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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

# Where you come from matters: temperature influences host–parasitoid interaction through parental effects

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## Abstract

Temperature alters host suitability for parasitoid development through direct and indirect pathways. Direct effects depend on ambient temperatures experienced by a single host individual during its lifetime. Indirect effects (or parental effects) occur when thermal conditions met by a host parental generation affect the way its offspring will interact with parasitoids. Using the complex involving eggs of the moth *Lobesia botrana* as hosts for the parasitoid *Trichogramma cacoeciae*, we developed an experimental design to disentangle the effects of (1) host parental temperature (temperature at which the host parental generation developed and laid host eggs) and (2) host offspring temperature (temperature at which host eggs were incubated following parasitism, i.e. direct thermal effects) on this interaction. The host parental generation was impacted by temperature experienced during its development: *L. botrana* females exposed to warmer conditions displayed a lower pupal mass but laid more host eggs over a 12-h period. Host parental temperature also affected the outcomes of the interaction. *Trichogramma cacoeciae* exhibited lower emergence rates but higher hind tibia length on emergence from eggs laid under warm conditions, even if they were themselves exposed to cooler temperatures. Such indirect thermal effects might arise from a low nutritional quality and/or a high immunity of host eggs laid in warm conditions. By contrast with host parental temperature, offspring temperature (direct thermal effects) did not significantly affect the outcomes of the interaction. This work emphasises the importance of accounting for parental thermal effects to predict the future of trophic dynamics under global warming scenarios.

**Keywords** Host eggs · Oophagous parasitoid · Parental effects · Temperature · Trophic dynamics

## Introduction

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

At the individual level, host suitability—defined as the accordance between a parasitoid's requirements to complete

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its development and a host's physiological, morphological and behavioural features (see Vinson and Iwantsch 1980)—is affected by temperature in several ways. First, temperature determines the amounts of several energetic compounds in the host, among them proteins, lipids, glycogen and free carbohydrates (Geister et al. 2009; Kishani Farahani et al. 2016; Iltis et al. 2019). Since a host is the sole source of nutrients for an immature parasitoid, this thermal variation in host nutritional quality in turn crucially impacts the development of parasitoids and several aspects of their fitness (e.g. longevity, fecundity) (Kishani Farahani et al. 2016). In addition, most parasitoids lack adult lipogenesis and are thus unable to synthesise fat reserves for survival and egg production, which strengthens their dependence on the nutritional resources obtained from their host during development (Visser and Ellers 2008). Second, temperature alters host immune functions (relying, mostly, on encapsulation and melanisation processes) that are aimed at killing parasitoids during their immature stages (Seehausen et al. 2017; Iltis et al. 2018, 2019). In this regard, high temperatures may in some cases stimulate the expression of host immune-related genes with negative consequences for parasitoid survival until emergence. This is especially true if warming concomitantly decreases the ability of the parasitoid to suppress the host immune system, for instance by inducing downregulation of polydnavirus transcription (Seehausen et al. 2017). In other cases, warmer conditions can elicit extensive weakening of the host's immunity, thereby enhancing host susceptibility to a parasitic attack (Iltis et al. 2018).

Thermal modulation of host suitability can arise from direct effects, whereby ambient temperatures temporarily or permanently experienced by a single host individual during its lifetime might affect the host's immunity (Iltis et al. 2018) and the resulting interaction with parasitoid eggs or larvae (Seehausen et al. 2017). These direct thermal effects are known to influence the outcomes of host–parasitoid interactions (e.g. host infestation rates, parasitoid development time and body mass on emergence, parasitoid emergence rates) (Bahar et al. 2012; Delava et al. 2016; Schreven et al. 2017). Besides direct effects, temperature can also indirectly shape host suitability through parental effects (Sgrò et al. 2016; Woestmann and Saastamoinen 2016; Donelson et al. 2018). Parental effects occur when conditions encountered by members of the parental generation influence the expression of a phenotype in the subsequent generation (Sgrò et al. 2016; Donelson et al. 2018). Indeed, environmental conditions experienced by a host parental generation—such as temperature, host plant nutritional quality or immune challenge—have demonstrated influence on a large variety of offspring traits related to their suitability for parasitoids (e.g. size, mass, amounts of energetic metabolites, immunity) (Geister et al. 2009; Janowitz and Fischer 2011; Eggert et al. 2015; Trauer-Kizilelma and Hilker 2015; Moreau et al. 2016). Beyond these effects at the individual level, to what extent such parental thermal effects might drive the dynamics of the host–parasitoid interaction remains unexplored, as does the relative importance of direct and parental effects for the outcomes of the interaction. From a global warming perspective, such a knowledge gap might limit our ability to forecast the impacts of rising temperatures for the future of host–parasitoid interactions. Indeed, this climatic disturbance will persist across generations and is, therefore, expected to affect species and interspecific relationships through direct and parental effects in a cumulative way (Sgrò et al. 2016; Donelson et al. 2018).

Here we investigated the consequences of direct and parental thermal effects for an interaction between host eggs and oophagous parasitoids. We developed an experimental design that allowed us to separate the relative impacts of (1) parental thermal effects, through differences in temperatures experienced by a host parental generation from larval development to egg laying (i.e. parental temperature), and (2) direct thermal effects, through differences in ambient temperatures at which host eggs were incubated following parasitism (i.e. offspring temperature). As an experimental imitation of global warming, we built two realistic, fluctuating regimes reflecting current and future thermal conditions in our focal area (Eastern France). We focused on the host–parasitoid complex constituted by eggs of one of the most harmful vineyard pests in the Palearctic region: the European grapevine moth *Lobesia botrana* (Lepidoptera: Tortricidae), as host for the oophagous parasitoid *Trichogramma cacoeciae* (Hymenoptera: Trichogrammatidae)—a candidate for the biological control of *L. botrana* populations (Pizzol et al. 2012; Thiéry et al. 2018). Considering that parental effects are known to be a major source of variation in offspring quality traits, particularly in the early life stages like eggs (reviewed by Woestmann and Saastamoinen 2016), we hypothesised that host egg suitability for parasitoids should be influenced by parental temperature to a greater extent than offspring temperature. Specifically, we expected lower parasitoid emergence rates from host eggs originating from warm conditions, as a consequence of a low suitability of these eggs. Indeed, higher temperatures experienced by *L. botrana* parents during development should shorten the duration of their larval stage and reduce their food intake—congruently with previous works conducted on this species (Iltis et al. 2018, 2019). Lower larval food intake should, in turn, negatively affect parental investment in egg quality, because *L. botrana* adults are non-feeding and their reproductive output, along with egg quality traits, tightly hinges on resources accumulated as caterpillars (Moreau et al. 2006, 2016).

## Materials and methods

### Thermal regimes

Thermal regimes used in this study reflected realistic current and future climatic conditions in Burgundy, Eastern France (Longvic–Dijon weather station, 47.27° N; 5.09° E; altitude = 219 m) (http://www.meteofrance.com). These regimes focused on the summer period, extending from 15 July to 15 Aug, because this date range is associated with high levels of activity for the host and the parasitoid in Eastern France, as shown by concomitant peaks of adult moth emergence and number of *L. botrana* eggs parasitised by *T. cacoeciae* (Barnay et al. 2001). The thermal regime designed to reflect conditions currently found in Burgundy, called the 'current regime', was generated according to the 20-year recordings of in situ hourly temperatures (1995–2014 period). The current regime was compared with the 'future regime', describing the summer thermal conditions (15 July to 15 Aug) likely to occur in Burgundy by the end of this century (2081–2100 period). To design the future regime, we combined six General Circulation Models and six Regional Climate Models, selecting the most pessimistic greenhouse gas emissions scenario: RCP 8.5 (see Beaumont et al. 2008; Harris et al. 2014 for an in-depth description of the use of climate models in ecology). Data are available on the Drias portal (http://www.drias-climat.fr). Daily cycles constituting the current regime and the future regime were composed of six temperature segments, each lasting 4 h and calculated (1) as the mean segment over the 30 days (15 July to 15 Aug) and the 20 years of in situ data for the current regime, or (2) as the mean segment over the six simulations run for the future regime (Fig. 1). Compared with the current regime, the future regime shows an increase in mean temperature of 5.3 °C (25.8 °C for the future regime versus 20.5 °C for the current regime) and an increase in thermal range (the difference between maximum and minimum daily temperatures) of 0.6 °C (8.5 °C for the future regime versus 9.1 °C for the current regime) (Fig. 1).

### Moth maintenance and host egg production

All *L. botrana* individuals used in this experiment belonged to a laboratory, diapause-free population maintained at the French National Institute for Agricultural Research (INRAe, Villenave d'Ornon, France). This large stock was comprised of several thousand adults per week, and was regularly supplemented with wild individuals collected from nearby vineyards (cultivar Sémillon) to preserve genetic diversity (Vogelweith et al. 2014). Moths were reared in a large cage at 20 ± 0.5 °C, 60 ± 5% relative humidity, under a light cycle of L17: D6 with 1 h of dusk. Luminosity reached 650 lx during photophase and fell to 100 lx at dusk. Two bands of waxed paper (5 × 10 cm) were hung inside the cage for egg laying. Every 3 days, these oviposition supports were renewed and transferred into plastic boxes covered by a moist piece of paper towel to protect eggs from desiccation until hatching.

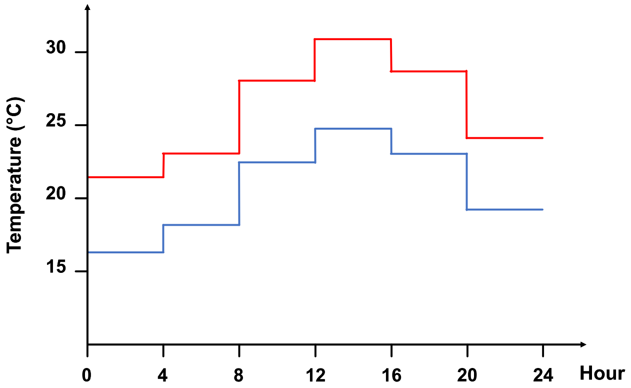


**Fig. 1** The two thermal regimes included in this study: 'current regime' (blue lines) and 'future regime' (red lines). Daily cycles were divided into six temperature segments of 4 h each. The current regime describes the thermal conditions recorded in Burgundy (Dijon) during summer (15 July to 15 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 (colour figure online)

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

Within 3 or 4 days following pupation, chrysalises were carefully extracted from their silk cocoons with fine forceps and weighed to the nearest 0.1 mg with a balance (Pioneer PA214C, OHAUS, Greifensee, Switzerland). Chrysalises were subsequently isolated in clean glass tubes (70 × 9 mm diameter) closed by cotton plugs before being returned to their rearing thermal regime. They were checked daily for imaginal emergence. Moths were sexed upon emergence and were supplied daily with water ad libitum through soaked cotton plugs. At dusk, one 24–48-h virgin female was randomly placed for one night in a clean glass mating tube (100 × 15 mm diameter) with one 24–72-h virgin male originating from the same thermal regime. We restricted the age ranges of sexual partners, and only used virgin individuals because age and mating history are known to affect several traits in this species that influence egg quality (e.g. spermatophore volume, number of eggs laid, egg size) (Moreau et al. 2006; Muller et al. 2016). Males were removed the following morning to avoid multiple mating, and were no longer used for the experiments. Females were allowed to oviposit freely in their mating tube closed by a daily soaked cotton plug as a water supply. Mating and egg laying occurred within the thermal regime from which the pair originated.

The number of eggs laid by females was recorded every morning via visual inspection. Only mating tubes containing at least 30 eggs laid within 12 h (i.e. during one single night) were used for parasitism tests. A lower limit of 30 eggs was set to ensure that host egg number was not a limiting factor for the parasitoid during parasitism tests and to reduce variation in host egg density. For the purpose of standardisation, host egg age was restricted to 12 h or less because it might affect the outcomes of interactions with *T. cacoeciae* (e.g. number of eggs parasitised, parasitoid emergence rates) (Moreno et al. 2009; Pizzol et al. 2012). In addition, using such freshly laid host eggs is appropriate to investigate parental thermal effects, because these eggs have been exposed to environmental conditions for a very short duration before parasitism tests. Hence, variation in their suitability for parasitoids should be importantly driven by parental effects. This selection procedure retained 512 mating tubes out of a total of 734 tubes, which represents 98% of the 523 tubes with eggs found inside. This high percentage can be explained by the fact that *L. botrana* females usually lay the largest amounts of eggs at the beginning of their oviposition period, especially during the first night succeeding to mating (Moreau et al. 2016). *Lobesia botrana* females were then removed and the tubes of freshly laid eggs were photographed using a stereomicroscope at 8x magnification (Stemi 508, Zeiss, Göttingen, Germany). For each tube, one picture including five eggs on the same horizontal plane was taken to reliably estimate mean egg size (surface area) within the clutch (Moreau et al. 2016). We then randomly selected 123 pictures ($n = 57$ for the current regime, $n = 66$ for the future regime) and assessed the surface area of five eggs for each picture (estimated as an elliptic surface, $S = \pi \times a \times b$ in mm$^2$, where $a$ and $b$ are the ellipse semi-axes) with a precision of ± 0.001 mm$^2$. The photographic data were analysed with ImageJ software (version 1.51j8, National Institutes of Health, Bethesda, USA).

## Parasitoid maintenance and parasitism procedure

Experimental lines of *T. cacoeciae* involved in this study were all thelytokous and, therefore, only constituted by females. We ran one single experiment using parasitoids belonging to four different strains to generalise our conclusions about the thermal modulation of host egg suitability to a generic parasitoid pressure. Hence, parasitoid strain was included as a treatment (involving four levels) in the experiment. These four strains were derived from field populations collected in June 2017 at four French localities: Aime (45.33° N; 6.39° E), Banyuls-sur-Mer (42.45° N; 3.09° E), Le Crouzet (44.38° N; 3.63° E) and Sophia Antipolis (43.61° N; 7.08° E). These sites were chosen because they are distant enough from each other to avoid any confounding genetic effect, given the relatively low dispersal abilities of *Trichogramma* species (Fournier and Boivin 2000). Wild populations were initially sampled on *Rosa* sp. and *Prunus* sp. with baits comprised of cards covered with ultraviolet-sterilised eggs of the Mediterranean flour moth *Ephestia kuehniella* (age < 5 days) as a substitute host. Parasitoids emerging from these baits were first identified as *T. cacoeciae* individuals based on molecular analyses involving PCR amplification of a microsatellite marker (Pizzol et al. 2005), and then used to establish laboratory colonies. Until the start of the experiments (i.e. over 9 months), they were reared in plastic culture tubes plugged with cotton (10 × 1 cm diameter) under controlled common conditions (23.1 ± 0.5 °C, 60 ± 5% relative humidity, photophase of L18: D6, 650 lx). One piece of cardboard (1 × 6 cm) covered with ultraviolet-sterilised eggs of *E. kuehniella* (age < 5 days) was provided for parasitoid multiplication. After 4 days of exposure, the cardboard pieces were transferred to clean rearing tubes for parasitoid emergence. A droplet of honey was deposited into each rearing tube to feed emerged adults. Prior to our parasitism tests, individuals originating from the four collected strains were genetically identified to ensure that no contamination had occurred within each strain (Pizzol et al. 2005).

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

Each day, host egg tubes originating from each thermal regime were equally distributed among *T. cacoeciae* strains to ensure temporal randomisation. Parasitism tests were conducted under a common temperature of 23.1 °C (± 0.5 °C, 60 ± 5% relative humidity, 650 lx) to standardise the effect of ambient temperature on parasitoid behaviour, and also because 23.1 °C is the rearing temperature of parasitoids as well as the intermediate temperature from which host egg tubes originated: between the mean temperatures of the current regime (20.5 °C) and the future regime (25.8 °C). Parasitoid mothers were introduced inside host egg tubes at 9:00 a.m. and delicately removed with a fine brush at 3:00 p.m. Exposure duration was set at 6 h to ensure parasitism was not limited by the number of host eggs available and to avoid superparasitism. Indeed, more than 6 h should be needed for one *T. cacoeciae* female to parasitise at least 30 eggs of *L. botrana* under the controlled conditions at which parasitism occurred (Moreno et al. 2009). No food or water was supplied to parasitoid mothers during the experiments. After their removal from host egg tubes, *T. cacoeciae* mothers were placed individually in clean Eppendorf tubes until their death. Using a stereomicroscope at 100 × magnification (Stemi 508, Zeiss, Göttingen, Germany), we then measured the length of their left hind tibia as an estimation of body size (precision ± 0.1 µm)—following the standard procedure described by Olson and Andow (1998). These measurements were taken to control for an effect of the body size of parasitoid mothers on the number of host eggs parasitised, the percentage of parasitoid emergence, and the hind tibia length of parasitoid daughters that emerged from parasitised eggs. Out of an initial 512 tubes, 12 tubes were removed from the dataset because the preservation state of the *T. cacoeciae* mothers used to parasitise these tubes did not permit reliable measurements of hind tibia length.

## Host egg incubation and data acquisition

Once parasitoid mothers were removed, host egg tubes were randomly incubated in either the current or the future regime (i.e. independently of the thermal regime they came from). This resulted in four combinations of thermal regimes (current/current, current/future, future/current, future/future), each combination being defined by one 'parental temperature' (regime within which host development, reproduction and egg laying occurred) and one 'offspring temperature' (regime within which host eggs were incubated following exposure to parasitoids). Each day, tubes of parasitised eggs were equally distributed between the two offspring temperatures for temporal randomisation. Incubation lasted 28 days before tube inspection. This duration was sufficient to enable the complete development of the host (hatching of *L. botrana* larvae from unparasitised eggs) and the parasitoid (emergence of *T. cacoeciae* daughters from parasitised eggs) until death (Moreau et al. 2009; Moreno et al. 2009). No cannibalism of parasitised eggs by newly hatched *L. botrana* caterpillars was observed. No parasitoid diapause was expected to occur under the environmental conditions—especially temperature and photoperiod—encountered by *T. cacoeciae* mothers and daughters during parasitism tests and post-parasitism incubation, respectively (Pizzol and Pintureau 2008).

After the incubation period, tubes were analysed under a stereomicroscope (Stemi 508, Zeiss, Göttingen, Germany) to record (1) the 'first-day fecundity' of the host (total number of eggs laid by one *L. botrana* female during one single night), (2) the 'apparent parasitism success' of the parasitoid mother (number of host eggs parasitised) and (3) the 'apparent emergence success' of parasitoid daughters (percentage of host eggs parasitised from which an adult *T. cacoeciae* successfully emerged) (Moreau et al. 2009). For the determination of apparent parasitism success, we considered an egg as parasitised when it turned from white to grey, given that such a change in colouration is widely acknowledged as a reliable indicator of parasitism by *Trichogramma* species (Hutchison et al. 1990) and because this criterion has been employed in previous studies that used *L. botrana* eggs as hosts for *Trichogramma* species (Moreau et al. 2009; Pizzol et al. 2012; Thiéry and Desneux 2018). Provided that blackening of the parasitised host eggs occurs at the time of parasitoid pupation (Hutchison et al. 1990), our metrics did not include cases where parasitoids died before the pupal stage and, therefore, provide information about the 'apparent' rather than the 'realised' parasitism of the host eggs. Apparent parasitism success was not expressed in percentages because host eggs were provided ad libitum to *T. cacoeciae* mothers during parasitism tests (Moreau et al. 2009). For the determination of apparent emergence success, we considered that the parasitoid daughter successfully emerged from the parasitised host egg when the blackened egg was found empty with an emergence hole on its surface. Hence, the difference between apparent parasitism success and apparent emergence success was that the former included all cases of apparent parasitism (all blackened eggs, with or without parasitoid emergence), whereas the latter only considered those that led to the emergence of the parasitoid daughter from the host egg (empty blackened eggs with an emergence hole on their surface). Sterile host clutches (28 tubes out of a total of 500 tubes) were discarded because they were laid by unmated *L. botrana* females and were, therefore, not subject to similar paternal effects as clutches resulting from successful mating. Host clutches were deemed sterile if no caterpillars emerged from the eggs. Tubes with no parasitised eggs found after exposure to a parasitoid mother ($n = 5$ for current/current, $n = 2$ for current/future, $n = 1$ for future/current, $n = 4$ for future/future) were conserved for statistical analysis focused on apparent parasitism success as no dead parasitoid mother had been observed after the 6 h of parasitism. Dead parasitoid daughters were carefully collected with a fine brush, and observed under a stereomicroscope at 100× magnification (Stemi 508, Zeiss, Göttingen, Germany) to measure the length of their left hind tibia with the same method used for mothers. As an estimation of body size, hind tibia length is positively correlated with a female's longevity and lifetime fecundity in *Trichogramma* species and can, therefore, be interpreted as a surrogate for individual performance (Doyon and Boivin 2005). The number of *T. cacoeciae* daughters extracted from each tube varied between zero and five, dependent on the number of daughters that had emerged from host eggs and their preservation state. Following the above selection procedure, 472 tubes were finally inspected ($n = 124$ for current/current, $n = 122$ for current/future, $n = 108$ for future/current, $n = 118$ for future/future), and hind tibia length measurements were taken from 826 parasitoid daughters collected from 373 tubes ($n = 96$ for current/current, $n = 107$ for current/future, $n = 89$ for future/current, $n = 81$ for future/future), equally distributed across the four parasitoid strains.

### Statistical analyses

This study was based on a 2 × 2 × 4 full-factorial design involving three factors: 'parental temperature' (two levels), 'offspring temperature' (two levels) and 'parasitoid strain' (four levels). The pupal mass of individuals of the *L. botrana* parental generation (i.e. parents which produced the host eggs) was studied with an analysis of variance (ANOVA) incorporating temperature experienced by this generation, sex and the interaction between these two explanatory variables. Egg surface area and first-day fecundity of the host (*L. botrana*) were analysed with statistical models that included parental temperature as an explanatory variable, and female and male pupal mass as two covariates. For host egg surface area, an analysis of covariance (ANCOVA) with mixed effects was performed to account for the random effect represented by the identity of each *L. botrana* female and male. The data for first-day fecundity of the host did not satisfy the assumption of homoscedasticity and were, therefore, compared between parental thermal regimes using a Generalised Linear Model (GLM)-negative binomial error with a log link function.

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

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

## Results

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

The pupal mass of individuals from the *L. botrana* parental generation was influenced by the interaction between rearing temperature and sex ($F_{1,940} = 9.11$, $P < 0.001$). In females, the pupal mass was negatively impacted by rearing temperature: individuals that developed in the future, warmer regime were significantly lighter than those originating from the current, cooler regime. Mean values of females' pupal mass were 13.6 mg for the current regime (95% confidence interval $CI_{95\%} = [13.4; 13.8]$, $n = 246$) and 13.1 mg for the future regime ($CI_{95\%} = [12.9; 13.3]$, $n = 226$). In males, the pupal mass was not significantly affected by rearing temperature. Mean values of males' pupal mass were 9.4 mg for the current regime ($CI_{95\%} = [9.3; 9.5]$, $n = 246$) and 9.3 mg for the future regime ($CI_{95\%} = [9.2; 9.5]$, $n = 226$). The surface area of *L. botrana* eggs was not significantly affected by parental temperature ($\chi^2_1 = 3.45$, $P = 0.06$). Eggs originating from the current regime had a mean surface area of 0.403 mm$^2$ ($CI_{95\%} = [0.399; 0.407]$, $n = 57$) and those originating from the future regime had a mean surface area of 0.411 mm$^2$ ($CI_{95\%} = [0.407; 0.415]$, $n = 66$). The first-day fecundity of *L. botrana* females was positively impacted by their rearing temperature ($\chi^2_1 = 36.4$, $P < 0.001$). Females reared in the future regime produced 19% more eggs within 12 h than females reared in the current regime. Mean values of first-day fecundity were 63 eggs for females reared in the current regime ($CI_{95\%} = [60; 65]$, $n = 246$) and 75 eggs for females which developed in the future regime ($CI_{95\%} = [71; 78]$, $n = 226$). Only first-day fecundity was affected by the covariates included in the models and this relationship was positive: it increased with female pupal mass ($\chi^2_1 = 6.31$, $P = 0.01$, slope $= 0.03$) and male pupal mass ($\chi^2_1 = 4.27$, $P = 0.04$, slope $= 0.03$).

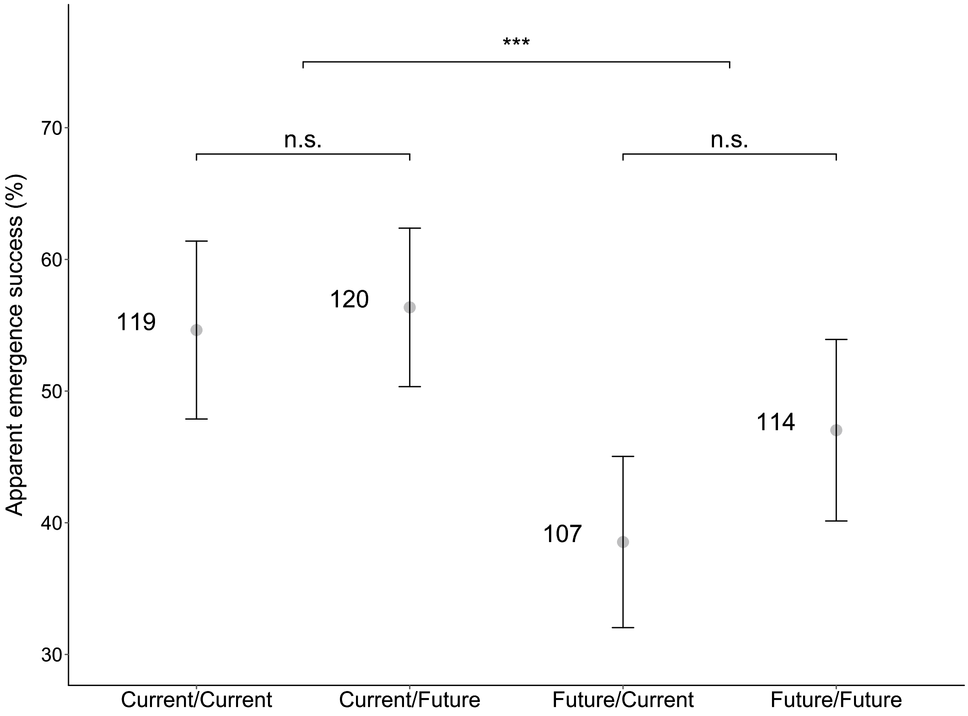
## Apparent parasitism success, apparent emergence success and hind tibia length of parasitoid daughters

Apparent parasitism success was not significantly affected by host parental temperature ($\chi^2_1 = 0.28$, $P = 0.60$). Among the three covariates included in the model (pupal mass of *L. botrana* female and male, hind tibia length of *T. cacoeciae* mother), apparent parasitism success was only positively influenced by the hind tibia length of *T. cacoeciae* mother ($\chi^2_1 = 9.80$, $P < 0.001$, slope $= 0.01$): the largest mothers parasitised significantly more eggs over 6 h than the smallest ones. As a random effect, parasitoid strain significantly affected apparent parasitism success ($\chi^2_1 = 17.8$, $P < 0.001$).

Apparent emergence success was modulated by host parental temperature ($\chi^2_1 = 9.44$, $P < 0.001$), but not by host offspring temperature ($\chi^2_1 = 0.39$, $P = 0.53$) or by the interaction between these two factors ($\chi^2_1 = 2.62$, $P = 0.11$). A lower percentage of parasitoid daughters emerged from host eggs originating from the future regime compared with host eggs coming from the current regime (Fig. 2). Among the three covariates included in the model (pupal mass of *L. botrana* female and male, hind tibia length of *T. cacoeciae* mother), apparent emergence success was only positively influenced by the pupal mass of *L. botrana* female ($\chi^2_1 = 40.0$, $P < 0.001$, slope $= 0.47$): the heavier the *L. botrana* female that laid the host eggs, the higher the apparent emergence success of parasitoid daughters from these eggs. As a random effect, parasitoid strain significantly affected apparent emergence success ($\chi^2_1 = 5.16$, $P = 0.02$).

The hind tibia length of *T. cacoeciae* daughters that emerged from parasitised *L. botrana* eggs was impacted by host parental temperature ($\chi^2_1 = 8.55$, $P < 0.001$), but not by host offspring temperature ($\chi^2_1 = 0.40$, $P = 0.53$) or by the interaction between these two factors ($\chi^2_1 = 0.02$, $P = 0.89$). Larger parasitoid daughters emerged from host eggs originating from the future regime in comparison with host eggs laid in the current regime (Fig. 3). None of the three covariates included in the model (pupal mass of *L. botrana* female

**Fig. 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 ± 95% confidence intervals. Asterisks highlight significant differences (****P* < 0.001, ***P* < 0.01, **P* < 0.05, *n.s.* non-significant) and numbers refer to sample sizes



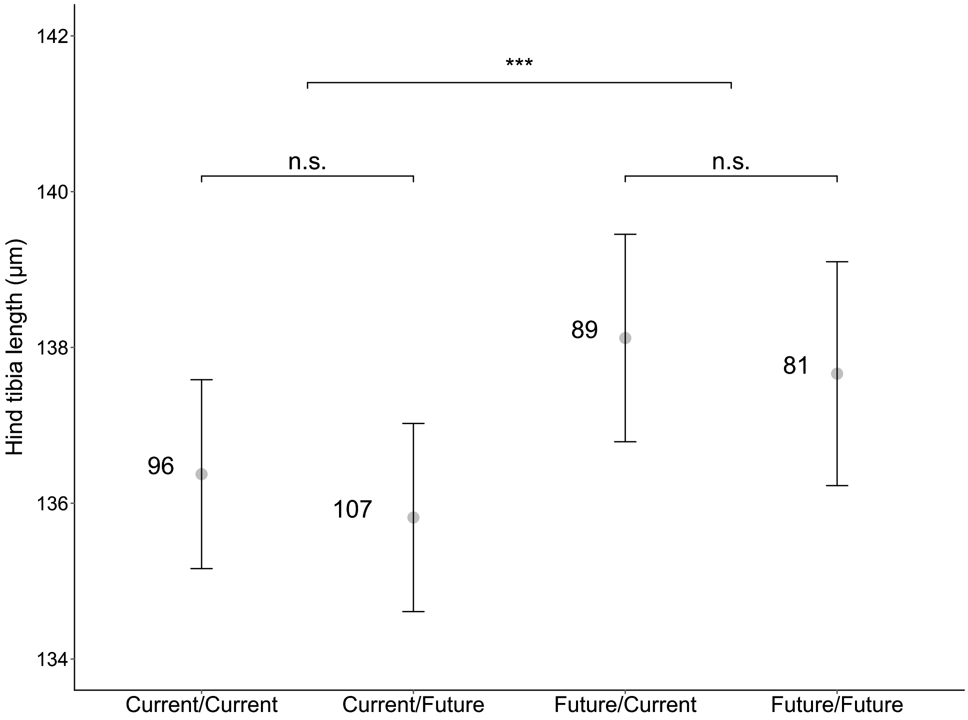


**Fig. 3** Effects of the combination of host parental temperature (thermal regime within which the host *L. botrana* developed and laid host eggs) and host offspring temperature (thermal regime within which host eggs were incubated following parasitism) on the length of left hind tibia (body size) of emerged parasitoid daughters. Represented values correspond to means ± 95% confidence intervals. Asterisks highlight significant differences (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, *n.s.* non-significant) and numbers refer to sample sizes

and male, hind tibia length of *T. cacoeciae* mother) significantly affected the hind tibia length of parasitoid daughters. As a random effect, parasitoid strain significantly affected the hind tibia length of *T. cacoeciae* daughters ($\chi_1^2 = 61.7$, $P < 0.001$).

## Discussion

The purpose of this work was to assess the relative importance of parental and direct thermal effects in determining the outcomes of the interaction between eggs of the European grapevine moth *L. botrana* and the oophagous parasitoid *T. cacoeciae*. Our most striking result was the considerable effect of host parental temperature, that is, temperature experienced by host parental generation, on parasitoid apparent emergence success and hind tibia length on emergence. *Trichogramma cacoeciae* experienced lower emergence rates, but displayed higher hind tibia length on emergence, from host eggs originating from warm conditions (laid in the future regime) compared with eggs produced under cold conditions (laid in the current regime). In contrast with parental effects, direct thermal effects did not perceptibly modulate the outcomes of the host–parasitoid interaction. These findings match our initial expectation that the interaction between freshly laid host eggs and an oophagous parasitoid should be primarily determined by indirect, parental effects. Our results emphasise the importance of accounting for such parental thermal effects with the aim to predict the future of trophic dynamics under global warming scenario. Interestingly, the modulation exerted by host parental temperature on the outcomes of the interaction was consistent over the four parasitoid strains included in the study, even if each strain displayed its own characteristics in terms of performance when parasitising *L. botrana* eggs (e.g. apparent parasitism and emergence success, hind tibia length of emerged parasitoid daughters). From an evolutionary perspective, this raises the question as to whether natural populations of *T. cacoeciae* experiencing a set of contrasting ecological conditions might respond in different ways to a rise in mean temperature, that is, whether parasitoid thermal adaptation may shape the evolutionary trajectory of the interaction in the context of climate change.

Two non-mutually exclusive hypotheses might account for the effects of host parental temperature on parasitoid apparent emergence success and hind tibia length on emergence. First, parasitoids are constrained by the limited amount of food contained in their single host, and might fail to complete their development if host eggs laid in the future regime provide an insufficient quantity or quality of nutritional resources (i.e. resource-based hypothesis) (Kishani Farahani et al. 2016). Whether this hypothesis is fully relevant to explain our results remains questionable, provided that we did not observe any effect of parental temperature on *L. botrana* egg surface area as a surrogate of host nutritional quality for the parasitoid. In addition, the resource-based hypothesis poorly explains differences regarding the hind tibia length of emerged parasitoids observed. Indeed, host eggs of low nutritional quality should produce smaller adult parasitoids (Kishani Farahani et al. 2016), while we instead observed a higher hind tibia length of *T. cacoeciae* daughters emerging from host eggs produced in warm conditions. As a next step, biochemical assays of the quantities of several energetic metabolites eggs are provisioned with (e.g. proteins, lipids, glycogen, soluble carbohydrates) would be needed to assess more thoroughly the plausibility of this resource-based explanatory hypothesis (Geister et al. 2009).

A second hypothesis, positing differences in egg immunity (i.e. immunity-based hypothesis), can be formulated to explain the importance of host parental temperature for the host–parasitoid relationship. There is a growing body of evidence showing that eggs of lepidopteran hosts are able to mount an immune response to fend off a myriad of invaders, and the efficiency of this endogenous immune barrier is an integral component of their suitability for parasitoids (Abdel-latief and Hilker 2008; Trauer-Kizilelma and Hilker 2015). Host immune defences against parasitism are modulated by parental experience (Triggs and Knell 2012; Trauer-Kizilelma and Hilker 2015), including parental exposure to a brief thermal stress (cold snap or heat spike) (Eggert et al. 2015). In our study, *L. botrana* parents might have faced daily stressful thermal conditions in the future regime—which included temperatures up to 30.5 °C for 4 h—while a decline in the performance of caterpillars of this species has been pointed out at temperatures exceeding 25 °C (Iltis et al. 2018, 2019). Such temporarily stressful temperatures met by the host parental generation might have promoted egg immunological defences, and could be potentially responsible for the negative effects of host parental temperature on parasitoid apparent emergence success. With respect to this immunity-based hypothesis, the proximate cause of the positive effect of host parental temperature on *T. cacoeciae* hind tibia length remains unknown at this stage. The reason could, for instance, involve a selective pressure exerted by the high immunity of eggs laid in warm conditions acting in favour of the largest parasitoid individuals. Such a phenomenon might occur if the efficiency of host encapsulation and melanisation processes decreases as the size of the foreign body to be encapsulated increases (Pomfret and Knell 2006). Hence, the largest parasitoid individuals could be more prone to survive the immune reaction expressed by their host. Considering that host egg immunity should operate during the first steps of the parasitism process, that is, acting on the early-life stages of *Trichogramma* parasitoids (Abdel-latief and Hilker 2008; Trauer-Kizilelma and Hilker 2015), one way to test the immunity-based hypothesis may consist of investigating the effects of host parental temperature on the early mortality of the parasitoid, before the blackening of the parasitised host eggs occurring at the time of parasitoid pupation (Hutchison et al. 1990). If this hypothesis is valid, a higher percentage of dead parasitoid eggs and larvae should be expected from host eggs originating from warm conditions compared with host eggs laid in cold conditions.

By contrast with parental thermal effects, direct thermal effects did not contribute to modulate the outcomes of the host–parasitoid interaction measured. In our study, host eggs were exposed to parasitoids shortly after being laid by *L. botrana* females (within 12 h). Hence, these freshly laid eggs experienced the direct thermal effects occurring before parasitism for a very short duration, which could mitigate the importance of these direct thermal effects in influencing egg suitability for the parasitoid. It would be worth investigating whether the absence of direct thermal effects would persist using host eggs older than 12 h. This is especially relevant considering that temperature primarily mediates embryonic development in insects (Howe 1967), and that the egg developmental stage in turn impacts most egg traits related to their susceptibility to *Trichogramma* parasitoids. For instance, the egg nutritional resources are progressively consumed for embryonic growth in a temperature-dependent manner (Geister et al. 2009); hence, direct thermal effects acting prior to parasitism may influence the amounts of reserves available for parasitoid development. Furthermore, in lepidopteran host eggs, the mechanisms underlying the host immune reaction to parasitoid attack could differ depending on the stage of host embryonic development. Host eggs at an early stage of embryogenesis presumably lack an immediately functional immune system (Strand and Pech 1995) and seem to rely on the upregulation of immune-related genes as an inducible response triggered by parasitoid oviposition (Abdel-latief and Hilker 2008). However, host eggs at a more advanced developmental stage could acquire an operating immune system through the appearance of immune cells involved in the encapsulation and melanisation of parasitoid eggs (Nardi 2004). Thus, the nature and possibly the efficiency of the immune barrier mounted by the eggs against parasitic infection could depend on the modulation of the egg development by temperatures encountered prior to parasitism.

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

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**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.

## Compliance with ethical standards

**Conflict of interest** The authors declare they have no conflict of interest.

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

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