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Thermal "red flags": impact of global warming and fungicide exposure on mate selection and reproductive behaviour of *Lobesia botrana*

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Abstract

While climate change and pesticide use expose insect pests to multiple stressors, their combined effects remain poorly studied. Rising temperatures can accelerate insect life cycles and alter reproductive behaviours, while pesticides can impair physiological functions, reproduction, and survival. Understanding how global warming and pesticide exposure interact is crucial for predicting pest population dynamics and their impact on agroecosystems. As mating behaviour, including mate choice, plays a fundamental role in population growth, studying how these combined environmental stressors influence reproduction is critical. This study investigated how Bordeaux mixture fungicide affects the development, mating behaviour of *Lobesia botrana* under current (2002–2021) and projected (2081–2100) climatic scenarios. Larvae were reared with two fungicide concentrations and under two climatic conditions. Larval mortality, development time, and adult longevity were monitored. Mating behaviour was assessed using no-choice and choice experiments, measuring pre-mating latency, mating success and duration, fecundity and fertility. Key life parameters (R_0, T, D_t, r_m, and λ) were estimated to investigate population dynamics. Results show that fungicide exposure negatively affected the development and survival of larvae until emergence, but these effects were modulated by climatic conditions. While Bordeaux mixture exposure prolonged development time, future climatic conditions shortened development time compared to current conditions. Choice experiments revealed that under future conditions, moths preferred unexposed partners, whereas no preference was observed under current conditions. These findings emphasize the importance of integrating climate change effects into pesticide risk assessments, as their interactions may have unexpected consequences for pest populations and sustainable management strategies in agroecosystems.

Keywords Climate change · Fungicide · Pest management · *Lobesia botrana* · Mate choice · Reproductive behaviour · Population dynamics

Introduction

Climate change and pesticide use are among the most significant drivers impacting the sustainability of agroecosystems (Fuhrer 2003; Agovino et al. 2019; Dhuldhaj et al. 2023; Subedi et al. 2023). Pesticides are extensively used in pest management strategies to protect crops from plant pathogens and herbivorous insects (Popp et al. 2013). However, pesticides can induce sublethal and lethal effects on non-target organisms (Desneux et al. 2007). Moreover, climate change is expected to exacerbate the spread of insect pests in new regions and increase the voltinism (i.e. number of generations per year) of pest populations (Diffenbaugh et al. 2008; Andrew and Hill 2017). In addition, the interaction between temperature and pesticide exposure may lead to synergistic or antagonistic effects on insect physiology, thereby

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influencing pest population growth (Boina et al. 2009; Ricupero et al. 2020; Iltis et al. 2022; Perrin et al. 2022; Kenna et al. 2023). Climate change alters insect sensitivity to pesticides, as temperature influences key physiological processes such as the absorption, distribution, metabolism, and excretion of pesticides (Holmstrup et al. 2010; Hooper et al. 2013). Conversely, pesticide exposure increases insect sensitivity to climate-related stressors, such as elevated temperatures and extreme weather events (Hooper et al. 2013). Consequently, the interplay between climate change and pesticide use may influence insect thermal tolerance, increase insect sensitivity to pesticide toxicity, or potentially enhance the development of pesticide resistance (Matzrafi 2018). As a result, climate change and pesticide applications can significantly alter pest populations and affect agroecosystems' equilibrium (Hooper et al. 2013; Delnat et al. 2019).

Examining life-history traits (e.g., mortality rates, development times, body conditions), and behaviours (e.g., dispersion, competition, reproduction) provides a foundational framework for predicting changes in pest population dynamics (Sutherland 1996; Nylin 2001; Smallegange and Ens 2018). Reproductive behaviours, encompassing precopulatory (e.g., mate recognition, courtship displays, and mate choice) (Bonduriansky 2001; Thomas 2011; Borrero-Echeverry et al. 2018; Baker et al. 2019; Mitoyen et al. 2019) and copulatory (e.g., body positioning, sperm transfer, and nutrient delivery such as nuptial gifts) behaviours, are particularly important as they directly influence mating success and offspring production (Vahed 1998; Milonas et al. 2011; Muller et al. 2015, 2016c; Friesen et al. 2016; Tong et al. 2017; Henneken and Jones 2017; Camacho-García et al. 2018). Among these reproductive behaviours, mate selection is of fundamental importance, as it not only directly impacts offspring fitness but also influences the genetic diversity of a population, which affects the survival and adaptation of future generations (Pilakouta and Ålund 2021). However, environmental stressors such as pesticide exposure and temperature can disrupt these reproductive processes. Pesticide exposure can impair key reproductive behaviours, such as mate recognition or courtship displays, thereby reducing reproductive performance (Müller et al. 2017; Tappert et al. 2017; Conrad et al. 2017; Boff et al. 2022). Similarly, many studies reported an influence of temperature on sexual selection, by affecting a wide range of traits such as courtship intensity, mate choice, and reproductive success (Conrad et al. 2017; Macchiano et al. 2019; García-Roa et al. 2020; Enos and Kozak 2021; Pilakouta and Baillet 2022). Yet, studies focused on the combined effects of temperature and pesticide exposure on reproductive behaviours remain scarce. Addressing this knowledge gap is crucial, as synergistic or antagonistic interactions between these stressors could significantly impact insect pests' reproductive performance and, consequently, disrupt pest population dynamics.

Moth species (e.g., Tortricidae family) are significant agricultural pests and serve as excellent models for studying reproductive behaviours (Brown 2021). These insects rely on various cues to assess partner quality, and their reproductive success is driven by a wide range of factors, including energy reserves accumulated during the larval stages, environmental conditions, the variety of host plant, and morphological traits that reflect individual quality (e.g., body size) (Roelofs and Brown 1982; Jiménez-Perez and Wang 2004; Muller et al. 2016c; Iltis et al. 2020). Understanding their reproductive biology is therefore critical for developing effective pest control strategies. Among these pests, the European grapevine moth *Lobesia botrana* is one of the most economically damaging species in viticulture (Benelli et al. 2023a, b; Thiéry et al. 2018). Larvae cause significant damage to grape production, and their recent spread to higher latitudes previously unaffected is a growing concern (Reineke and Thiéry 2016, 2004; Gutierrez et al. 2018). Reproductive behaviours of *L. botrana* include pre-copulatory actions, such as pheromone production by females, which allows males to detect and locate potential mates over long distances (Roelofs and Cardé 1973). In addition to pheromone-based signalling, *L. botrana* may also rely on visual and/or olfactory cues for mate selection (Muller et al. 2016a, c). Given its strong reliance on chemical signalling and other morphological cues, *L. botrana* is a valuable model for studying how external stressors modulate insect mating systems. Environmental pressures such as elevated temperatures and routine pesticide application can alter courtship behaviour, potentially compromising reproductive outcomes. Understanding how such factors influence the reproductive behaviours of *L. botrana* is therefore essential for improving pest control strategies and predicting population responses under changing environmental conditions.

Viticulture is an important socio-economical sector that faces the dual pressure of climate change and extensive pesticide applications (Patinha et al. 2018; van Leeuwen et al. 2024). Copper-based fungicides, such as the Bordeaux mixture, are widely used to manage fungal pathogens, like downy mildew *Plasmadora viticola* and powdery mildew *Eryphise necator*, which can significantly reduce grape yields (Gessler et al. 2011; Pertot et al. 2017). These fungicides are particularly prevalent in vineyards due to their authorization for use in both conventional and organic farming systems (European Commission 2018; ANSES 2022). While copper-based fungicides are used against fungal pathogens, numerous studies have reported unintended effects on non-target organisms in viticultural agroecosystems, including pests and their natural enemies (Pennington et al. 2018; Vogelweith and Thiéry 2018; Garinie et al. 2024; Nusillard et al. 2024b). These non-target effects are further influenced by temperature changes (Iltis et al. 2022; Nusillard et al. 2024a). For instance, global warming may increase the tolerance of *L. botrana* larvae to Bordeaux mixture (Iltis et al. 2022) and negatively impact natural enemies (Nusillard et al. 2024a), potentially altering management. Such interactions can compromise the success of biological control strategies and exacerbate *L. botrana* population growth under future climatic conditions (Pennington et al. 2018). In addition, Iltis et al. (2020) reported that under future climatic conditions, female *L. botrana* exhibited reduced mating success compared to current conditions. This finding highlights the need for a better understanding of how climate change impacts reproductive behaviours. However, despite their importance in shaping pest population dynamics trends, the combined effects of climate change and copper-based fungicides on the reproductive behaviours of *L. botrana* remain poorly understood. Investigating these interactions is essential to predict future pest population trends and to develop sustainable pest management strategies in viticultural agroecosystems facing a changing climate.

In this context, we investigated the effects of Bordeaux mixture on the reproductive behaviour, mate selection, and life-history traits of *L. botrana*, and examined how these effects are modulated by climate change (i.e., elevated temperatures and increased drought conditions). Specifically, the present study aimed to (i) evaluate the effects of fungicide exposure on development, including survival, time to emergence, pupal mass, and adult longevity; (ii) investigate the influence of projected future climatic conditions (2081–2100) on these developmental traits; (iii) assess reproductive behaviour and mate selection under different treatment conditions and measure the impacts of fungicide exposure on female fecundity and fertility; and (iv) estimate potential shifts in population dynamics by calculating key life table parameters.

Materials and methods

Insect rearing and fungicide exposure

Moths originated from a laboratory-reared population of diapause-free *L. botrana* maintained at the National Research Institute for Agriculture, Food and the Environment (INRAe, Villenave d'Ornon, France). Eggs were collected on waxed paper strips suspended inside moth cages. Strips were then transferred into plastic containers and placed under moistened paper towels, rehydrated daily until egg hatching. Rearing was conducted under controlled laboratory conditions, with a temperature of 22 ± 1 °C, a relative humidity of 60 ± 10%, and a 16:8 h light:dark photoperiod. Upon hatching, neonate larvae (< 12 h old) were individually collected and placed into 2 mL Eppendorf® tubes containing 1.5 mL of artificial diet. The diet composition per litre included: 1000 mL of water, 15 g of agar, 86.6 g of corn flour, 41.3 g of wheatgerm, 45.5 g of beer yeast, 6 g of ascorbic acid, 3.4 g of mineral salt (Wesson salt mixture), 128 mg of pyrimethanil, 2.7 g of benzoic acid, 2.8 g of methyl 4-hydroxybenzoate, and 5 mL of 95% ethanol (adapted from Thiéry and Moreau 2005). For our experiments, Bordeaux mixture—composed of copper sulphate ($CuSO_4$, the active ingredient) and lime (CaO)—was employed as it is widely used in vineyards. The copper sulphate concentration used in this study was chosen to reflect the maximum levels typically observed in vineyard environments (Lai et al. 2010; Mackie et al. 2012; Hummes et al. 2019). In natural conditions, larvae may consume berries that have been directly sprayed with Bordeaux mixture or that have accumulated copper through soil leaching and root uptake by the vine after repeated applications and rainfalls (Mackie et al. 2012). Therefore, to simulate realistic copper exposure in viticultural environments, larvae in the fungicide treatment group were fed a diet supplemented with 10 mL of Bordeaux mixture (BB Caffaro WG, containing 20% copper sulphates), diluted in distilled water to obtain the desired copper sulphate concentration of 100 $mg.kg^{-1}$ (measured as mg of copper sulphates per kg of artificial diet). Finally, control larvae received a diet supplemented with 10 mL of distilled water, with no added copper ($[Cu] = 0$ $mg.kg^{-1}$).

Climatic scenarios

Larvae, both exposed and unexposed to fungicide, were placed into climate-controlled chambers (Memmert HPP260eco, Schwabach, Germany) programmed to simulate current and future summer climatic conditions (i.e., temperature and relative humidity) in Burgundy (Eastern France, Longvic-Dijon weather station, 47.27°N; 5.09°E; altitude = 219 m; Fig. 1). The selected period, from July 15th to August 15th, aligns with the peak development of *L. botrana* due to warm temperatures and coincides with a critical stage in grape berry development, highlighting the increased need for crop protection (Benelli et al. 2023a, b). This period also overlaps with the application window for Bordeaux mixture, which generally extends from early May to late July. For the current climatic scenario, temperatures were set using average hourly values over a 30-day period, derived from 20 years of historical data (2002–2021). The future climate scenario was designed to replicate projected summer conditions in Burgundy, at the end of the twenty-first century (2081–2100), based on the SSP5-8.5 scenario, which represents the worst-case greenhouse gas emission pathway (Calvin et al. 2023). These projections were generated using the average output from 18 CMIP6 General Circulation Models (GCMs) and further refined with a quantile mapping method to downscale and correct the model outputs, employing data from the Dijon weather station

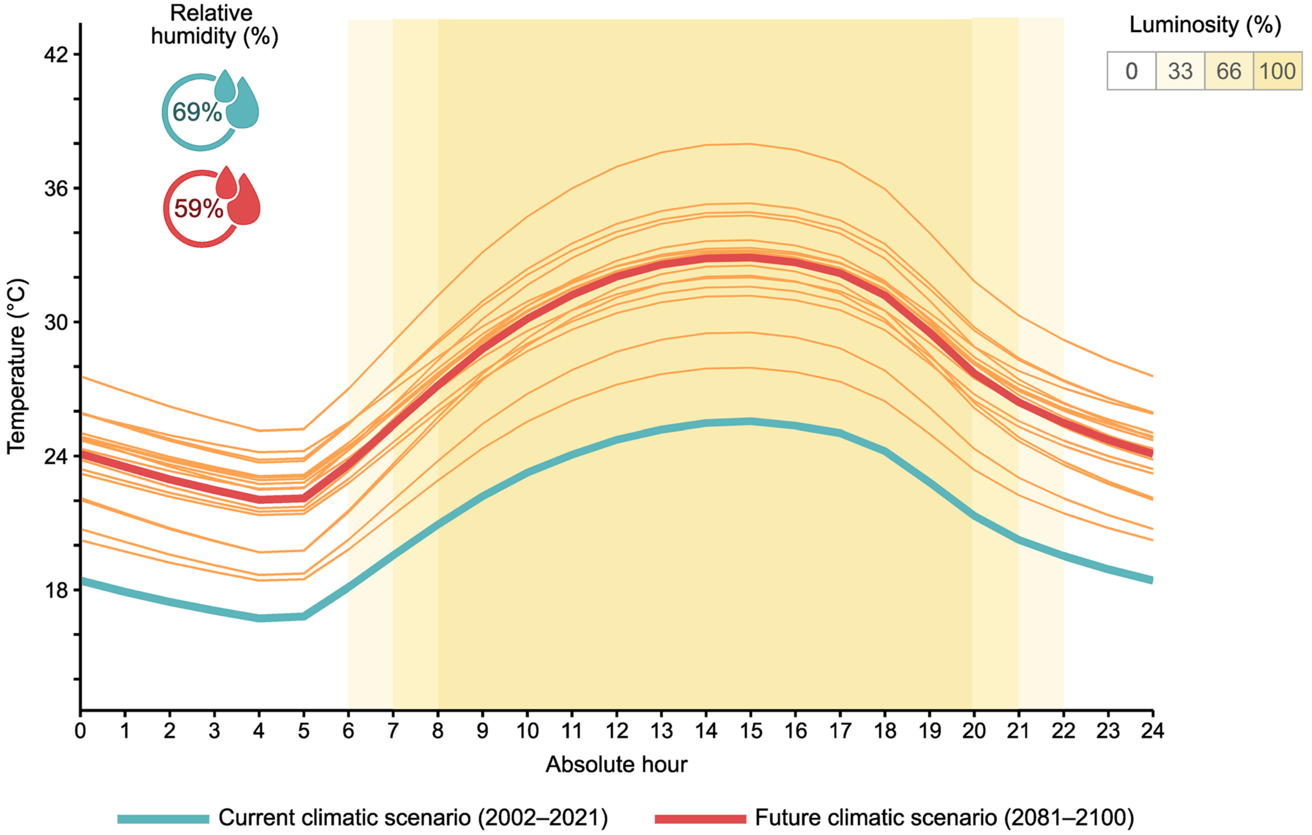

Fig. 1 Experimental projected and current climatic conditions. The blue curve represents the current daily temperature fluctuations, while the red curve shows projected future temperatures based on the average of 18 climatic models (individual model outputs are shown as fine orange lines). The relative humidity (%) programmed in each climatic chamber is displayed in the top left, and the luminosity (%) in the top right, with shades of yellow indicating increasing light levels. Lighting conditions consisted of a combined system of cool white (6500 K) and warm white (2700 K) illumination. At full intensity (100%), the light output was measured at 2000 lx

(see method in Zito 2021). Temperature was programmed to follow natural daily fluctuations with gradual ramp-up and ramp-down transitions and was maintained with a precision of ± 0.1 °C (Fig. 1). To prevent condensation of the nutrient medium, relative humidity was kept constant over the 24-h cycle at the daily average value for each climate scenario (Fig. 1). Relative humidity was controlled within ± 5%, and both temperature and humidity were continuously monitored throughout the experiment. Lighting followed a 16:8 h light:dark photoperiod, with gradual transitions to simulate sunrise and sunset. Light intensity increased to 33% and 66% during the first hours of illumination and decreased in the same pattern during the final hours. Lighting was provided by a combination of cool (6500 K) and warm (2700 K) white LEDs, reaching a maximum of 2000 lx (Fig. 1). These lighting conditions align with standard practices commonly used in *L. botrana* rearing (Roditakis and Karandinos 2001).

Experimental design

Larvae were subjected to two climatic conditions: current (2002–2021) and future (2081–2100) conditions (Fig. 2). Within each climatic regime, larvae were fed either a diet supplemented with Bordeaux mixture (100 mg.kg^{-1} copper, “exposed”) or an untreated diet (0 mg.kg^{-1} copper, “unexposed”). Development was monitored from egg hatching until adult emergence. For reproduction experiments, adult moths were divided into two experimental groups: (i) no-choice mating and (ii) choice mating. In the choice experiments, two combinations were tested for each climatic condition: (i) an unexposed male (focal individual) was presented with both an unexposed female and an exposed female, and (ii) an unexposed female (focal individual) was presented with both an unexposed male and an exposed male. After each choice experiment, individuals were sacrificed and not used in any further experiments. In the no-choice experiments, four pairings were conducted in current and future climatic conditions: (i) unexposed female × unexposed male, (ii) unexposed female × exposed male, (iii) exposed

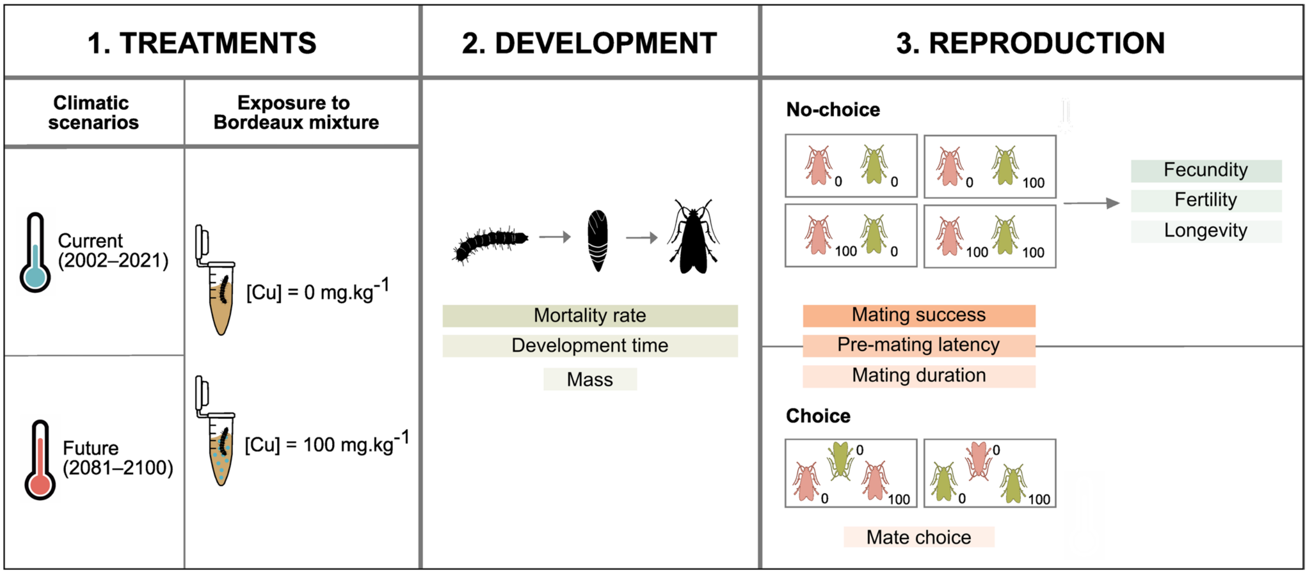

Fig. 2 Overview of the experimental approach to test the influence of temperature and fungicide exposure on mate selection and the reproductive behaviour of *L. botrana*. In no-choice and choice experiments, females are represented in pink and males in green. The index next to the moths indicates the concentration of Bordeaux mixture they developed on (0: unexposed, 100: exposed)

female × unexposed male, and (iv) exposed female × exposed male. After the no-choice experiments, individuals were preserved to assess reproductive performance, including fecundity, fertility, and longevity.

Pest development response to Bordeaux mixture under different climatic scenarios

A total of 5113 neonate larvae were randomly assigned to one of four experimental conditions: current ($n = 1561$ for 0 mg.kg^{-1}, $n = 1342$ for 100 mg.kg^{-1}) and future ($n = 1036$ for 0 mg.kg^{-1}, $n = 1174$ for 100 mg.kg^{-1}) climate regime. Larvae were monitored daily until pupation. Each pupa was weighed, individually placed into glass tubes, and checked daily for adult emergence. Upon emergence, moths were sexed by inspecting the ventral tips of the abdomen. Developmental variables were measured, including (i) mortality rate (proportion of larvae and pupae that died relative to the total number of larvae initially placed in Eppendorf® tubes), (ii) pupal mass (mg), (iii) development time (days from egg hatching to adult emergence), and (iv) longevity (days from adult emergence to death).

Pest reproduction response to Bordeaux mixture under different climatic scenarios

General conditions

Mating experiments were conducted under controlled temperature and humidity conditions specific to each climatic regime, using red light (100 lx) to simulate low-light conditions (dusk-like conditions). For each climatic regime, the temperature was set based on the average temperature observed over a 4-h mating period (8 a.m. to 12 a.m.). For the current climate scenario, this temperature was maintained at 20 ± 0.5 °C with a relative humidity (RH) of 60 ± 5%, while in the future climatic scenario, it was set to 26.5 ± 0.5°C with the same RH of 60 ± 5%. All pairings involved virgin individuals: females aged 1 ± 1 days and males aged 2 ± 1 days. Each experiment lasted up to 3 h or until mating occurred, as the likelihood of mating drops to nearly zero beyond this period (Muller et al. 2016b).

Experiment 1: no-choice mating

Four experimental combinations were tested: (i) F0 × M0, unexposed female with unexposed male (current: $n = 61$, future: $n = 43$), (ii) F0 × M100, unexposed female with exposed male (current: $n = 56$, future: $n = 87$), (iii) F100 × M0, exposed female with unexposed male (current: $n = 53$, future: $n = 76$), and (iv) F100 × M100, exposed female with exposed male (current: $n = 57$, future: $n = 86$). In each experiment, a female was placed into a glass tube for a 5-min acclimatization period before introducing the male. Once introduced, male–female interactions between males and females were recorded for 3 h using a Moticam 1080 camera and Motic Images Plus 3.0 software. Video footage was analysed to estimate: (i) mating success, considered successful if the pair remained coupled for more than one minute, indicating successful intromission (Muller 2016),

(ii) pre-mating latency, time elapsed between first contact and mating initiation, and (iii) mating duration, time from the start of mating until separation. Following mating, the female was retained in the mating tube to lay eggs on the inner surface of the tube, while the male was moved to a separate tube. Both were monitored daily to assess longevity (days from adult emergence to death). Eggs were incubated under the same developmental rearing conditions for at least ten days (during which the female died, and the eggs hatched), after which the following reproductive metrics were assessed: (i) fecundity (total number of eggs laid per female), and (ii) fertility (proportion of eggs that successfully hatched).

Experiment 2: choice mating

To investigate partner selection by a focal individual when in contact with two potential partners (one fungicide-exposed and one unexposed), triad experiments were conducted under two setups: (i) an unexposed female (F0) with two male partners, one fungicide-exposed (M100) and one unexposed (M0) (current $n = 42$, future: $n = 46$), (ii) an unexposed male (M0) with two female partners, one fungicide-exposed (F100) and one unexposed (F0) (current $n = 62$, future: $n = 60$). To differentiate between exposed and unexposed individuals, each partner was randomly marked with either yellow or red acrylic paint the day before testing. These colours were selected to minimize interference with the moths' colour perception (Crook et al. 2022). Moths were anesthetized on ice to immobilize them for marking with a fine brush applied to the base of the right wing. On the testing day, the focal individual was placed into a transparent plastic box (17 × 10.5 × 9 cm) for a 5-min acclimatization period, after which two partners were introduced simultaneously, positioned equidistantly from the focal moth. Observations were conducted visually for up to 3 h. If a mating occurred, the non-selected partner was removed to avoid intrasexual competition, with its identity confirmed by the colour marking. For each experiment, the following metrics were marked down: (i) mating success, defined as successful if the pair remained coupled for more than one minute, (ii) mate choice, indicating whether the focal individual mated with a fungicide-exposed or unexposed partner, (iii) pre-mating latency, and (iv) mating duration. To prevent cross-contamination, the plastic boxes were cleaned with acetone after each test.

Pest population dynamics responding to Bordeaux mixture under different climatic scenarios

Following the procedure described by Maia et al. (2000), key life table parameters (i.e., R_0, T, Dt, r_m and λ) were estimated using mortality data, developmental variables (i.e., development times, sex ratio, longevity) and reproductive outcomes (i.e., fecundity and fertility) from the development and the no-choice experiments. The following life table parameters were estimated:

- Net reproductive rate (R_0), which represents the mean net contribution of a female to the next generation, is expressed as the total number of female offspring produced per female during the entire oviposition period.
- Mean generation time (T), which indicates the mean time (in days) between the birth of individuals (neonate emergence) in one generation and the birth of individuals at the same stage in the subsequent generation.
- Doubling time (Dt), which refers to the time (in days) required for doubling the initial population.
- Intrinsic rate of increase (r_m), which is derived from the exponential growth population potential, assuming a stable age distribution.
- Finite rate of increase (λ), which is a multiplication factor of the original population at each time period. The decimal portion of λ reflects the daily growth rate, expressed as a percentage.

Using the jackknife procedure, values of R_0, T, Dt, r_m and λ were estimated, enabling variance calculations for each parameter (Maia et al. 2000). These values were subsequently analysed using a Generalized Linear Model (GzLM) to compare differences between fungicide exposure combinations and climatic conditions, with an appropriate family distribution fitted to ensure accurate statistical modelling.

Statistical analyses

Datasets were analysed using Generalized Linear Models (GzLMs) to evaluate the effects of Bordeaux mixture exposure, climate scenarios, and their interaction on the studied response variables. Pupal mass was included as a covariate in all GzLMs, based on a priori hypothesis that individual and sexual partner mass could influence development (Muller et al. 2015, 2016c; Iltis et al. 2022; Garinie et al. 2024). For binomial data (e.g., mortality and mating success), GzLMs with a binomial distribution were applied to assess the effects and interaction of fungicide exposure and climate scenario. To ensure optimal models fit, different error distribution families (e.g., Gaussian, Poisson, quasi-Poisson, Gamma and negative binomial) were tested and applied as appropriate to model the error structure of each response variable, including population dynamics parameters (R_O, T, r_m, λ, and D_t). GzLM models were followed by ANOVA using a Chi-square test for the Poisson family, an F-test for the quasi-Poisson family, and a likelihood ratio (LR) test for the negative binomial family to assess model significance.

When significant effects were detected, *post-hoc* tests were performed using the *emmeans* package (version 1.8.1.1) (Searle et al. 1980) to identify which specific conditions (i.e., fungicide exposure and climate scenario) significantly differed, and *p-values* were adjusted using the Tukey method. For the choice mating experiments, exact binomial tests were employed to assess whether observed choice proportions deviated significantly from 50%, indicating a preference beyond random choice. GzLMs were conducted using the *MASS* package (version 7.3.58.2) (Venables and Ripley 2002). All statistical analyses were performed using the R software (4.3.2, R Core Team 2023).

Results

Pest development response to Bordeaux mixture under two climatic scenarios

Larval and pupal mortality were significantly influenced by the climatic regime and Bordeaux mixture exposure, with a significant interaction between these factors (Fig. 3a; GzLM, binomial distribution, effect of Bordeaux mixture: $\chi^2_{1,5049} = 82.869$, $p < 0.001$; effect of climatic regime: $\chi^2_{1,5050} = 4.254$, $p = 0.039$; interaction effect: $\chi^2_{1,5048} = 29.383$, $p < 0.001$). Under the current climatic regime, individuals exposed to Bordeaux mixture had a significantly higher mortality rate (+ 19%) than unexposed individuals, whereas under the future climatic conditions, Bordeaux mixture exposure led to a smaller but significant increase in mortality (+ 4%) (Fig. 3a). Individuals exposed to Bordeaux mixture exhibited significantly lower pupal mass in both males and females compared to unexposed individuals, with no significant effect of the climatic regime on pupal mass (Fig. 3c, Table S1). Bordeaux mixture exposure also significantly extended development time in males and females, regardless of the climatic regime (Fig. 3b, Table S1). Moreover, development time was shorter for both sexes under the future climate scenario compared to the current climate scenario (Fig. 3b, Table S1). In contrast, adult longevity was unaffected by Bordeaux mixture but significantly decreased under future climatic conditions compared to current climatic conditions (– 50% for males and – 18% for females; Fig. 3d, Table S1). In addition, moths of both sexes with shorter development times exhibited significantly higher

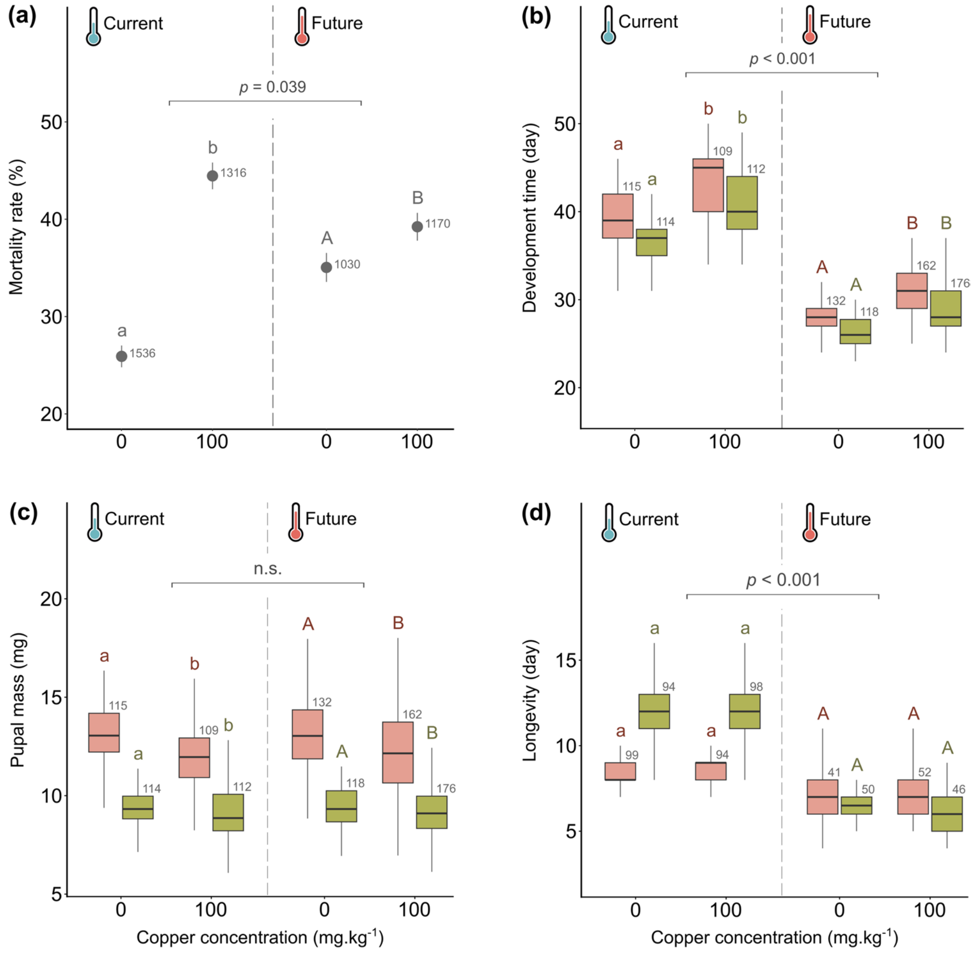

Fig. 3 Effects of Bordeaux mixture exposure (0 or 100 mg.kg^{-1}) on life-history traits related to development and longevity under current (2002–2021) and future (2081–2100) climatic conditions, with: **a** mortality rate (%) (mean ± SEM), **b** development time until moth emergence (day), **c** pupal mass (mg), and **d** adult longevity (day). Females are represented in pink and males in green. Boxplots denote the first and third quartiles of the relative exposures, with the median denoted by a bold horizontal line. Letters in dark pink and blue indicate significant differences ($p < 0.05$, *post-hoc* test) in traits for females and males separately, between exposure concentrations (lowercase for current climate and uppercase for future climate). *P*-values (*p*) above the bars denote significant differences between the two climatic conditions for males and for females (n.s. indicates non-significant differences). Gray numbers associated with data points or boxes indicate sample sizes

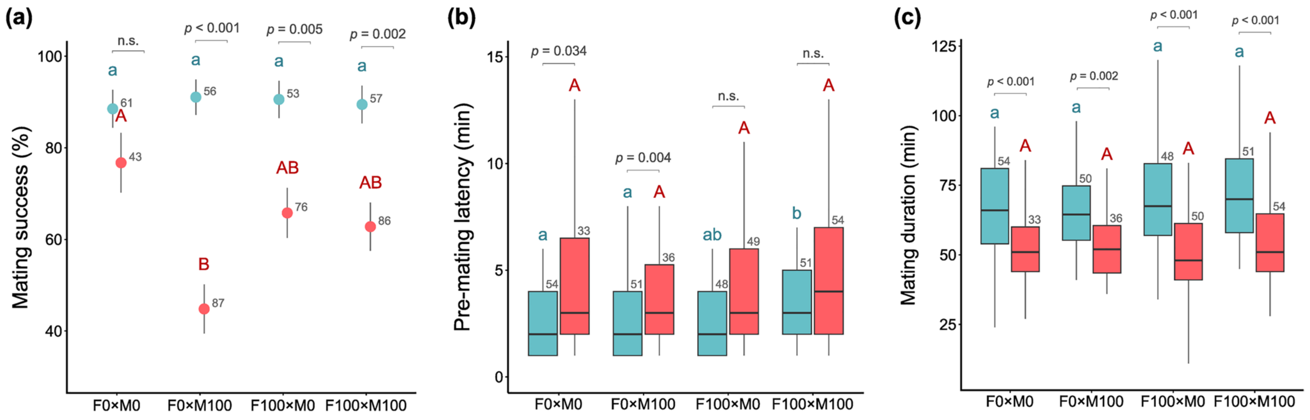

Fig. 4 Effects of pairwise exposure combinations (F0 × M0, F0 × M100, F100 × M0, and F100 × M100) in no-choice mating experiments under current (blue) and future (red) climatic scenarios on: **a** mating success (%) (mean ± SD), **b** pre-mating latency (min), and **c** mating duration (min). Pairwise exposure combinations are represented on the x-axis as Female (F) × Male (M), where 100 indicates exposure to Bordeaux mixture and 0 indicates no exposure. Boxplots denote the first and third quartiles of the relative exposures, with the median denoted by a bold horizontal line. Lowercase blue and uppercase red letters indicate significant differences between pairwise exposure combinations under current and future climatic scenarios, respectively ($p < 0.05$, *post-hoc* test). *P*-values (*p*) above the bars denote significant differences between the two climatic regimes for each pairwise combination, and n.s. indicates non-significant differences. Gray numbers adjacent to points or boxes represent sample sizes

pupal mass (Table S1; regression coefficient of females: $\beta = -0.013$, $p = 0.002$; and males: $\beta = -0.018$, $p = 0.004$). However, while male moths with greater longevity also had a significantly higher pupal mass, this effect was not observed in females (Table S1; $\beta = 0.014$, $p = 0.011$).

Pest reproduction response to Bordeaux mixture under two climatic scenarios

No-choice experiments: mating success and behaviours

In no-choice experiments, the mating success of moths was significantly lower under future climatic conditions compared to current climatic conditions (Fig. 4a, Table S2). Under the current climate, mating success averaged 90% and remained consistent across all four exposure combinations. However, under future climatic conditions, mating success averaged 77% in control pairs (F0 × M0) and decreased when one of the partners was exposed to the fungicide (Fig. 4a). The lowest mating success (45%) was observed in pairs where only the male was exposed to the Bordeaux mixture (F0 × M100). Mating success under future climatic conditions was moderately reduced when only the female was exposed (F100 × M0) or when both partners were exposed (F100 × M100), averaging 66% and 63% (Fig. 4a). Mating success was also significantly influenced by female mass; heavier females exhibited lower mating success rates (Table S2, $\beta = -0.215$, $p < 0.001$).

Pre-mating latency was significantly affected by climatic conditions and fungicide exposure (Table S2). Under future climatic conditions, pre-mating latency was significantly longer for unexposed females compared to unexposed females for current climatic conditions (Fig. 4b, Table S2). Under current climatic conditions, pre-mating latency was significantly extended when both partners were exposed to Bordeaux mixture (F100 × M100) (Fig. 4b, Table S2). In contrast, under future climate conditions, fungicide exposure had no significant effect on pre-mating latency (Fig. 4b, Table S2). Finally, mating duration was significantly reduced under future climatic conditions, compared to current conditions, but fungicide exposure had no significant effect regardless of the climatic scenario (Fig. 4c, Table S2).

No-choice experiments: reproductive performance

Moths reared under future climatic conditions laid significantly fewer eggs (−28%) compared to those reared under current conditions (Fig. 5a, Table S2). While fungicide exposure significantly reduced overall female fecundity (Table S2), this effect was not statistically significant in *post-hoc* tests. Female fecundity was significantly influenced by body weight, with heavier females laying more eggs (Table S2, $\beta = 0.075$, $p < 0.001$). Female fertility was also significantly reduced under the future climatic conditions, decreasing by 39% compared to current conditions. A large variance in female fertility was measured under future conditions (Fig. 5b). However, Bordeaux mixture exposure had no significant effect on fertility (Fig. 5b, Table S2).

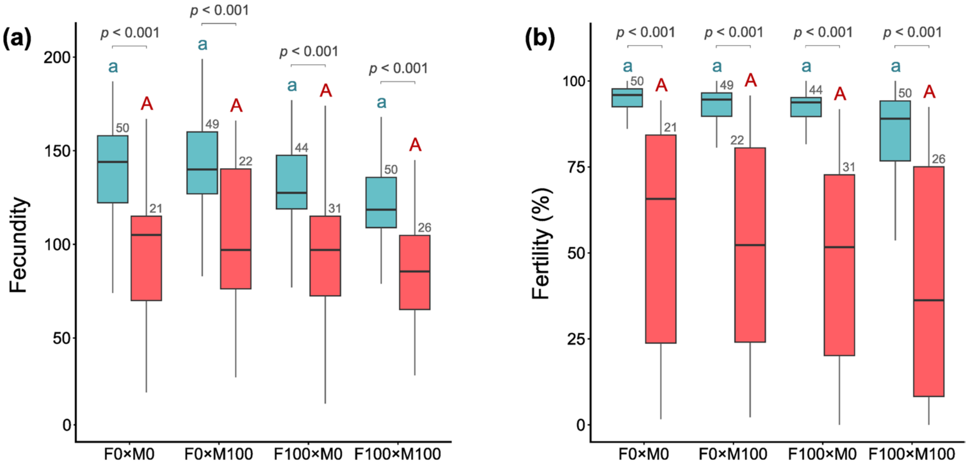

Fig. 5 Effects of pairwise exposure combinations in no-choice mating experiments under current (blue) and future (red) climatic scenarios on: **a** fecundity (total number of eggs laid), and **b** fertility (percentage of hatched eggs). Pairwise exposure combinations are represented on the x-axis as Female (F) × Male (M), where 100 indicates exposure to Bordeaux mixture and 0 indicates no exposure. Boxplots denote the first and third quartiles of the relative exposures, with the median denoted by a bold horizontal line. Lowercase blue and uppercase red letters indicate significant differences between pairwise exposure combinations under current and future climatic scenarios, respectively ($p < 0.05$, *post-hoc* test). *P*-values (*p*) above the bars denote significant differences between the two climatic regimes for each pairwise combination. Gray numbers adjacent to boxes represent sample sizes

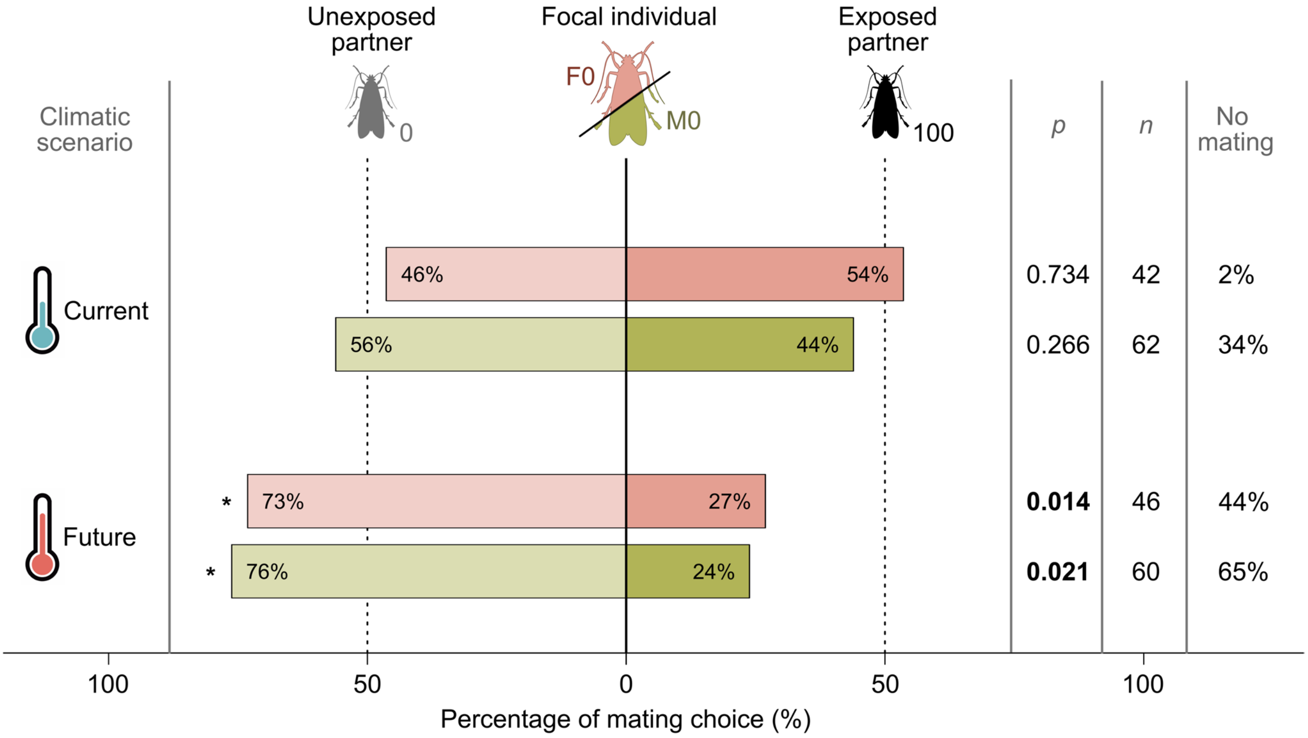

Fig. 6 Mate choice responses of focal individuals (females in pink and, males in green) when presented with two partners: one exposed (100) and one unexposed (0) to Bordeaux mixture, under current and future climatic conditions. Coloured bars indicate the percentage of choices made for each partner type. *P*-values (*p*) and asterisks denote significant preferences for unexposed partners (exact binomial test). Sample sizes (*n*) and the percentage of no-choice (instances where no preference was shown) are displayed in the right column

Choice experiments: mating success and behaviours

In choice mating experiments, when focal individuals were presented simultaneously with two potential partners, one exposed to the Bordeaux mixture and one unexposed, climatic condition significantly influenced mating outcomes (Table S3). Under current climatic conditions, no significant difference in mate choice was observed between unexposed and fungicide-exposed partners, regardless of whether the focal individual was male or female (Fig. 6). However, under future climatic conditions, focal individuals mated more frequently with unexposed partners than with fungicide-exposed partners (Fig. 6). The no-choice rate (instances where no mating occurred during the triad test) was significantly higher under future climatic conditions than under current conditions (Figure S1a, Table S3). Under current conditions, the no mating rate was low for female focal individuals (2%) but substantially higher for males (34%). Under future conditions, the no mating rate increased significantly to 44% for females and 65% for males (Fig. 6, Figure S1a). Pre-mating latency was significantly longer for female focal individuals under future conditions compared to female pre-mating latency under current conditions, while pre-mating latency for males remained unaffected by climatic scenarios (Figure S1b, Table S3). Additionally, mating duration was significantly shorter under future climatic conditions compared to current conditions, with no significant difference between male and female focal individuals (Figure S1c, Table S3).

Pest population dynamics responding to Bordeaux mixture under two climatic scenarios

Under current and future climatic conditions, exposure of both partners to Bordeaux mixture, compared to unexposed partners, significantly reduced the net reproductive rate (R_0) (GzLM quasi-Poisson distribution, $F_{3,288} = 24.061$, $p < 0.001$), the intrinsic rate of increase (r_m) (GzLM Gamma distribution, $\chi^2_{3,252} = 3.065$, $p < 0.001$), and the finite rate of increase (λ) (GzLM Gamma distribution, $\chi^2_{3,252} = 0.013$, $p < 0.001$), while significantly increasing the mean generation time (T) (GzLM quasi-Poisson distribution, $\chi^2_{3,252} = 19.982$, $p < 0.001$) (Fig. 7). In addition, exposure to Bordeaux mixture led to a significant increase in doubling time (Dt) under both climatic conditions, compared to unexposed partners (GzLM quasi-Poisson distribution, $\chi^2_{3,252} = 29.430$, $p < 0.001$) (Fig. 7).

For the same fungicide exposure combinations between partners, comparisons between climatic conditions showed that the net reproductive rate (R_0) was significantly lower under future climatic conditions, with an average reduction of 55% compared to current conditions (GzLM quasi-Poisson distribution, $F_{1,291} = 175.706$, $p < 0.001$) (Fig. 7). Additionally, the mean generation time (T) was significantly shorter under future climatic conditions, with an average reduction of 27% (GzLM quasi-Poisson distribution, $\chi^2_{1,255} = 221.240$, $p < 0.001$) (Fig. 7). While a significant overall difference in doubling time (Dt) was found between the two climatic conditions (GzLM quasi-Poisson distribution, $\chi^2_{1,255} = 7.021$, $p = 0.039$), pairwise comparisons did

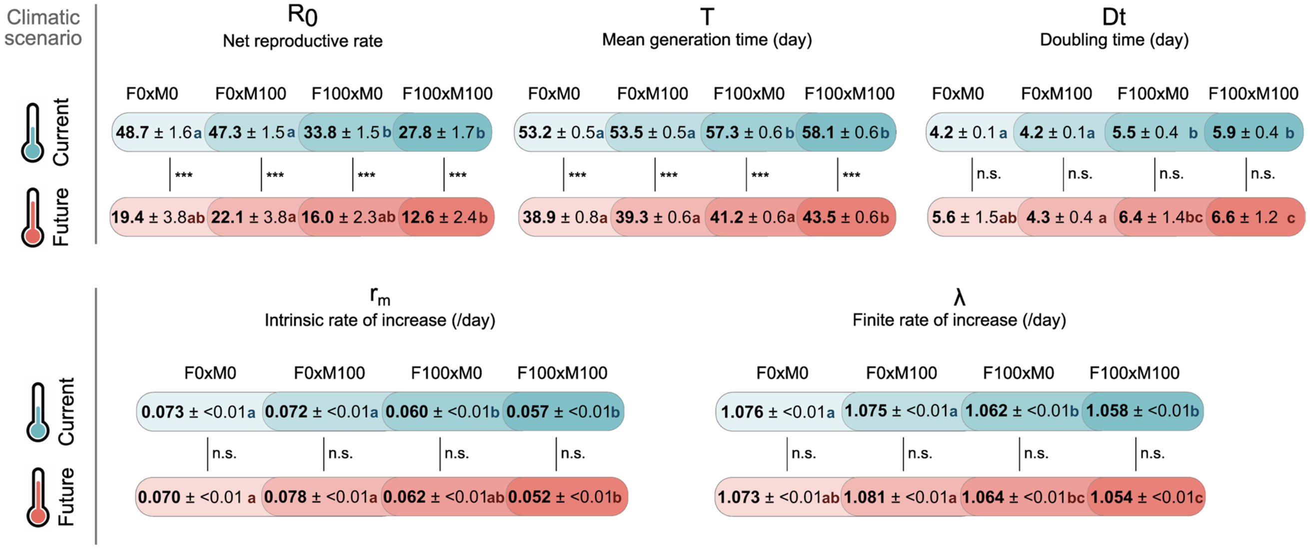

Fig. 7 Estimated life table parameters (mean ± SEM) of *Lobesia botrana* under pairwise exposure combinations of Bordeaux mixture (F0 × M0, F0 × M100, F100 × M0, and F100 × M100) under current and future climatic conditions. For each parameter within a given climatic condition, means (± SEM) followed by the same letters are not significantly different based on *post-hoc* pairwise comparisons. Significant differences between current and future climatic conditions are indicated by asterisks (***$p < 0.001$; n.s., not significant)

not reveal significant differences between climatic conditions within each treatment (Fig. 7). In contrast, no significant differences were found in the intrinsic rate of increase (r_m) (GzLM Gamma distribution, $\chi^2_{1,255} = 0.133$, $p = 0.109$), or the finite rate of increase (λ) (GzLM Gamma distribution, $\chi^2_{1,255} = 0.001$, $p = 0.080$) between climatic conditions (Fig. 7).

Discussion

In this study, we investigated the effects of the widely used Bordeaux mixture fungicide on mate selection and reproductive behaviour of the moth pest *L. botrana* under both current and projected end-of-century climatic scenarios. Our results showed that fungicide exposure influenced mate choice, modulated by climatic conditions. Under future climatic conditions, moths mated more frequently with unexposed partners than with fungicide-exposed partners, whereas this preference was not observed under current climatic conditions. Developmental experiments revealed that Bordeaux mixture exposure prolonged the development time, while elevated temperatures accelerated it. Fungicide exposure also resulted in higher mortality. However, the multi-stress effects of temperature and fungicide exposure interacted under future conditions, mitigating the fungicide's lethal impact. Finally, the estimation of life parameters provided insights into potential shifts in *L. botrana* population dynamics under a future climate scenario with fungicide exposure. These findings highlight the complex interplay between pesticide exposure and climate change, emphasizing the need to consider both factors when predicting pest population trajectories and designing sustainable pest management strategies in a changing climate.

Mechanisms of "red flag" detection

Choice experiments revealed that under future climatic conditions, focal individuals (males and females) mated more frequently with unexposed partners than with fungicide-exposed ones. Additionally, a notable percentage of no-choice events—instances where no mating occurred during the test—arose, with 44% of focal females and 65% of focal males failing to mate. No-choice experiments further supported this finding, showing a decline in mating success under future climatic conditions, particularly when fungicide-exposed females were paired with unexposed males. These results indicate that mating behaviour is significantly disrupted when one partner has been exposed to Bordeaux mixture under future climatic conditions.

The mate selection towards an unexposed partner suggests that fungicide exposure alters the quality of mate selection cues under future climatic conditions. This implies that fungicide-exposed individuals act as "red flags", defined here as a warning cue indicating lower mate suitability. Indeed, mate choice in insects is influenced by several modalities, including visual, olfactory, and physical cues, which can interact synergistically (Bonduriansky 2001). Temperature is a well-known modulator of sexual communication in insects, particularly in species that use acoustic and vibratory signals. For example, temperature-coupling phenomenon whereby both male signal production and female preferences shift together in response to temperature changes has been observed in crickets and the acoustic moth *Achroia grisella* (Pires and Hoy 1992; Greenfield and Medlock 2007). This coordinated adaptation allows individuals to maintain effective communication despite environmental fluctuations. In contrast, other species such as the solitary bee *Osmia bicornis* and the treehopper *Enchenopa binotata* show no such coupling (Conrad et al. 2017; Jocson et al. 2019). Instead, elevated temperatures amplify differences in male signal quality, thereby enhancing female discrimination. In these systems, only males capable of maintaining robust, attractive signals in warm conditions are consistently accepted, while less adapted males are more likely to be rejected. Temperature can also affect chemical communication by altering the production and perception of volatile compounds, disrupting signal reliability (Linn et al. 1988; Woodrow et al. 2000; Conrad et al. 2017). Although insects use different temperature-sensitive mechanisms to select mates, the impact of warming on sexual communication is likely to differ between species (Brandt et al. 2018). In *L. botrana*, olfactory cues play a key role in mate recognition and attraction, as females release pheromones to enable males to locate them (Witzgall et al. 2005). These volatile compounds facilitate mate recognition and favour successful courtship (Johansson and Jones 2007). Previous studies have highlighted the role of CHCs as a signal of individual identity and quality during close-range courtship, and as "honest signals"—reliable indicators of an individual's fitness or genetic quality—for mate evaluation (Johansson and Jones 2007; Ingleby 2015). We hypothesize that physiological changes induced by larval fungicide exposure may alter internal chemistry, leading to modifications in CHC production during adulthood. In moths, such changes often manifest as variations in the quantity or relative concentrations of chemical compounds released (Heuskin et al. 2014; Ngumbi et al. 2020).

Aside from the disruption of chemical or visual cues, other sublethal effects of fungicide exposure may contribute to the observed disruption in mating behaviour (Desneux et al. 2007). The combined effects of sublethal fungicide exposure and thermal stress can reduce moth activity, inhibit female calling behaviour, or impair male locomotion, thereby disadvantaging exposed individuals (Knight and Flexner 2007; Bernardes et al. 2022). This reduction in sexual activity could explain the higher mating success of unexposed individuals, compared to fungicide-exposed individuals, and the occurrence of mating failure. In our experimental setup where individuals were free to move, physical capacities and sexual motivation likely contributed to mating success. A complementary study assessing partner motivation, such as measuring female calling activities and male locomotion activity, could provide further information about the behavioural mechanisms underlying these effects (Muller et al. 2016a). Overall, these results highlight the vulnerability of mating systems to combined environmental stressors. In *L. botrana*, fungicide exposure during larval development under warming disrupts the complex interplay of sensory cues involved in mate selection, leading to reduced mating success. Investigating the physiological basis of these disruptions could provide valuable insights into the combined effects of agrochemicals and climate change on insect reproductive systems.

Mechanisms influencing partner quality

Beyond the direct cues influencing mate perception in moths, fungicide exposure primarily impacts larval development, a critical period in which physiological changes can have lasting consequences in adulthood. Especially for capital breeders, whose reproductive success depends on energy reserves accumulated during the larval stages (Muller et al. 2015, 2016c). Environmental stressors, such as temperature fluctuations and fungicide exposure, can disrupt the synthesis of these reserves, reducing mate quality and impairing reproductive outcomes (Muller et al. 2016c; Iltis et al. 2020; Garinie et al. 2024; Nusillard et al. 2024a). The decline in partner quality, observed under future climatic conditions, but not under current ones, may be attributed to physiological mechanisms, potentially linked to developmental disruptions caused by fungicide exposure.

Fungicide exposure prolonged *L. botrana* development time by approximately four days (+ 10%) and reduced male and female pupal mass for both climatic scenarios. This extended development time regardless of climatic condition suggests a potential trade-off, where energy typically allocated to growth is redirected towards detoxification processes (Fujii et al. 2020). Detoxification enzymes present in *L. botrana*, such as glutathione S-transferases (GSTs) and metallothioneins, facilitate the neutralization of heavy metals, including the copper found in Bordeaux mixture (Navarro-Roldán et al. 2020; Tibbett et al. 2021; Gekière 2025). Temperature directly influences the activity of detoxification enzymes (Li et al. 2023). Higher temperatures under future conditions can alter enzyme efficiency, potentially reducing an organism's ability to neutralize copper, then inducing greater physiological damages to larvae impacting adult behaviour and life-history traits. In addition, development time under current climatic conditions was significantly longer by approximately 10 days (28%) compared to future conditions. While this longer development may increase larval exposure to the fungicide, it could also provide additional time for the detoxification and metabolization of this fungicide. We hypothesize that under future climatic conditions, the combination of faster development and temperature-driven changes in detoxification efficiency results in greater physiological impairments. This, in turn, reduces the quality of adults as mating partners.

Our study indicates that the adverse consequences of fungicide exposure on partner quality under future climatic conditions may be attributable to a combination of factors, including reduced development time, diminished detoxification capacity, and temperature-induced changes in detoxification efficiency. These elements ultimately exert an influence on mate selection and reproductive success.

Implications for pest management

Assessing the life parameters of *L. botrana* has provided insights into the potential evolution of its population dynamics in response to Bordeaux mixture exposure under a changing climate. Our results indicate an important shift in life parameters, particularly when females were exposed to the fungicide—regardless of whether they mated with an exposed or unexposed partner. This effect was especially pronounced under current climatic conditions. This finding underscores the pivotal role of female exposure in reducing reproductive output and population growth. Overall, larval exposure negatively affected development and reproduction across both climatic scenarios, in accordance with Garinie et al. (2024) which reported the adverse effects of Bordeaux mixture under constant climatic conditions.

Concerning climate influence, our results suggest that population growth parameters, including doubling time (Dt), intrinsic rate of increase (r_m), and finite rate of increase (λ), did not significantly differ between scenarios. However, future climatic conditions had negative effects on survival rates and showed a general trend towards reduced reproductive output. This decline in reproductive rate (R_0) was partially offset by an accelerated mean generation time (T), which was significantly shorter under future conditions, thereby explaining similarities between population growth observed between current and future climatic scenarios. However, our study examines the effects of global warming on a first-generation population, which has not undergone prior adaptations or been exposed to this stress previously. Therefore, our results do not account for potential evolutionary adaptations that may mitigate the negative impacts of rising temperatures on *L. botrana* survival and reproduction over multiple generations (Bale et al. 2002; Hoffmann 2017; González-Tokman et al. 2020). Evidence for other insect

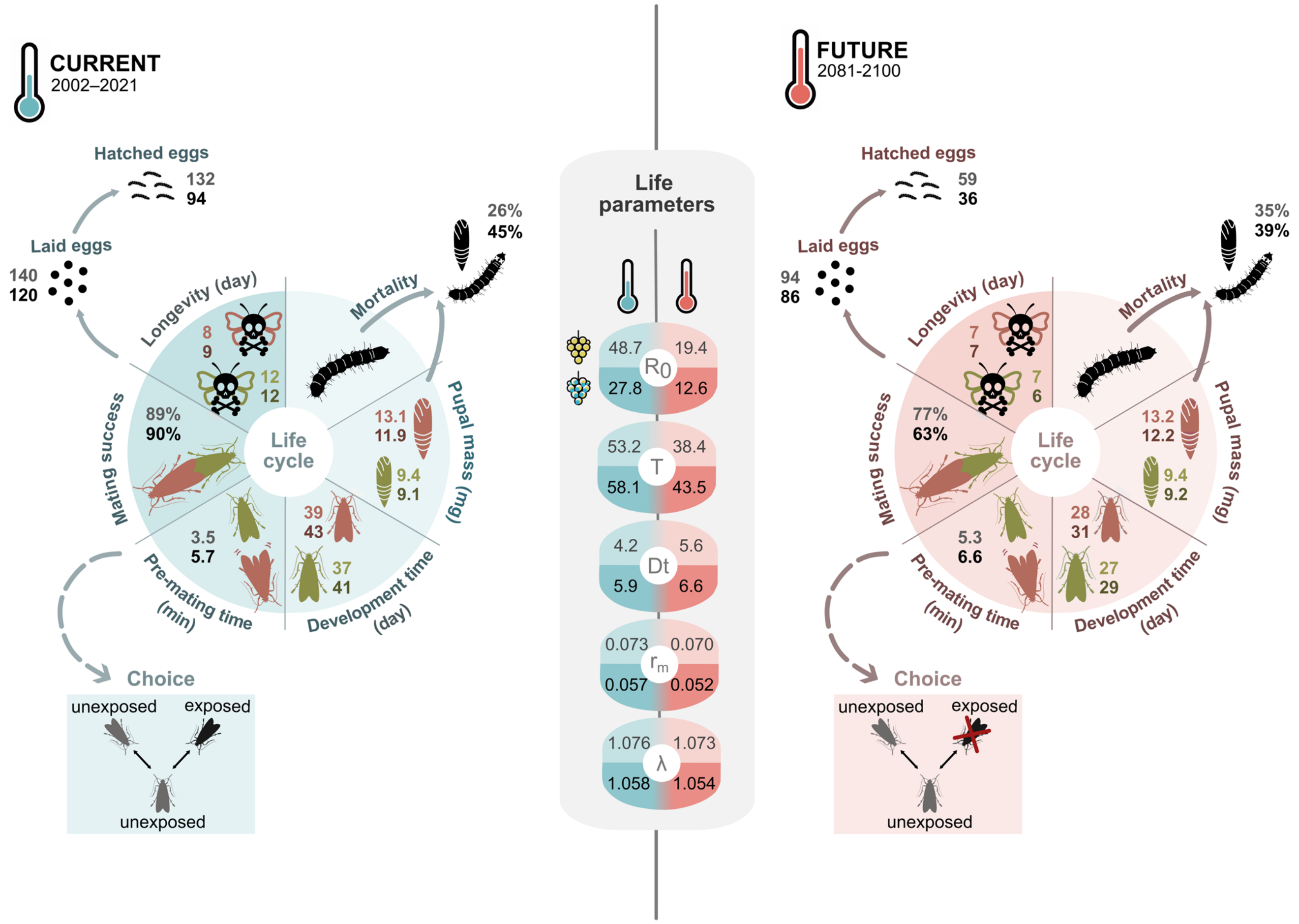

Fig. 8 Schematic representation summarizing the effects of Bordeaux mixture on *Lobesia botrana* life cycle and life table parameters under current and end-of-century climatic conditions. The central section presents estimated life table parameters, while the left and right sections illustrate the life cycle under current (blue) and future (red) climatic conditions. Within each cycle, average developmental variables and results from no-choice mating tests are displayed. Females are represented in pink and males in green. Lighter colours indicate averages for control individuals (not exposed to the fungicide), while darker colours represent fungicide-exposed individuals. Rectangles denote results from choice experiments

species suggests that phenotypic plasticity and genetic variation shape responses to elevated temperatures (Sgrò et al. 2016; Hill et al. 2021). Similarly, *L. botrana* may rely on plasticity to buffer temperature changes (e.g. behavioural and morphological), but long-term survival will likely depend on local adaptation (Sgrò et al. 2016; Hill et al. 2021).

A northward shift in *L. botrana* populations may occur as climate change causes summer temperatures in southern regions to approach their upper thermal limit (Gutierrez et al. 2018). Future research should examine how plasticity and genetic variation interact to shape *L. botrana* response to climate change. Differences between generation time and doubling time, due to fungicide exposure and/or climatic conditions, could also influence biotic interactions, particularly biocontrol strategies targeting *L. botrana*. Parasitoids, commonly used in biological control methods, can be directly or indirectly affected by thermal and chemical stressors. For example, Iltis et al. (2022) reported enhanced immune activity for *L. botrana* under future climatic conditions compared to current ones. In addition, Nusillard et al. (2024b) showed that future climatic conditions reduced the number of parasitized eggs, emergence rate and offspring quality (size, longevity, fecundity) in *T. oleae*, particularly when the host *L. botrana* had been exposed to Bordeaux mixture. These findings suggest that climate change and Bordeaux mixture exposure may reduce the effectiveness of biological control strategies against *L. botrana*. A better understanding of the combined effects of global warming and Bordeaux mixture on *L. botrana* and its natural enemies is thus needed. These studies will be essential for refining biocontrol programs, ensuring they can adapt to evolving pest dynamics, and remain as effective when facing fungicide exposure and future climatic conditions. Finally, while this study simulated a future climatic scenario by controlling temperature and humidity, climate change encompasses a broad range of environmental shifts that cannot be fully replicated in climate chambers, such as elevated CO_2 and ozone levels, or altered precipitation patterns. Moreover, the controlled and laboratory conditions within climate chambers limit insects' behavioural thermoregulation. In natural environments, *L. botrana* can exploit a wide range of microhabitats, seeking out shaded, cooler, or more humid sites to reduce exposure to adverse temperatures and light. Future experiments in natural environment are thus needed to better understand the impact of climate change and pesticide exposure on mate selection and the reproductive behaviour of most pests.

Conclusion

This study highlights the intricate and multifaceted effects of Bordeaux mixture on *L. botrana* in a context where global warming is reshaping pest pressures in vineyards worldwide, potentially altering pest dynamics and complicating management strategies. Our results show that increased temperatures and drought conditions will have an impact on larval development and the adult stage of *L. botrana*, and alter the influence of fungicide exposure.

Under current climatic conditions, fungicide exposure primarily disrupts larval development, with limited impact on the adult stage (Fig. 8). However, fungicide exposure under the future climatic scenario had broader consequences, altering both larval development and adult reproductive behaviour. Behavioural choice experiments revealed that focal individuals significantly preferred unexposed sexual partners over those exposed to the fungicide. These findings suggest that the adverse effects of fungicide exposure reduce individual performance at elevated temperatures, thereby allowing mate selection to occur under these conditions. This has significant potential to impact the reproductive success and population dynamics of *L. botrana*. Such behavioural shifts may also reflect a broader ecological phenomenon in which chemical stressors interact with global warming to influence insect life histories and mating mechanisms. In addition, this study provides valuable information into population dynamics under future environmental stress. While no increase in population growth was observed under warmer conditions, the potential adaptive capacity of insects to stressful environments must be considered (Sgrò et al. 2016; Hoffmann 2017; Hill et al. 2021). Overall, our results emphasize the need for further investigation into the collateral effects of agricultural practices, such as fungicide application, in the context of climate change. The interaction between chemical exposure and global warming has the potential to alter insect life cycles, reproductive strategies, and population dynamics in complex and unexpected ways. By shedding light on the complex interactions between global change and fungicide exposure, our research contributes to a deeper understanding of the challenges pest management is facing in an era of rapid environmental change.

Author contributions

TG and JM conceived and designed the research study. TG and ALM maintained the insect stock and conducted the experiments. TG and YL analysed the data. All authors contributed to the writing process and revised the manuscript.

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Data availability Data involved in this study are available upon request.

Declarations

Conflict of interest The authors have no known conflicts of interest to declare.

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