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# 1           **Has North Africa turned too warm for a Mediterranean** 2                           **forest pest because of climate change?**

3  
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22 **Abstract**

23 Climate warming is inducing dramatic changes in species distribution. While many studies report the  
24 poleward range expansion of some species, some others report the range retraction and extinction  
25 risk of other species. Here we explore how climate warming affects the southern edge in North Africa  
26 of the pine processionary moth, *Thaumetopoea pityocampa*, which is a model insect currently  
27 expanding northwards and toward higher elevation in Europe. This Mediterranean forest insect was  
28 found in southern Tunisia until 2003. Field surveys were conducted to map the current southern  
29 edge of the species in Tunisia. Pheromone traps were installed on a north-south gradient, a  
30 translocation experiment of egg-masses was conducted on this gradient and local temperature  
31 change was analysed. We thus proved that the pine processionary moth has disappeared from  
32 southern Tunisia, and that no more adult males were actually flying there. We also found a decrease  
33 of egg-hatching and of the proportion of individuals able to reach larval stages along this gradient,  
34 while daily minimal and maximal temperatures globally increased. Furthermore, we showed that  
35 daily maximal and minimal temperatures as well as indices of extremely high temperatures have  
36 substantially increased during the study period (1980-2019). This study reveals the retraction of the  
37 pine processionary moth from southern Tunisia due to higher mortality rates that could be attributed  
38 to a significant local warming. The role of other factors (mainly the response of host trees and  
39 natural enemies to climate change) may amplify this direct effect and should be further explored.

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46 **Keywords:** pine processionary moth; *Thaumetopoea pityocampa*; climate warming; range  
47 retraction; *Pinus*; Tunisia

## 48 **1 Introduction**

49

50

51 Climate change is currently evidencing an unequivocally increase in temperature with an average  
52 warming of 0.85°C during the period 1880-2012 (IPCC 2014). Extreme weather events, notably  
53 heatwaves, have also increased in both intensity and frequency in most parts of the world since  
54 1950, and in particular in North Africa. For instance, in Tunisia, the mean annual temperature has  
55 increased by 1.4°C in the 20<sup>th</sup> century and the increase has even reached +3°C locally in Tunis  
56 (northern Tunisia)(Verner et al. 2013). Climate warming is significant throughout Tunisia, even in  
57 southern regions where average maximum temperatures can already exceed 40°C (Verner et al.  
58 2013). Climate change scenarios suggest that maximal temperature could further rise, for instance by  
59 2.5-3.3°C in Tunis by the 2080s (Verner et al. 2013).

60 Higher temperatures and more frequent and intense heatwaves threaten lives as well as ecosystems  
61 (Parmesan et al. 2000). Indeed, a consequence of the ongoing global warming is a set of dramatic  
62 impacts on a broad range of organisms, particularly plants and invertebrates (Parmesan and Yohe  
63 2003; Robinet and Roques 2010; Walther et al. 2002). One of these impacts is the distributional  
64 change for species whose geographic range is mainly limited by temperature. Until recently, most of  
65 the studies have reported that many species were expanding their distribution toward the poles and  
66 higher elevations due to climate change (Andersen et al. 2019; Parmesan et al. 1999; Thomas and  
67 Lennon 1999). Few species-level extinctions were reported so far, namely species of anurans  
68 including the golden toad (*Bufo periglenes*) (e.g., Pounds et al. 1999) but, following species  
69 distribution models, Thomas et al. (2004) estimated that 15-37% of the studied species (Taxa of  
70 mammals, birds, frogs, reptiles, butterflies, other invertebrates and plants) could become extinct by  
71 2050. The extinction risk is actually predicted to accelerate with the temperature increase, and up to  
72 one species out of six could become extinct in the worst climate change scenario (RCP8.5; 4.3°C rise  
73 compared to pre-industrial temperatures) (Urban 2015). The overall positive or negative impacts of  
74 climate change on species distribution are thus very difficult to predict. It is notably unclear how the  
75 southern range is impacted for species that move their northern range limit northwards (e.g.  
76 southern pine beetle, *Dendroctonus frontalis*, in the United-States, Lesk et al. 2017, or the pine  
77 processionary moth, *Thaumetopoea pityocampa*, in Europe, Battisti et al. 2005). Modeling  
78 techniques such as species distribution models or phenological models can be used to predict insect  
79 distributions and thus assess the potential shifts of northern and southern limits (e.g., for the spruce  
80 budworm, *Choristoneura fumiferana*, in North America, Régnière et al. 2012). However, the southern  
81 limit is often not studied in the field and we have so far poor biological evidence to say whether

82 some species face a real range expansion (e.g., the northern limit shifts northwards and the southern  
83 limit remains the same) or instead a range shift (i.e., both northern and southern limits shift  
84 northwards at about the same rate).

85 The pine processionary moth (PPM), *Thaumetopoea pityocampa*, is a well-known Mediterranean  
86 species that has been recognized by the Intergovernmental Panel on Climate Change (IPCC) to be one  
87 of the few species for which the underlying mechanism of response to climate warming was clearly  
88 demonstrated (Rosenzweig et al. 2007). Indeed, PPM is expanding northwards in Europe as an  
89 indirect effect of the rise of minimal temperatures on insect survival during the cold season (Battisti  
90 et al. 2005; Robinet et al. 2007). The northern edge of its distribution has then been considered as an  
91 indicator of global warming in France (French Ministry of Ecology, ONERC 2010).

92 PPM is distributed not only in Southern Europe but also in Asia Minor and North Africa (Roques et al.  
93 2015), where summer temperatures can reach extremely high values. PPM occurrence has been  
94 documented at its southern edge in North Africa (Roques et al. 2015) but the effect of climate  
95 change on the PPM distribution edge is unclear. PPM has expanded its distribution in the south of  
96 Algeria because of the massive pine planting program, The Green Dam, to combat desertification.  
97 Climate conditions were likely suitable for the PPM establishment before these pine plantations. In  
98 Morocco, PPM has also spread due to large afforestation activities and introduction of exotic pine  
99 species. In addition, its southern limit is blurred by its altitudinal limit in the High Atlas. In Tunisia, no  
100 large afforestation was done since the 1990s and no mountainous barrier may limit the southern  
101 range of PPM. Thus, it offers a unique place to investigate the effects of climate change on the  
102 species' southern distribution. PPM had been seen in southern Tunisia until 2003 (Azizi 2015).  
103 However, since 2014, PPM has not been seen in this region during occasional field travels (Ben  
104 Jamâa, 2017), and it is unclear whether PPM is still present. Since monthly maximal temperatures  
105 above 25°C are detrimental for PPM populations (Démolin and Rive 1968; Robinet et al. 2015), and  
106 maximal temperatures usually exceed 40°C in July and August in southern Tunisia, the effects of their  
107 rise on these southern PPM populations are questioned.

108 In this context, two major objectives for this study were: 1) to update our knowledge about the PPM  
109 spatial distribution at its southern edge in Tunisia, and 2) to determine the effects of climate change  
110 on this possible distribution retraction. For this purpose, we first surveyed the current southern  
111 distribution of PPM. We installed pheromone traps to test the presence/absence of adult males, and  
112 we installed PPM colonies on a latitudinal gradient to measure their survival rate in relation with  
113 weather conditions. We also analyzed long time-series of temperatures along this gradient to  
114 characterize locally the intensity of observed climate change. This study on a model species known to

115 expand northwards provides the first clear evidence about adverse effects of climate warming on its  
116 southern range.

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## 120 **2 Materials and methods**

121

### 122 **2.1 Study species**

123 The pine processionary moth (PPM), *T. pityocampa* (Denis & Schiffermüller) (Lepidoptera,  
124 Notodontidae), is a univoltine forest insect species largely distributed in Mediterranean countries  
125 (Démolin 1969; Roques 2015). In Tunisia, adults generally fly in summer from 15<sup>th</sup> July to 1<sup>st</sup> August at  
126 high altitudes, and from 10<sup>th</sup> August to 7<sup>th</sup> September at mid-altitudes (Démolin et al.1968; Ben  
127 Jamâa et al. 1999). Females lay eggs on pine needles, larvae hatch about one month later and  
128 develop in five instars (L1 to L5; generally from autumn to spring), they feed on pine needles and  
129 build collectively white silk nests on pine branches during the cold season. At the end of their  
130 development, larvae make a procession (occurring from the end of January to March depending on  
131 winter severity) to leave the tree and burry in the soil and pupate. In fact, pupation occurs in  
132 February in the mountains, whereas it occurs in September and January-February in the regions of  
133 coastline. After a flexible period of diapause, adults emerge. Each PPM life-stage has some thermal  
134 constraints given the time window at which they are exposed to. For instance, late instar larvae are  
135 vulnerable to cold in winter (< 0°C) while eggs and first instar larvae are vulnerable to heat in  
136 summer-autumn (> 25°C) across its range in Mediterranean countries (Démolin 1969; Robinet et al.  
137 2015). In relation with these constraints, PPM phenology varies across bioclimate regions (i.e., adult  
138 emergence and egg hatching occur later in warmer areas, thus young larvae are less exposed to the  
139 highest summer temperatures ; Huchon and Démolin 1970) and this phenology could furthermore be  
140 affected by climate change (Robinet et al. 2015). PPM, which is the most important insect defoliator  
141 of pine forests in Mediterranean countries, causes substantial impact on the tree growth (Jacquet et  
142 al. 2013). In addition, PPM also causes important allergy risks to humans and animals because larvae  
143 can release urticating setae (Battisti et al. 2017). This species is thus not only a good model species to  
144 study the effects of climate change but also an important pest in everyday life in forestry and public  
145 health.

### 146 **2.2. Historical distribution of the PPM in Tunisia**

147 The PPM is one of the most serious pests of Aleppo pine forests in Tunisia (Rive 1966) and thus, it has  
148 been episodically surveyed in the past. This insect is historically present in all pine stands from north  
149 to south (Démolin and Rive 1968; Roques et al. 2015) (Fig. 1B). First, Démolin et al. (1968) conducted  
150 surveys to determine the potential dates of adult emergence across different localities. This dataset  
151 can be used to have PPM occurrence points in the 1960s (Fig. SM1-A). In the 1990s, PPM nests have  
152 been seen in three regions (Jebel Sidi Driss, Jebel Toulal and Techine) around Gabes according to  
153 forestry technicians (Fig. SM1-B). Later, PPM occurrence was studied through egg-masses sampled by  
154 INRGREF in September-October 1992, 1993 and 1995 throughout different localities going from  
155 northern regions to the southernmost edge of natural Aleppo pine stands (Kasserine) (Fig. SM1-B).  
156 Thereafter, PPM nests have been last seen in Tataouine in 2003 (Azizi 2015) during field travels in  
157 Jebel Broumet (Fig. SM1-C). In 2010, its presence can be inferred from egg-masses collected by  
158 INRGREF, and in 2013-2014 through field surveys conducted by Azizi (2015) (Fig. SM1-C). PPM  
159 absence was firstly assessed in 2013-2014 in Tataouine, Gabes and Medenine (Azizi 2015).

160

### 161 **2.3. Mapping the southern edge of the PPM distribution in Tunisia**

162 Due to characteristic signs of PPM presence (white silk nests, egg-masses, or signs of pine tree  
163 defoliation), the presence of PPM is relatively easy to detect on the field. However, recording  
164 locations of PPM presence was not enough to map the southern edge of the PPM distribution. We  
165 needed to record locations where PPM was absent as well in order to actually define the border. The  
166 mapping of PPM northern distribution in France has been standardized over a regular cell grid at a  
167 spatial resolution of 8 km × 8 km (see protocol for field sampling described by Rousselet et al. 2013).  
168 We tried to derive a similar approach to map the southern edge of the PPM distribution in Tunisia.  
169 However, it was difficult, if not impossible, to adapt this protocol since we had no baseline edge to  
170 rely on, and host trees could be very scarce and scattered in southern Tunisia. Therefore, we adopted  
171 an intermediate protocol: we reported the occurrence (presence/absence) of the PPM in potentially  
172 critical areas. In 2018, from the 2<sup>nd</sup> to the 4<sup>th</sup> of January, we visited the regions supposed to be at the  
173 southern edge or beyond (near Sidi Bouzid, Gabes and Tataouine; Fig. 1-2). We notably surveyed  
174 areas where pine stands were reported by the General Direction of Forests in Tunis (Fig. 2A), and the  
175 main roads along which some isolated pine trees could eventually be found. Trees outside forests  
176 could effectively play an important role in habitat connectivity and the presence of the PPM (Rossi et  
177 al. 2016). In addition to this extensive survey, we added observations done on October 10<sup>th</sup>, 2017  
178 near Gafsa during a preliminary survey trip.

179

## 180 **2.4 Pheromone trapping**

181 Sexual pheromone traps (BuxaTrap®) were installed at different dates in summer 2018 as PPM adults  
182 generally fly later in warmer areas (Huchon and Démolin 1970). These traps were distributed on a  
183 latitudinal gradient going from north to south: Tunis, Testour, Kef, Sidi Bouzid, Gabes and Tataouine  
184 (Fig. 1). One to three traps per site were attached on the branches of Aleppo pine trees, *Pinus*  
185 *halepensis*, placed at 1.5 meter high, and checked weekly until the trap removal (end of September  
186 to end of October 2018). When several traps were installed on the same site, they were distant to 50  
187 meters from each other.

188

## 189 **2.5 Translocation of egg masses**

190 *General method.* In order to assess the mortality rate under different bioclimatic zones, we chose to  
191 work on a thermal gradient consisting of three locations (with Aleppo pines): Zaghouan (core area),  
192 Sidi Bouzid (supposedly on the southern edge) and Tataouine (from where PPM may have  
193 disappeared) (Fig. 1). Since early larval stages are particularly sensitive to high temperatures (Robinet  
194 et al. 2015), we aimed to measure how maximal temperatures recorded in Tunisia in autumn could  
195 impact the survival of eggs and early larval stages. Some PPM colonies were thus translocated and  
196 exposed to field weather conditions from September 2019 to January-February 2020 on this  
197 gradient. Then, they were retrieved before they left their nest (e.g., just before the end of their larval  
198 development and the processions). In this way, we avoid their potential establishment in the area  
199 where it has likely disappeared (even if the establishment risk was supposedly very low). This  
200 experiment was inspired from those done in France and Italy to explore the effects of low winter  
201 temperatures on the PPM survival at its northern and altitudinal edge (Battisti et al. 2005).

202 *Field experiment in more details.* Egg-masses were collected on *P. halepensis* near Sidi Bouzid on  
203 September 17<sup>th</sup>, 2019 (i.e., as soon as egg-masses could be found in this site). The translocation of  
204 egg-masses was done on a latitudinal gradient, going from north (Zaghouan, within the PPM core  
205 distribution) to south (Tataouine, where PPM has likely disappeared), with an intermediate location  
206 at its southern limit (Sidi Bouzid) (Fig. 1). Our initial objective was to translocate 30 egg-masses at  
207 each location, but given the low population density, it was not possible and we decided to keep only  
208 30 egg-masses for Tataouine. A total of 15 egg-masses have been translocated at Zaghouan on Sept  
209 25<sup>th</sup>, 2019 (three egg-masses per pine tree, on five trees), 15 egg-masses at Sidi Bouzid on Sept 17<sup>th</sup>,  
210 2019 (three egg-masses per pine tree, on five trees), and 30 egg-masses have been translocated at  
211 Tataouine on Sept 18<sup>th</sup>, 2019 (five egg-masses per pine tree, on six trees). Since a very low number of  
212 pine trees were available for this experiment, we had to place more egg-masses per tree (five instead

213 of three). Egg-masses and nests were then collected on Jan 7<sup>th</sup>, 2020 from Tataouine and Sidi Bouzid,  
214 and on Feb 5<sup>th</sup>, 2020 from Zaghouan.

215 *Analysis of egg-masses and nests collected from field experiments.* Egg-masses and nests retrieved  
216 from the previous experiments were brought to the laboratory at INRGREF (Tunis) and kept at  
217 ambient air temperature (25±2°C). For each egg-mass, scales covering the eggs were removed to  
218 count eggs and split them into four categories (Tsankov et al. 1996; Imbert 2012) following their  
219 observation under a binocular magnifier:

- 220 (1) hatched eggs, presenting a characteristic large and round larval emergence hole,
- 221 (2) non-hatched-eggs, having no larval nor parasitoid emergence holes,
- 222 (3) parasitized eggs, showing a characteristic small parasitoid emergence hole and/or having a dead  
223 parasitoid inside, and/or having a characteristic parasitoid meconium inside, and finally
- 224 (4) other eggs, including dried, flat and non viable eggs, and dead PPM larva that failed to emerge  
225 and showed an irregular larval emergence hole.

226 For each nest, all the living and dead larvae were counted, and their larval instar was determined.

227 *Temperature records.* Small data loggers (iButtons<sup>®</sup>) have been installed on the three locations from  
228 Dec 18<sup>th</sup>, 2018 to Jan 7<sup>th</sup>, 2020 in Tataouine, from Jan 9<sup>th</sup>, 2019 to Jan 7<sup>th</sup>, 2020 in Sidi Bouzid and  
229 from Feb 2<sup>nd</sup>, 2019 to Feb 5<sup>th</sup>, 2020 in Zaghouan to record temperature every two hours. Each logger  
230 was attached in the shade of a branch of the selected pine tree among trees used for the  
231 translocation experiment. On each location, several temperature statistics were calculated to  
232 compare weather conditions: (1) monthly statistics: absolute minimal and maximal temperatures of  
233 each month, and mean temperature of each month, and (2) daily statistics: daily minimal and  
234 maximal temperatures, and daily mean temperature. Data analysis was done using the R software (R  
235 Core Team, 2018).

236

## 237 **2.6 Statistical analysis related to the translocation experiments**

238 As the percentages of the different egg categories and the living/dead larvae were not normally  
239 distributed, a Kruskal-Wallis H test (followed by a post-hoc Dunn's pairwise tests if the K-W test was  
240 significant) was performed to compare the results from the different studied locations. A pairwise  
241 Wilcoxon signed Rank test was applied to compare temperatures among the locations of the  
242 latitudinal gradient.

243

## 244 **2.7 Analysis of climate data**

245 *Climate data source.* Daily minimal and maximal temperatures were kindly provided by the National  
246 Institute of Meteorology (INM) in Tunis at the following stations: (1) Mograne (representative of the  
247 weather in Zaghouan, located 6.7 km away) during the period 1991 – 2011, (2) Medenine (located at  
248 47.6 km from Tataouine, characterized by desert climate as the latter) during the period 1980 – 2011,  
249 (3) Sidi Bouzid during the period 1980 – 2014, and (4) Tunis during the period 1980 – 2014.  
250 Hereafter, for simplification, we will refer to the name of experimental sites: Zaghouan for the  
251 Mograne weather station, and Tataouine for the Medenine weather station. Since these datasets  
252 had missing data and do not provide recent weather conditions (between 2011 or 2014 to 2019), we  
253 also retrieved daily temperatures from Tutiempo Network  
254 (<https://fr.tutiempo.net/climat/tunisie.html>). For the four stations, we checked that there was a  
255 good agreement between the two datasets (i.e., we compared daily temperatures in 2011 and they  
256 correctly matched). We thus considered the combination of these two datasets to have full time-  
257 series without missing data until 2019.

258 *Calculation of annual maximal, minimal and mean temperatures.* To explore the local warming trend  
259 during the period 1980-2019 in Tunis, Sidi Bouzid and Tataouine and during the period 1991-2019 in  
260 Zaghouan, we calculated the annual mean of daily maximal, minimal and mean temperatures (Tmax,  
261 Tmin, and Tmean, respectively). Then, we made a linear regression for each variable (Tmax, Tmin,  
262 Tmean) as a function of the years to elucidate the magnitude of warming on each site. These  
263 analyses were performed using R software (R Core Team 2018).

264 *Calculation of indices of extreme temperatures.* Nine indices related to temperatures from those  
265 defined by the Expert Team on climate change Detection Monitoring and Indices (ETCCDMI) were  
266 considered (Table 1; Peterson 2005; Zhang and Yang 2004). The calculation of these indices as well as  
267 statistical analyses were performed using the RclimDex package of R software  
268 (<https://github.com/ECCC-CDAS/RclimDex>). Slopes of the annual trends of these extreme climate  
269 indices were calculated based on a least square linear fitting. A locally weighted linear regression  
270 using a loess smoother function in R (Zhang and Yang 2004) was also applied to each index. The  
271 statistical significance of trends was assessed based on the Student's t-test for the estimate of the  
272 slope at the 95% level ( $p$  value < 0.05). In addition to these annual trends, we explored on a monthly  
273 basis (from June to October) the fluctuation of the number of days at which daily maximal  
274 temperature exceeded 35 and 40°C.

275

### 276 **3 Results**

277

### 278 **3.1 Mapping the PPM southern edge in Tunisia**

279 In total, 186 locations were investigated. PPM was found in 25 locations (including one location  
280 visited in 2017 in north-east Gafsa) and absent in 161 locations (including one location visited in 2017  
281 in south-east Gafsa) (Fig. 2B). All the southern sites visited around Gabes and Tataouine were free  
282 from PPM, whereas the most southern sites infested by PPM were the north-east of Gafsa and  
283 south-east of Sidi Bouzid.

284

### 285 **3.2 Pheromone trapping**

286 No PPM male adult was caught in the pheromone traps in Gabes and Tataouine, thus confirming that  
287 PPM is absent in the most southern sites. In contrast, 40-58 adults per trap were caught in the  
288 regions of Sidi Bouzid, Kef (wherein the highest number of captures occurred), Testour and Tunis  
289 (Table 2).

290

### 291 **3.3 Translocation of egg masses**

292 *Comparison of hatched eggs.* The proportion of hatched eggs clearly decreased from north to south  
293 (gradient Zaghouan – Sidi Bouzid - Tataouine) (Fig. 3; Tables SM2-SM4). In addition, in Tataouine, one  
294 whole egg-mass out of 30 (3%) has not hatched, whereas all egg-masses from Sidi Bouzid and  
295 Zaghouan provided some hatched eggs (Tables SM2SM4). There was a statistically significant  
296 difference in the percentage of hatched (Kruskal-Wallis  $\chi^2 = 7.06$ ,  $df = 2$ ,  $P = 0.029$ ) and unhatched eggs  
297 (Kruskal-Wallis  $\chi^2 = 12.19$ ,  $df = 2$ ,  $P = 0.002$ ) between the different locations. There was a significant  
298 difference in hatched eggs between Tataouine and Zaghouan (Dunn's pairwise test;  $P = 0.028$ ,  
299 adjusted using the Bonferroni correction), and there was a significant difference in unhatched eggs,  
300 between Tataouine and Zaghouan ( $P = 0.003$ , adjusted by the Bonferroni correction), and between  
301 Sidi Bouzid and Zaghouan ( $P = 0.012$ , adjusted by the Bonferroni correction).

302 *Comparison of parasitized eggs and other mortality factors.* Surprisingly the rate of parasitized eggs  
303 was higher in Tataouine, including both the generalist egg parasitoids, *Ooencyrtus pityocampae*, and  
304 the supposedly specialist egg parasitoids, *Baryscapus servadeii*, and most of parasitoids survived and  
305 emerged because we found parasitoid meconium more than dead parasitoids inside eggs.  
306 Nevertheless, this parasitism rate was very low (6% on average) and did not vary significantly from  
307 the other regions ( $\chi^2 = 1.67$ ,  $df = 2$ ,  $P = 0.433$ ). Other factors of egg mortality had little impacts (less

308 than 11.5% on average) and did not show any clear pattern on the latitudinal gradient. The  
309 percentage of other egg mortality was not significantly different among locations ( $X^2 = 0.35$ ,  $df = 2$ ,  
310  $P=0.836$ ).

311 *Comparison of larval survival.* Unfortunately, when we retrieved PPM nests, none of them was found  
312 on the site of Zaghouan (they were likely removed by people). As a result, we could only compare  
313 larval survival between Sidi Bouzid and Tataouine. The proportion of living larvae was lower in  
314 Tataouine than in Sidi Bouzid (Fig. 3; Tables SM2-SM4). Surprisingly a few larvae succeeded to survive  
315 in Tataouine (46% of eggs succeeded their development in larvae). The percentage of larvae that  
316 succeeded to survive was not significantly different between Tataouine and Sidi Bouzid ( $X^2 = 0.83$ ,  
317  $df=1$ ,  $P= 0.361$ ). However, the percentage of dead larvae was significantly higher in Tataouine (12%)  
318 than in Sidi Bouzid ( $X^2= 4.03$ ,  $df=1$ ,  $P=0.04$ ). The highest larval mortality affected mainly young instars  
319 (L2 and L3) in Tataouine (table SM2). Besides, larval development was relatively faster in Tataouine  
320 compared to Sidi Bouzid. Percentages of L2, L3, L4 and L5 instars were respectively 11 *versus* 18%, 41  
321 *versus* 54%, 41 *versus* 27% and 7 *versus* 1% in Tataouine compared to Sidi Bouzid (Tables SM2 and  
322 SM3).

323 *Comparison of temperatures.* Temperatures globally increased from north to south (gradient  
324 Zaghouan – Sidi Bouzid - Tataouine) (Fig. 4). The average from Sept 1<sup>st</sup> 2019 to Feb 5<sup>th</sup> 2020 of daily  
325 minimal, mean and maximal temperatures was: 15.1°C, 20.1°C and 26.5°C in Tataouine; 14.3°C,  
326 19.0°C and 26.0°C in Sidi Bouzid, and 11.7°C, 16.1°C and 24.0°C in Zaghouan. Daily minimal and mean  
327 temperatures were significantly different among the three locations ( $P < 10^{-4}$  and  $P < 10^{-9}$ ), while the  
328 maximal daily temperature was significantly different only between Tataouine and Zaghouan  
329 ( $P = 0.005$ ), and Sidi Bouzid and Zaghouan ( $P=0.02$ ) but not between Tataouine and Sidi Bouzid  
330 ( $P = 0.33$ ) (pairwise Wilcoxon Signed Rank Test) (Fig. 5).

331

332

### 333 **3.4 Analysis of climate data**

334

335 *Trends in annual maximal, minimal and mean temperatures.* All temperature variables (Tmax, Tmin  
336 and Tmean) showed a significant rising trend for all sites (Fig. 6; Table 3). Within 39 years (1980-  
337 2019), maximal temperatures have thus increased by 1.2°C, 1.7°C, 1.2°C respectively in Tunis, Sidi  
338 Bouzid, Tataouine and they have increased by 0.8°C within 28 years (1991-2019) in Zaghouan.  
339 Minimal temperatures have increased by 2.6°C, 1.5°C and 1.7°C within 39 years respectively in Tunis,

340 Sidi Bouzid, Tataouine, and they have increased by 2°C within 28 years in Zaghouan. The highest  
341 annual temperatures are recorded in Tataouine with  $T_{max} = 28^{\circ}\text{C}$ ,  $T_{min} = 16.5^{\circ}\text{C}$  and  $T_{mean} = 22.5^{\circ}\text{C}$   
342 (Fig. 6).

343 *Trends in extreme temperatures: warm indices.* The number of warm nights (TN90p) significantly  
344 increased at all the stations (Table 4). Similarly, there was a positive trend on the number of warm  
345 days (TX90p) with significant increase observed only at Tunis and Sidi Bouzid. There was a positive  
346 trend on TXx at all stations (except Zaghouan, presented a negative insignificant trend) with a  
347 significant increase observed at Sidi Bouzid. Trend analysis for TNx showed a positive trend with  
348 significant increase throughout the study areas. The other indices (except SU40 and SU35, in  
349 Zaghouan) indicated an increasing trend. The number of days with a daily maximal temperature (TX)  
350 above 40°C (SU40) showed a significant increase at Sidi Bouzid and Tataouine. There was a highly  
351 significant increase in the number of days with a daily maximal temperature (TX) above 35°C (SU35)  
352 at Tunis, Sidi Bouzid and Tataouine. The number of days with a daily maximal temperature (TX)  
353 above 25°C (SU25) presented a highly significant increase at Tunis, Sidi Bouzid and a significant  
354 increase at Tataouine (Fig. SM5-SM7).

355 *Trends in extreme temperatures: temperature fluctuation indices.* In diurnal temperature range  
356 (DTR), three sites (Tunis, Zaghouan and Tataouine) had significant downward trends (Table 4). The  
357 lowest DTR value was recorded in Tunis (in 2004), followed by Zaghouan (in 2018) and Tataouine (in  
358 2017). Unlike the other regions, there was a positive but not significant trend for DTR at Sidi Bouzid.

359 *Number of days with temperatures above 35°C and 40°C from June to October.* Different patterns  
360 were observed among months (SM8-SM13). Both Tataouine and Sidi Bouzid recorded extremely high  
361 temperatures from June to August, while Tataouine appears to be even warmer than Sidi Bouzid  
362 from September to October. Indeed, more than half of July and August months had temperatures  
363 higher or equal to 35°C in the southern regions (Sidi Bouzid and Tataouine) nearly each year (Fig.  
364 SM9 ; Fig. SM10). Similarly, the number of days with temperatures higher or equal to 40°C (even  
365 exceeded 45°C) was more frequent in the southern regions than the northern ones (SM9-SM10). In  
366 September, high temperatures were more frequent in Tataouine (exceeding 35°C for 8-20 days and  
367 40°C for 1-8 days ; Fig. SM11) than in other sites. In October, temperatures exceeded frequently 35°C  
368 (up to 10 days) in Tataouine (Fig. SM12). Although such phenomenon was observed also in the past  
369 (in 1990 and 1992), it was less frequent. Recently, several consecutive years reached such high  
370 temperatures (at least 4 days above 35°C were recorded each year from 2012 to 2016; Fig. SM12).

371

## 372 **4 Discussion**

373

374 Climate change has been demonstrated to be a major factor affecting populations of forest pests in  
375 numerous ways. Recent literature has mainly reported species expanding their distribution, such as  
376 *T. pityocampa* (Roques et al. 2015). In this species, range expansion in Europe has been explained by  
377 higher winter temperatures and thus more favorable weather conditions to survive in winter. On the  
378 other hand, temperature increase and drought may affect the southern edge of the species  
379 distribution (in North Africa). Thus, the present study explored the effects of climate warming on  
380 possible southern retraction based on experimental approaches conducted in the field.

### 381 **4.1 Field evidence of a southern retraction**

382 PPM was historically present in southern Tunisia (the presence was confirmed through the  
383 observation of PPM nests), notably in Tataouine (Azizi 2015). Following the survey of the PPM's  
384 southern edge, it appears that the PPM was not found neither around Gabes nor Tataouine, whereas  
385 it was present in the north-east of Gafsa and south-east of Sidi Bouzid. Pheromone traps confirmed  
386 that no PPM males were actually flying in these two areas. Former PPM nests (i.e., nests built the  
387 previous year(s)) were not found either. Following these results, we proved that PPM has effectively  
388 disappeared from south Tunisia and the reason for this southern retraction has then been explored.

### 389 **4.2 Lower survival in warmer southern sites.**

390 We observed a global decrease of egg hatching and proportion of living larvae (Fig. 3), and an  
391 increase of temperatures (Fig. 4) along the latitudinal gradient from north to south. Maximal  
392 temperatures as well as egg hatching rates were however not statistically different between the  
393 southern PPM edge (Sidi Bouzid) and the area where it has disappeared (Tataouine), but they were  
394 different from the northernmost site (Zaghouan) (Fig. 5). Minimal and mean temperatures were  
395 though statistically higher in Tataouine than in Sidi Bouzid during the study period (Fig. 5), and thus  
396 may not explain the same low level of hatching rates in both Sidi Bouzid and Tataouine. However, it  
397 could explain why larval development was substantially faster in Tataouine than in Sidi Bouzid  
398 (Tables SM2-SM3). Indeed these higher (minimal and mean) temperatures could trigger a more rapid  
399 development since insect development rate is usually linearly correlated to temperature, at least up  
400 to an optimal temperature threshold (Rebaudo and Rabhi 2018). Maximal temperatures could be the  
401 main driver of the PPM mortality and disappearance in southern Tunisia. If the development rate of  
402 eggs increases with increasing mean temperatures, then young larvae hatching from these eggs  
403 appear earlier in autumn and are thus likely exposed to higher maximal and potentially lethal

404 temperatures. We could thus expect a further retraction from the region of Sidi Bouzid in the coming  
405 years if minimal and mean temperatures continue increasing with climate warming. Difficulties in  
406 collecting egg-masses in this region provide evidence of the PPM population decline at its current  
407 southern edge.

#### 408 **4.3 Retrospective analysis of the role of local climate warming**

409 Average annual maximal, mean and minimal temperatures significantly increased between 1980 and  
410 2019 in all investigated sites. Except in Sidi Bouzid, minimal temperatures increased faster than  
411 maximal temperatures (Table 3). As already mentioned, increase of minimal temperature is likely  
412 beneficial to the development rate of the insect. However, if eggs could develop faster, young larvae  
413 would be exposed to higher summer temperatures (due to both their occurrence at an earlier time-  
414 window in the season, and an increase – even if more moderate – of maximal temperatures) and this  
415 would potentially foster mortality rates. In Tataouine, given the observed warming trend (Table 3),  
416 the annual minimal and maximal temperatures have increased respectively by 0.7°C and 0.5°C over  
417 16 years (since PPM was observed in 2003), which is a substantial warming. More importantly,  
418 extremely high temperature values are recorded more and more often in southern regions (Sidi  
419 Bouzid and Tataouine; SU40, SU35, TXX in Table 4). The increasing trend of these heat indices may  
420 have a detrimental effect on the early instars larvae and thus contribute to higher mortality rates,  
421 which may explain the disappearance of PPM from southern Tunisia. Although we found that some  
422 larvae could develop in Tataouine in 2019-2020, maximal temperatures were much lower that year  
423 than the previous years (Fig. 6) and heat extremes (e.g., TXX and SU35) were also lower (Fig. SM5).  
424 Higher temperatures have mostly been recorded between 2009 and 2016 (Fig. 6).

#### 425 **4.4 Life-stages potentially impacted by extremely high temperatures**

426 Looking at summer data more specifically, temperatures usually exceeded 35°C on more than 15  
427 days per month, even 40°C for a few days, and reached sometimes 45°C in the southern regions in  
428 July and August (Fig. SM9-SM10). This period corresponds to the flight of adults, which may be  
429 subject to lethal temperatures (Ben Jamâa 2017). However, we should note that both Sidi Bouzid and  
430 Tataouine had very similar maximal temperatures in summer (Fig. SM9-SM10). Regarding the  
431 autumn data, in September (period that coincides with the beginning of oviposition), temperatures  
432 above 35°C and 40°C were more frequent in Tataouine (Fig. SM11). These temperatures (in  
433 September) could negatively affect egg survival if they reach unusually high values. Indeed, Robinet  
434 et al. (2013) showed that egg-masses from a French PPM population were able to survive a daily  
435 maximal temperature of 40°C during 12 consecutive days. However, Rocha et al. (2017) showed that  
436 negative effects appeared on egg-masses from a Tunisian PPM population at 42°C after only three

437 days of heatwaves, and none of them survived at 44°C. In October (period that corresponds to the  
438 development of young larvae), temperatures exceeded 35°C (up to 10 days) in Tataouine (Fig. SM12).  
439 Young larvae are particularly sensitive to high temperatures (Robinet et al. 2015). First instar larvae  
440 from French and Portuguese winter PPM populations have a substantial mortality rate at 36°C  
441 (Santos et al. 2011). Thus, we suggest that high temperatures recorded especially in autumn in  
442 southern Tunisia had contributed to higher mortality rates and to the disappearance of the PPM  
443 from this area.

#### 444 **4.5 Other factors to explore**

445 Even if the increase of temperatures could be largely involved in the retraction of the PPM southern  
446 range, other factors also need to be explored. Firstly, as already briefly mentioned, a change in PPM  
447 phenology could also potentially explain changes in its geographical distribution (Robinet et al. 2015)  
448 and should be further explored in association with the direct effect of climate warming on PPM  
449 survival. Secondly, climate change can also affect the PPM host trees. The last IPCC report (2014)  
450 revealed that the frequency and intensity of droughts has likely increased in the Mediterranean areas  
451 especially in arid regions. Droughts could considerably reduce the needles' length (Borghetti et al.  
452 1998) and decrease the leaf life span (Girard et al. 2012), and this may disturb the layout of egg-  
453 masses around the pine needles. In addition, it is currently unknown whether climate change affects  
454 the pine needles' composition and how this change could alter the larval survival. This indirect effect  
455 of climate change on host trees could be an additional mortality factor to consider. The effect of  
456 drought on host preference and performance was indeed demonstrated for the Mediterranean pine  
457 shoot beetle, *Tomicus destruens*, on maritime pine, *Pinus pinaster* (Branco et al. 2010). In addition,  
458 according to Henriksson et al. (2003), leaf water content is one of the most important factors  
459 affecting the growth of defoliating larvae such as *Epirrita autumnata*. Hence, drought stress may  
460 have a detrimental effect on insect performance reflected as decrease in leaf water content, and/or  
461 increase in leaf toughness and in secondary metabolites concentration. However, there is little  
462 information available regarding the effect of drought on the PPM performance. Thirdly, increase of  
463 both droughts and temperatures in most arid conditions would increase *P. halepensis* stress, thus  
464 impacting their own growth and survival (Cherif et al. 2019; Vicente-Serrano et al. 2010). In general,  
465 phenological plasticity of some tree species (such as *Pinus sylvestris* in Europe) may not allow the  
466 tree species to adapt to climate change at their distributional edge (Duputié et al. 2015). If the PPM  
467 host trees would no longer be able to survive in some regions, the PPM would also no longer be able  
468 to be there, unless shifting on other hosts. Lastly, another mortality factor to consider is parasitism.  
469 Indeed, the rate of parasitized eggs was relatively high in Tataouine (Fig. 3). Although this parasitism  
470 rate increases mortality, it is quite low (6 % on average) compared to other parts of the PPM

471 distribution (e.g. 24.4 % in France (Orléans) and 29 % in Bulgaria (Maglizh), Georgiev et al. 2020) and  
472 may not be a key factor in the PPM retraction.

#### 473 **4.6 Contrasted effects of climate change on insects' range and outbreaks**

474 Increase of outbreaks and spread of pests are often reported. Bark beetles, for example, can cause  
475 tree mortality due to severe droughts, which are amplified by higher temperatures, and this could  
476 trigger a positive feedback on the reproductive rate of the insect populations (Raffa et al. 2008; Raffa  
477 et al. 2015). In contrast, range reduction and extinction risks are often reported for other species. In  
478 Britain, fine-resolution mapping revealed extinction gradients since 1970 for three of the four  
479 northern butterfly species: *Aricia artaxerxes* and *Erebia aethiops* retracted northwards, and *Erebia*  
480 *epiphron* retracted uphill (Franco et al. 2006). Actual shifts of insect distribution are poorly  
481 documented so far, apart from predictions of bioclimate models. A good example documenting a  
482 shift in outbreaks is the larch bud moth, *Zeiraphera griseana*. Its cyclical outbreaks are actually  
483 shifting from medium to high elevations in the Alps, and this could be attributed to a better host-  
484 insect synchronization with climate warming at those high elevations (Johnson et al. 2010; Rozenberg  
485 et al. 2020). The study presented in this article, in association with the previous study of Battisti et al.  
486 (2005) done on the PPM northern range expansion, thus provides the very first well-documented  
487 shift in species distribution due to climate warming, and it also reveals the causal mechanisms.

#### 488 **4.7 Conclusions**

489 Increase of outbreaks and spread are often reported for some species while range reduction and  
490 extinction risks are often reported for other species. The scientific community is usually focusing on  
491 what is threatening (e.g., more damages due to pests, or disappearance of protected species), but  
492 the overall and comprehensive impact of climate change is not so often explored. Here we  
493 demonstrate that climate could become too warm for a Mediterranean forest pest in the south of its  
494 distribution. The next question to tackle is whether forest trees that could finally get rid of pests or  
495 pathogens could actually persist in such extreme climate conditions.

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672

673 **Declarations**

674 **Funding**

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679

680 **Conflicts of interest/Competing interests**

681 The authors declare no conflicts of interest.

682

683 **Availability of data and material**

684 Most of the datasets are provided in the article and supplementary material. Other datasets are  
685 available from the corresponding author on request.

686

687 **Code availability**

688 The R code of analyses is available from the corresponding author on request.

689

690 **Authors' contributions**

691 CR and MBJ designed the study. AB conducted the field experiments, the laboratory analysis and the  
692 statistical analyses ; CR and MBJ supervised her work. AB, MBJ and CR wrote and revised the article.

693

694 **Ethics approval**

695 This study was conducted on an insect species (the pine processionary moth, *Thaumetopoea*  
696 *pityocampa*), which is a pest species commonly controlled. In addition, this is a model species for  
697 science which has been exempted from any declaration regarding the Nagoya protocole.

698

699 **Consent to participate**

700 Not applicable.

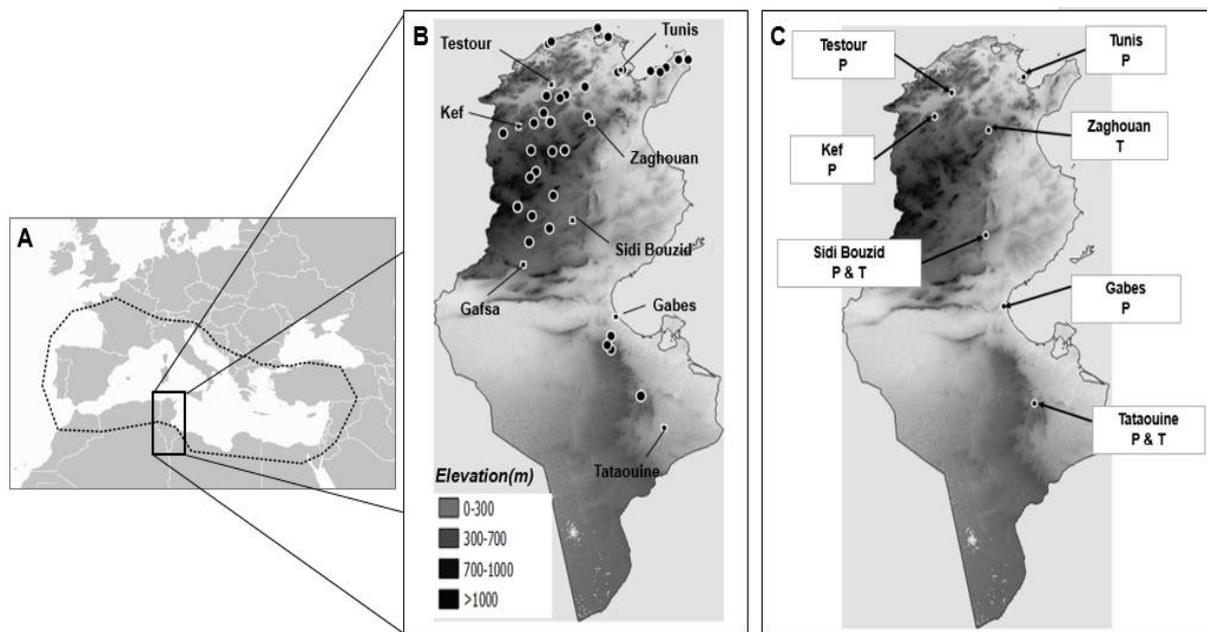
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702 **Consent for publication**

703 The authors of this article consent to publish the study.

704

705 **Figures**



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709 **Fig. 1:** (A) The rough distribution of the PPM across its range represented by the dashed line (derived  
710 from Roques et al., 2015), (B) the historical occurrence of the PPM in Tunisia (elevation background  
711 from SRTM, is provided by ESRI), and (C) location of pheromone traps (P) and translocation  
712 experiments on egg-masses (T) across a latitudinal gradient in Tunisia.

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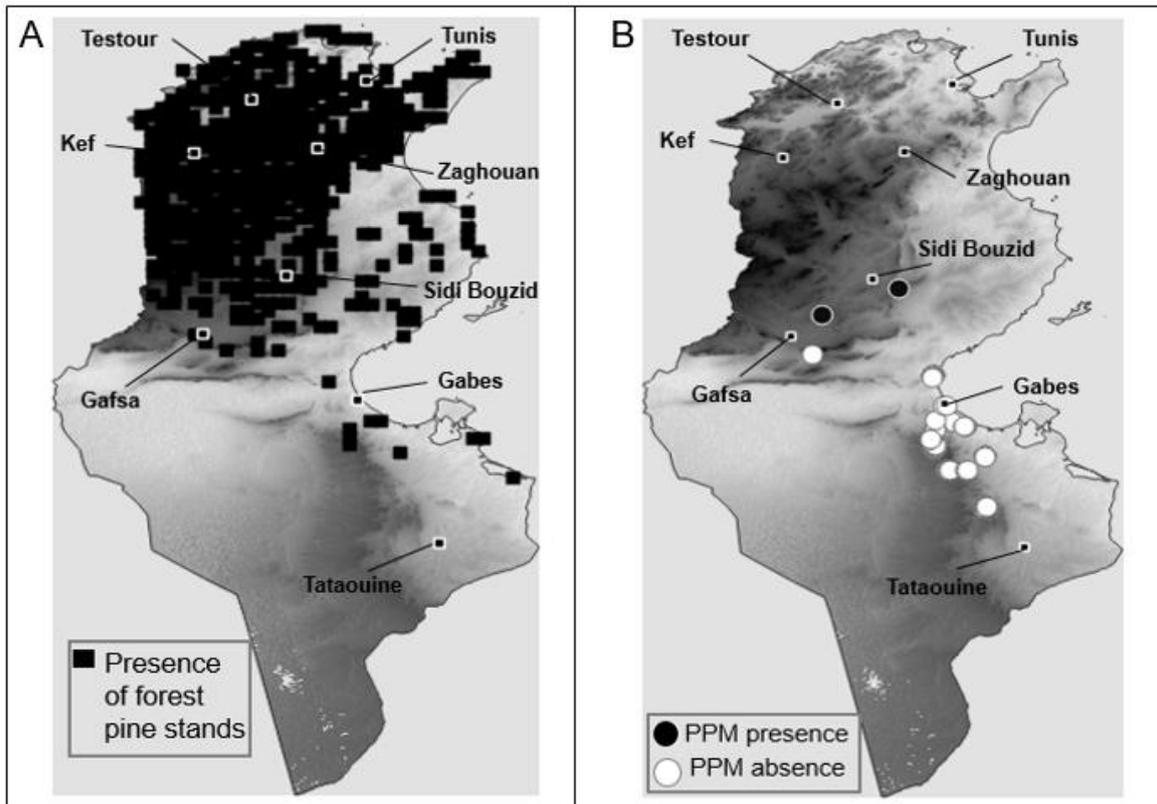
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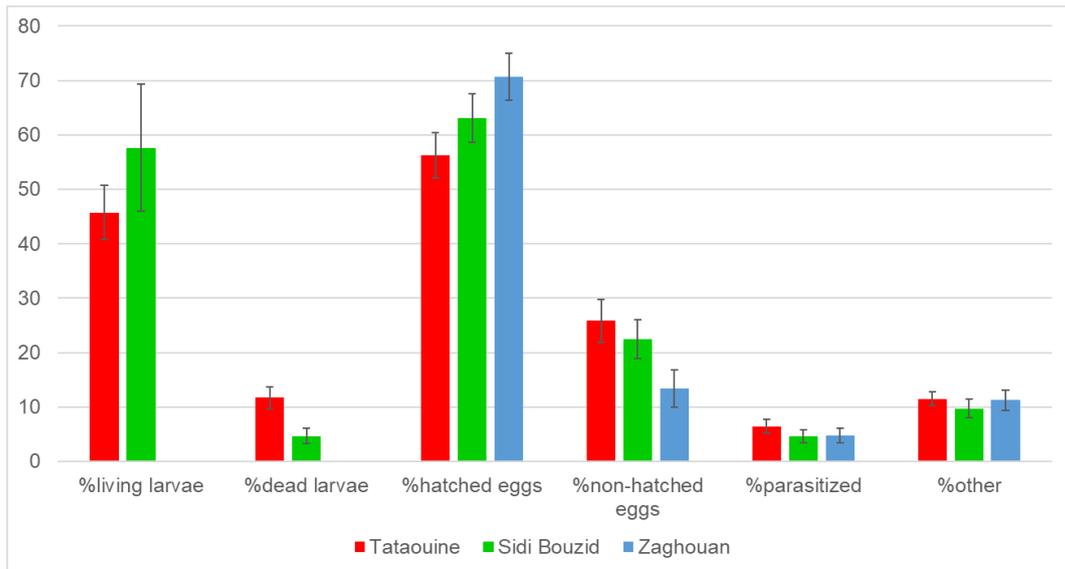


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724 **Fig. 2:** (A) Map of forest pine stands on the 8 km x 8 km grid, as reported by the General Direction of  
 725 Forests in Tunisia, and (B) map of the PPM presence and absence in South Tunisia.

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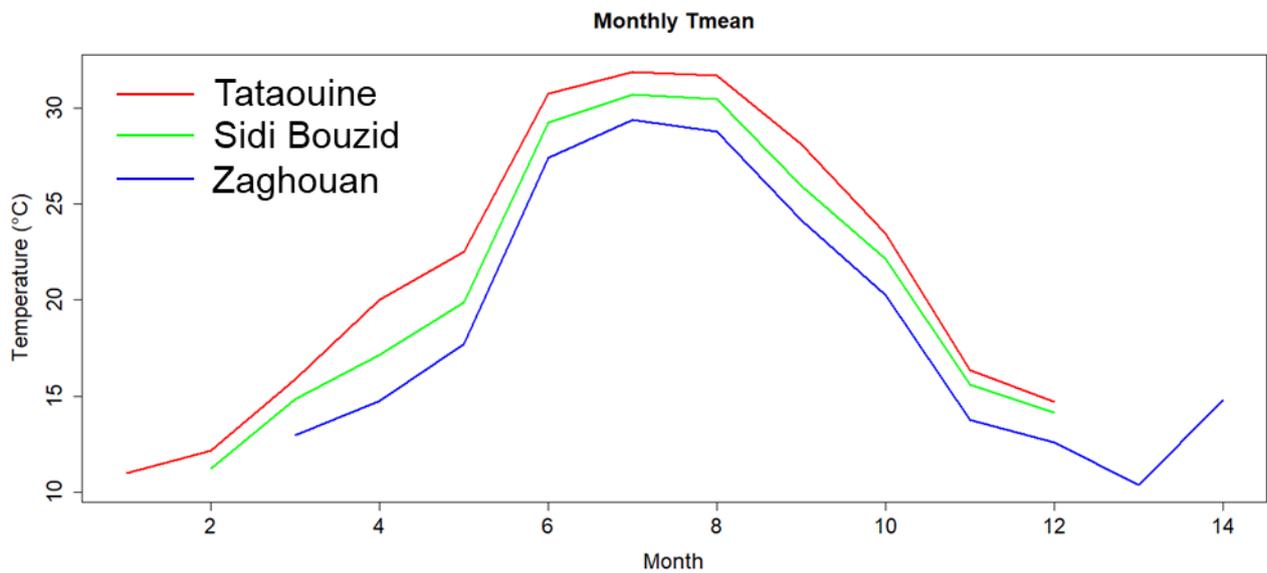


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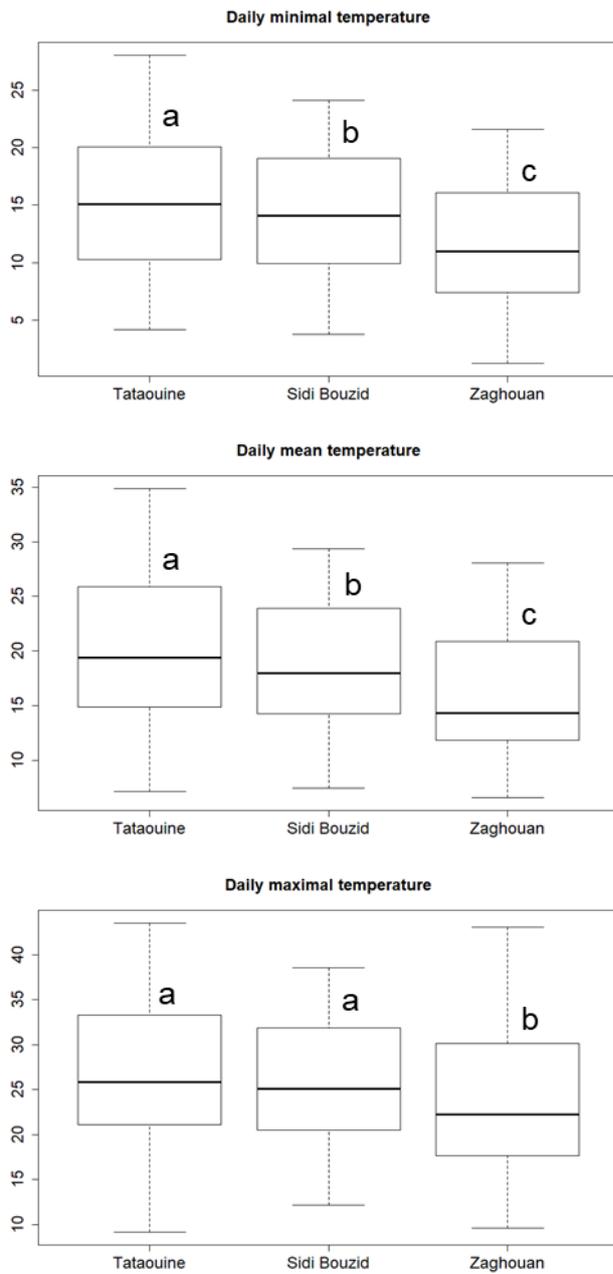
729 **Fig. 3:** Comparison of larval survival, egg hatching, parasitized eggs and other causes of egg mortality  
 730 along the latitudinal gradient going from Zaghouan (within the PPM core distribution in North  
 731 Tunisia), Sidi Bouzid (the southern PPM limit) and Tataouine (region of disappearance in South  
 732 Tunisia). Error bars indicate the standard error.

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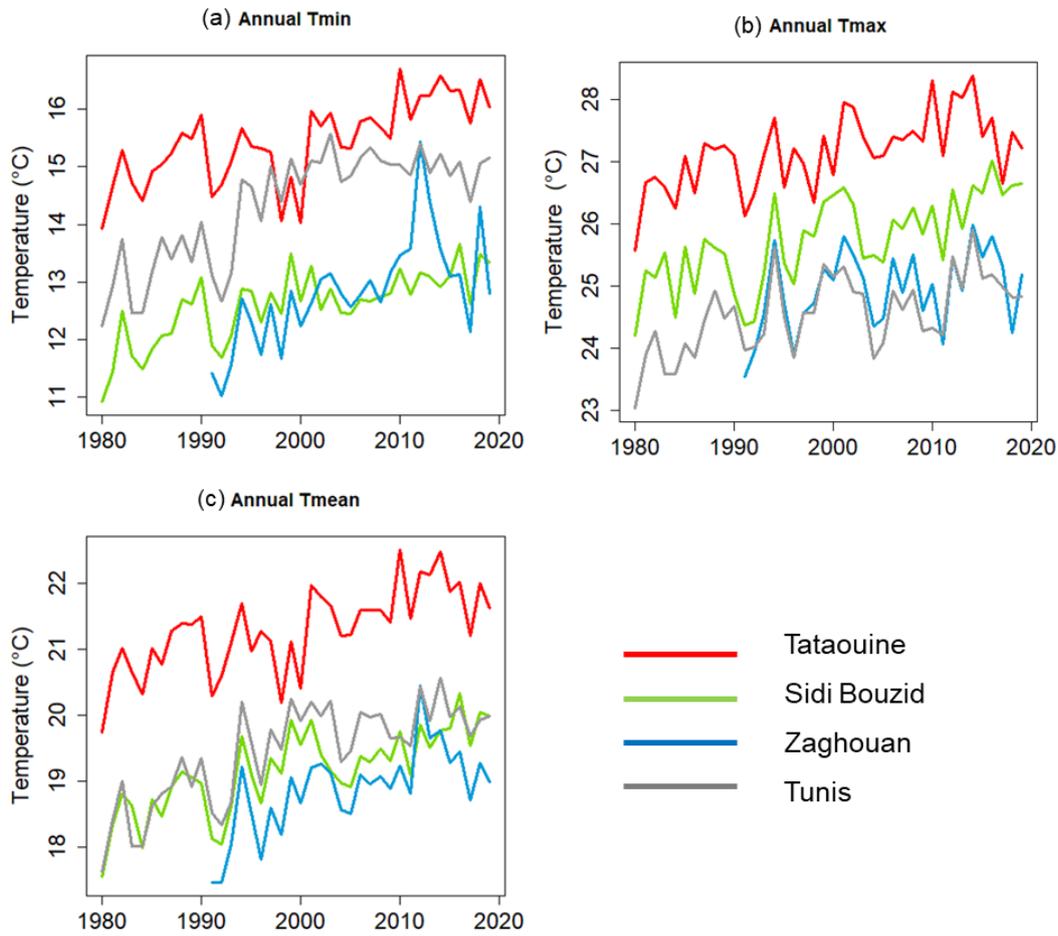
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735 **Fig. 4:** Comparison of monthly mean temperatures in Tataouine, Sidi Bouzid and Zaghouan between  
 736 January 2019 (month 1) and February 2020 (month 14) following data loggers installed on field sites.



737

738 **Fig. 5:** Boxplot of daily minimal, mean and maximal temperatures recorded on sites from Sept 1<sup>st</sup>  
 739 2019 to Feb 5<sup>th</sup> 2020. Different letters on each panel indicate a statistical difference using a pairwise  
 740 Wilcoxon Signed Rank Test.



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742

743 **Fig. 6:** Annual mean of daily (a) minimal, (b) maximal, and (c) mean temperatures on a south-north  
 744 gradient (going from Tataouine, Sidi Bouzid, Zaghuan to Tunis) between 1980 and 2019.

745

746 **Tables**

Index	Description	Definition	Units
SU40	Very hot days	Annual count when TX (daily maximum) > 40°C	days
SU35	Very hot days	Annual count when TX (daily maximum) > 35°C	days
SU25	Summer days	Annual count when TX (daily maximum) > 25°C	days
TXx	Max Tmax: hottest day	Annual maximum value of daily maximum temp	°C
TNx	Max Tmin: hottest night	Annual maximum value of daily minimum temp	°C
TR25	Tropical Nights	Annual count when TN (daily minimum) > 20°C	days
TX90p	Warm days frequency	Percentage of days when TX > 90 <sup>th</sup> percentile	%
TN90p	Warm nights frequency	Percentage of days when TN > 90 <sup>th</sup> percentile	%
DTR	Diurnal temperature range	Monthly mean difference between TX and TN	°C

747 **Table 1:** List of extreme temperature indices used in this study.

748

Gradient	Site	Installation date	Removal date	Number of traps	Number of captures (per trap)
North Tunisia ↓	Tunis	June 28 <sup>th</sup>	Sept 28 <sup>th</sup>	1	40 (40)
	Testour	July 4 <sup>th</sup>	Oct 16 <sup>th</sup>	3	167 (56)
	Kef	July 3 <sup>rd</sup>	Oct 16 <sup>th</sup>	3	173 (58)
	Sidi Bouzid	June 19 <sup>th</sup>	Oct 24 <sup>th</sup>	3	148 (49)
	Gabes	July 31 <sup>st</sup>	Oct 24 <sup>th</sup>	1	0 (0)
South Tunisia	Tataouine	July 31 <sup>st</sup>	Oct 24 <sup>th</sup>	3	0 (0)

749 **Table 2:** Trap captures in summer 2018 along the latitudinal gradient in Tunisia.

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Location	Tmin		Tmax		Tmean	
	Slope $\pm$ SE	<i>P</i>	Slope $\pm$ SE	<i>P</i>	Slope $\pm$ SE	<i>P</i>
Tunis	0.067 $\pm$ 0.008	< 0.001	0.031 $\pm$ 0.006	< 0.001	0.048 $\pm$ 0.006	< 0.001
Zaghouan	0.073 $\pm$ 0.015	< 0.001	0.029 $\pm$ 0.013	0.03	0.051 $\pm$ 0.01	< 0.001
Sidi Bouzid	0.039 $\pm$ 0.005	< 0.001	0.044 $\pm$ 0.006	< 0.001	0.041 $\pm$ 0.005	< 0.001
Tataouine	0.043 $\pm$ 0.006	< 0.001	0.031 $\pm$ 0.006	< 0.001	0.037 $\pm$ 0.006	< 0.001

754

755 **Table 3:** Analysis of temperature trend during 1980-2019 (except for Zaghouan: 1991-2019). The756 slope ( $\pm$  standard error, SE), with its significance probability (*P*), represents the trend (unit: °C/year).

Station	SU40	SU35	SU25	TXx	TNx	TR25	TX90p	TN90p	DTR
Tunis	0.044	0.429**	0.457**	0.017	0.075**	0.233**	0.114*	0.318**	-0.035**
Zaghouan	-0.044	-0.082	0.345	-0.062	0.097*	0.222**	0.072	0.426**	-0.044*
Sidi Bouzid	0.221*	0.712**	0.601**	0.048*	0.097**	0.100*	0.164**	0.228**	0.005
Tataouine	0.200*	0.520**	0.448*	0.022	0.066**	0.553**	0.086	0.226**	-0.021*

**Table 4:** Decadal trends of the extreme indices of temperatures along four stations in Tunisia. For Zaghouan, we considered missing values between 1980 and 1990 to conduct the same decadal analysis. \* indicates significance at 5% level ( $P < 0.05$ ) and \*\* significance at 1% level ( $P < 0.01$ ).

