_1(50)$ ) for 50% of a batch of seeds to germinate was  $117.164 \pm 0.636$  °C. The Probit model's fit percentage was higher than 91%. On the other hand, the average thermal time for the supraoptimal temperatures ( $\theta_2(50)$ ) was  $51.327 \pm 0.523$  °Cd, and the model fit was greater than 60% (Table 2).

The likelihood of a higher percent germination increased as heat accumulation increased, as demonstrated by the thermal time in the suboptimal range (Fig. 3a). It is interpreted that when approaching the thermal sum of ( $\theta_1(50)$ )  $117.164 \pm 0.636$  °Cd, it reaches higher germination percentages. The analysis revealed significant variation in germination along the suboptimal thermal gradient ( $X^2 = 459.225$ ,  $df = 7$ ,  $P = 0.002$ ). Within the supraoptimal range (Fig. 3b), the accumulation of more heat negatively affects germination, and percentages decrease. Therefore, the thermal time of the supraoptimal range is less. But with that value the germination of 50% of the batch of seeds is achieved. The analysis revealed significant variation in germination along the supraoptimal thermal gradient ( $X^2 = 432.675$ ,  $df = 7$ ,  $P = 0.001$ ).

Parameters	Suboptimal	Supraoptimal
R <sup>2</sup>	91.8	60.2
K	- 3.1873 ± 0.14	- 0.9149 ± 0.047
$\sigma$	0.0272 ± 0.0013	0.017 ± 0.0011
$\theta$ (50) (°Cd)	117.164 ± 0.636	51.327 ± 0.523

**Table 2.** Thermal time values for suboptimal and supraoptimal temperatures for 50% of the seed lot, and thermal time parameters estimated by Probit analysis. The values represent mean ± standard deviation. R<sup>2</sup> regression coefficient, K intercept constant,  $\sigma$  standard deviation;  $\theta$  (50) thermal time (thermal sum).



**Fig. 3.** Probit scale germination as a function of thermal time for: (a) suboptimal range,  $\theta_1$ , (b) supraoptimal range,  $\theta_2$ , of temperatures. The red lines represent the germination confidence intervals. Estimated data is shown by the blue line. The points represent the experimental data's average.

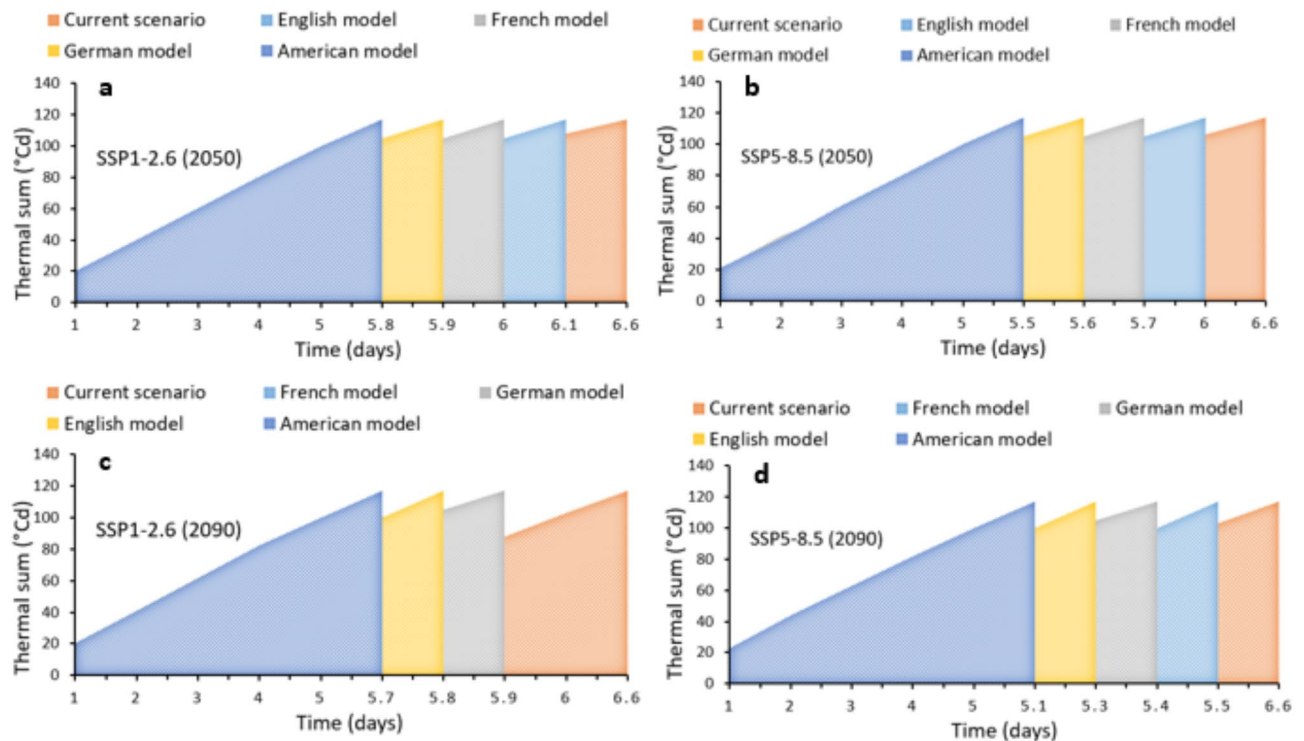
### Germination under climate change scenarios

According to climate change scenarios, germination is predicted to occur in less time, because the thermal sum necessary for germination to occur is completed in less time. In the current scenario, *I. jinicuil* seed dispersal occurs in the month of May, with an average temperature of 22.4 °C. For germination to begin, the seeds need to accumulate the thermal time of ( $\theta_1$  (50)) 117.164 ± 0.636 °Cd, which accumulates in 6.6 days (Fig. 4). In the intermediate future (year 2050) and under the optimistic scenario (SSP1 2.6 Watts/m<sup>2</sup>), all models predict a temperature increase in May. Under the English model (HADGEM2-ES), an increase of 1.6 °C is predicted for this month, while average temperatures of 1.8, 2.1 and 2.5 °C are expected for the French (CNRMCM5), German (MPI-ESM-LR), and American (GFDL-CM3) models, respectively. Accordingly, germination start times are reduced, with thermal time accumulating in just 6.1, 6.0, 5.9, and 5.8 days for the English, French, German, and American models, respectively (Fig. 4a). For the pessimistic climate change scenario (SSP5-8.5 Watts/m<sup>2</sup>), increases of 3.0, 3.1, 3.3, and 3.6 °C were predicted in May for the English (HADGEM2-ES), French (CNRMCM5), German (MPI-ESM-LR), and American (GFDL-CM3) models. This corresponds to a faster accumulation of the thermal time ( $\theta_1$  (50)) of 117.164 ± 0.636 °C required for germination, varying between 6 days for the English model and 5.5 days for the American model. Which is up to 27 h earlier than the current scenario (Fig. 4b).

For the distant future (year 2090), under the optimistic climate change scenario (SSP1 2.6 Watts/m<sup>2</sup>), increases of 2.1, 2.3, 2.8, and 2.9 °C were predicted in May for the French (CNRMCM5), German (MPI-ESM-LR), English (HADGEM2-ES), and American (GFDL-CM3) models. This corresponds to a faster accumulation of the thermal time ( $\theta_1$  (50)) of 117.164 ± 0.636 °Cd required for germination, varying from 5.9 days for the French model and 5.7 days for the American model. Which is up to 20 h earlier than the current scenario (Fig. 4c). For the most pessimistic climate change scenario (SSP5-8.5 Watts/m<sup>2</sup>), increases of 3.7, 4.1, 4.5, and 5.1 °C were predicted in May for the French (CNRMCM5), German (MPI-ESM-LR), English (HADGEM2-ES), and American (GFDL-CM3) models. This corresponds to a faster accumulation of the thermal time ( $\theta_1$  (50)) of 117.164 ± 0.636 °Cd required for germination, varying between 5.5 days for the French model and 5.1 days for the American model. Which is up to 1.5 days earlier than the current scenario (Fig. 4d).

### Potential distribution under climate change scenarios

For the construction of species distribution models, environmental variables of temperature and precipitation are included, in addition to soil variables; but by including species-specific physiological variables, such as optimal germination temperatures (OGT), ecological niche models are strengthened and enriched, and the precision of their projections is improved since they are usually more restrictive. Table 3 shows how the inclusion of OGT typically reduced the predicted distribution of *I. jinicuil*. In theory, considering OGT results in more accurate models of a species' distribution, thus increasing the probability of finding *I. jinicuil* in predicted areas. According to the models, if the optimal temperatures for germination are included, models predict a decrease of 37.6% in the current distribution opposed to models without this variable. Under future scenarios the predicted



**Fig. 4.** Time required to accumulate the thermal time ( $^{\circ}\text{Cd}$ ) in the optimistic ( $\text{SSP1-2.6 W/m}^2$ ) and pessimistic ( $\text{SSP5-8.5 W/m}^2$ ) scenarios for the month of May in the current scenario and in different climate models. (a) Time required to accumulate the thermal time for the month of May in the optimistic scenario ( $\text{SSP1-2.6 W/m}^2$ ) for the near future (year 2050), for the current scenario, and in different models. (b) Time required to accumulate the thermal time for the month of May for the pessimistic scenario ( $\text{SSP5-8.5 W/m}^2$ ) for the near future (year 2050). (c) Time required to accumulate the thermal time for the month of May, in the optimistic scenario ( $\text{SSP1-2.6 W/m}^2$ ), for the distant future (year 2090). (d) Time required to accumulate the thermal time for the month of May in the pessimistic scenario ( $\text{SSP5-8.5 W/m}^2$ ) for the distant future (year 2090).

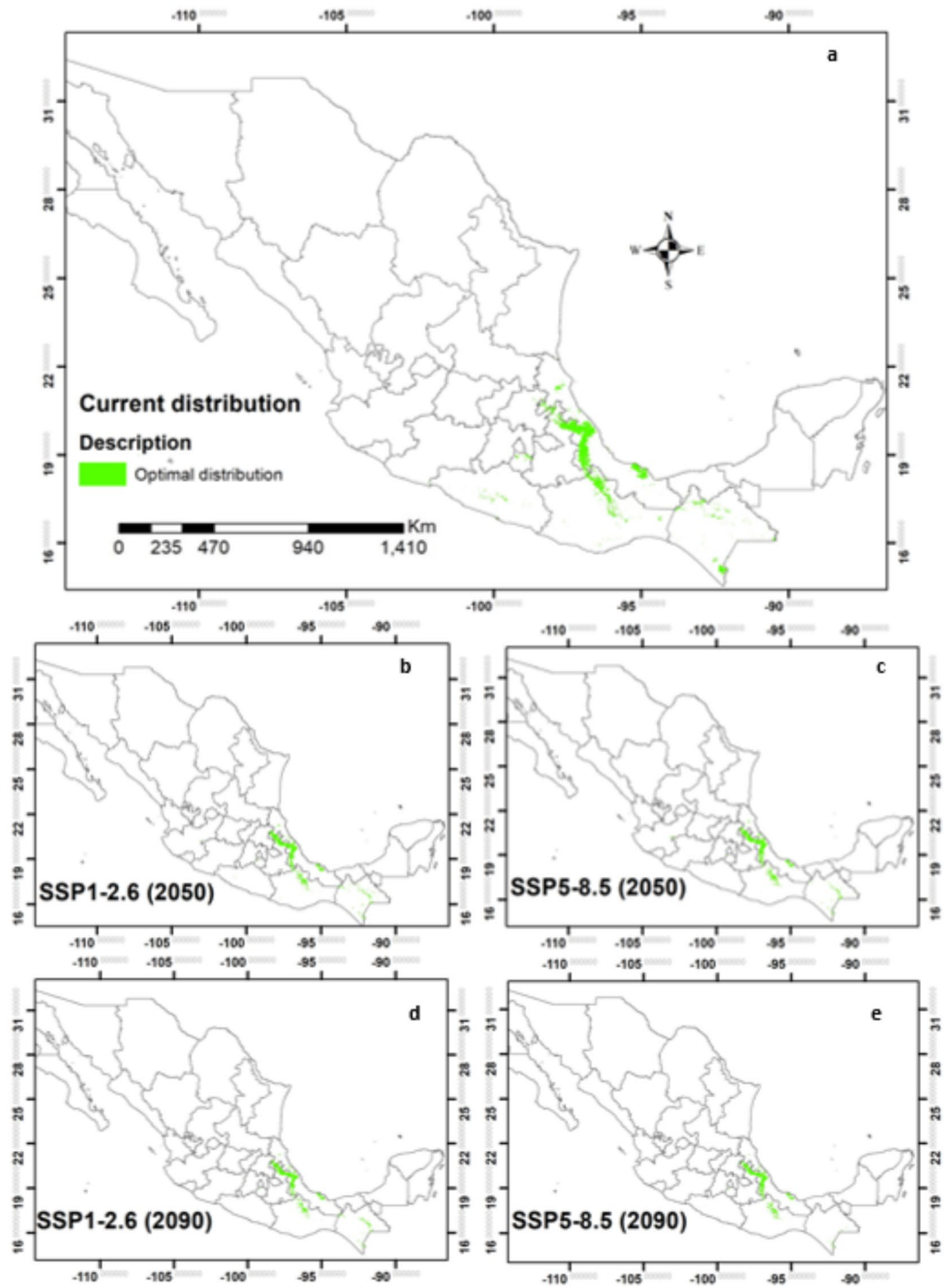
Description	Optimal temperatures approach	Current	2050 ( $\text{km}^2$ )		2090 ( $\text{km}^2$ )	
		( $\text{km}^2$ )	SSP1-2.6	SSP5-8.5	SSP1-2.6	SSP5-8.5
Suitability area ( $\text{km}^2$ )	No	28,882.04	18,828 (34.8%)	16,343 (43.4%)	18,135 (37.2%)	15,593 (46.0%)
Suitability area ( $\text{km}^2$ )	Yes	18,019	17,799 (1.2%)	17,123 (5.0%)	15,223 (15.5%)	13,776 (23.5%)
Decline in area ( $\text{km}^2$ )		10,866	1029	- 780	2912	1817
Percentage decline (%)		37.6	5.4	- 4.7	16	11.6

**Table 3.** Models of the distribution of *I. jinicuil* considering or not the effects of optimal temperatures for germination, across different temporal horizons and under optimistic (2.6) and pessimistic (8.5) climate change scenarios according to the GISS-E2-1-G model.

reductions in species distributions with the addition of this variable are less pronounced (5.4–16%) and might result in a small increase in the species distribution (near future SSP5-8.5). Comparing predicted distribution changes under each climate change scenario versus the actual distribution reveals that losses in species distribution are expected under all climate change scenarios but these are more marked in models without the variable of optimal germination temperature (Table 3).

Results of the species distribution models, including optimal temperature, had AUC values of  $0.97 \pm 0.01$ ; indicating a good model fit to the data, with a greater than 50% probability of finding the species in predicted areas. According to the climate change scenarios of the GISS-E2-1-G model the distribution of *I. jinicuil* populations in the future will decrease between 34 and 46% of their current distribution (Fig. 5). Jackknife procedures identified annual precipitation (38.5%), type of soil (19.5%), precipitation during the driest period (13.4%), the altitude (8.2%), and average temperature of the driest month (5.1%) as the variables that most contributed to the construction of the MaxEnt model of the current species distribution.

In the near future (2050), under optimistic (2.6) and (8.5) pessimistic emissions scenarios a reduction of the species distribution by 1.21 and 4.96%, respectively, is expected as compared to the current distribution (Table 4). In the lower  $\text{CO}_2$  emissions scenario (SSP1-2.6), a decrease of just over 1% of the current distribution



**Fig. 5.** Distribution maps under climate change scenarios for *I. jinicuil* in Mexico, projected for the near future (year 2050) and distant future (year 2090). In the optimistic scenario (SSP1-2.6 W/m<sup>2</sup>) and the drastic scenario (SSP5-8.5 W/m<sup>2</sup>). **(a)** Current distribution of *I. jinicuil* in Mexico. **(b)** Potential distribution of *I. jinicuil*, projected for the year 2050 in the optimistic scenario (SSP1-2.6 w/m<sup>2</sup>). **(c)** Potential distribution of *I. jinicuil*, projected for the year 2050 in the pessimistic scenario (SSP5-8.5 w/m<sup>2</sup>). **(d)** Potential distribution of *I. jinicuil*, projected for the year 2090 in the optimistic scenario (SSP1-2.6 w/m<sup>2</sup>). **(e)** Potential distribution of *I. jinicuil*, projected for the year 2090 in the pessimistic scenario (SSP5-8.5 w/m<sup>2</sup>).

is expected. Colima, Quintana Roo and Tamaulipas are expected to suffer reductions in the distribution of the study species, while increases are predicted in Jalisco (98.7%), Hidalgo (68.8%), Puebla (24.8%) and Chiapas (19%). The climatic variables that contributed the most to the model were: annual precipitation (29.9%), precipitation during the driest period (28.2%), soil type (15.4%) and altitude (8.1%). Under the higher CO<sub>2</sub>

State	Current (km <sup>2</sup> )	2050 (km <sup>2</sup> )		2090 (km <sup>2</sup> )	
		SSP1-2.6	SSP5-8.5	SSP1-2.6	SSP5-8.5
Chiapas	2008.11	2480.73	2005.69	1964.47	538.69
Colima	1.57	0.00	0.00	0.00	0.00
Guerrero	452.09	27.74	15.36	13.58	13.90
Hidalgo	220.35	707.84	576.86	608.81	495.12
Jalisco	1.10	87.35	113.00	71.22	0.00
Mexico	27.17	24.95	26.05	26.45	13.17
Michoacan	13.28	0.55	0.55	0.55	0.00
Morelos	274.47	68.42	71.54	64.65	68.75
Oaxaca	3570.94	3076.41	3031.64	2387.35	2604.90
Puebla	2528.21	3365.28	3295.90	3066.25	2996.17
Quintana Roo	1.11	0.00	0.00	0.00	0.00
Tabasco	29.28	1.74	0.44	0.63	1.33
Tamaulipas	10.48	0.00	0.00	0.00	0.00
Veracruz	8877.95	7957.63	7986.35	7018.91	7043.92
Suitability area (km <sup>2</sup> )	18016.11	17798.64	17123.38	15222.88	13775.94
Decrement area (km <sup>2</sup> )		217.46	892.73	2793.23	4240.16
Percentage of decrement (%)		1.21	4.96	15.50	23.54

**Table 4.** Estimated areas (km<sup>2</sup>) for *I. jinicuil* in Mexico, according to the GISS-E2-1-G model. Projected in the optimistic scenario (SSP1-2.6 W/m<sup>2</sup>) and drastic scenario (SSP5-8.5 W/m<sup>2</sup>). For the intermediate future (year 2050) and distant future (year 2090), according to climate change scenarios.

emissions scenario (SSP5-8.5), the distribution of the species decreases 3.75% more than in the scenario (SSP1-2.6). In general, spatial trends are similar to those reported for the lower CO<sub>2</sub> emissions scenario. The variables that contributed the most to the model were: precipitation during the driest period (33.3%), annual precipitation (22.6%), soil type (15.5%) and altitude (6.6%).

In the distant future (2090), a reduction in the species' distribution between 15.5 and 23.5% is expected versus the current distribution (Table 3). In the SSP1-2.6 scenario, Colima, Quintana Roo and Tamaulipas lose all suitable area for the species. Tabasco (97.8%), Guerrero (97%), Michoacan (95.8%), Morelos (76.4%), Oaxaca (33.1%) and Veracruz (21%) will lose optimal area for the species, while Jalisco should add 71.22 km<sup>2</sup> of suitable area compared to the current scenario with 1.10 km<sup>2</sup>. In addition, Hidalgo will increase its surface area by 270% and Puebla should exhibit an increase of 21.3%. The variables that contributed the most to the construction of this model were: annual precipitation (32.6%), precipitation during the driest period (26.1%), soil type (14.3%) and altitude (6.6%). In the SSP5-8.5 scenario, an overall decrease 46% in the species distribution is predicted relative to the current distribution. The states of Colima, Jalisco, Michoacán, and Tamaulipas are expected to lose all suitable area for the species. The variables that contributed the most to the model construction were: precipitation during the driest period (39.1%), annual precipitation (19%), soil type (14.2%) and altitude (6.2%).

## Discussion

### Germination

*I. jinicuil* seeds have the ability to germinate in a wide range of temperatures, which gives it a competitive advantage in a successional ecological niche<sup>31</sup>. Therefore, temperature plays an important role in seed germination performance and the geographic distribution patterns of the species<sup>32</sup>. *I. jinicuil* is distributed in the humid Mexican tropics, so in the months of April and May it can present temperatures higher than the average optimal temperature (31.52 ± 1.43 °C); the seeds during this time will experience stress due to high ambient temperatures, which also coincide with their dispersion. Although, seeds at temperatures close to T<sub>0</sub> usually present a higher germination rate<sup>33</sup>.

Previous studies by Leão et al.<sup>15</sup>, Rodrigues et al.<sup>16</sup> and Barros-Guimarães et al.<sup>17</sup> reported that 20 to 25 °C was the ideal temperature range for Inga seed germination and suggest that the minimum temperature for germination could be in the range of 10 to 15 °C. Our study used a broader temperature gradient (5–40 °C) for evaluating the germination of *I. jinicuil* resulting in a broader thermal niche than previously reported. According to the results, the highest germination percentages occurred at 25 ± 0.5 °C, which is in line with the studies of *Inga vera* Willd<sup>17</sup>. Nevertheless, this is below the ideal temperature (T<sub>0</sub>: 31.6 ± 1.1) and is consistent with findings for other tropical species such as *Cedrela odorata* L<sup>27</sup> and *Swietenia macrophylla* King<sup>25</sup>.

Our findings support previous work indicating that optimal temperature is not always the site of maximum germination<sup>34</sup>. It is possible that recalcitrant tropical species seeds, which are susceptible to low temperatures and lose viability at temperatures below 15 °C, are the reason why the lowest percentage of germination occurred in seeds exposed to the lowest temperatures (5 ± 0.5 °C)<sup>35</sup>. Low temperatures also cause germination processes' metabolic rates to decrease<sup>36</sup>. As a result, the conditions under which the seeds mature and disperse will determine whether germination takes place at low temperatures (≤ 10 °C)<sup>18</sup>.

### Cardinal temperatures

The three nonlinear models and the linear model developed for the study all showed good prediction, since realistic values were observed according to the experiment data. However, the lower RMSE values of B1 and the SL1 indicated they had the best fit to the empirical data. Due to the non-linear nature of the peak model was more flexible but also tended to underestimate the values of the maximum temperature similar to previous studies<sup>27</sup>.

To estimate the cardinal temperatures for germination of *I. jinicuil*, a wide temperature gradient (from 5 to 40 °C) was required. As a result, the models showed a good fit (>92%)<sup>37</sup>. The studied species used a wide temperature interval, defining the thermal niche for germination of  $4.8 \pm 1.3$  to  $49.2 \pm 3.64$  °C between  $T_b$  and  $T_c$ , respectively. Given that all climate change scenarios predicted temperature increases, as a means of adapting to the rapid changes in climate, the ability to germinate across a broad temperature range might be considered<sup>27</sup>.

$T_o$  be attained in May, the hottest month, which coincides with the dispersal of seeds<sup>14</sup> and corresponds directly to the increased germination rates<sup>36</sup>. The above is especially important in seeds with recalcitrant behavior such as *I. jinicuil*, which have a very short period of viability during optimal ambient temperatures. Daibes et al.<sup>38</sup> report a range of 20 to 40 °C, which includes the optimal temperatures for germination of tropical species in the western Brazilian Amazon. Therefore, a similar thermal range for *I. jinicuil* coincides with tropical species from Mexico such as *C. odorata*<sup>27</sup> and *S. macrophylla*<sup>25</sup>.

When optimum temperatures are surpassed germination rates decreases<sup>39</sup>. This may be due to effects in cell membranes initiating protein denaturation and can lead to embryo death<sup>40</sup> or, at the very least, a reduction in the germination metabolic processes<sup>41</sup>. At 40 °C, the species registered just over 60% germination on average, which coincides with the germination of *Astronium lecointel* Ducke, *Parkia nitida* Miq., *Schizolobium amazonicum* Ducke<sup>38</sup>; in addition to *C. odorata*<sup>27</sup> and *S. macrophylla*<sup>25</sup> in the same thermal gradient.  $T_c$  for germination was close to 50 °C, which may offer a competitive advantage for germination in more open fragmented habitats where surface temperatures can reach or surpass 45 °C<sup>42,43</sup>. *I. jinicuil* had an average germination of 12.5% at 5 °C, which was the lowest percentage recorded in the study. Because seeds' metabolism is less active in colder temperatures, germination will take longer<sup>44</sup> and suggests that  $T_b$  accurately predicts the phenological stages of a species<sup>37</sup>.

### Thermal time

Thermal time calculation has a high predictive value for the different phenological stages of plants, which allows its application to be extended to predict the effects of climate change on germination, plant emergence, and species distribution, especially those sensitive to desiccation that will be the most affected by the increase in temperature. This, in turn, opens up the possibility of designing management and conservation strategies for these species<sup>45</sup>. This study provides the first reports of thermal time for *I. jinicuil*, an important climatic parameter for analyzing how temperature impacts seeds metabolism, germination percentages, and rates<sup>46</sup>. In May, seeds are released ( $22.4$  °C  $T_m$ ), but germination occurs once a threshold thermal time has been obtained and germination can begin<sup>47</sup>. This was reached in 6.6 days on average under current conditions, when the emergence of seedlings maximized, thus affecting establishment success and the survival and regeneration of the species<sup>38</sup>. Using agroclimatic models, the accumulated temperature (°Cd) is used to characterize the phenological phases, such as germination, and has an impact on phenological variation<sup>48</sup> and thermodormancy. In terms of bioclimatic regulation of germination processes, temperature is the most significant factor<sup>49</sup>. Late successional species typically take longer than early successional species to reach phenological stages such as germination<sup>50</sup>. The thermal time ( $\theta_1(50)$ ) for *I. jinicuil* of  $117.164 \pm 0.636$  °Cd was lower than that reported previously for *S. macrophylla* ( $189.091 \pm 4.239$  °Cd)<sup>25</sup>, *Cedrela fissilis* Vell. of ( $157 \pm 20$  °Cd)<sup>38</sup> and *C. odorata* ( $132.74 \pm 2.60$  °Cd)<sup>27</sup>.

### Germination under climate change scenarios

The results indicate that the increase in temperature will reduce the germination performance of *I. jinicuil*, since a response to abiotic stress such as temperature is regulated by hormones, mainly abscisic acid (ABA), which involves several key proteins<sup>51</sup>. Temperature stress (heat shock) is aggravated by climate change; increasing temperature is a factor that can alter the physiological and metabolic processes of seeds<sup>52</sup>. Therefore, germination in the face of thermal stress has an impact on the survival of species and the resilience of ecosystems to climate change<sup>53</sup>. The impact of rising temperatures on flowering, fruiting, and germination periods (which in turn impact the functioning of tropical ecosystems) is typically assessed in studies on how climate change may affect tropical tree<sup>43</sup>. The models that forecast the impact of climate change on *I. jinicuil* germination in this study indicate a 1.6–2.9 °C increase. When compared to the current situation, this will reduce the amount of time required to accumulate the thermal time (°Cd) for *I. jinicuil* seed germination. According to Funes et al.<sup>47</sup>, quicker germination confers an advantage in the competition for available spaces and guarantees the establishment of individuals. Thus, climate changes can affect the competitive capacity of a species, which in turn can affect its distribution and germination rate. The sustainability and smooth operation of forest ecosystems may be negatively impacted by such modifications, which may also result in a decrease in tree diversity<sup>54</sup>. Adaptation to new climatic conditions requires migrations in altitude and latitude that are not easy and can result in evolutionary changes including the colonization of new environmental niches<sup>55</sup>.

### Potential distribution under climate change scenarios

The distribution models for *I. jinicuil* overlap with the distribution of tropical montane cloud forest and areas of shade-grown coffee production suffering from land use change and associated losses of biodiversity<sup>56</sup>, including loss of biodiversity, mainly of native trees. In addition, the increase in temperature due to climate change predicts a decrease of up to more than 23% in the area with optimal conditions for the distribution of the species<sup>38</sup>. Which highlights the urgent need to propose strategies for the conservation of the species. Based on the NASA

GISS-E2-1-G model the optimal distribution of *I. jinicuil* is expected to decrease in the up to 23.5% due to climate change. The model's appropriate resolution for regional impact studies led to the decision to employ it<sup>57</sup>. Therefore, the projections had an excellent fit (AUC > 0.96), depending on the area under the curve<sup>58</sup>. The two variables that had the greatest effects on the models used to create the distribution of the species under study were annual precipitation and precipitation during the driest period. The study species' geographic range may be further restricted by the combination of altered rainfall patterns and rising temperatures brought on by climate change, which will accelerate soil water evaporation, possibly prolong droughts, and exacerbate drought stress<sup>59</sup>. There are no previous studies on the potential biogeographic distribution for *I. jinicuil*, and providing such information for this species in Mexico was a central focus of this study. The findings imply that to preserve the genetic diversity of populations at risk from climate change, seeds should be collected in areas where suitable conditions for their distribution will be lost and in populations located at higher temperature levels<sup>25</sup>.

Since propagation by seeds is obligatory for this and most other tropical tree species, information on the responses of seeds to changing environmental conditions, it is essential to understand the physiological mechanisms underlying the growth and development of trees<sup>60</sup>. Effects on the hormone mechanisms involved in fruiting and flowering requires additional research<sup>61</sup>, as does the potential impacts of dispersal, competition, and establishment and resulting predictions of changes in species distributions<sup>62</sup>. Since the physiology of seeds is influenced by temperature from the maternal environment, changing seed maturation, seed research must therefore be conducted from the perspective of climate change<sup>63</sup>. Warmer-weathered fruits produce seeds with less moisture, increasing the likelihood that seeds susceptible to desiccation will not survive. This would eventually restrict the ability of seeds to proliferate and the range of species that can exist. As far as we are aware, this is the first investigation into cardinal temperatures, thermal time, and the impact of climate change on *I. jinicuil* germination and dispersal. This species is distributed in the remnants of the tropical montane cloud forest, a fragile ecosystem, making it a species vulnerable to extinction. The productivity and profitability of growing shade coffee, however, will be impacted by the decline in the range of this multipurpose tree, which is the species most commonly used as shade on coffee plantations. Therefore, the study could be the basis for developing strategies for the management, conservation, and conservation of the tree biodiversity in the country's coffee-growing regions.

## Materials and methods

### Origin of the seeds

Ripe fruits of *I. jinicuil* were collected from 35 trees in 5 shade-grown coffee farms, established in the community of Los Carriles (718806.96 E and 2152610.24 N; 1189 m a.s.l.), located in the coffee-growing region of Coatepec, in the center of the state of Veracruz. Collections were carried out in early May 2023. Seed collection was carried out in accordance with the IUCN policy statement on research with species at risk of extinction, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and the General Law on Ecological Balance and Environmental Protection (LGPEA) and its regulations. Which govern the conservation and sustainable use of wildlife and its habitat in Mexico. The weather in this area is moist temperate, with year-round rainfall (Cf)<sup>64</sup>, usual annual precipitation of 1761 mm, and an average annual temperature of 19.4 °C. Figure 6 graphs showing the average monthly temperature and precipitation. The volcanic soils are of the humic andosol type, with a pH of 6.5, good drainage, and a clay-sandy texture<sup>3</sup>.

### Plant authentication

The collection of fruits and herbario specimens was carried out by the PRONATURA team in accordance with the standards established by the Kew Millennium Seed Bank Partnership. The authentication of the plant material, of fruits and seeds, was carried out by Biol. Armando Ponce Vargas. The herbarium specimen was deposited in the internal collection of the FESI-UNAM Seed Bank, with folio number BSMAMG50. It is available to the general public for educational and research purposes.

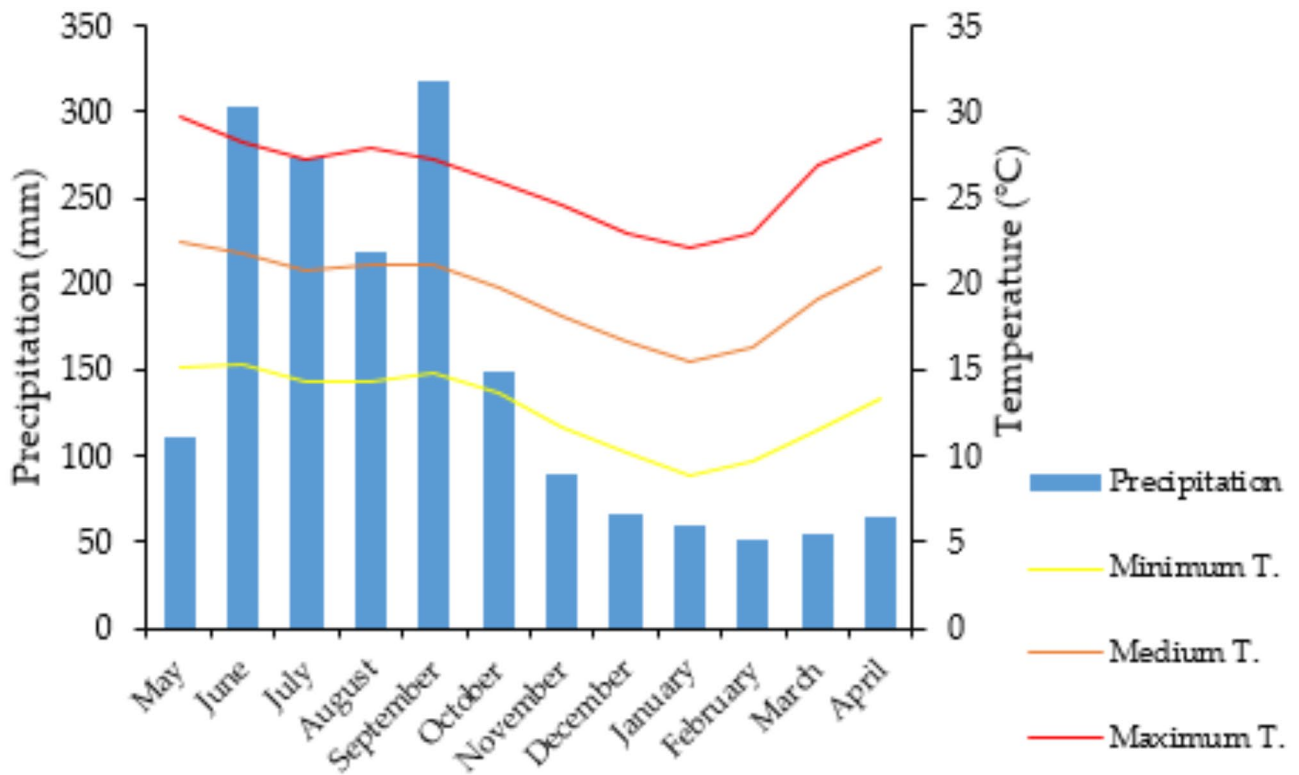
Fruits pods were placed in breathable cloth bags and sent immediately to a laboratory in Tlalnepantla, state of Mexico. The pods were opened with tweezers in the Plant Physiology Laboratory of FESI, UNAM. After manually removing the seeds from their pods, they were placed in paper bags (15 °C and 55–60% humidity) for 24 h prior to tests of germination and moisture content including the experiment of cardinal temperatures. To determine the moisture content of the seeds it was done according to the weight differences<sup>34</sup>.

### Initial germination test

Germination test consisted of placing 10 seeds on agar medium (10 g L<sup>-1</sup>) in Petri dishes (6 cm diameter), using ten replicates of a random design. The Petri dishes were kept in a controlled environment chamber (SPX-150 Model, Brand LUZEREN) with a relative humidity of 70% and a temperature of 25 ± 0.5 °C. A seed was considered germinated when the radicle measured ≥ 1 mm<sup>65–67</sup>. Non-germinated seeds were subjected to a cutting test at the conclusion of the experiment to determine viability.

### Experimental design and statistical analysis

For the cardinal temperatures treatments, a completely randomized design was used; 10 seeds were sown in a Petri dish, and 10 replicates were performed for each temperature treatment. The Petri dishes were placed in germinators with a thermal gradient of 5 to 40 °C and a light photoperiod of 12 h. Germination was recorded daily for 45 days. Ungerminated seeds were subjected to a shear test at the end of the experiment to determine viability. Since the percentage germination results did not meet the normalcy assumptions, the analysis of variance was performed using Kruskal–Wallis, and the multiple comparisons were performed using Dunn's post hoc test. For the analysis of regression models, the effectiveness and adjustment were determined through the analysis of RMSE, R<sup>2</sup> and adjusted<sup>25,36</sup> R<sup>2</sup>.



**Fig. 6.** Temperature and accumulated precipitation (mm month<sup>-1</sup>) information for the Coatepec, Veracruz, area where *I. jinicuil* seeds were collected. Historical monthly averages are reported for the period 1981–2010. Data obtained from a global climate database (<http://es.climate-data.org/>). T. temperature.

### Effect of temperature on germination

The methodology described by Sampayo et al.<sup>26</sup> was applied in order to evaluate the effect of temperature on germination. In Petri dishes, 10 seeds were planted in 10 replicates using a completely randomized design on agar medium (10 g L<sup>-1</sup>). Using halogen lamps with a light intensity of 28.05 μmol m<sup>-2</sup> s<sup>-1</sup> (Quantum Meter Apogee Mod. QMSW-SS, Logan, UT, USA), petri dishes were placed in germinators with a thermal gradient of 5 to 40 °C and a 12-h photoperiod of light. Germination was recorded daily for 45 days. Non-germinated seeds were subjected to a cutting test at the conclusion of the experiment to determine viability.

### Evaluated variables

The following formula was used to determine the total germination for each temperature treatment: (1)<sup>68,69</sup>:

$$G (\%) = \frac{n}{N} * 100 \quad (1)$$

where n is the number of germinated seeds in each Petri dish and N is the total number of seeds.

The following Eq. (2)<sup>70</sup> was used to calculate the germination rate, which was an estimate of the quantity of seeds that germinated each day:

$$GR = \frac{G_1}{N_1} + \frac{G_2}{N_2} + \dots + \frac{G_i}{N_i} + \dots + \frac{G_n}{N_n} = \sum_{i=1}^n \frac{G_i}{N_i} \quad (2)$$

where  $G_i$  is the quantity of seeds that germinate, and  $N_i$  is the number of days that the experiment began.

To estimate the  $T_{50}$ , the time in which 50% of the total seeds germinated for each temperature was determined.

### Determination of cardinal temperature using nonlinear regression models

To estimate the cardinal temperatures of *I. jinicuil*, the method proposed by Cabrera-Santos et al.<sup>25</sup> was used; linear and non-linear regression models were used to determine the most effective and best-fitting model to predict the effect of temperature on germination, based on a thermal gradient<sup>71</sup>.

The two segmented models used to determine cardinal temperatures were a pair of two-segment linear regressions, each for suboptimal and supraoptimal ranges, respectively. The x-intercept of each regression line and, consequently, the base temperature ( $T_b$ ) were estimated using the first segment of the regression in the suboptimal range. The second regression segment was utilized to estimate the x-intercept and, consequently, the ceiling temperature ( $T_c$ ) for the supraoptimal range<sup>72</sup>. Calculating the  $T_b$  and  $T_c$  involved averaging the x-intercept of fractions in the suboptimal and supraoptimal temperature range<sup>73</sup>. The optimum temperature ( $T_o$ ) be determined as the point where the second and first segments of the suboptimal and supra-optimal range regression lines, respectively, intersect<sup>74</sup>.

Segmented models (S1 and S2) were built with two segments of the linear regression in the suboptimal range, where  $X$  = any value of  $X$  and  $X_0$  = the  $X$  coordinate value at the intersection of the two segments. The first segment's condition was  $X < X_0$ , and the second segment's condition was  $X > X_0$ <sup>25</sup>. According to the empirical data, this was observed where there were statistically different changes in the slope of the  $1/VG$  in function of temperature at 20 °C in the suboptimal range and between 35 and 40 °C in the supraoptimal range; consequently,  $X_0$  for S1 were restricted at 20 °C and 35 °C for sub- and supraoptimal ranges; while  $X_0$  for S2 were restricted to 20 °C and 40 °C, respectively. Segmented models were run for 10–80% of the seed population.

The non-linear curvilinear Asymmetric Peak Function was run for 10–70% of the seed population with the following Eq. (3)<sup>25,75</sup>:

$$Y = \left( a^x \left( \exp \left( (-b^x (x/c)^{-1})^2 + 1/(x-d) \right) \right) \right) \quad (3)$$

where  $a$  is the maximal germination rate in each curve,  $b$  is  $1/\sigma^2$  of the asymmetric Peak Function,  $c$  is the temperature where the germination rate is highest, and  $d$  is the interception between the abscise axis and temperature in the descending extreme of the Peak Function.  $T_b$  and  $T_c$  temperatures were defined as the temperatures in the intersection between the tangent at the inflection points of the Peak Function and the abscise axis. The thermal time was defined as the reciprocal of the slope of the tangent at the inflection points of the function<sup>76</sup>.

In each case, the best goodness-of-fit parameters (RMSE,  $R^2$  and, adjusted  $R^2$ ) of the models (4) were used, according to:

$$RMSE = \sqrt{\left( \frac{1}{n} \right) \sum (Y_{obs} - Y_{pred})^2} \quad (4)$$

where  $Y_{obs}$  presents the measured value,  $Y_{pred}$  estimated amount, and  $n$  the quantity of samples<sup>77</sup>, and with the regression coefficient ( $R^2$ ) determining the models' goodness of fit:

$$R^2 = SSR/SST \quad (5)$$

where  $SSR$  indicates the sum of squares (SS) for regression  $\left( \sum_{i=1}^n (\hat{Y}_i - \bar{Y}) \right)$  and  $SST$  the total  $SS \left( \sum_{i=1}^n (Y_i - \bar{Y}) \right)$ . The observed value is  $Y_i$ , and the corresponding estimated value is  $Y$ .

### Determination of cardinal temperature using linear regression model

Following the methodology of Cabrera-Santos et al.<sup>25</sup>,  $T_b$  was calculated by computing the time for germination in percentiles. Their inverse was then calculated and plotted against temperature to see how the data was trending, locate the inflection point, and identify the range of suboptimal temperatures that  $T_b$  and  $T_o$  define. In accordance with Ellis et al.<sup>73</sup>, linear regression was used to determine the parameters for each germination percentage. The base temperature was then determined by calculating the average value of  $(\beta_0)$ . The temperature range between  $T_o$  and  $T_c$  is defined as supraoptimal by Hardegree<sup>74</sup>, which can be used to estimate the  $T_c$ .  $T_c$  for germination was determined using linear regression and expressed in percentiles. The  $T_c$  value was the average value of  $(\beta_0)$  that was obtained. In the end,  $T_o$  was determined as the intersection of the first and second segments of the supraoptimal and suboptimal range regression lines, respectively.

### Thermal time

Thermal time, as defined by Sampayo-Maldonado et al.<sup>26</sup>, is the daily temperature accumulation needed for 50% of the seed lot to germinate<sup>18</sup>. For each temperature treatment, the number of germinations was measured in percentiles. The likelihood that a seed will germinate in a specific amount of time was calculated using Probit analysis<sup>78</sup>. The following Eq. (6) represents the range of suboptimal temperatures for which Probit values were expressed as a function of  $\theta_1$ <sup>79</sup>:

$$Probit (G) = K + [\theta_1 / \sigma] \quad (6)$$

where: When thermal time is zero,  $K$  is the intercept constant, and  $\sigma$  is the standard deviation of the  $\theta_1$  thermal time response. Using the same equation, the thermal time needed for 50% ( $\theta_1$  (50)) of the population to germinate was calculated.

As a function of  $\theta_2$ , Probit values were expressed for the range of supra-optimal temperatures. Equation (7) was employed to explain the germination response, in accordance with Covell et al.<sup>79</sup>:

$$\text{Probit}(G) = Ks + (T + \theta_2/t(G)) / \sigma \quad (7)$$

where:  $\sigma$  is the standard deviation of the maximum temperature  $T_c$ ,  $(T + \theta_2/t(G))$  is the maximum temperature  $T_c$ , and  $Ks$  is an intercept constant when the thermal time is zero. The thermal time needed for 50% germination ( $\theta_2$  (50)) of the population was calculated.

Potential effects of climate change on germination.

Sampayo-Maldonado et al.<sup>24</sup> methodology was followed in this analysis, which made use of maps of the combined projections<sup>80</sup> of the global circulation models' average temperature layers from the Digital Climate Atlas for Mexico, which were available for the French (CNRMCM5), American (GFDL-CM3), English (HADGEM2-ES), and German (MPI-ESM-LR) models (<http://atlasclimatico.unam.mx/AECC/servmaps/>). These models were developed using the Regional Models of Phase 6 for the Intergovernmental Panel on Climate Change's Coupled Model Intercomparison Project (IPCC), with projections for the medium future (2045–2069) and the distant future horizon (2075–2099). The assumptions for CO<sub>2</sub> emissions and associated radiative forcing were 2.6 and 8.5 (SSP5) Watts/m<sup>2</sup>, respectively<sup>81</sup>. We were able to predict the average temperatures for May, which is when seed dispersal starts, using these maps<sup>82</sup>.

For each scenario, the time it would take for *I. jinicuil* seeds to accumulate the thermal time required for 50% of a seed batch to germinate was predicted. The analysis was performed using the Thermal time method<sup>83,84</sup>:

$$\text{Thermal time } (^{\circ}\text{Cd}) = (Env T_m - T_b) t_m \quad (8)$$

where: the average base germination temperature ( $T_b$ ), the average temperature for the month ( $T_m$ ), number of days in the month until the average value of the thermal time is reached ( $t_m$ ), and the accumulated degree days ( $^{\circ}\text{Cd}$ ) are all given.

Modelling potential distributions under climate change scenarios.

The maps of the various climate change scenarios were created using the methodology described in Sampayo et al.<sup>85</sup>. Specimens of *I. jinicuil* collected in the nation were georeferenced in a database from the Global Biodiversity Information Facility (GBIF) platform<sup>86</sup> (<https://www.gbif.org/>), which was one of the data sources used in distributional modeling. Of the total records, only those records found at the optimum germination temperature were used, in the range of 29.5 to 33.5 °C (average value of  $T_0 \pm 2$  °C standard deviation). This is refined with bioclimatic variables from WorldClim, in this case the average temperature of the warmest quarter (Bio10). Therefore, records with temperatures above or below the  $T_0$  range are not included in the analysis. The analysis only included 93% of the total georeferenced points for the species<sup>24</sup>. Data from 1970 to 2000 were used to parameterize 19 climatic variables from BioClim (v2.0), using 1 km<sup>2</sup> pixels<sup>87,88</sup>, and land use and layers of land use and cover and the elevation layer of the country's relief<sup>89</sup>.

Program MaxEnt 3.3.3 was used to run the current distribution models. Georeferenced sites reporting the presence of *I. jinicuil* within its ideal germination temperature range were used to parameterize the models. The relative contribution of each BioClim climatic variable to the model was calculated using the Jackknife method<sup>90</sup>. The program was run again to produce maps of the expected current species distribution in ideal climatic habitat after these crucial climate variables were determined. The number of pixels was obtained and converted to km<sup>2</sup> using the ArcMap 9.3' tool<sup>24</sup>. Lastly, maps showing the species' distribution in the current climatic conditions were produced with a probability higher than 50%.

To obtain the surface with optimal climatic habitat for future distribution, BioClim (v2.0) was used together with MaxEnt 3.3.3 software<sup>90</sup>. We downloaded the climatic layers of the General Circulation Model (GCM) of the Goddard Institute for Space Studies (GISS) of the National Aeronautics and Space Administration (NASA) of the United States of America (GISS-E2-1-G). These layers were produced from the Regional Models of the Coupled Models Intercomparison Project Phase 6 of the Intergovernmental Panel on Climate Change (IPCC), with projections for 2050 as a medium future horizon (average for 2041–2060) and 2090 as a distant future horizon (average for 2081–2100). Given two Shared Socioeconomic Pathways (SSP1) with radiative forcing of 2.6 and 8.5 (SSP5) Watts/m<sup>2</sup> (respectively, decreasing and increasing CO<sub>2</sub> emissions)<sup>91</sup>. The sites were georeferenced and contained populations of the species, spread across the ideal temperature range for germination (29.5 to 33.5 °C). The climatic factors that made the biggest contributions to the distribution model were assessed using the Jackknife method. Counting the pixels and converting them to square kilometers using the ArcMap 9.3' tool. Ultimately, maps showing the species' distribution in projected future climates were produced, with a probability higher than 50%.

To examine if the environmental variables were multicollinearity, Pearson correlation coefficients were employed<sup>92</sup>. The type of response to the environmental variable, being uncorrelated ( $r \leq 0.8$ ) with the normal distribution, and having the highest contribution as indicated by the Jackknife test were the three criteria used to

select the predictive variables. Furthermore, areas that present barriers to the species' dispersal were eliminated, thereby restricting the results of biogeographical regions.

## Conclusions

The study's findings showed that both the linear and non-linear models examined fit the empirical data on *I. jinicuil* germination in response to temperature reasonably well. The linear and beta models, on the other hand, fit the data better than the segmented ones and both precisely define the cardinal temperatures for the species. Temperature had an impact on *I. jinicuil*'s ability to germinate. According to the regression models, the minimum temperature for germination was in the range of 4.8 to 9.45 °C (average  $T_b$ :  $6.21 \pm 2.23$  °C). With increasing temperature, the germination rate reached its maximum rate at the optimum temperature and highest germination speed, which was found in the range of 29.58 to 33.02 °C (average  $T_o$ :  $31.52 \pm 1.43$  °C). With temperatures higher than the optimum temperature, the maximum temperature at which germination occurred was found at the ceiling temperature, in the range of 44.51 to 49.20 °C (average  $T_c$ :  $47.6 \pm 2.73$  °C). At 25 °C, the percentage of germination reached its maximum, and at  $31.6 \pm 1.1$  °C, the rate of germination was fastest. The calculated thermal time ( $(\theta_{-1}(50))$   $117.164 \pm 0.636$  °Cd) takes 6.6 days to reach under the current climate conditions. Temperature rises are predicted by climate change models, which will reduce the amount of time it takes for seeds to reach the temperature required for germination. The Goddard Institute for Space Studies (GISS) of NASA's GISS-E2-1-G model predicts that, in comparison to its current distribution, the future distribution of *I. jinicuil* populations will decline by 1.2–23.5%. The results obtained in the work indicate an adequate resolution of the distribution of the species based on the optimal germination range and the realization of a design with greater temperature resolution in the optimal germination range is perceived as a perspective of the work. In addition, in areas where the climate will no longer be ideal, it is advised to collect seeds and conduct provenance tests in accordance with models of the species' potential distribution in order to preserve valuable genotypes for future environments. It is also possible to create commercial plantations of the species and acquire seeds of exceptional genetic quality by planting seed orchards. Distribution modeling of *I. jinicuil* led to the identification of locations where temperature will maximize establishment and adaptation under various climate change scenarios by positively influencing seed germination. The results presented in this work have the potential to establish the bases for future research on cardinal temperatures in successive stages of development, such as the establishment and growth of the species. In addition, develop a plant conservation program, based on the climate change approach, generate habitat restoration projects for *I. jinicuil*, according to the new areas with suitable conditions for the species, as well as disseminate information to shade coffee producers on adaptation and mitigation actions in the face of climate change.

## Data availability

The datasets used and/or analysed during the current study available from the corresponding author on reasonable request to cmflores@unam.mx.

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## Author contributions

C.M.F.O. and T.U. Conceived the idea and designed the experiment. S.S.M. and D.C.S. Performed the experiments. N.I.R.A. and G.S.Q. Carried out the seed collections. T.U., M.W., M.G. and E.B. Verified the analytical methods. P.D.A., A.D.O.S. and R.H.M. Supervised the development of this work and analysed the data. S.S.M., D.C.S. and C.M.F.O. Wrote a draft of the manuscript. All authors interpreted the results and reviewed the final manuscript.

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## Declarations

### Competing interests

The authors declare no competing interests.

### Additional information

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