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Intraspecific variation in lizard heat tolerance alters estimates of climate impact

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Abstract

1. Research addressing the effects of global warming on the distribution and persistence of species generally assumes that population variation in thermal tolerance is spatially constant or overridden by interspecific variation. Typically, this rationale is implicit in sourcing one critical thermal maximum (CT_{max}) population estimate per species to model spatiotemporal cross-taxa variation in heat tolerance. Theory suggests that such an approach could result in biased or imprecise estimates and forecasts of impact from climate warming, but limited empirical evidence in support of those expectations exists.

2. We experimentally quantify the magnitude of intraspecific variation in CT_{max} among lizard populations, and the extent to which incorporating such variability can alter estimates of climate impact through a biophysical model. To do so, we measured CT_{max} from 59 populations of 15 Iberian lizard species (304 individuals).

3. The overall median CT_{max} across all individuals from all species was 42.8 ºC and ranged from 40.5 to 48.3 ºC, with species medians decreasing through xeric, climate-generalist and mesic taxa. We found strong statistical support for intraspecific differentiation in CT_{max} by up to a median of 3 ºC among populations. We show that annual restricted activity (operative temperature > CT_{max}) over the Iberian distribution of our study species differs by a median of > 80 hours per 25-km^2 grid cell based on different population-level CT_{max} estimates. This discrepancy leads to predictions of spatial variation in annual restricted activity to change by more than 20 days for six of the study species.

4. Considering that during restriction periods, reptiles should be unable to feed and reproduce, current projections of climate-change impacts on the fitness of ectotherm fauna could be under- or over-estimated depending on which population is chosen to represent the physiological spectra of the species in question. Mapping heat tolerance over the full geographical ranges of single species is thus critical to address cross-taxa patterns and drivers of heat tolerance in a biologically comprehensive way.

Abstract (Spanish version)

1. En macroecología, cuando se evalúan los efectos del calentamiento global en la distribución y persistencia de las especies, generalmente se asume que la tolerancia térmica entre poblaciones es constante a lo largo de la distribución de las especies, o despreciable en comparación con su variación interespecífica. Tal planteamiento es implícito cuando se utiliza el máximo crítico termal (CT_{max}) de una población por especie para modelar la variación espacio-temporal de la tolerancia termal entre especies. Teóricamente, esto puede sesgar o añadir imprecisión en las estimaciones y proyecciones de impacto por el calentamiento asociado al cambio global, pero la evidencia empírica de tales previsiones es limitada.

2. Cuantificamos experimentalmente la magnitud de la variación intraespecífica en CT_{max} entre poblaciones de lagartijas, y hasta qué punto la incorporación de esta variabilidad puede alterar la evaluación del impacto del clima a través de un modelo biofísico. Para ello, medimos el CT_{max} en 59 poblaciones de 15 especies de lagartijas ibéricas (304 individuos).

3. La mediana general del CT_{max} fue 42.8 ℃ entre todos los individuos de todas las especies, y varió desde 40.5 hasta 48.3 ℃, mientras que las medianas por especie decrecieron de taxones de hábitats secos, pasando por generalistas, hasta taxones de hábitats húmedos. Encontramos un fuerte apoyo estadístico para la diferenciación intraespecífica del CT_{max} de hasta de 3 ℃ (mediana) entre poblaciones. Mostramos que la actividad restringida anual (temperatura operativa $> CT_{max}$) en la distribución ibérica de las especies de estudio difirió en > 80 horas por celda espacial de 25-km^2 (mediana) en función del CT_{max} poblacional. Esta discrepancia conduce a que las predicciones de la variación espacial de la actividad restringida anual difieran en más de 20 días en seis de las especies investigadas.

4. Teniendo en cuenta que durante los periodos de restricción, los reptiles son incapaces de alimentarse y reproducirse, las proyecciones actuales de impactos del cambio climático sobre el *fitness* de la fauna ectotérmica pueden infra- o sobre-estimarse dependiendo de la población elegida para representar el espectro fisiológico de cada especie. Cartografiar la tolerancia termal sobre el rango geográfico completo de especies individuales es por lo tanto crucial, antes de que podamos examinar patrones y mecanismos de variación entre múltiples especies de una manera biológicamente comprensiva.

INTRODUCTION

The response of individuals to climate warming and, ultimately, the combined effects on populations and species, is mediated through interactions between physiology and behaviour (Pörtner & Farrell 2008; Somero 2012; Sunday *et al.* 2014). Organisms eat, move and reproduce within a thermal window bounded by their thermal tolerance, or performance limits, generally

101 known as critical thermal maximum (CT_{max}) and minimum (CT_{min}) (Cowles & Bogert 1944; Huey

102 & Stevenson 1979). When environmental temperatures are at or around critical limits, biological

103 activity is constrained and, if temperature extremes are prolonged, they might compromise

104 individual and population survival (Somero 2011; Clarke 2014). The policy consequences of these

105 interactions, in the context of both impacts and adaptation, have been stressed by the

106 Intergovernmental Panel on Climate Change in its Fifth Assessment Report: "…*surpassing*

107 *temperature thresholds means going into time-limited tolerance, and more extreme temperature*

108 *changes lead to exceedance of thresholds that cause metabolic disturbances and ultimately onset of*

109 *cell damage*" (Field *et al.* 2014).

110   Thermal metrics, including upper thermal limits, have been documented for many species

111 and compiled into global databases (Bennett *et al.* 2018). Collectively, these data constitute a

112 valuable resource for research aiming at determining how clines in thermal tolerance might affect

113 biotic responses to local, regional and global environmental change (Deutsch *et al.* 2008; Angilletta

114 2009; Sunday, Bates & Dulvy 2012; we review examples focusing on climate change in Table S1).

115 For instance, conservatism of CT_{max} implies that many species might have exhausted the

116 evolutionary potential for developing further tolerance to climate warming (Araújo *et al.* 2013;

117 Grigg & Buckley 2013; Hoffmann, Chown & Clusella-Trullas 2013). And extinction risk due to

118 increased temperatures is expected to peak in the tropics because tropical species seem to be closer

119 to their upper thermal limits than temperate species (Deutsch *et al.* 2008; Sunday, Bates & Dulvy

120 2010; Gunderson & Stillman 2015). Such research is based on sizeable datasets, typically collated

121 from multiple primary-literature sources, whereby the thermal tolerance of individual species is

122 most often characterized based on one population (Fig. 1). The approach is based on the implicit

123 working assumption that interspecific variation is larger than intraspecific variation or, the least,

124 that variation among populations is so small as to have negligible impact on overall patterns.

125 Invariably, a potentially large source of physiological variation at the species level has been to date

126 rarely considered to forecast biological responses to environmental change (Valladares *et al.* 2014,

127 see below). This aspect is important because spatial mosaics of thermal tolerance might reduce the

128 vulnerability of species to climate warming, consequently altering estimates of impact and plans for

129 conservation and management (Sears, Raskin & Angilletta 2011; Cochrane *et al.* 2015a).

130   The thermal performance of species along environmental gradients is expected to vary

131 considerably across both altitude and latitude and might include ontogenic and evolutionary

132 components (Clusella-Trullas & Chown 2014; Sinclair *et al.* 2016). Theoretical developments have

133 demonstrated that incorporating intraspecific variability in life-history traits into modelling could

134 substantially improve forecasts of how species ranges might respond to environmental shifts such as

135 climate change (Valladares *et al.* 2014; Ikeda *et al.* 2017). This has been corroborated in a few

136 applied studies, particularly with plants (Benito Garzón *et al.* 2011; Cochrane *et al.* 2015b; Smith *et*

137 *al.* 2017), and including thermal traits in ectotherms such as insects (Lancaster 2016), reptiles

138 (Artacho *et al.* 2017) and amphibians (Kolbe, Kearney & Shine 2010). However, little effort has

139 been made to quantify the magnitude, and the likely predictive importance of population differences

140 in CT_{max} for multiple species in a common biogeographical context. To address this issue, we

141 quantify intraspecific variability in CT_{max} across 59 populations of 15 species of Iberian lizards, and

142 determine the extent to which among-population variability is likely to modify forecasts and

143 predictions of annual restricted activity when environmental temperatures exceed CT_{max}.

144

MATERIALS AND METHODS

Sampling

147 Through spring and summer 2013 and 2014, we sampled 304 adult males from 59 populations and

148 15 Iberian species of lacertid lizards (Table 1). Our study populations comprised wide- and

149 restricted-range taxa (nine endemic to the Iberian Peninsula) covering all of the major climatic

150 regions through Spain and Portugal (Fig. S1 and S2). Given the substantial sampling effort

151 involved, sampling was tailored to cover a grid of localities maximizing species richness,

152 minimizing travelled distance (see sampling map in Fig. S2), and capturing in most cases more than

153 50 % of the length of the climate gradient occupied by each species in the Iberian Peninsula

154 (climate gradients reconstructed in Fig. S3).

155 Individuals were caught by noosing. We sampled 2 to 5 populations per species (median = 4

156 populations per species with 90% interquantile ranges of [3, 5]), and 3 to 10 males per population

157 (Table 1). The former intrapopulation sample size is within the range of that used in many studies of

158 lizard thermal tolerance (e.g., Beal, Lattanzio & Miles 2014; Muñoz *et al.* 2016). However, we

159 assessed optimal sample size from six datasets including population CT_{max} from 8 to 25 adult

160 lizards from the Americas, Asia and Europe (Huang & Tu 2008; Muñoz *et al.* 2014; Buckley,

161 Ehrenberger & Angilletta 2015; Andrango, Sette & Torres-Carvajal 2016; Belasen *et al.* 2016; and

162 unpublished data), and concluded that a sample size of 3 males should accurately capture the mean

163 population CT_{max} estimated from larger population sizes (Table S2; Fig. S4 to S7).

164

CT_{max} estimation

166 To minimize local-ambient effects prior to CT_{max} estimation, all lizards were housed at 25 °C (8:00-

167 18:00 hours, lights-on) and 15 °C (18:00-8:00 hours, lights-off) for 14 days. Throughout, lizards

168 were kept individually in terraria layered with coconut fibre and a ceramic brick for shelter. We fed

169 lizards daily with house crickets (*Acheta domesticus*), and provided them daily with spring water in

170 a Petri dish. Following the former acclimation period, we determined CT_{max} through the 'dynamic

171 method' after Lutterschmidt and Hutchison (1997) as follows. We inserted a thermocouple some 1

172 to 2 cm (depending on body size) into the cloaca of each lizard – to avoid internal damage, the

173 thermocouple was covered with pure vaseline and the apical sensor was rounded with a minute drop

174 of dry nail polish. The thermocouple was wired to a HH-25TC Omega Thermometer via a 1 m-long

175 cable made up of flexible polytetrafluoroethylene. For each lizard, we fastened a 2×5 cm^2 strip of

176 parafilm that immobilized the distal part of the cable (equipped with the thermocouple) ventrally

177 against the cloacal and genital area. Thereafter, lizards were kept some 30 cm from a red-light lamp,

178 and body temperatures were ramped up at 1 ºC $\times$ min^{-1}. Throughout each trial, we monitored body

179 temperature and behaviour, and ultimately estimated CT_{max} as the cloacal temperature at which a

180 lizard lost its righting response (Lutterschmidt & Hutchison 1997). Ramping rates affect CT_{max}

181 estimation (Terblanche *et al.* 2007), so we controlled for this factor by using a single rate across all

182 individuals examined. Immediately after thermal shocks, we immersed lizards down to their necks

183 in a bath of cool water to prevent physiological/physical damage, thereafter providing water and

184 food *ad libitum* to all individuals for up to five consecutive days following the day of CT_{max}

185 estimation. We released all individuals at their point of capture.

186

Modelling

188 *Linear model: local versus regional effects on CT_{max}*

189 We ranked statistical support for two models through the Akaike's information criterion adjusted to

190 finite sample size (Sugiura 1978), using model probabilities (wAIC$_c$, which are scaled to a 0 to 1

191 interval), and evidence ratios of wAIC$_c$ of the first-ranked model to the wAIC$_c$ of the other model

192 (Burnham & Anderson 2002). For each species separately, the model set contrasted the hypothesis

193 that CT_{max} varies according to the geographic location of populations (locality effect: $CT_{max} \sim loc$,

194 i.e., a unique intercept or mean CT_{max} for each population, with *loc* being a categorical variable

195 coding for population identity) against the alternative (null) hypothesis that CT_{max} is homogeneous

196 across all populations studied (region effect: $CT_{max} \sim 1$, i.e., a unique intercept or mean CT_{max}

197 across all populations within a species). Throughout, we assumed Gaussian errors (corroborated in

198 the saturated model [$CT_{max} \sim loc$] by means of Q-Q and fit-versus-residual plots), and discarded

199 heteroscedasticity effects using Bartlett's tests (Bartlett 1937). The 'lm' function in the *R* package

200 'stats' was used for the linear models and all data plots hereafter were generated in 'graphics' (*R*

201 Development Core Team 2016).

202   Since we sampled 3 to 10 males per population (Table 1, see above), statistical support for

203 our two models might be influenced by different sample sizes among populations. We controlled

204 for this factor by sampling randomly 3 individuals per population (the minimum sample size

205   collected from any one population) and contrasting our model set for each study species (locality

206   versus region effects on CT_{max} as above), and repeating this procedure 100 times each including a

207   different triplet of individuals per population.

208

209   *Biophysical model: restriction times based on CT_{max}*

210   To assess the extent to which single-population estimates generate varying predictions of lizard

211   responses to climatic variation, we used activity restriction times as the biological response. Sinervo

212   *et al.* (2010) defined 'restriction time' for lizards as the amount of time per day in which 'operative

213   temperatures' (T_e, see below) are above preferred body temperatures. We use a more conservative

214   metric whereby 'restriction time' equates with the amount of hours over which a lizard's T_e exceeds

215   CT_{max}; this metric is biologically realistic because diurnal lizards are bound to be active when T_e

216   surpasses their preferred temperature (Gunderson & Leal 2015). Effectively, our metric equates

217   with *diurnal* restriction times because there is no solar radiation, nor (in our species set) lizard

218   activity, at night. Overall, our purpose was to generate a metric of restriction time that is

219   biologically meaningful and comparable among populations, rather than to construct a fully

220   parameterized model of the thermal niche (e.g., Kearney & Porter 2004), or a model characterizing

221   the magnitude of the erosion of the thermal niche (e.g., Sinervo *et al.* 2010).

222   Prior to calculating restriction times, we estimated T_e by solving the biophysical model by

223   Porter *et al.* (1973), namely $Q_E = (Q_S+Q_I) – (Q_T+Q_C)$, which includes climate (fluxes of ground

224   radiation, air temperature and wind speed) and biological (e.g., skin emissivity and absorbance)

225   information. Succinctly, this model formulates the heat flow between an organism and its

226   environment (Q_E) as a function of the solar shortwave (Q_S) and infrared (Q_I) radiations absorbed by

227   an individual, minus the heat the animal exchanges by thermal radiation (Q_T) and convection (Q_C).

228   T_e is one of the factors in the four-order equation for Q_T given the surface area (S) and emissivity

229   (ε) of the animal, and the Stephan-Boltzman constant (σ), i.e., $Q_T = S \times \varepsilon \times \sigma \times T_e^4$. Equations and

230   variables are fully described in Table S4.

231   For each population, we estimated T_e every hour daily for an entire calendar year, resulting

232   in 8784 maps (24 hours per day × 366 days per year, where 366 days account for leap years in our

233   model of regional climate, see below) using the *R* package 'RnetCDF' (Michna & Woods 2013). To

234   do so, we obtained hourly estimates of the climate variables (averaged over the period 1955 to

235   2010) from a 'Regional Climate Model' specifically elaborated for the Iberian Peninsula at a 5×5

236   km^2 grid-cell resolution (Dasari *et al.* 2014); the former represents an improvement for the study

237   area relative to other datasets with coarser resolution and global scope (e.g., Kearney, Isaac &

238   Porter 2014). For every 5x5 km^2 grid cell, we summed the number of hours when T_e was larger

239   than CT_{max} for each population separately (= annual restriction time) using the 'Climate Data

240 Operators' package (Kaspar, Schulzweida & Mueller 2010). The resulting maps were clipped to the

241 geographical distribution of each species, and converted to geo-tiff format through the package

242 'GDAL/OGR' (GDAL/OGR contributors 2016). Species distributions (presence-absence data in

243 10×10 km^2 grid cells) were obtained from Araújo *et al.* (2011), and from additional sources for

244 recently described species (see Supporting Information). We therefore downscaled species

245 distribution data to 5×5 km^2 grid cells to match the resolution of the climate data, and standardized

246 annual restriction times by the total number 5×5 km^2 grid cells occupied by each species in the *R*

247 packages 'raster' (Hijmans & van Etten 2012) and 'rgdal' (Keitt *et al.* 2010).

248

249 **RESULTS**

250 The median CT_{max} across all 304 individuals (59 populations, 15 species) was 42.8 ºC with 90 %

251 interquartile limits of [41.0, 46.0]. The CT_{max} across all individual lizards varied by 8 ºC, from 40.2

252 ºC (Catalonian wall lizard *Podarcis liolepis* from Cuellar, Segovia-Castilla and León) to 48.3 ºC

253 (spiny-footed lizard *Acanthodactylus erythrurus* from Matalascañas, Huelva-Andalucía) (Fig. 2a).

254 The median of the population CT_{max} medians varied from 41.2 [41.0, 41.9] in the western green

255 lizard *Lacerta bilineata* to 45.6 [44.5, 47.3] ºC in *A. erythrurus* (Table 1). CT_{max} medians tended to

256 decrease from arid- to mesic-adapted species, with climate generalists in between (Table 1).

257 We found strong statistical support for the hypothesis that CT_{max} differed among populations

258 within each species separately (locality effect: different mean CT_{max}), against the alternative

259 hypothesis that CT_{max} did not differ (region effect: same mean CT_{max} among populations) – we

260 report AIC metrics per species in Table S3. Across species, the locality- and region-effect

261 hypotheses had a median probability of 0.83 [0.52, 0.96] and 0.17 [0.04, 0.48], respectively (Fig.

262 2b), and we obtained similar support for both models when we controlled for intrapopulation

263 sample size (see Methods, Fig. S10). The locality-effect model explained up to 32 % of the

264 variation in CT_{max}, and scored between 2 to 32 times higher model probabilities (wAIC$_c$, see

265 Methods) than the region-effect model for 12 of the 15 study species (Table S3). Both models had

266 similar support for the Vaucher's wall lizard *P. vaucheri*, the Geniez's wall lizard *P. virescens*, and

267 the Spanish large psammodromus *Psammodromus algirus* (Table S3). Median and mean

268 differences in CT_{max} between populations remained mostly between 1 and 3 ºC (Table 1).

269 The median annual restriction time across the 59 sampled populations was 281 [63, 670]

270 hours per 5×5 km^2 grid cell (Fig. 3) in the known Iberian distribution of the 15 study species.

271 Assuming an average daily activity of 7 hours, those restriction times mean lack of diurnal activity

272 due to overheating over 40 [9, 96] days in a calendar year. Annual restriction times over the 59

273 populations varied from 31 (common wall lizard *P. muralis* from Navacerrada, Madrid) to 596

274 (Schreiber's green lizard *L. schreiberi* from Gata, Caceres-Extremadura) hours per grid cell. Within

275   species, the median population-level range of restriction times was 83 [43,201], varying from 43

276   (large psammodromus *P. algirus*) to 232 (Geniez's wall lizard *P. virescens*) hours per grid cell

277   (Table 1). In particular, for 6 of the 15 study species (*A. erythrurus*, *L. schreiberi*, *P. virescens*,

278   *Lacerta bilineata*, *P. liolepis*, Vaucher's wall lizard *P. vaucheri*) predicted annual restriction times

279   differed by > 140 hours per grid cell among populations (Table 1, Fig. 3); for the former species,

280   therefore, depending on which population-level CT_{max} was included in the biophysical model,

281   intraspecific discrepancies of > 20 days in the number of seven-hour days free of lizard activity

282   could result. Additionally, for the 4 study species with the lowest predicted annual restriction times

283   (median among populations < 90 hours per grid cell; *P. muralis*, Carbonell's wall lizard *P.*

284   *carbonelli*, Iberian rock lizard *I. monticola*, Spanish psammodromus *P. hispanicus*), the range of

285   restriction times among populations was larger or nearly equal to the smallest restriction time

286   estimated for a single population (Table 1, Fig. 3).

287

288   **Discussion**

289   We show that intraspecific heat tolerance varies considerably across the Iberian Peninsula, with

290   CT_{max} differences of up to 3 °C (median) among populations of single species. Those differences

291   comprise ~75% of the CT_{max} range observed across our 15 study species (Table 1). This pattern

292   holds true across Iberian lineages of lacertids —all represented in our species set (see Pyron,

293   Burbrink & Wiens 2013).

294   In contrast, whenever multiple population data are available, in those studies that have

295   related heat tolerance to climate change across multiple ectothermic species (Fig. 1, Table S1),

296   authors often average or take the maximum CT_{max} of a limited number of populations (e.g., Sinervo

297   *et al.* 2010; Clusella-Trullas, Blackburn & Chown 2011; Araújo *et al.* 2013), or otherwise use

298   several CT_{max} values for some species and, mostly, only one for others (e.g., Huey *et al.* 2009;

299   Hoffmann, Chown & Clusella-Trullas 2013; Gunderson & Stillman 2015). Our results demonstrate,

300   however, that the population, or population estimate, taken to represent a full species can result in

301   starkly different cross-taxon patterns of heat tolerance, be they for CT_{max} or, potentially, any of its

302   composites such as thermal performance curves (Sinclair *et al.* 2016), 'safety margins' (e.g.,

303   Sunday *et al.* 2014; Gunderson & Stillman 2015) or 'warming tolerance' (e.g., Deutsch *et al.* 2008;

304   Hoffmann, Chown & Clusella-Trullas 2013). The rationale behind a 'one species, one thermal trait'

305   approach (Sinclair *et al.* 2016) is partly the fact that thermal limits have been estimated only once

306   for most species whose thermal physiology has been investigated; and partly because popular

307   statistical methods to analyse those datasets while accounting for phylogenetic relatedness among

308   species (e.g., phylogenetic least-squares regression) were originally designed to deal with one data

309   point per species. However, from a purely analytical viewpoint (see Ives, Midford & Garland 2007;

310   Stone, Nee & Felsenstein 2011), the effect of heterogeneous sampling can be as important as

311   phylogenetic bias, and should be considered in comparative studies (Garamszegi & Møller 2010).

312   For six of the 15 study species, our prediction of annual restriction times, using different

313   population-level CT_{max} estimates, translated into species-level variation of 20 days and longer

314   during which environmental (operative) temperatures would be above CT_{max}. This variation can

315   dramatically modify inferences about behavioural patterns and fitness (Adolph & Porter 1993) and,

316   therefore, estimations of climate impacts accounting for trait (Cochrane *et al.* 2015a) or niche

317   (Pearman *et al.* 2010) variation within species. For instance, phenotypic and species distributions

318   can track different aspects of climate change (e.g., temperature *versus* precipitation) and both

319   complement impact assessments (Smith *et al.* 2017), climate effects can be masked by

320   thermoregulation interacting with topography (Sears, Raskin & Angilletta 2011) and spatial scale

321   (Barton, Clusella-Trullas & Terblanche 2018), latitudinal enhancement of heat tolerance might

322   signal recent poleward range expansions (Lancaster 2016), while species distribution models can

323   fail to detect constrains in population expansion (Kolbe, Kearney & Shine 2010) or area of

324   occupancy (Benito Garzón *et al.* 2011) owing to trait plasticity. To illustrate this point, we predicted

325   annual restriction times of 596, 668, 697 and 715 hours per 5×5 km^2 grid cell using the CT_{max} of

326   each of four populations of the Schreiber's green lizard *Lacerta schreiberi* (CT_{max} range = 40.5 to

327   42.9 °C across individuals, and 41.0 to 42.1 °C among population medians). This species is endemic

328   to the Iberian Peninsula, where it is mostly restricted to riparian shrubs in mountain ranges and low

329   temperate forests close to mountain slopes (Monasterio *et al.* 2013). Our population-based modeling

330   variation above would imply differences in predicted annual restriction times for the species from

331   85 to 102 seven-hour days per grid cell during which individuals would be forced to shelter from

332   overheating. This is biologically important because body growth and reproductive rates are

333   compromised by high temperatures in this species (Monasterio *et al.* 2013), while extended periods

334   of shelter might come at the expense of feeding and reproductive opportunities for ectothermic

335   fauna (Sinervo *et al.* 2010).

336   Our study supports the idea that single populations are bound to represent a snapshot of the

337   continuum of phenotypic variability in species' heat tolerances, and reinforces the proposition that

338   intraspecific variability in thermal limits is a key factor to project reliably how species might

339   respond to climate warming (Valladares *et al.* 2014). Physiological flexibility represents an

340   important mechanism by which species can persist in variable environments (Chevin & Hoffmann

341   2017) and adapt to environmental change (Chown *et al.* 2010). This is a major area of research with

342   regard to the ways in which species responses to climate change are mediated by the interplay

343   between microevolutionary processes and plasticity (Gienapp *et al.* 2008). Considering the

344   heterogeneity of climatic conditions across the Iberian Peninsula and within the range of most

Iberian lacertids, and the projected loss of climate space (higher temperatures, lower precipitation) for reptiles in the south-west of Europe (Araújo, Thuiller & Pearson 2006), it is unsurprising that current and future variability in CT_{max} might be the result of natural selection and adaptation at the population level. The genetic basis of this variation in lizards still needs to be disentangled. Heritability of some thermal traits may be low (Logan, Cox & Calsbeek 2014; Martins et al. 2018), and determining how common such low heritability might be requires wider taxonomical coverage and larger sample sizes. Recent studies do illustrate that ectotherm thermal limits can evolve in a few generations in response to climate events (Geerts *et al.* 2015; Campbell-Staton *et al.* 2017), while rapid climate change can also elicit complex evolutionary patterns combining directional (Gilbert & Miles 2017; Logan *et al.* 2018) and correlational (Artacho *et al.* 2015; Gilbert & Miles 2017) selection across populations (Logan, Cox & Calsbeek 2014; Martins *et al.* 2018). These mechanisms can shed light on the role of plasticity and evolutionary forcing in high *versus* low latitudes (Lancaster 2016), and at the margins of the distribution of species where extinction and dispersal processes in response to environmental change might be most frequent and intense (Valladares *et al.* 2014).

It is also unclear whether intraspecific variability in heat tolerance could buffer proposed rates of extinction of ectothermic species under climate change (see Sinervo *et al.* 2010), and interact with other life-history traits to constrain activity times and elicit concomitant effects on population fitness (Kearney 2012; Kearney 2013). For instance, in insects intraspecific variation in thermal breadth ($CT_{max} - CT_{min}$) seems latitudinally invariant only for stable and declining species, so those taxa currently not experiencing range expansions might be unfit to tolerate further warming at high altitudes, especially in the case of insular, endemic or, overall, narrowly distributed species (Lancaster 2016). An assessment of the biological implications of this phenomenon seems highly relevant for the ecology and conservation of species, particularly those with long generation times and slow genetic responses to rapid environmental change (Hoffmann & Sgrò 2011), and could be integrated into modelling approaches available for the study of climate-change impacts on biodiversity (Pacifici *et al.* 2015). The generation of novel physiological data for more species from the tree of life is indeed a pressing endeavour (Pörtner & Farrell 2008). Thus, the recent collation of the *GlobTherm* database (Bennett *et al.* 2018: species-level metrics of thermal tolerance for 2133 taxa globally) highlights voids of knowledge in the most diverse eukaryotic groups (algae, plants, invertebrates) and in vast stretches of northernmost Africa, America and Eurasia. Bennett *et al.* (2018) foresee the inclusion of intraspecific variation in future versions of the dataset, and those updates will quantify the existing bias in thermal-trait information for species *versus* populations. All the same, acquiring estimates of thermal traits over broader expanses of the geographical ranges of single species seems essential (Chown & Gaston 2016) before we might be able to address cross-

taxa patterns and drivers of heat tolerance in a biologically comprehensive way. This endeavour could be logistically prohibitive for very wide-ranging species (which are an uncommon phenomenon), but could be realized for species with restricted distributions, and represents an important area of future development.

AUTHORS' CONTRIBUTIONS

SHP, DRV and MBA conceived the idea. MBA and CM designed the project and the full set of experiments. CM, VG and WB did field and experimental work. SHP run hypothesis contrasts and assessed optimal sample size, FFY modelled restriction times, and WB generated polygon data of species distributions. SHP led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All physiological data associated with this study (CT_{max} for 304 male lizard individulas) have been deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1553pc3 (Monasterio *et al.*

415 2018). As further data analyses are in progress, release of data has been embargoed for 1 year from

416 the date of publication.

417

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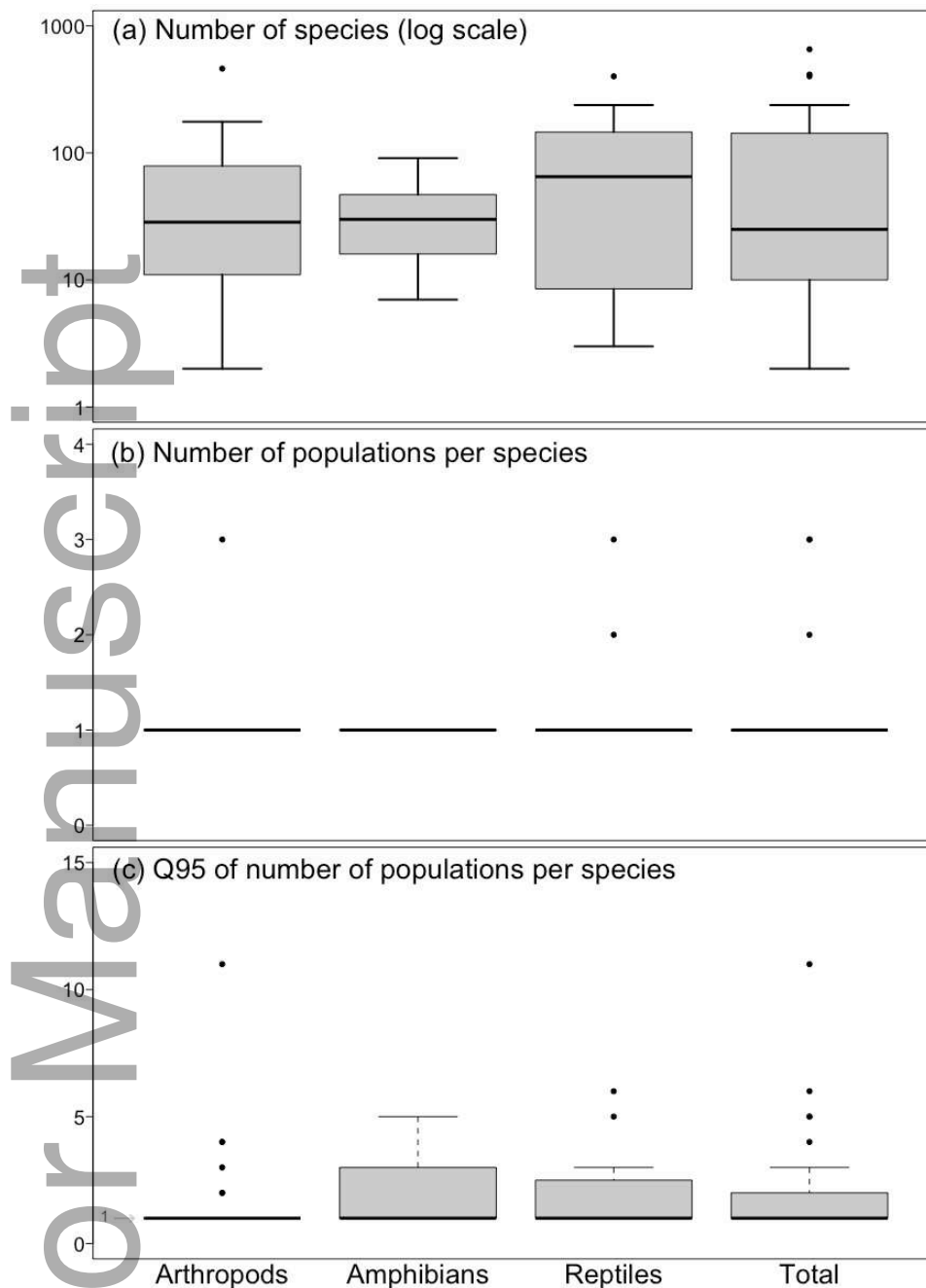
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646   **FIGURE 1** Species and population sample sizes in climate-change studies using critical thermal

647   maxima (CT_{max}) of multiple species of three groups of terrestrial ectotherms. Thick lines in boxes

648   indicate medians across all studies[1] ($N = 38$) for broad taxa separately (arthropods, amphibians,

649   reptiles) and all taxa together (total). Q95 is the 95 % interquartile range.

(a) Number of species (log scale)

(b) Number of populations per species

(c) Q95 of number of populations per species

Arthropods   Amphibians   Reptiles   Total

650
651 [1] Studies comprise primary literature where CT_{max} has been estimated by the 'dynamic method' (see

652 Methods; taxa, hypotheses and conclusions summarized in Table S1). We assume that one

653 population represents one species in the minority of cases in which a species' CT_{max} is taken to be

654 the average of the CT_{max} of several populations.

655 **FIGURE 2** Population-level critical thermal maxima (CT_{max}) of 15 Iberian species of lacertid

656 lizards. Left panel (a) shows CT_{max} over 304 adult male lizards from 59 populations of the 15 study

657 species. Single boxplots represent discrete populations, sample-size median per population is 5

658 adult males with 90 % interquantile ranges of [5, 6], and dashed lines indicate mean and median

659 CT_{max} across all individuals. In the right panel (b), black boxplots represent cross-species median

660 model probabilities ($wAIC_c$) of two models: CT_{max} varies with population locality versus CT_{max}

661 does not vary among populations. AIC metrics per species reported in Table S3.

662 (a)   40   42   44   46   48   Iberian Lacertidae CTmax (ºC)   Locality effect   Region effect   (b)
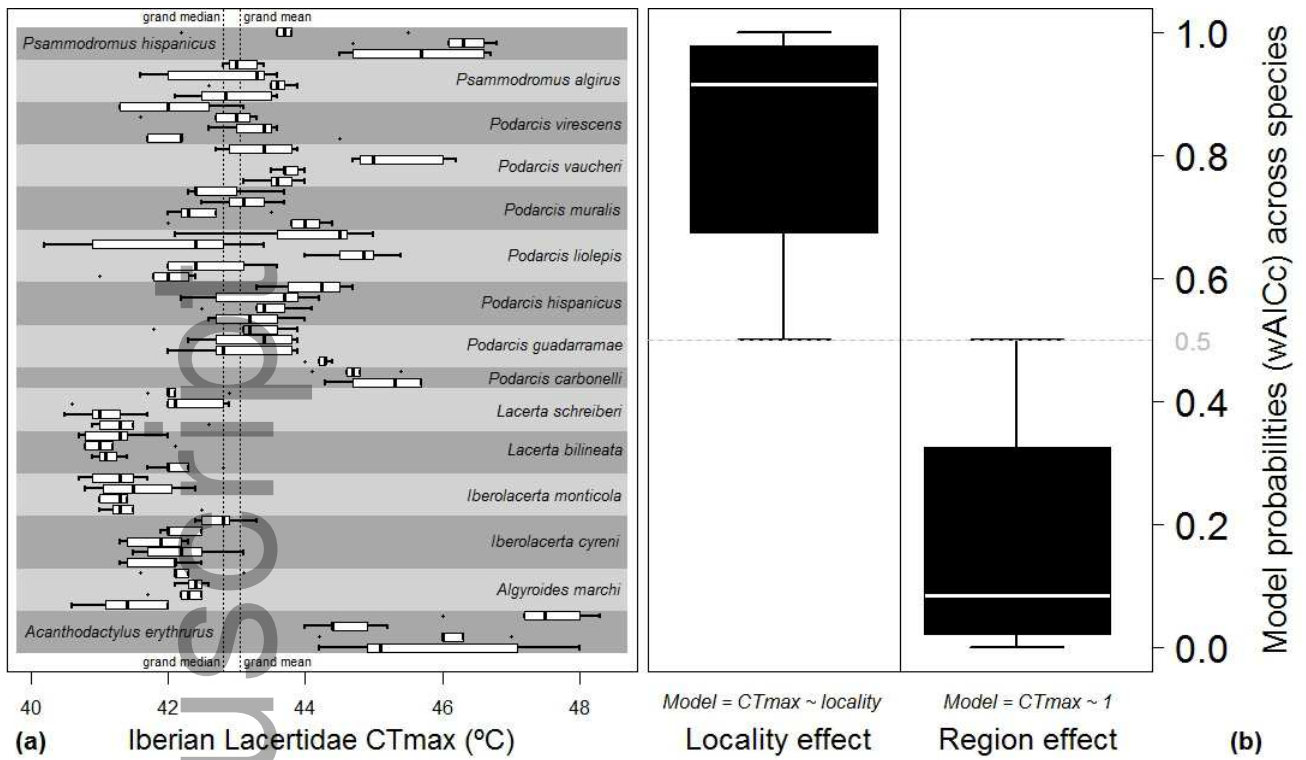
663 **FIGURE 3** Prediction of annual restriction times[1] from 59 populations of Iberian species of

664 lacertid lizards (ordered by median values). Each box represents intraspecific variation in

665 predictions based on the median CT_{max} of single populations.
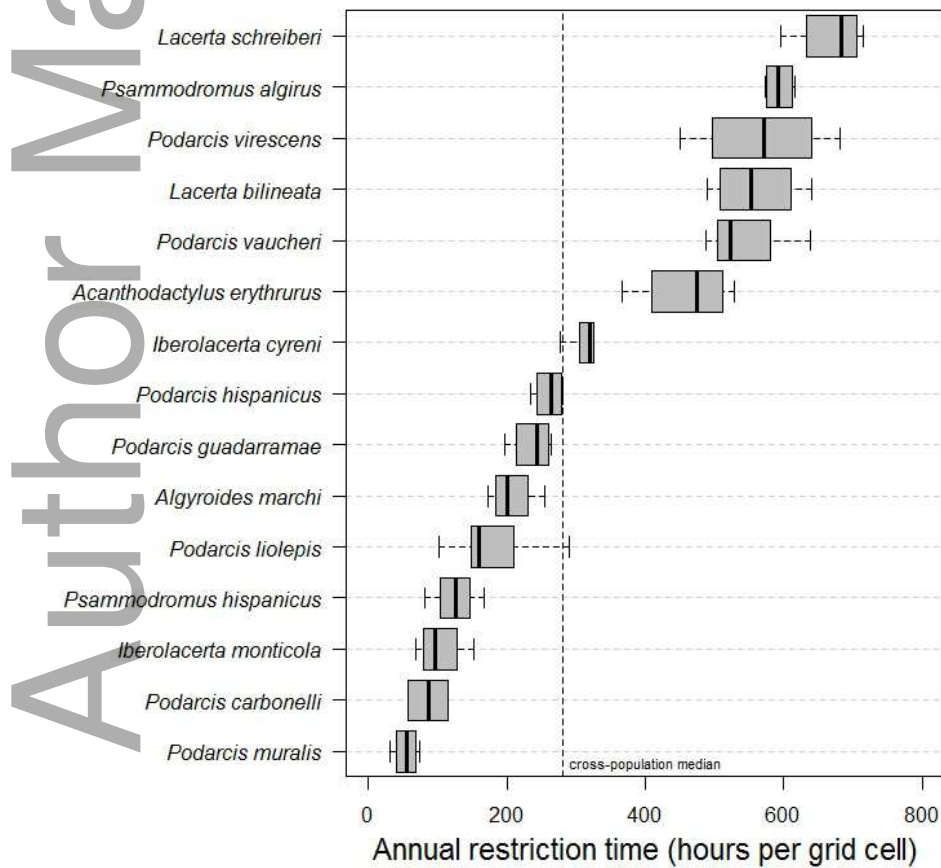
666

667   [1] Restriction time defined as number of diurnal hours over a calendar year when operative

668   temperatures are above the population CT_{max} per 5×5 km^2 grid cell within the known Iberian

669   distribution of each species. Sample sizes reported in Table 1.

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670 **TABLE 1** Intraspecific variability in critical thermal maxima (CT_{max}, ºC) and annual restriction times (RT, hours per 5×5 km^2 grid cell) based on 59

671 populations from 15 Iberian species of lacertid lizards[1]. Species listed in order of decreasing median CT_{max}. See description of variables below[2].

Study species	Populations (individuals)	CT_{max} median	CT_{max} range	RT median	RT range	Broad climate type	Precipitation	Temperature
Acanthodactylus erythrurus	4 (22)	45.6 [44.5, 47.3]	3.1	475 [379, 524]	163	dry, warm	46 [15,83]	22.6 [6.5,25.0]
Podarcis carbonelli	2 (10)	45.0 [44.7, 45.3]	0.6	87 [61,112]	57	generalist	64 [25,97]	19.6 [18.3,22.1]
Psammodromus hispanicus	3 (15)	44.7 [43.1, 46.2]	3.3	127 [87,164]	86	generalist	53 [17,107]	22.0 [169,234]
Podarcis vaucheri	4 (20)	43.7 [43.4, 44.8]	1.6	522 [493,621]	150	dry, warm	18 [14,31]	22.8 [193,241]
Podarcis hispanicus	4 (19)	43.6 [43.2, 44.2]	1.1	265 [238, 281]	46	generalist	54 [23,103]	22.4 [4.8,24.9]
Podarcis guadarramae	4 (20)	43.3 [42.9, 44.2]	1.5	244 [203, 263]	66	generalist	73 [45,132]	19.5 [16.2,23.3]
Psammodromus algirus	4 (25)	43.1 [42.1, 43.6]	1.6	592 [574,615]	43	generalist	58 [18,142]	21.9 [3.6,25.1]
Podarcis virescens	4 (20)	43.0 [42.3, 43.4]	1.2	572 [464,670]	232	generalist	36 [19,72]	23.2 [19.7,25.7]
Podarcis muralis	4 (20)	42.8 [42.3, 43.9]	1.7	57 [34,73]	44	mesic, cold	159 [96,248]	16.6 [11.0,19.1]
Podarcis liolepis	5 (26)	42.4 [42.1, 44.8]	2.3	160 [111,274]	188	generalist	112 [58,209]	16.8 [19.0,22.5]
Algyroides marchi	4 (20)	42.2 [41.5, 42.4]	1.0	202 [177, 247]	81	mesic, warm	61 [38,74]	21.2 [19.7,23.4]
Iberolacerta cyreni	5 (25)	42.1 [41.9, 42.7]	0.9	320 [283, 326]	49	mesic, cold (alpine)	78 [53,96]	17.6 [16.1,21.5]
Lacerta schreiberi	4 (20)	41.7 [41.0, 42.1]	1.1	683 [607,712]	119	mesic, cold	121[47,176]	17.9 [15.2,22.3]
Iberolacerta monticola	4 (24)	41.3 [40.8, 41.5]	0.2	97 [72,145]	83	mesic, cold (alpine)	138 [94,176]	16.7 [13.7,18.9]
Lacerta bilineata	4 (18)	41.2 [41.0, 41.9]	1.0	553 [495,631]	150	mesic, cold	161 [108,245]	17.0 [27.0,19.1]

672 [1] *Podarcis hispanicus* and *Psammodromus hispanicus* are recently redefined species that keep the names of former species complexes (Speybroeck *et al.* 2016).

673 [2] First column shows number of populations (total number of individuals) sampled per species. Second and third columns show the grand median CT_{max} (among population

674 medians), and the RT median (obtained through a biophysical model); both are reported along with 90 % interquartile limits. CT_{max} ranges are the differences between maximum and

675 minimum median population estimates, and RT ranges are the absolute difference between maximum and minimum population restriction times for each species. Broad climate

676 types, in which each species is found in the Iberian Peninsula, follow Speybroeck *et al.* (2016). Precipitation and temperature (median and 90 % interquantile ranges over all 10×10

677 km^2 grid cells in the Iberian distribution of each species) are rainfall of the wettest quarter (mm) and temperature of the hottest quarter (ºC) from the 'Bioclim' suite (Hijmans *et al.*

678 2005).

SUPPORTING INFORMATION

Expanded methods and results

TABLE S1. List of 38 studies linking CT_{max} (estimated through the 'dynamic method' – see Methods) and climate change in > 2 terrestrial ectotherm species.

TABLE S2. Lizard CT_{max} datasets collated from the primary literature and own sources.

TABLE S3. AIC_c metrics of model support for CT_{max} being regionally homogenous (Region effect = $CT_{max} \sim 1$) against varying according to population locality (Locality effect = $CT_{max} \sim loc$) for each of the 15 study species of Iberian lizards.

TABLE S4. Summary of variables used in the biophysical model by Porter et al. (1973). Climate variables included in the model highlighted in red.

FIGURE S1. Photographs of the 15 study species of Iberian lizards (Lacertidae) from one of the study localities (* = Iberian endemism).

FIGURE S2. Map of locations of the 59 sampled populations of the 15 study species of Iberian lizards (Family Lacertidae).

FIGURE S3. Climate gradients occupied by the 59 study populations of the 15 study species (Family Lacertidae).

FIGURE S4. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 7 populations of *Sceloporus undulatus* in the USA.

FIGURE S5. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 6 species of *Liolaemus* spp. in Chile.
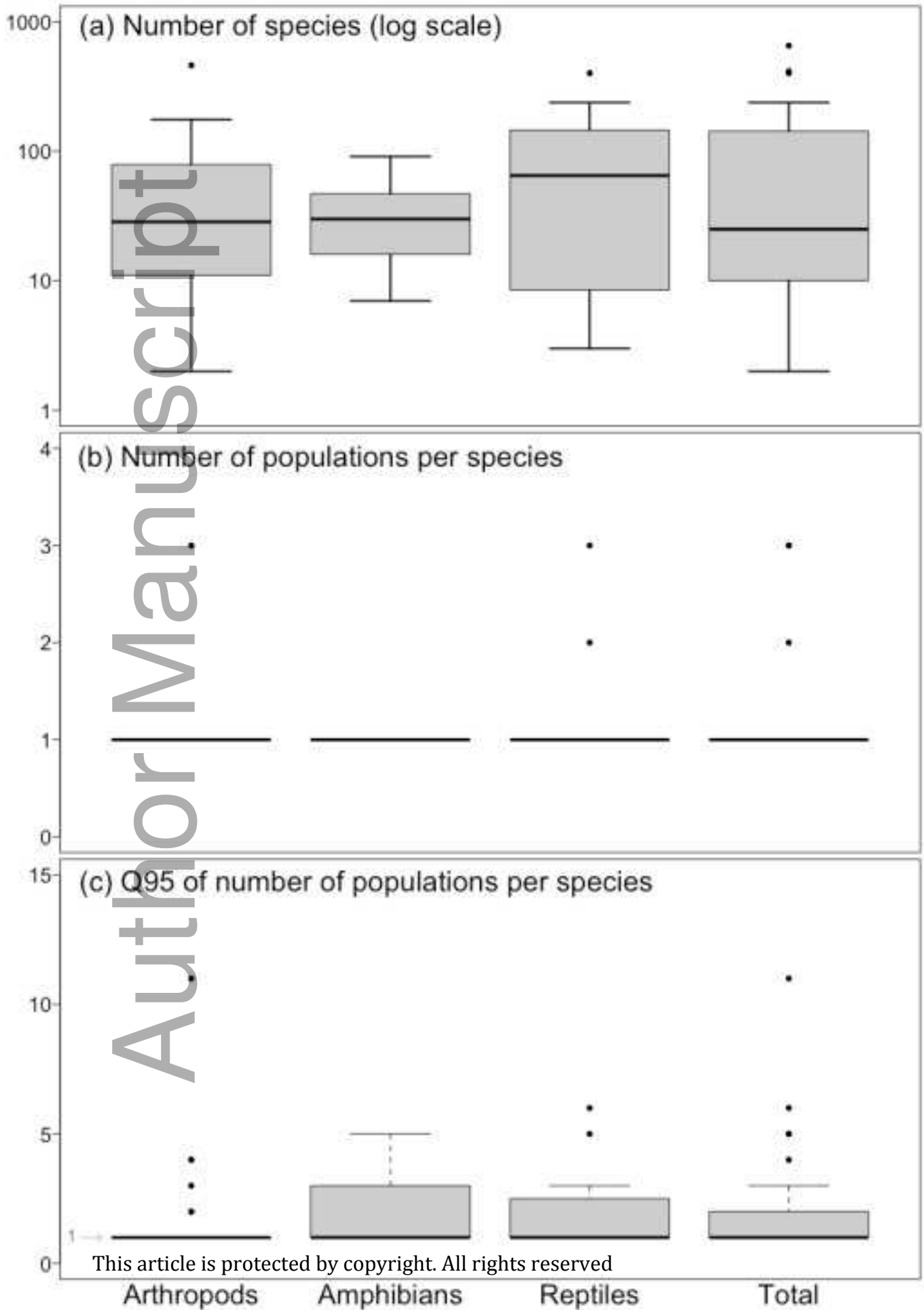
FIGURE S6. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 1 population of *Scenocercus guentheri* from the Northern Andes in Ecuador.
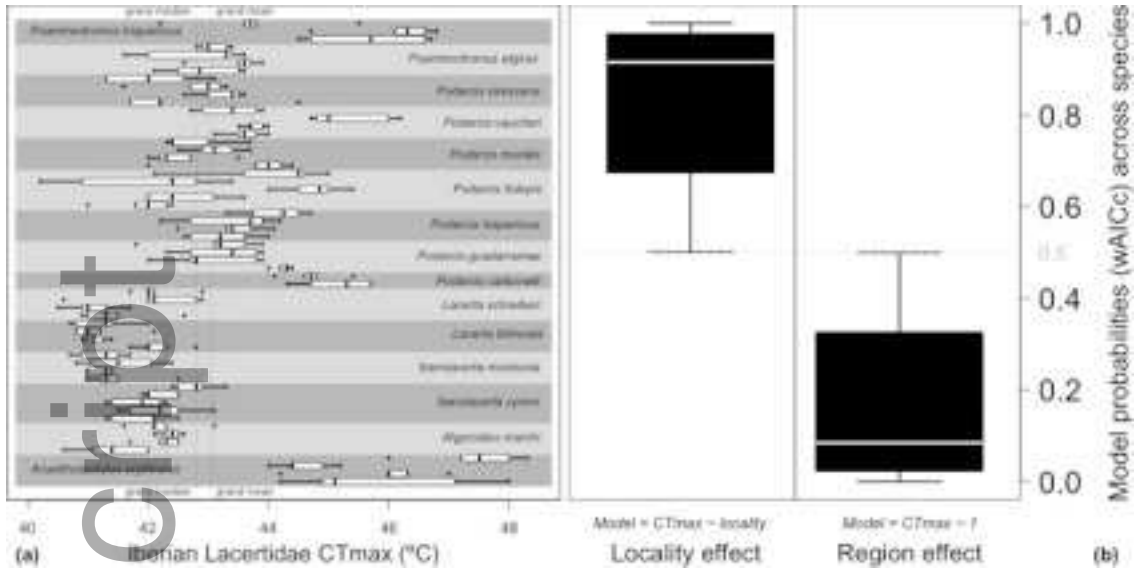
FIGURE S7. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 6 populations of *Anolis cybotes* in the Dominican Republic.

FIGURE S8. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 1 population of *Scenocercus guentheri* from the Northern Andes in Ecuador.
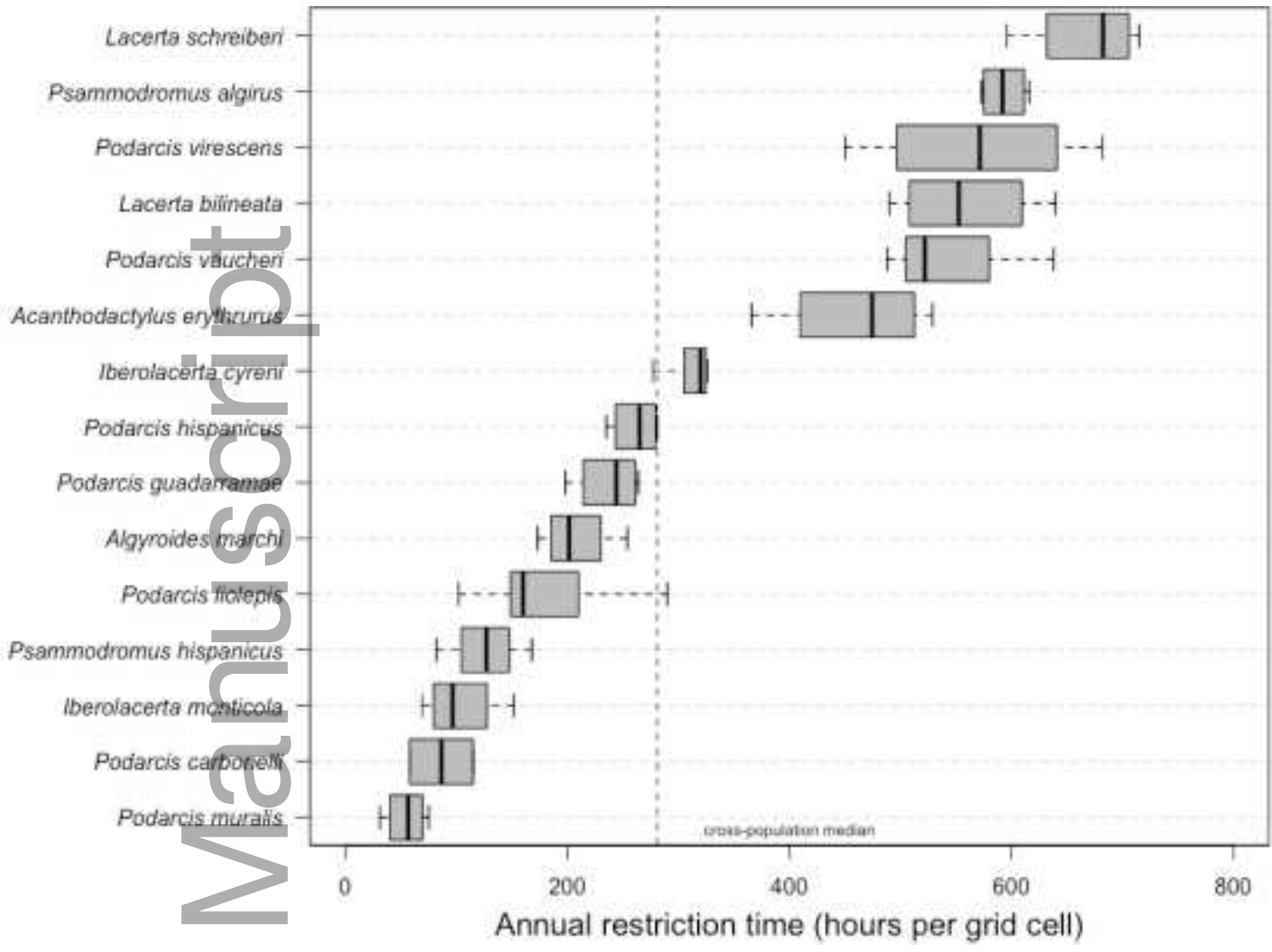
FIGURE S9. Effect of increasing sample size (number of males = N_i) on the accuracy of mean CT_{max} for 6 populations of *Podarcis erhardii* in Greece.

FIGURE S10. Controlling for intrapopulation sample size in model contrasts.

(a) Number of species (log scale)

(b) Number of populations per species

(c) Q95 of number of populations per species

Arthropods Amphibians Reptiles Total

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