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1 **Where you come from matters: temperature influences host-**
2 **parasitoid interaction through parental effects**

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¹ Author contribution statement

All authors conceived and designed the experiments. CI and CM performed the experiments. CI, CM and PL analysed the data. CI, PL and JM led the writing of the manuscript. All authors critically revised the intellectual content of the draft and gave their approbation for the final version to be published

11 **Abstract**

12 Temperature alters host suitability for parasitoid development through direct and indirect
13 pathways. Direct effects depend on ambient temperatures experienced by a single host
14 individual during its lifetime. Indirect effects (or parental effects) occur when thermal
15 conditions met by a host parental generation affect the way its offspring will interact with
16 parasitoids. Using the complex involving eggs of the moth *Lobesia botrana* as hosts for the
17 parasitoid *Trichogramma cacoeciae*, we developed an experimental design to disentangle the
18 effects of: (i) host parental temperature (temperature at which the host parental generation
19 developed and laid host eggs) and (ii) host offspring temperature (temperature at which host
20 eggs were incubated following parasitism, i.e. direct thermal effects) on this interaction. The
21 host parental generation was impacted by temperature experienced during its development: *L.*
22 *botrana* females exposed to warmer conditions displayed a lower pupal mass but laid more
23 host eggs over a 12-hour period. Host parental temperature also affected the outcomes of the
24 interaction. *Trichogramma cacoeciae* exhibited lower emergence rates but higher hind tibia
25 length on emergence from eggs laid under warm conditions, even if they were themselves
26 exposed to cooler temperatures. Such indirect thermal effects might arise from a low
27 nutritional quality and/or a high immunity of host eggs laid in warm conditions. By contrast
28 with host parental temperature, offspring temperature (direct thermal effects) did not
29 significantly affect the outcomes of the interaction. This work emphasises the importance of
30 accounting for parental thermal effects to predict the future of trophic dynamics under global
31 warming scenarios.

32 **Key words**

33 Host eggs, oophagous parasitoid, parental effects, temperature, trophic dynamics.

34 **Introduction**

35 Host-parasitoid interactions modulate the composition of communities and the functioning of
36 ecosystems in both natural and agricultural landscapes (Godfray 1994). Parasitoids exert top-
37 down control on the structure of food webs by regulating the abundance of phytophagous
38 arthropods, while hosts in turn drastically constrain the size of parasitoid populations through
39 bottom-up control (Walker and Jones 2001; Stireman et al. 2005; Thomson et al. 2010). The
40 strength of these top-down and bottom-up forces is governed by a set of biotic and abiotic
41 factors, among which temperature is unequivocally recognised as a key determinant of host-
42 parasitoid interactions (Hance et al. 2007; van Baaren et al. 2010; Jeffs and Lewis 2013).
43 Undeniably, the body temperature and performance of the host and the parasitoid depend on
44 thermal variation among both latitudes and microhabitats (Hance et al. 2007; van Baaren et al.
45 2010; Furlong and Zalucki 2017). The thermal sensitivity of these two antagonistic partners
46 makes host-parasitoid interactions likely to be disrupted by global warming (Jeffs and Lewis
47 2013; Furlong and Zalucki 2017). For instance, Furlong and Zalucki (2017) suggest that
48 increasing global temperatures will produce a greater negative impact on parasitoid
49 distributions, than on their hosts, due to their lower optimal temperature and narrower thermal
50 tolerance range.

51 At the individual level, host suitability – defined as the accordance between a
52 parasitoid’s requirements to complete its development and a host’s physiological,
53 morphological and behavioural features (see Vinson and Iwantsch 1980) – is affected by
54 temperature in several ways. First, temperature determines the amounts of several energetic
55 compounds in the host, among them proteins, lipids, glycogen and free carbohydrates (Geister
56 et al. 2009; Kishani Farahani et al. 2016; Iltis et al. 2019). Since a host is the sole source of
57 nutrients for an immature parasitoid, this thermal variation in host nutritional quality in turn
58 crucially impacts the development of parasitoids and several aspects of their fitness (e.g.

59 longevity, fecundity) (Kishani Farahani et al. 2016). In addition, most parasitoids lack adult
60 lipogenesis and are thus unable to synthesise fat reserves for survival and egg production,
61 which strengthens their dependence on the nutritional resources obtained from their host
62 during development (Visser and Ellers 2008). Second, temperature alters host immune
63 functions (relying, mostly, on encapsulation and melanisation processes) that are aimed at
64 killing parasitoids during their immature stages (Seehausen et al. 2017; Iltis et al. 2018, 2019).
65 In this regard, high temperatures may in some cases stimulate the expression of host immune-
66 related genes with negative consequences for parasitoid survival until emergence. This is
67 especially true if warming concomitantly decreases the ability of the parasitoid to suppress the
68 host immune system, for instance by inducing downregulation of polydnavirus transcription
69 (Seehausen et al. 2017). In other cases, warmer conditions can elicit extensive weakening of
70 the host's immunity, thereby enhancing host susceptibility to a parasitic attack (Iltis et al.
71 2018).

72 Thermal modulation of host suitability can arise from direct effects, whereby ambient
73 temperatures temporarily or permanently experienced by a single host individual during its
74 lifetime might affect the host's immunity (Iltis et al. 2018) and the resulting interaction with
75 parasitoid eggs or larvae (Seehausen et al. 2017). These direct thermal effects are known to
76 influence the outcomes of host-parasitoid interactions (e.g. host infestation rates, parasitoid
77 development time and body mass on emergence, parasitoid emergence rates) (Bahar et al.
78 2012; Delava et al. 2016; Schreven et al. 2017). Besides direct effects, temperature can also
79 indirectly shape host suitability through parental effects (Sgrò et al. 2016; Woestmann and
80 Saastamoinen 2016; Donelson et al. 2018). Parental effects occur when conditions
81 encountered by members of the parental generation influence the expression of a phenotype in
82 the subsequent generation (Sgrò et al. 2016; Donelson et al. 2018). Indeed, environmental
83 conditions experienced by a host parental generation – such as temperature, host plant

84 nutritional quality or immune challenge – have demonstrated influence on a large variety of
85 offspring traits related with their suitability for parasitoids (e.g. size, mass, amounts of
86 energetic metabolites, immunity) (Geister et al. 2009; Janowitz and Fischer 2011; Eggert et al.
87 2015; Trauer-Kizilelma and Hilker 2015; Moreau et al. 2016). Beyond these effects at the
88 individual level, to what extent such parental thermal effects might drive the dynamics of the
89 host-parasitoid interaction remains unexplored, as does the relative importance of direct and
90 parental effects for the outcomes of the interaction. From a global warming perspective, such
91 a knowledge gap might limit our ability to forecast the impacts of rising temperatures for the
92 future of host-parasitoid interactions. Indeed, this climatic disturbance will persist across
93 generations and is therefore expected to affect species and interspecific relationships through
94 direct and parental effects in a cumulative way (Sgrò et al. 2016; Donelson et al. 2018).

95 Here we investigated the consequences of direct and parental thermal effects for an
96 interaction between host eggs and oophagous parasitoids. We developed an experimental
97 design that allowed us to separate the relative impacts of: (i) parental thermal effects, through
98 differences in temperatures experienced by a host parental generation from larval
99 development to egg laying (i.e. parental temperature), and (ii) direct thermal effects, through
100 differences in ambient temperatures at which host eggs were incubated following parasitism
101 (i.e. offspring temperature). As an experimental imitation of global warming, we built two
102 realistic, fluctuating regimes reflecting current and future thermal conditions in our focal area
103 (Eastern France). We focused on the host-parasitoid complex constituted by eggs of one of
104 the most harmful vineyard pests in the Palearctic region: the European grapevine moth
105 *Lobesia botrana* (Lepidoptera: Tortricidae), as host for the oophagous parasitoid
106 *Trichogramma cacoeciae* (Hymenoptera: Trichogrammatidae) – a candidate for the biological
107 control of *L. botrana* populations (Pizzol et al. 2012; Thiéry et al. 2018). Considering that
108 parental effects are known to be a major source of variation in offspring quality traits,

109 particularly in the early life stages like eggs (reviewed by Woestmann and Saastamoinen
110 2016), we hypothesised that host egg suitability for parasitoids should be influenced by
111 parental temperature to a greater extent than offspring temperature. Specifically, we expected
112 lower parasitoid emergence rates from host eggs originating from warm conditions, as a
113 consequence of a low suitability of these eggs. Indeed, higher temperatures experienced by *L.*
114 *botrana* parents during development should shorten the duration of their larval stage and
115 reduce their food intake – congruently with previous works conducted on this species (Iltis et
116 al. 2018, 2019). Lower larval food intake should, in turn, negatively affect parental
117 investment in egg quality, because *L. botrana* adults are non-feeding and their reproductive
118 output, along with egg quality traits, tightly hinges on resources accumulated as caterpillars
119 (Moreau et al. 2006, 2016).

120 **Materials and methods**

121 *Thermal regimes*

122 Thermal regimes used in this study reflected realistic current and future climatic conditions in
123 Burgundy, Eastern France (Longvic-Dijon weather station, 47,27°N; 5,09°E; altitude = 219
124 m) (www.meteofrance.com). These regimes focused on the summer period, extending from
125 15-July to 15-Aug, because this date range is associated with high levels of activity for the
126 host and the parasitoid in Eastern France, as shown by concomitant peaks of adult moth
127 emergence and number of *L. botrana* eggs parasitised by *T. cacoeciae* (Barnay et al. 2001).
128 The thermal regime designed to reflect conditions currently found in Burgundy, called the
129 ‘current regime’, was generated according to 20-year recordings of *in situ* hourly temperatures
130 (1995-2014 period). The current regime was compared with the ‘future regime’, describing
131 the summer thermal conditions (15-July to 15-Aug) likely to occur in Burgundy by the end of
132 this century (2081-2100 period). To design the future regime, we combined six General

133 Circulation Models and six Regional Climate Models, selecting the most pessimistic
134 greenhouse gas emissions scenario: RCP 8.5 (see Beaumont et al. 2008; Harris et al. 2014 for
135 an in-depth description of the use of climate models in ecology). Data are available on the
136 Drias portal (www.drias-climat.fr). Daily cycles constituting the current regime and the future
137 regime were composed of six temperature segments, each lasting 4h and calculated (i) as the
138 mean segment over the 30 days (15-July to 15-Aug) and the 20 years of *in situ* data for the
139 current regime, or (ii) as the mean segment over the six simulations run for the future regime
140 (Fig. 1). Compared with the current regime, the future regime shows an increase in mean
141 temperature of 5.3°C (25.8°C for the future regime *versus* 20.5°C for the current regime) and
142 an increase in thermal range (the difference between maximum and minimum daily
143 temperatures) of 0.6°C (5.6°C for the future regime *versus* 5.0°C for the current regime) (Fig.
144 1).

145 *Moth maintenance and host egg production*

146 All *L. botrana* individuals used in this experiment belonged to a laboratory, diapause-free
147 population maintained at the French National Institute for Agricultural Research (INRA,
148 Villenave d'Ornon, France). This large stock was comprised of several thousand adults per
149 week, and was regularly supplemented with wild individuals collected from nearby vineyards
150 (cultivar Sémillon) to preserve genetic diversity (Vogelweith et al. 2014). Moths were reared
151 in a large cage at $20 \pm 0.5^\circ\text{C}$, $60 \pm 5\%$ relative humidity, under a light cycle of L17: D6 with
152 one hour of dusk. Luminosity reached 650 lx during photophase and fell to 100 lx at dusk.
153 Two bands of waxed paper (5 x 10 cm) were hung inside the cage for egg laying. Every 3
154 days, these oviposition supports were renewed and transferred into plastic boxes covered by a
155 moist piece of paper towel to protect eggs from desiccation until hatching.

156 Over two months, a total of 5520 freshly hatched larvae (age < 24h) were collected
157 with a fine brush and isolated in Eppendorf tubes filled with 1.5 ml of artificial medium that is
158 typically used for the laboratory rearing of this species (composition for 1000 ml: 1000 ml
159 water, 15 g agar, 86.6 g maize flour, 41.3 g wheat germ, 45.5 g beer yeast, 6 g ascorbic acid,
160 3.4 g mineral salt, 0.32 g Scala, 2.7 g benzoic acid, 2.8 g Nipagin and 5 ml 95% ethanol)
161 (Thiéry and Moreau 2005; Muller et al. 2016; Iltis et al. 2018). Individual rearing in
162 Eppendorf tubes avoided larval competition and subsequent food deprivation (Thiéry et al.
163 2014). Tube caps were drilled for air circulation and covered with a piece of fine mesh fabric
164 to prevent larvae from escaping. Individuals were randomly assigned to four incubators (ST
165 2/2 BASIC, Pol-Eko Aparatura, Wodzisław Śląski, Poland), two of which being programmed
166 to run the current regime and the other two to run the future regime (temperature $\pm 0.1^{\circ}\text{C}$, 50
167 $\pm 10\%$ relative humidity, L18: D6, 650 lx). Twice a week, larvae from a given thermal regime
168 were switched between the two climate chambers running this regime, as well as the relative
169 locations of individuals inside these chambers. Temperatures inside the devices were recorded
170 by independent data loggers (Hobo, Onset Computer Corporation, Bourne, USA) and
171 conformed to the thermal regimes programmed during the whole course of the experiments.
172 To limit disturbance, larval viability and pupation were monitored only when swapping
173 rearing tubes between incubators (i.e. twice a week).

174 Within 3 or 4 days following pupation, chrysalises were carefully extracted from their
175 silk cocoons with fine forceps and weighed to the nearest 0.1 mg with a balance (Pioneer
176 PA214C, OHAUS, Greifensee, Switzerland). Chrysalises were subsequently isolated in clean
177 glass tubes (70 x 9 mm diameter) closed by cotton plugs before being returned to their rearing
178 thermal regime. They were checked daily for imaginal emergence. Moths were sexed upon
179 emergence and were supplied daily with water *ad libitum* through soaked cotton plugs. At
180 dusk, one 24-48h virgin female was randomly placed for one night in a clean glass mating

181 tube (100 x 15 mm diameter) with one 24-72h virgin male originating from the same thermal
182 regime. We restricted the age ranges of sexual partners, and only used virgin individuals
183 because age and mating history are known to affect several traits in this species that influence
184 egg quality (e.g. spermatophore volume, number of eggs laid, egg size) (Moreau et al. 2006;
185 Muller et al. 2016). Males were removed the following morning to avoid multiple mating, and
186 were no longer used for the experiments. Females were allowed to oviposit freely in their
187 mating tube closed by a daily soaked cotton plug as a water supply. Mating and egg laying
188 occurred within the thermal regime from which the pair originated.

189 The number of eggs laid by females was recorded every morning via visual inspection.
190 Only mating tubes containing at least 30 eggs laid within 12h (i.e. during one single night)
191 were used for parasitism tests. A lower limit of 30 eggs was set to ensure that host egg
192 number was not a limiting factor for the parasitoid during parasitism tests and to reduce
193 variation in host egg density. For the purpose of standardisation, host egg age was restricted
194 to 12h or less because it might affect the outcomes of interactions with *T. cacoeciae* (e.g.
195 number of eggs parasitised, parasitoid emergence rates) (Moreno et al. 2009; Pizzol et al.
196 2012). In addition, using such freshly laid host eggs is appropriate to investigate parental
197 thermal effects, because these eggs have been exposed to environmental conditions for a very
198 short duration before parasitism tests. Hence, variation in their suitability for parasitoids
199 should be importantly driven by parental effects. This selection procedure retained 512
200 mating tubes out of a total of 734 tubes, which represents 98% of the 523 tubes with eggs
201 found inside. This high percentage can be explained by the fact that *L. botrana* females
202 usually lay the largest amounts of eggs at the beginning of their oviposition period, especially
203 during the first night succeeding to mating (Moreau et al. 2016). *Lobesia botrana* females
204 were then removed and the tubes of freshly laid eggs were photographed using a
205 stereomicroscope at 8x magnification (Stemi 508, Zeiss, Göttingen, Germany). For each tube,

206 one picture including five eggs on the same horizontal plane was taken to reliably estimate
207 mean egg size (surface area) within the clutch (Moreau et al. 2016). We then randomly
208 selected 123 pictures ($n = 57$ for the current regime, $n = 66$ for the future regime) and
209 assessed the surface area of five eggs for each picture (estimated as an elliptic surface, $S =$
210 $\pi \times a \times b$ in mm², where a and b are the ellipse semi-axes) with a precision of ± 0.001
211 mm². The photographic data were analysed with ImageJ software (version 1.51j8, National
212 Institutes of Health, Bethesda, USA).

213 *Parasitoid maintenance and parasitism procedure*

214 Experimental lines of *T. cacoeciae* involved in this study were all thelytokous, and therefore
215 only constituted by females. We ran one single experiment using parasitoids belonging to four
216 different strains in order to generalise our conclusions about the thermal modulation of host
217 egg suitability to a generic parasitoid pressure. Hence, parasitoid strain was included as a
218 treatment (involving four levels) in the experiment. These four strains were derived from field
219 populations collected in June 2017 at four French localities: Aime (45,33°N; 6,39°E),
220 Banyuls-sur-Mer (42,45°N; 3,09°E), Le Crouzet (44,38°N; 3,63°E) and Sophia Antipolis
221 (43,61°N; 7,08°E). These sites were chosen because they are distant enough from each other
222 to avoid any confounding genetic effect, given the relatively low dispersal abilities of
223 *Trichogramma* species (Fournier and Boivin 2000). Wild populations were initially sampled
224 on *Rosa sp.* and *Prunus sp.* with baits comprised of cards covered with ultraviolet sterilised
225 eggs of the Mediterranean flour moth *Ephestia kuehniella* (age < 5 days) as a substitute host.
226 Parasitoids emerging from these baits were first identified as *T. cacoeciae* individuals based
227 on molecular analyses involving PCR amplification of a microsatellite marker (Pizzol et al.
228 2005), and then used to establish laboratory colonies. Until the start of the experiments (i.e.
229 over 9 months), they were reared in plastic culture tubes plugged with cotton (10 x 1 cm
230 diameter) under controlled common conditions ($23.1 \pm 0.5^{\circ}\text{C}$, $60 \pm 5\%$ relative humidity,

231 photophase of L18: D6, 650 lx). One piece of cardboard (1 x 6 cm) covered with ultraviolet
232 sterilised eggs of *E. kuehniella* (age < 5 days) was provided for parasitoid multiplication.
233 After 4 days of exposure, the cardboard pieces were transferred to clean rearing tubes for
234 parasitoid emergence. A droplet of honey was deposited into each rearing tube to feed
235 emerged adults. Prior to our parasitism tests, individuals originating from the four collected
236 strains were genetically identified to ensure that no contamination had occurred within each
237 strain (Pizzol et al. 2005).

238 Only *T. cacoeciae* females, less than 24h old, were picked for the experiments. These
239 females had not parasitised any host eggs before their contact with *L. botrana* eggs during the
240 parasitism tests. Parasitoid age was restricted (< 24h) to standardise its effects on the total
241 number of host eggs parasitised (Pizzol et al. 2012). Tubes of freshly emerged parasitoids
242 were gently tapped until *T. cacoeciae* females fell from the tubes. A tube of host eggs was
243 then inversely placed over the parasitoid until it climbed the walls of the tube. We only
244 selected actively moving parasitoids tipped from their rearing tubes to make sure their
245 physical integrity had not been altered during manipulation. To avoid any confusion, *T.*
246 *cacoeciae* females used to parasitise *L. botrana* eggs will be referred to as ‘mothers’ and those
247 that emerged from these eggs will be called ‘daughters’.

248 Each day, host egg tubes originating from each thermal regime were equally
249 distributed among *T. cacoeciae* strains to ensure temporal randomisation. Parasitism tests
250 were conducted under a common temperature of 23.1°C ($\pm 0.5^\circ\text{C}$, $60 \pm 5\%$ relative humidity,
251 650 lx) to standardise the effect of ambient temperature on parasitoid behaviour, and also
252 because 23.1°C is the rearing temperature of parasitoids as well as the intermediate
253 temperature from which host egg tubes originated: between the mean temperatures of the
254 current regime (20.5°C) and the future regime (25.8°C). Parasitoid mothers were introduced
255 inside host egg tubes at 9:00 AM and delicately removed with a fine brush at 3:00 PM.

256 Exposure duration was set at 6h to ensure parasitism was not limited by the number of host
257 eggs available and to avoid superparasitism. Indeed, more than 6h should be needed for one *T.*
258 *cacoeciae* female to parasitise at least 30 eggs of *L. botrana* under the controlled conditions at
259 which parasitism occurred (Moreno et al. 2009). No food or water was supplied to parasitoid
260 mothers during the experiments. After their removal from host egg tubes, *T. cacoeciae*
261 mothers were placed individually in clean Eppendorf tubes until their death. Using a
262 stereomicroscope at 100x magnification (Stemi 508, Zeiss, Göttingen, Germany), we then
263 measured the length of their left hind tibia as an estimation of body size (precision $\pm 0.1 \mu\text{m}$) –
264 following the standard procedure described by Olson and Andow (1998). These
265 measurements were taken to control for an effect of the body size of parasitoid mothers on the
266 number of host eggs parasitised, the percentage of parasitoid emergence, and the hind tibia
267 length of parasitoid daughters that emerged from parasitised eggs. Out of an initial 512 tubes,
268 12 tubes were removed from the dataset because the preservation state of the *T. cacoeciae*
269 mothers used to parasitise these tubes did not permit reliable measurements of hind tibia
270 length.

271 *Host egg incubation and data acquisition*

272 Once parasitoid mothers were removed, host egg tubes were randomly incubated in either the
273 current or the future regime (i.e. independently of the thermal regime they came from). This
274 resulted in four combinations of thermal regimes (current/current, current/future,
275 future/current, future/future), each combination being defined by one ‘parental temperature’
276 (regime within which host development, reproduction and egg laying occurred) and one
277 ‘offspring temperature’ (regime within which host eggs were incubated following exposure to
278 parasitoids). Each day, tubes of parasitised eggs were equally distributed between the two
279 offspring temperatures for temporal randomisation. Incubation lasted 28 days before tube
280 inspection. This duration was sufficient to enable the complete development of the host

281 (hatching of *L. botrana* larvae from unparasitised eggs) and the parasitoid (emergence of *T.*
282 *cacoeciae* daughters from parasitised eggs) until death (Moreau et al. 2009; Moreno et al.
283 2009). No cannibalism of parasitised eggs by newly hatched *L. botrana* caterpillars was
284 observed. No parasitoid diapause was expected to occur under the environmental conditions –
285 especially temperature and photoperiod – encountered by *T. cacoeciae* mothers and daughters
286 during parasitism tests and post-parasitism incubation, respectively (Pizzol and Pintureau
287 2008).

288 After the incubation period, tubes were analysed under a stereomicroscope (Stemi 508,
289 Zeiss, Göttingen, Germany) to record (i) the ‘first-day fecundity’ of the host (total number of
290 eggs laid by one *L. botrana* female during one single night), (ii) the ‘apparent parasitism
291 success’ of the parasitoid mother (number of host eggs parasitised) and (iii) the ‘apparent
292 emergence success’ of parasitoid daughters (percentage of host eggs parasitised from which
293 an adult *T. cacoeciae* successfully emerged) (Moreau et al. 2009). For determination of
294 apparent parasitism success, we considered an egg as parasitised when it turned from white to
295 grey, given that such a change in colouration is widely acknowledged as a reliable indicator of
296 parasitism by *Trichogramma* species (Hutchison et al. 1990) and because this criterion has
297 been employed in previous studies that used *L. botrana* eggs as hosts for *Trichogramma*
298 species (Moreau et al. 2009; Pizzol et al. 2012; Thiéry and Desneux 2018). Provided that
299 blackening of the parasitised host eggs occurs at the time of parasitoid pupation (Hutchison et
300 al. 1990), our metrics did not include cases where parasitoids died before the pupal stage, and
301 therefore provide information about the ‘apparent’ rather than the ‘realised’ parasitism of the
302 host eggs. Apparent parasitism success was not expressed in percentages because host eggs
303 were provided *ad libitum* to *T. cacoeciae* mothers during parasitism tests (Moreau et al.
304 2009). For determination of apparent emergence success, we considered that the parasitoid
305 daughter successfully emerged from the parasitised host egg when the blackened egg was

306 found empty with an emergence hole on its surface. Hence, the difference between apparent
307 parasitism success and apparent emergence success was that the former included all cases of
308 apparent parasitism (all blackened eggs, with or without parasitoid emergence), whereas the
309 latter only considered those that led to the emergence of the parasitoid daughter from the host
310 egg (empty blackened eggs with an emergence hole on their surface). Sterile host clutches (28
311 tubes out of a total of 500 tubes) were discarded because they were laid by unmated *L.*
312 *botrana* females and were therefore not subject to similar paternal effects as clutches resulting
313 from successful mating. Host clutches were deemed sterile if no caterpillars emerged from the
314 eggs. Tubes with no parasitised eggs found after exposure to a parasitoid mother ($n = 5$ for
315 current/current, $n = 2$ for current/future, $n = 1$ for future/current, $n = 4$ for future/future) were
316 conserved for statistical analysis focused on apparent parasitism success as no dead parasitoid
317 mother had been observed after the 6h of parasitism. Dead parasitoid daughters were carefully
318 collected with a fine brush, and observed under a stereomicroscope at 100x magnification
319 (Stemi 508, Zeiss, Göttingen, Germany) to measure the length of their left hind tibia with the
320 same method used for mothers. As an estimation of body size, hind tibia length is positively
321 correlated with a female's longevity and lifetime fecundity in *Trichogramma* species and can
322 therefore be interpreted as a surrogate for individual performance (Doyon and Boivin 2005).
323 The number of *T. cacoeciae* daughters extracted from each tube varied between zero and five,
324 dependent on the number of daughters that had emerged from host eggs and their preservation
325 state. Following the above selection procedure, 472 tubes were finally inspected ($n = 124$ for
326 current/current, $n = 122$ for current/future, $n = 108$ for future/current, $n = 118$ for
327 future/future), and hind tibia length measurements were taken from 826 parasitoid daughters
328 collected from 373 tubes ($n = 96$ for current/current, $n = 107$ for current/future, $n = 89$ for
329 future/current, $n = 81$ for future/future), equally distributed across the four parasitoid strains.

330 *Statistical analyses*

331 This study was based on a 2x2x4 full-factorial design involving three factors: ‘parental
332 temperature’ (two levels), ‘offspring temperature’ (two levels) and ‘parasitoid strain’ (four
333 levels). The pupal mass of individuals of the *L. botrana* parental generation (i.e. parents
334 which produced the host eggs) was studied with an Analysis of Variance (ANOVA)
335 incorporating temperature experienced by this generation, sex and the interaction between
336 these two explanatory variables. Egg surface area and first-day fecundity of the host (*L.*
337 *botrana*) were analysed with statistical models that included parental temperature as an
338 explanatory variable, and female and male pupal mass as two covariates. For host egg surface
339 area, an Analysis of Covariance (ANCOVA) with mixed effects was performed to account for
340 the random effect represented by the identity of each *L. botrana* female and male. The data
341 for first-day fecundity of the host did not satisfy the assumption of homoscedasticity and were
342 therefore compared between parental thermal regimes using a Generalised Linear Model
343 (GLM)-negative binomial error with a log link function.

344 For apparent parasitism success, apparent emergence success and hind tibia length of
345 parasitoid daughters, three covariates were included in the models (pupal mass of *L. botrana*
346 female and male, hind tibia length of *T. cacoeciae* mother). As no transformation enabled to
347 reach normality for these discrete data, apparent parasitism success was analysed using a
348 Generalised Linear Mixed Model (GLMM)-negative binomial error with a log link function,
349 incorporating host parental temperature as a fixed effect and parasitoid strain as a random
350 effect. For apparent emergence success, data were expressed in proportions and a GLMM-
351 binomial error with a logit link function was performed to assess the fixed effects of host
352 parental temperature, host offspring temperature and their interaction while accounting for
353 parasitoid strain as a random effect. Lastly, variation in hind tibia length of parasitoid
354 daughters was analysed by means of an ANCOVA with mixed effects, including host parental

355 temperature, host offspring temperature and their interaction as fixed effects; and the identity
356 of *L. botrana* female, male, parasitoid mother and parasitoid strain as random effects.

357 For all statistical analyses conducted, the best statistical model was selected following
358 a stepwise backward procedure from initial models that included all simple fixed effects and
359 their interactions. Normality and homoscedasticity were evaluated with a Shapiro-Wilk and
360 Bartlett test, respectively. Post-hoc tests based on contrasts among the least square means
361 were conducted to tease out significant differences. A Bonferroni correction was applied to
362 prevent Type I errors. All statistical analyses were carried out using R software (version 3.6.1,
363 R Development Core Team).

364 **Results**

365 *Pupal mass, egg surface area and first-day fecundity of L. botrana host*

366 The pupal mass of individuals from the *L. botrana* parental generation was influenced by the
367 interaction between rearing temperature and sex ($F_{1,940} = 9.11$, $P < 0.001$). In females, the
368 pupal mass was negatively impacted by rearing temperature: individuals that developed in the
369 future, warmer regime were significantly lighter than those originating from the current,
370 cooler regime. Mean values of females' pupal mass were 13.6 mg for the current regime (95%
371 confidence interval $CI_{95\%} = [13.4; 13.8]$, $n = 246$) and 13.1 mg for the future regime ($CI_{95\%} =$
372 $[12.9; 13.3]$, $n = 226$). In males, the pupal mass was not significantly affected by rearing
373 temperature. Mean values of males' pupal mass were 9.4 mg for the current regime ($CI_{95\%} =$
374 $[9.3; 9.5]$, $n = 246$) and 9.3 mg for the future regime ($CI_{95\%} = [9.2; 9.5]$, $n = 226$). The surface
375 area of *L. botrana* eggs was not significantly affected by parental temperature ($\chi^2_1 = 3.45$, $P =$
376 0.06). Eggs originating from the current regime had a mean surface area of 0.403 mm^2 ($CI_{95\%}$
377 $= [0.399; 0.407]$, $n = 57$) and those originating from the future regime had a mean surface area
378 of 0.411 mm^2 ($CI_{95\%} = [0.407; 0.415]$, $n = 66$). The first-day fecundity of *L. botrana* females

379 was positively impacted by their rearing temperature ($\chi_1^2 = 36.4$, $P < 0.001$). Females reared
380 in the future regime produced 19% more eggs within 12h than females reared in the current
381 regime. Mean values of first-day fecundity were 63 eggs for females reared in the current
382 regime (CI_{95%} = [60; 65], $n = 246$) and 75 eggs for females which developed in the future
383 regime (CI_{95%} = [71; 78], $n = 226$). Only first-day fecundity was affected by the covariates
384 included in the models and this relationship was positive: it increased with female pupal mass
385 ($\chi_1^2 = 6.31$, $P = 0.01$, slope = 0.03) and male pupal mass ($\chi_1^2 = 4.27$, $P = 0.04$, slope = 0.03).

386 *Apparent parasitism success, apparent emergence success and hind tibia length of parasitoid*
387 *daughters*

388 Apparent parasitism success was not significantly affected by host parental temperature ($\chi_1^2 =$
389 0.28, $P = 0.60$). Among the three covariates included in the model (pupal mass of *L. botrana*
390 female and male, hind tibia length of *T. cacoeciae* mother), apparent parasitism success was
391 only positively influenced by the hind tibia length of *T. cacoeciae* mother ($\chi_1^2 = 9.80$, $P <$
392 0.001, slope = 0.01): the largest mothers parasitised significantly more eggs over 6 hours than
393 the smallest ones. As a random effect, parasitoid strain significantly affected apparent
394 parasitism success ($\chi_2^2 = 17.8$, $P < 0.001$).

395 Apparent emergence success was modulated by host parental temperature ($\chi_1^2 = 9.44$,
396 $P < 0.001$), but not by host offspring temperature ($\chi_1^2 = 0.39$, $P = 0.53$) or by the interaction
397 between these two factors ($\chi_1^2 = 2.62$, $P = 0.11$). A lower percentage of parasitoid daughters
398 emerged from host eggs originating from the future regime compared with host eggs coming
399 from the current regime (Fig. 2). Among the three covariates included in the model (pupal
400 mass of *L. botrana* female and male, hind tibia length of *T. cacoeciae* mother), apparent
401 emergence success was only positively influenced by the pupal mass of *L. botrana* female
402 ($\chi_1^2 = 40.0$, $P < 0.001$, slope = 0.47): the heavier the *L. botrana* female that laid the host eggs,

403 the higher the apparent emergence success of parasitoid daughters from these eggs. As a
404 random effect, parasitoid strain significantly affected apparent emergence success ($\chi_1^2 = 5.16$,
405 $P = 0.02$).

406 The hind tibia length of *T. cacoeciae* daughters that emerged from parasitised *L.*
407 *botrana* eggs was impacted by host parental temperature ($\chi_1^2 = 8.55$, $P < 0.001$), but not by
408 host offspring temperature ($\chi_1^2 = 0.40$, $P = 0.53$) or by the interaction between these two
409 factors ($\chi_1^2 = 0.02$, $P = 0.89$). Larger parasitoid daughters emerged from host eggs originating
410 from the future regime in comparison with host eggs laid in the current regime (Fig. 3). None
411 of the three covariates included in the model (pupal mass of *L. botrana* female and male, hind
412 tibia length of *T. cacoeciae* mother) significantly affected the hind tibia length of parasitoid
413 daughters. As a random effect, parasitoid strain significantly affected the hind tibia length of
414 *T. cacoeciae* daughters ($\chi_1^2 = 61.7$, $P < 0.001$).

415 Discussion

416 The purpose of this work was to assess the relative importance of parental and direct thermal
417 effects in determining the outcomes of the interaction between eggs of the European
418 grapevine moth *L. botrana* and the oophagous parasitoid *T. cacoeciae*. Our most striking
419 result was the considerable effect of host parental temperature, that is, temperature
420 experienced by host parental generation, on parasitoid apparent emergence success and hind
421 tibia length on emergence. *Trichogramma cacoeciae* experienced lower emergence rates, but
422 displayed higher hind tibia length on emergence, from host eggs originating from warm
423 conditions (laid in the future regime) compared with eggs produced under cold conditions
424 (laid in the current regime). By contrast with parental effects, direct thermal effects did not
425 perceptibly modulate the outcomes of the host-parasitoid interaction. These findings match
426 our initial expectation that the interaction between freshly laid host eggs and an oophagous

427 parasitoid should be primarily determined by indirect, parental effects. Our results emphasise
428 the importance of accounting for such parental thermal effects with the aim to predict the
429 future of trophic dynamics under global warming scenario. Interestingly, the modulation
430 exerted by host parental temperature on the outcomes of the interaction was consistent over
431 the four parasitoid strains included in the study, even if each strain displayed its own
432 characteristics in terms of performance when parasitising *L. botrana* eggs (e.g. apparent
433 parasitism and emergence success, hind tibia length of emerged parasitoid daughters). From
434 an evolutionary perspective, this raises the question as to whether natural populations of *T.*
435 *cacoeciae* experiencing a set of contrasting ecological conditions might respond in different
436 ways to a rise in mean temperature, that is, whether parasitoid thermal adaptation may shape
437 the evolutionary trajectory of the interaction in the context of climate change.

438 Two non-mutually exclusive hypotheses might account for the effects of host parental
439 temperature on parasitoid apparent emergence success and hind tibia length on emergence.
440 First, parasitoids are constrained by the limited amount of food contained in their single host,
441 and might fail to complete their development if host eggs laid in the future regime provide an
442 insufficient quantity or quality of nutritional resources (i.e. resource-based hypothesis)
443 (Kishani Farahani et al. 2016). Whether this hypothesis is fully relevant to explain our results
444 remains questionable, provided that we did not observe any effect of parental temperature on
445 *L. botrana* egg surface area as a surrogate of host nutritional quality for the parasitoid. In
446 addition, the resource-based hypothesis poorly explains differences regarding the hind tibia
447 length of emerged parasitoids observed. Indeed, host eggs of low nutritional quality should
448 produce smaller adult parasitoids (Kishani Farahani et al. 2016), while we instead observed a
449 higher hind tibia length of *T. cacoeciae* daughters emerging from host eggs produced in warm
450 conditions. As a next step, biochemical assays of the quantities of several energetic
451 metabolites eggs are provisioned with (e.g. proteins, lipids, glycogen, soluble carbohydrates)

452 would be needed to assess more thoroughly the plausibility of this resource-based explanatory
453 hypothesis (Geister et al. 2009).

454 A second hypothesis, positing differences in egg immunity (i.e. immunity-based
455 hypothesis), can be formulated to explain the importance of host parental temperature for the
456 host-parasitoid relationship. There is a growing body of evidence showing that eggs of
457 lepidopteran hosts are able to mount an immune response to fend off a myriad of invaders,
458 and the efficiency of this endogenous immune barrier is an integral component of their
459 suitability for parasitoids (Abdel-latief and Hilker 2008; Trauer-Kizilelma and Hilker 2015).
460 Host immune defences against parasitism are modulated by parental experience (Triggs and
461 Knell 2012; Trauer-Kizilelma and Hilker 2015), including parental exposure to a brief
462 thermal stress (cold snap or heat spike) (Eggert et al. 2015). In our study, *L. botrana* parents
463 might have faced daily stressful thermal conditions in the future regime – which included
464 temperatures up to 30.5°C for 4h – while a decline in the performance of caterpillars of this
465 species has been pointed out at temperatures exceeding 25°C (Iltis et al. 2018, 2019). Such
466 temporarily stressful temperatures met by the host parental generation might have promoted
467 egg immunological defences, and could be potentially responsible for the negative effects of
468 host parental temperature on parasitoid apparent emergence success. With respect to this
469 immunity-based hypothesis, the proximate cause of the positive effect of host parental
470 temperature on *T. cacoeciae* hind tibia length remains unknown at this stage. The reason
471 could, for instance, involve a selective pressure exerted by the high immunity of eggs laid in
472 warm conditions acting in favour of the largest parasitoid individuals. Such a phenomenon
473 might occur if the efficiency of host encapsulation and melanisation processes decreases as
474 the size of the foreign body to be encapsulated increases (Pomfret and Knell 2006). Hence,
475 the largest parasitoid individuals could be more prone to survive the immune reaction
476 expressed by their host. Considering that host egg immunity should operate during the first

477 steps of the parasitism process, that is, acting on the early-life stages of *Trichogramma*
478 parasitoids (Abdel-latif and Hilker 2008; Trauer-Kizilelma and Hilker 2015), one way to test
479 the immunity-based hypothesis may consist of investigating the effects of host parental
480 temperature on the early mortality of the parasitoid, before the blackening of the parasitised
481 host eggs occurring at the time of parasitoid pupation (Hutchison et al. 1990). If this
482 hypothesis is valid, a higher percentage of dead parasitoid eggs and larvae should be expected
483 from host eggs originating from warm conditions compared with host eggs laid in cold
484 conditions.

485 By contrast with parental thermal effects, direct thermal effects did not contribute to
486 modulate the outcomes of the host-parasitoid interaction measured. In our study, host eggs
487 were exposed to parasitoids shortly after being laid by *L. botrana* females (within 12h).
488 Hence, these freshly laid eggs experienced the direct thermal effects occurring before
489 parasitism for a very short duration, which could mitigate the importance of these direct
490 thermal effects in influencing egg suitability for the parasitoid. It would be worth
491 investigating whether the absence of direct thermal effects would persist using host eggs older
492 than 12h. This is especially relevant considering that temperature primarily mediates
493 embryonic development in insects (Howe 1967), and that the egg developmental stage in turn
494 impacts most egg traits related with their susceptibility to *Trichogramma* parasitoids. For
495 instance, the egg nutritional resources are progressively consumed for embryonic growth in a
496 temperature-dependent manner (Geister et al. 2009), hence direct thermal effects acting prior
497 to parasitism may influence the amounts of reserves available for parasitoid development.
498 Furthermore, in lepidopteran host eggs, the mechanisms underlying the host immune reaction
499 to parasitoid attack could differ depending on the stage of host embryonic development. Host
500 eggs at an early stage of embryogenesis presumably lack an immediately functional immune
501 system (Strand and Pech 1995) and seem to rely on the upregulation of immune-related genes

502 as an inducible response triggered by parasitoid oviposition (Abdel-latif and Hilker 2008).
503 However, host eggs at a more advanced developmental stage could acquire an operating
504 immune system through the appearance of immune cells involved in encapsulation and
505 melanisation of parasitoid eggs (Nardi 2004). Thus, the nature and possibly the efficiency of
506 the immune barrier mounted by the eggs against parasitic infection could depend on the
507 modulation of the egg development by temperatures encountered prior to parasitism.

508 In summary, our study lends support to the hypothesis that temperatures experienced
509 by a host parental generation affect the outcomes of a host-parasitoid interaction through
510 parental thermal effects, regardless of the temperature at which the host-parasitoid complex
511 was incubated (i.e. direct thermal effects). Transgenerational plasticity should play a major
512 role in ensuring the local persistence of species in face of global warming (Sgrò et al. 2016;
513 Donelson et al. 2018). However, species do not respond in isolation to climate disturbance, as
514 they tightly depend on each other through ecological linkages, particularly in cases of obligate
515 associations such as host-parasitoid trophic relationships (Jeffs and Lewis 2013). In this
516 regard, our study is the first to demonstrate that parental thermal effects might influence
517 trophic dynamics beyond effects on individual performance. However, to what extent parental
518 thermal effects persist across ontogenetic stages to affect trophic interactions involving larvae
519 – such as host-parasitoid systems including larval hosts and larval parasitoids, or other kinds
520 of trophic relationships (e.g. host-parasite, insect-plant) – remains to be explored, and could
521 be the focus of further investigations.

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532 **Compliance with ethical standards**

533 Conflict of interest: The authors declare they have no conflict of interest.

534 Ethical approval: All applicable institutional and/or national guidelines for the care and use of
535 animals were followed.

536 Data availability: Data will be made publicly available at Dryad once the paper accepted.

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688

Figure legends

Figure 1 The two thermal regimes included in this study: ‘current regime’ (blue lines) and ‘future regime’ (red lines). Daily cycles were divided into six temperature segments of 4h each. The current regime describes the thermal conditions recorded in Burgundy (Dijon) during summer (15-July to 15-Aug) over recent period (1995-2014). The future regime forecasts the summer thermal conditions that might be observed in Burgundy by the end of the century (2081-2100), positing massive and growing future emissions of greenhouse gas. This regime is based on the predictions given by six combinations of climate models.

Figure 2 Effects of the combination of host parental temperature (thermal regime within which the host *L. botrana* developed and laid host eggs) and host offspring temperature (thermal regime within which host eggs were incubated following parasitism) on the percentage of parasitised host eggs from which a parasitoid emerged (apparent emergence success of the parasitoid). Represented values correspond to means \pm 95% confidence intervals. Asterisks highlight significant differences (** $P < 0.01$, * $P < 0.05$, n.s. non-significant) and numbers refer to sample sizes.

Figure 3 Effects of the combination of host parental temperature (thermal regime within which the host *L. botrana* developed and laid host eggs) and host offspring temperature (thermal regime within which host eggs were incubated following parasitism) on the length of left hind tibia (body size) of emerged parasitoid daughters. Represented values correspond to means \pm 95% confidence intervals. Asterisks highlight significant differences (** $P < 0.01$, * $P < 0.05$, n.s. non-significant) and numbers refer to sample sizes.

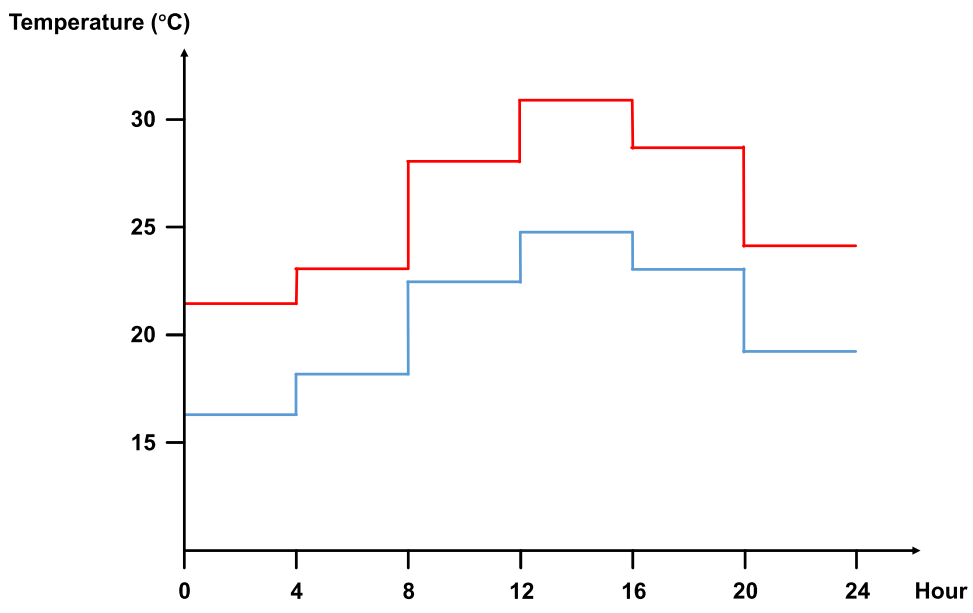


Figure 1

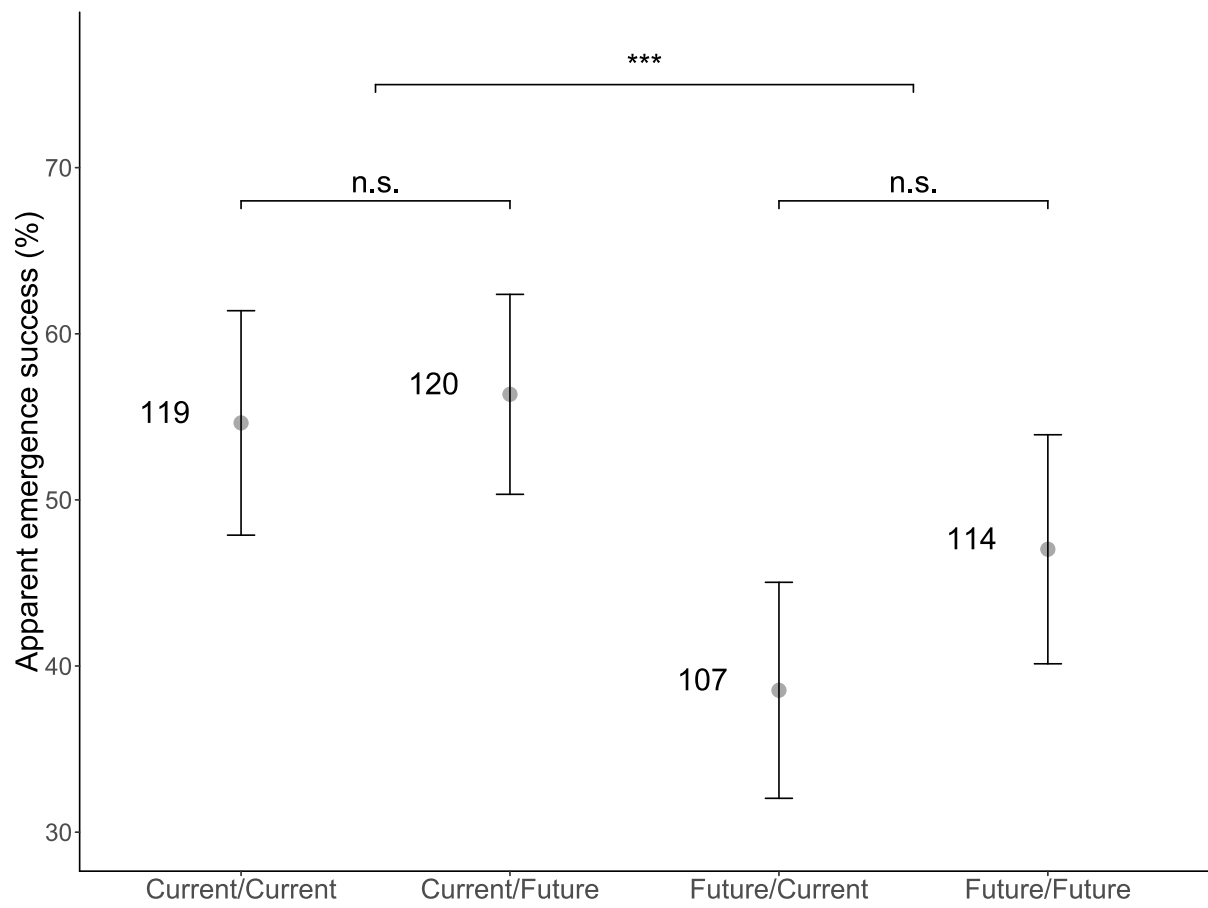


Figure 2

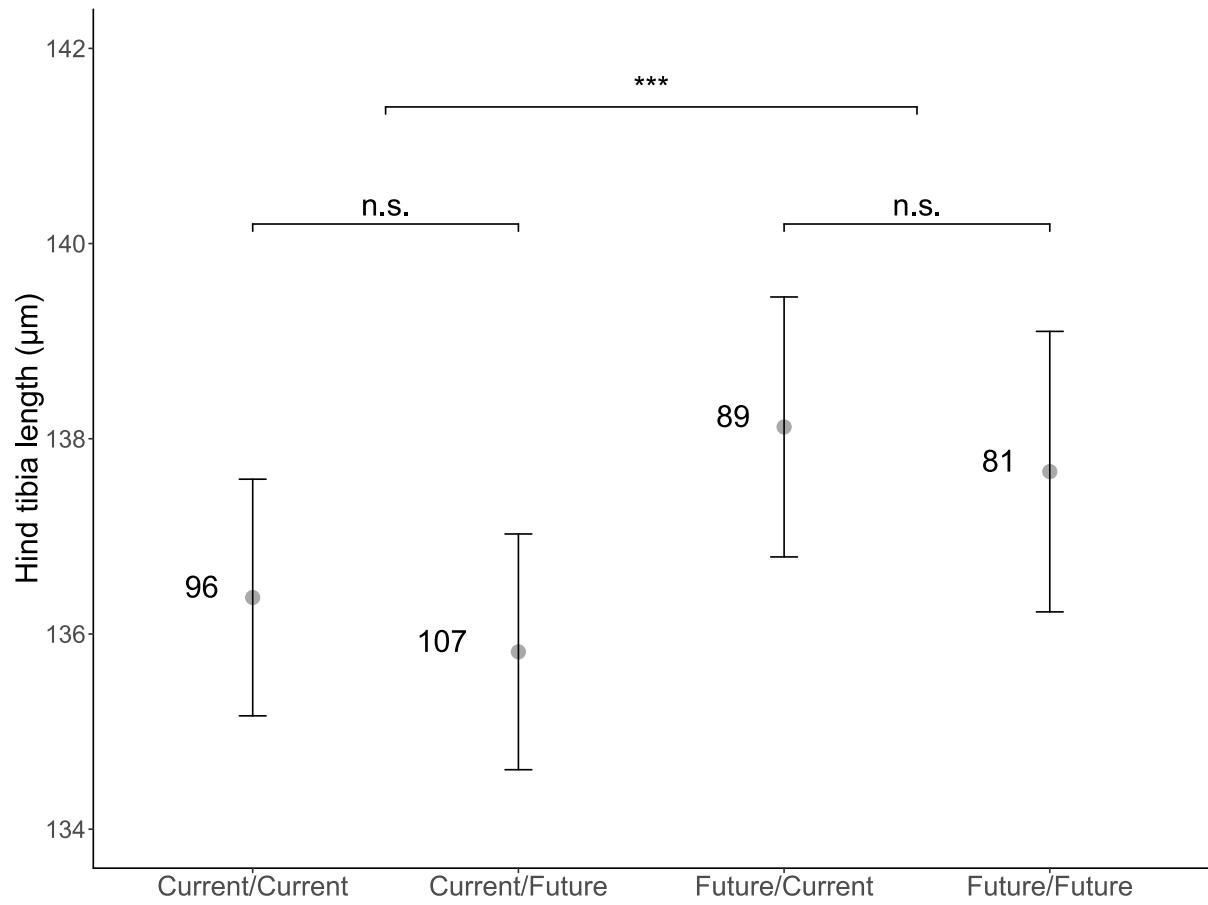


Figure 3