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journal homepage: www.elsevier.com/locate/cropro

# Current and future perspectives on *Lobesia botrana* pest oviposition behavior in the context of climate change and fungicide applications

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ARTICLE INFO

Keywords: Global warming Pest management Viticulture Copper-based fungicide Oviposition behavior

#### ABSTRACT

Climate change-induced temperature increases are likely to promote the spread of insect pests into new regions, requiring adaptations in pest management strategies. Copper-based fungicides are widely used in viticulture to manage fungal diseases, but may also impact non-target insect pests. This study investigated the effects of Bordeaux mixture on the oviposition behavior and egg survival of the grapevine pest Lobesia botrana, under simulated current (2002-2021) and future (2081-2100) climatic scenarios. Laboratory choice and no-choice experiments were conducted to assess oviposition preferences, potential deterrent effects of Bordeaux mixture, and its toxicity to eggs. In the choice experiment, L. botrana females showed significant preference for untreated grapes under both climatic conditions. However, in the no-choice experiment, Bordeaux mixture neither significantly deterred oviposition nor affected egg hatching rate in either scenario. While Bordeaux mixture had minimal influence on oviposition behavior, future climatic conditions significantly reduced female longevity and fecundity. This reduction in reproductive output may suggest lower pest pressure, but accelerated generation turnover and increased voltinism under warmer conditions could amplify pest pressure in the long term. This study provides insights on the collateral effects of Bordeaux mixture on L. botrana under a future climatic scenario and emphasizes the need for further research on its potential impacts on other key life history traits (e.g., development, reproduction). These findings highlight the importance of integrating climate change projections into pest management strategies to ensure sustainable viticultural practices.

# 1. Introduction

Climate change is expected to have significant impacts on agroecosystems (Jägermeyr et al., 2021). By the end of the century, temperatures are projected to increase by 1.4°C–4.4°C, accompanied by substantial changes in precipitation patterns (IPCC, 2023). This will lead to an increase in rainfall in some regions and a decrease in others, thereby raising the risks of floods and droughts (IPCC, 2023). Viticulture, which is highly dependent on meteorological conditions, is particularly sensitive to these environmental changes (Molitor and Junk, 2019). This climatic trend may have a direct impact on most components of the viticultural ecosystem (Reineke and Thiéry, 2016; van Leeuwen et al., 2024), such as the advancement of vine phenology (Fraga et al., 2018), the alteration of aromatic profiles in grapes (Drappier et al., 2017), or the suitability of regions for viticulture (Fraga et al., 2018; Hannah et al., 2013). These changes in weather conditions and their underlying impacts will not be homogeneous across wine-growing regions. While viticulture in southern regions is particularly vulnerable to drought (Santos et al., 2020), regions at higher latitudes, such as Western and Central Europe, may face new challenges, including the emergence of pests and diseases in areas that were previously unaffected (Gutierrez et al., 2018; Reineke and Thiéry, 2016). In addition, milder winters are expected to increase insect pest survival, and warmer conditions in all seasons are likely to accelerate larval

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https://doi.org/10.1016/j.cropro.2025.107198

Received 13 January 2025; Received in revised form 27 February 2025; Accepted 10 March 2025 Available online 11 March 2025 0261-2194/© 2025 The Authors, Published by Elsevier Ltd. This is an open access article under the CC BY licer

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development, which may lead to an increased number of generations within a given year (Caffarra et al., 2012; Reineke and Thiéry, 2016). The damage caused by pests feeding on plant tissue creates favorable conditions for the proliferation of pathogenic fungi, such as downy mildew, powdery mildew, and gray mold, negatively affecting grape production and wine quality (Ioriatti et al., 2012). Given the multiple threats that climate change poses to the long-term sustainability of vineyards, projecting future climate impacts on pest population dynamics and disease prevalence has become a major concern in viticul-tural research.

Fungicides are widely used to prevent fungal diseases in grapevines (Dagostin et al., 2011; ANSES, 2022). Bordeaux mixture, a copper-based fungicide (CuSO<sub>4</sub>), is authorized in both organic and conventional production and is one of the most commonly used (ANSES, 2022; European Commission, 2018; Gessler et al., 2011). Although primarily used to manage fungal infections, Bordeaux mixture can also inadvertently aid in controlling insect pests in vineyards (Vogelweith and Thiéry, 2018). Indeed, this copper-based fungicide has been shown to affect the survival, development, and reproduction of the vinevard pest Lobesia botrana (Lepidoptera, Tortricidae), potentially affecting its population dynamics (Garinie et al., 2024; Nusillard et al., 2024a). However, climatic conditions can influence the impact of these fungicides on non-target pests, as the body temperature and physiological performance of ectothermic insects are closely linked to environmental temperature (Hooper et al., 2013; Martin and Huey, 2008; Sinclair et al., 2016). Indeed, temperature affects the absorption, distribution, metabolism, and excretion of toxic substances in these organisms (Hooper et al., 2013). For instance, warmer temperatures may increase pest tolerance to copper-based fungicides by increasing their immune response (e.g., phenoloxidase activity) or larval survival (Iltis et al., 2022). Although the physiological effects of fungicides on insect pests are well documented (Garinie et al., 2024; Iltis et al., 2022; Margus et al., 2023; Nusillard et al., 2024a; Saifullah et al., 2022), their effects on behavior, particularly oviposition, are poorly understood. In addition, previous studies have examined the interaction of fungicide and temperature effects on the larval and pupal stages (Iltis et al., 2022; Nusillard et al., 2024b), leaving a gap in the understanding of their effects on the adult stage and especially female oviposition behavior.

Oviposition site selection is critical for the reproductive success of phytophagous insects, especially for species whose newly hatched larvae have limited dispersal abilities (Awmack and Leather, 2001). Both olfactory receptors located on the antennae (Tasin et al., 2006) and chemoreceptors, including gustatory receptors on the tarsi and ovipositor, have been extensively studied in L. botrana (Maher and Thiéry, 2004a; Maher and Thiéry, 2006). These sensory receptors enable these insects to detect specific compounds emitted by plants, helping them assess whether plants are suitable as potential hosts. In addition, mechanoreceptors that process tactile cues allow insects to perceive the physical characteristics of plants, such as leaf texture and surface roughness (Maher and Thiéry, 2004a, 2004b; Städler, 1984). The use of fungicides can disrupt most of these cues by altering plant odors, causing olfactory repulsion, or altering the suitability of the oviposition site surface, potentially reducing egg deposition on treated plants (Amat et al., 2024; Carrasco et al., 2015). For example, copper-based fungicides used in olive cultivation have been shown to inhibit oviposition of the olive fruit fly Bactrocera oleae (Diptera, Tephritidae) (Checchia et al., 2022). Similarly, sulfur-based fungicides have been found to deter oviposition in the European grapevine moth L. botrana, with females preferring to lay eggs on untreated grapes when given a choice (Tacoli et al., 2020). This study also showed that the toxicity of these substances can reduce hatching rates. In this context, copper-based fungicides used in viticulture may function as oviposition deterrents, highlighting their potential utility in integrated pest management strategies. However, the combined effects of temperature and fungicide exposure on pest oviposition behavior, as well as their impact on the rate of egg hatching, remain unexplored. Filling this gap is critical to understanding the dynamics of grape pest populations under climate change, including the effects of existing management treatments.

The grapevine moth *L. botrana*, is a major global pest of grapevines worldwide, and its biology and management have recently been reviewed (Benelli et al., 2023a, 2023b; Thiéry et al., 2023). In this species, wild females lay hundreds of fertilized eggs on grapevines, primarily on grape berries, providing the larvae with immediate access to food resources. (Thiéry, 2011). The aim of this study was to evaluate the unexpected effects of Bordeaux mixture on the oviposition behavior and egg survival of L. botrana and to examine how these effects might be influenced by climate change projections for the end of the century. Bordeaux mixture treatments can be applied to grapevines before or after oviposition, depending on the meteorological conditions associated with fungal development. To assess these effects, choice and no-choice experiments were conducted in the laboratory to evaluate the preference of L. botrana for fungicide-treated versus untreated grapes and to determine the deterrent effect of Bordeaux mixture. Additionally, the toxicity of Bordeaux mixture on L. botrana eggs was tested. All experiments were conducted under controlled conditions, with scenarios designed to represent both present-day climates and those expected under future climate change. Previous studies have shown that sulfur dust sprayed on grapes may alter L. botrana oviposition behavior (Tacoli et al., 2020) and that copper-based fungicides can deter oviposition in other pests (Checchia et al., 2022; Mojdehi et al., 2022; Prophetou-Athanasiadou et al., 1991). While Bordeaux mixture does not appear to be toxic to insect eggs (Silva de Armas et al., 2019), high temperatures have been shown to reduce the hatching rate of L. botrana eggs (Kiaeian Moosavi et al., 2017). This study investigates the interaction between Bordeaux mixture applications and temperature conditions, providing insights into the potential impacts of climate change on the oviposition behavior and reproductive success of L. botrana in viticulture.

# 2. Materials and methods

## 2.1. Lobesia botrana rearing

All insects used in the experiments were provided by a laboratory strain of Lobesia botrana (INRAe, Villenave d'Ornon, France). Moth eggs were collected using bands of waxed paper suspended in a cage. When a sufficient number of eggs had accumulated on the surface of the paper, it was transferred to a plastic box containing a semi-artificial diet (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), as described previously (Thiéry and Moreau, 2005). Larvae were kept at a controlled density and monitored daily until pupation. Pupae were weighed on a microbalance (±0.01 mg; SECURA225D-1CFR, Sartorius®, Germany) and individualized in glass tubes (70  $\times$  9 mm diameter) sealed with cotton plugs. Pupae were checked daily, and newly emerged adults were sexed by a visual examination of the ventral tip of the abdomen. Rearing was carried out under standard laboratory conditions (22  $\pm$  1°C, 60  $\pm$  10% relative humidity, under a 16:8 h light:dark photoperiod).

## 2.2. Climatic scenarios

Experiments were conducted in climatic chambers (Memmert HPP260eco, Schwabach, Germany) programmed to replicate both current and future climatic scenarios, with adjustments to temperature, humidity, and photoperiod to reflect conditions representative of Burgundy, Eastern France (Longvic-Dijon weather station, 47.27°N; 5.09°E; altitude = 219 m) (Fig. 1). The two scenarios were designed to simulate summer conditions (July 15th –August 15th), coinciding with the peak activity of *L. botrana* and the associated vineyard damage (Castex et al., 2023; Martín-Vertedor et al., 2010). The regime for the current climatic scenario was based on average hourly values over a 30-day period, based





**Fig. 1.** Abiotic conditions programmed in the climatic chambers to simulate current and future climatic scenarios in terms of: (a) luminosity (%), (b) temperature (°C), and (c) relative humidity (%). The thin orange curves represent the 18 individual climatic models used to generate the mean for the future climatic regime applied in this study (red curves). The red and blue curves correspond to the programmed future and current climatic conditions, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

on data from 20-year period (2002–2021), to represent the average diurnal cycle of temperature and relative humidity. The future climatic scenario was designed to replicate summer conditions in Burgundy at the end of the century (2081–2100). Climatic projections for the future scenario were derived from the average of 18 CMIP6 GCMs (General Circulation Model) run with the SSP5 8.5 scenario, which represents the highest greenhouse gas emission pathway (Calvin et al., 2023). Downscaling and correction of the models were performed using a quantile mapping method, calibrated with data from the Dijon weather station (method described in Zito, 2021). In climatic chambers, abiotic conditions were continuously monitored and controlled (temperature:  $\pm 0.1^{\circ}$ C, relative humidity:  $\pm 5\%$ ).

# 2.3. General procedure

Fertilized females of *L. botrana* were obtained by randomly selecting a 1-day-old virgin female from the general rearing and mating the subject with a two-day-old virgin male in a glass tube ( $100 \times 15$  mm diameter) at dusk (under red light), under standard conditions of temperature ( $22 \pm 1^{\circ}$ C) and humidity ( $60 \pm 10\%$ ). The mating process was monitored for a 3-h period with a camera (Moticam 1080). Analysis of the video allowed the determination of effective mating, which was considered a 'successful mating' when the two subjects remained paired for more than 5 min (Muller and Garinie, personal observation). Three distinct experiments were conducted: (C) choice oviposition trials, (NC) no-choice oviposition trials, and (T) Bordeaux mixture toxicity on eggs. In both (C) choice and (NC) no-choice experiments, fertilized females were retained individually in the mating tube after mating and placed in the climatic chambers (under either future or current conditions) for 24 h before being transferred to the experimental boxes. This procedure ensured that only females that had initiated oviposition were used, thus ensuring that the absence of oviposition during the experiment was due to treatment effects and not a delay in oviposition behavior. The eggs laid in the mating tube prior to the female's transfer to the experimental box were counted to establish a correlation with the number of eggs laid during the experimental trials. Females were transferred directly to their respective experimental boxes immediately after mating for the Bordeaux mixture toxicity to eggs (T) experiment.

# 2.4. Bordeaux mixture spraying

Mature grapes of the cultivar Vittoria (Italy) were used in both the choice (C) and no-choice (NC) experiments. This cultivar was selected for its longer production period compared to other cultivars, ensuring a constant supply of mature grapes throughout the entire duration of the experiments (from October 11 to November 19, 2023). Prior to the bioassays, the grapes were washed in distilled water for 5 min, dried at  $22^{\circ}C \pm 1^{\circ}C$  (room temperature), and stored in a refrigerator at  $7^{\circ}C$  to prevent overripening. The maximum storage time was limited to one week. On the day of spraying, the grapes were removed from the refrigerator 3 h before fungicide application to allow them to reach room temperature, preventing condensation during the application of the Bordeaux mixture. Immediately before spraying, the grapes were divided into bunches of 10 berries and weighed. No significant

difference in mass was observed between untreated samples (C: 79.7  $\pm$  16.6 g; NC: 60.1  $\pm$  16.1 g) and Bordeaux mixture-treated samples (C: 77.8  $\pm$  15.7 g; NC: 57.9  $\pm$  12.4 g), indicating that grape mass did not influence oviposition behavior (C: paired *t*-test, t<sub>54</sub> = -1.780, *p* = 0.077; NC: linear model (LM), *F*<sub>1,109</sub> = 0.648, *p* = 0.423). Plastic sheets (4.5  $\times$  7 cm) were used as a substrate for female oviposition in the Bordeaux mixture toxicity on eggs (T) experiment. Following standard vineyard management practices, Bordeaux mixture (20 g.L<sup>-1</sup>; 20% copper content, BB Caffaro WG) diluted with distilled water was applied to treated grapes and plastic sheets using a glass reagent sprayer (CAMAG). Untreated grapes and sheets were sprayed with distilled water as a control. The grapes and sheets were then dried overnight before being placed in the experimental boxes.

#### 2.5. Oviposition and toxicity experiments

## 2.5.1. Experiment 1: choice oviposition

The choice oviposition trials (current: n = 28; future: n = 27, at least one fertilized egg observed on grapes) were conducted to investigate the oviposition site selection of L. botrana in response to Bordeaux mixture. All the experiments were conducted under the current or future climatic scenarios. An average of seven trials was conducted daily over a nineday period. In each trial, a single mated female (two days old) was presented with two grapes - one treated with Bordeaux mixture and one untreated – inside a box (29 x  $19 \times 15.1$  cm) lined with black felt to prevent oviposition on the plastic surface. Berries from the same grape cluster were used, and the position of the grapes (treated vs. untreated) was alternated between sides for each trial to avoid maturity and position bias, while the boxes were randomly placed within the climatic chamber. The female was allowed to oviposit on both grapes for 24 h. After this oviposition period, the female was transferred from the box to a glass tube (100  $\times$  15 mm diameter), and the grapes were placed separately in plastic boxes (10 x 10 imes 15 cm). Females were monitored daily until death to assess longevity. Ten days after the experiment, the number of eggs laid on each grape was counted, distinguishing hatched eggs (transparent with an empty chorion) from aborted eggs (dead larva visible inside the chorion). The following variables were measured: (i) number of eggs laid on each grape (treated and untreated), (ii) hatching rate, and (iii) longevity of females.

# 2.5.2. Experiment 2: no-choice oviposition

The no-choice oviposition trials (current, treated: n = 26; current, untreated: n = 30; future, treated: n = 26; future, untreated: n = 29, at least one fertilized egg was observed) were conducted to assess oviposition site avoidance by L. botrana in response to Bordeaux mixture spraying under both current and projected future climatic conditions. An average of eleven trials was conducted daily over an eleven-day period. The same protocol was used as in the oviposition choice trials described above, but only one grape - treated or untreated - was presented to a single mated female for 24 h in a box (18 x 11.5  $\times$  7 cm) covered with black felt. The maturity of the berries was assessed by measuring the sugar concentration in the grapes using a refractometer (HHTEC, Brix 0-90%) to avoid any bias related to grape maturity. No significant differences in sugar concentration were found between the experimental conditions (generalized linear model (GzLM), binomial negative distribution, climate:  $LR_{1,109} = \langle 0.001, p = 0.991 \rangle$ ; treatment:  $LR_{1,108} = \langle 0.001, p = 0.940 \rangle$ . The following variables were measured: (i) the number of eggs laid on the grapes, (ii) the hatching rate, and (iii) the longevity of females.

# 2.5.3. Experiment 3: Bordeaux mixture toxicity on eggs

The toxicity of the Bordeaux mixture on the eggs of *L. botrana* was assessed both before and after spraying treatment under current and projected future climatic conditions (current, sprayed before laying: n = 21; current, sprayed after laying: n = 25; current, untreated: n = 23; future, sprayed before laying: n = 24; future, sprayed after laying: n = 2

22; future, untreated: n = 25). An average of thirteen trials was conducted daily over a twelve-day period. Immediately after mating and for a 48-h period, a single female was placed with a band of plastic paper – treated or untreated – in a box (18 x 11.5 × 7 cm) covered with black felt. Half of the untreated papers on which females had laid eggs were sprayed with Bordeaux mixture prior to incubation to assess its toxicity. Ten days later, the eggs were inspected and counted as described above. The following variables were measured: (i) the number of eggs laid on untreated and treated surfaces, (ii) the hatch rate on surfaces before and after spraying treatment and on the untreated surface, and (iii) the longevity of females.

## 2.6. Statistical analyses

A linear mixed-effects model (LMM) was employed for the choice oviposition trials to evaluate the effects of grape type (untreated or treated with Bordeaux mixture) and climatic conditions on the number of eggs laid. The mass of the female and the number of eggs laid before the experiment were included as covariates to control for individual differences in body size and laying history. The response variable, the number of eggs laid, was square-root transformed to meet assumptions of normality and homoscedasticity. The experimental box identity was included as a random effect in the model to address non-independence within the experimental setup. Backward selection based on the Akaike information criterion (AIC) was used to identify the most parsimonious model (Zuur et al., 2009). For the no-choice oviposition trials, a generalized linear model (GzLM) with a quasi-Poisson distribution was used to assess the effect of Bordeaux mixture spraying and climatic scenario on the number of eggs laid on grapes, as this model best fit the data with non-normally distributed egg counts. These factors were included as covariates in the analysis based on the expectation that female pupal mass and the number of eggs laid prior to the no-choice trial could influence the number of eggs laid during the test. For each experiment (i.e., C, NC, and T), a linear model (LM) was used to analyze the effect of Bordeaux mixture spraying and climatic scenarios on the female longevity, and the total number of eggs laid throughout the female's lifespan. When residuals did not meet normality assumptions, log or square-root transformations were applied to improve data distribution. If these transformations did not achieve normality, a GzLM was used with a quasi-Poisson or negative binomial distribution, depending on which provided the best fit to the data. For the hatching rate, GzLM was employed with a quasi-binomial or negative binomial distribution. Pupal mass was included as a covariate in each test. All statistical analyses were performed using the R software (4.3.2, R Core Team, 2023). The MASS (Venables and Ripley, 2002) and lme4 (Bates et al., 2015) packages were used for the corresponding analyses.

## 3. Results

#### 3.1. Experiment 1: choice oviposition

Females laid significantly more eggs on untreated grapes compared to grapes sprayed with Bordeaux mixture under both climatic conditions (Fig. 2a; LMM,  $\chi_1^2$ =6.164, p = 0.013). The effect of climatic conditions on egg-laying was not significant (Fig. 2a; LMM,  $\chi_1^2$  = 0.060, p = 0.807). On average, 58% of the eggs were laid on untreated grapes and 42% were laid on treated grapes across both climatic conditions. The number of eggs laid prior to the experiment significantly influenced the number of eggs laid during the experiment (LMM,  $\chi_1^2$  = 6.638, p = 0.010), with a decrease in egg-laying observed as the number of pre-experiment eggs increased ( $\beta$  = -0.024, p = 0.013). Additionally, the number of eggs laid was not influenced by females' mass (LMM,  $\chi_1^2$  = 3.721, p = 0.054).

## 3.2. Experiment 2: no-choice oviposition

The number of eggs laid was not significantly different between



**Fig. 2.** Number of eggs laid on untreated grapes (green) compared to grapes sprayed with Bordeaux mixture (blue) under two climatic scenarios (current and future); with **(a)** choice and, **(b)** no-choice experiments. The horizontal edges of the rectangles represent the first and third quartiles, the horizontal line inside the box indicates the median, the black circle represents the mean, and the vertical lines extend to the minimum and maximum values within the data range. Asterisks highlight significant differences (\*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05, n.s. non-significant). Numbers (*n*) above grapes and moths refer to the number of females tested. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

untreated grapes and grapes treated with Bordeaux mixture in either the current or future climatic scenarios (Fig. 2b; GzLM, quasi-Poisson distribution,  $F_{1,108} = 1.976$ , p = 0.163). However, females laid fewer eggs in the current climatic scenario (-18%) compared to the future climatic context ( $F_{1,107} = 11.4$ , p = 0.001). The decrease in oviposition on grapes depended on the number of eggs laid in the mating tube before the female's contact with the grape ( $F_{1,106} = 44.604$ , p < 0.001). Specifically, a higher number of eggs laid in the tube was associated with a lower number of eggs laid on the grapes. Overall, the number of eggs laid increased with female pupal mass ( $\beta = 0.074$ , p = 0.001).

## 3.3. Experiment 3: Bordeaux mixture toxicity on eggs

The proportion of hatching eggs was not affected by the Bordeaux mixture treatment, regardless of whether it was applied before or after egg-laying, with an average hatching rate of  $91 \pm 13\%$  (Table 1; GzLM, quasi-binomial distribution,  $F_{2,136} = 0.435$ , p = 0.648). Similarly, climatic scenarios and female mass had no effect on hatching rate (Table 1,  $F_{1,138} = 2.018$ , p = 0.158;  $F_{1,135} = 0.102$ , p = 0.750). These findings were consistent across both choice and no-choice experiments. In both cases, Bordeaux mixture treatments did not influence egg hatchability (Table 1, C: GzLM, quasi-binomial distribution,  $F_{1,105} = 0.045$ , p = 0.686; NC: GzLM, negative-binomial distribution,  $LR_{1,108} = 0.893$ , p = 0.345) as well as climatic scenarios (Table 1, C: GzLM, negative-binomial distribution,  $LR_{1,108} = 0.686$ ; NC: GzLM, quasi-binomial distribution,  $LR_{1,109} = 0.048$ , p = 0.686; NC: GzLM, quasi-binomial distribution,  $LR_{1,109} = 0.048$ , p = 0.827)

## 3.4. Longevity and number of eggs laid throughout the lifespan

Across the three experiments (C, NC, and T), female longevity was significantly lower under future climatic conditions compared to the current climatic conditions (on average, -34%; Fig. 3a; (C) LM,  $F_{1,49} = 51.978$ , p < 0.001; (NC)  $F_{1,101} = 181.748$ , p < 0.001; (T)  $F_{1,134} = 134.028$ , p < 0.001) and laid fewer eggs (on average, -18%) (Fig. 3b; (C) GLM, quasi-Poisson distribution,  $F_{1,51} = 4.871$ , p = 0.032; (NC) GLM, quasi-Poisson distribution,  $F_{1,100} = 9.384$ , p = 0.003; (T) LM,  $F_{1,134} = 37.466$ , p < 0.001). In contrast, Bordeaux mixture had no significant effect on female longevity (Fig. 3a; (NC) LM, log-transformation,  $F_{1,101} = 0.114$ , p = 0.737; (T) LM, root-square transformation,  $F_{2,134} = 0.336$ , p = 0.716) or the total number of eggs laid during the female's lifespan (Fig. 3b; (NC)  $F_{1,99} = 1.311$ , p = 0.255; (T)  $F_{2,134} = 0.071$ , p = 0.932).

## 4. Discussion

The aim of this study was to evaluate the effects of the copper-based fungicide, Bordeaux mixture, on the oviposition behavior and egg survival of *Lobesia botrana* and to investigate how these effects may respond to future climatic conditions projected for the end of the century. We found that females showed a slight preference for ovipositing on untreated grapes regardless of the climatic scenario. Despite this

## Table 1

Hatching rate (%) across experiments under two climatic conditions (current or future) and treatments (untreated or treated with Bordeaux mixture applied either before or after egg laying). Values are presented as mean  $\pm$  standard deviation (SD), with sample sizes indicated in parentheses (*n*).

Current	Untreated	Treated before	Treated after
No-choice (NC) Choice (C) Toxicity (T)	$\begin{array}{l} 99.5\pm0.9~(26)\\ 96.8\pm5.8~(28)\\ 92.8\pm13.1~(23) \end{array}$	$\begin{array}{c} 96.5\pm 6.8~(29)\\ 96.9\pm 5.8~(28)\\ 90.3\pm 14.1~(21) \end{array}$	- - 94.3 ± 10.1 (25)
Future			
No-choice (NC) Choice (C) Toxicity (T)	$\begin{array}{c} 97.9 \pm 2.5 \ (26) \\ 96.1 \pm 8.1 \ (27) \\ 86.8 \pm 15.1 \ (25) \end{array}$	$\begin{array}{c} 97.9 \pm 4.7 \ (29) \\ 96.5 \pm 7.4 \ (25) \\ 92.0 \pm 6.4 \ (24) \end{array}$	- - 90.0 ± 15.7 (22)

preference, there was no evidence of a deterrent effect of the Bordeaux mixture under either climatic condition, and the fungicide did not induce significant toxicity in the eggs. These results indicate that the fungicide does not have a substantial collateral impact on *L. botrana* oviposition. However, future climatic conditions significantly decreased female longevity and total fecundity, meaning fewer eggs laid per generation but potentially accelerating the pest's life cycle and increasing voltinism.

Females showed a preference for laying their eggs on untreated grapes when given a choice, suggesting that they can detect grapes sprayed with Bordeaux mixture and prefer not to oviposit on them. This discrimination is likely mediated by visual, olfactory, or tactile cues emitted by the Bordeaux mixture, which may signal an unsuitable substrate for egg deposition (Städler, 2008). Lobesia botrana relies on olfactory cues to locate grapes, which play a crucial role in shaping its oviposition behavior (Tasin et al., 2011). Changes in the odor profile of Vitis vinifera plants have been reported to inhibit the attractiveness of these plants to L. botrana (Salvagnin et al., 2018). David et al. (2022) reported that fungicide odor pollution might disrupt bumblebee floral odor recognition by interfering with their ability to learn and respond to plant signals. We hypothesized that the Bordeaux mixture odor may interact with the grape's natural odor profile, potentially exerting a deterrent effect or inhibiting plant recognition, which could explain the preference for laying eggs on untreated grapes. However, while odor may play a role in oviposition site selection, visual and tactile cue stimuli are also known to interact with olfaction in this process (Tasin et al., 2011). The small surface area of our set-up meant that females inevitably encountered both grapes, suggesting that oviposition decisions were more likely influenced by post-landing cues rather than pre-landing stimuli. Indeed, after landing, L. botrana females use sensory structures located at the tips of their legs, proboscis, antennal tips, and the ventral surface of the ovipositor to detect physical (i.e., mechanoreceptors) and chemical (i.e., chemoreceptors) stimuli (Maher and Thiéry, 2004a). Mechanoreceptors assess the roughness and shape of the substrate, while chemoreceptors detect various chemicals (Maher and Thiéry, 2004a, 2004b). The surface of the oviposition site is important for egg fixation, and it has been shown that its texture and physical properties can influence this process (Maher and Thiéry, 2004a; Al Bitar et al., 2012). The Bordeaux mixture creates a protective coating on the grapes that can be detected by mechanoreceptors. This coating may be perceived as a barrier, potentially preventing egg deposition and prompting females to choose a more suitable surface. Additionally, chemoreceptors may chemically and gustatorily detect Bordeaux mixture upon contact, which could further inhibit oviposition (Amat et al., 2024). Interestingly, climatic conditions did not influence the preference of females to lay eggs on untreated or treated grapes, suggesting no effect of temperature on their ability to discriminate between the two.

Lobesia botrana showed a significant preference for untreated grapes. Specifically, an average of 58% of the eggs were laid on untreated grapes compared with 42% on treated grapes, indicating that Bordeaux mixture does not act as a strong repellent for L. botrana oviposition. In line with the small effect of the Bordeaux mixture in the choice experiment, the oviposition behavior of L. botrana females was not affected by the Bordeaux mixture, regardless of whether the grapes were treated or untreated in the no-choice experiment. This result was consistent under both current and future climatic scenarios, supporting the hypothesis that Bordeaux mixture does not act as a deterrent to this moth under any climatic conditions. The absence of a repellency effect from this copperbased fungicide contrasts with findings from previous studies. Prophetou-Athanasiadou et al. (1991) and Mojdehi et al. (2022) reported that copper hydroxide, another copper-based fungicide, deterred oviposition in the olive fruit fly Bactrocera oleae (Diptera). The differences in the deterrent effect observed may be attributed to the type of copper-based fungicide used in our study, which employed copper sulfate. In addition, variations in copper concentrations may also contribute to the observed



**Fig. 3.** Life history traits measured in (i) choice, (ii) no-choice, and (iii) toxicity experiments under current (blue) and future (red) climatic scenarios as a function of the treatment to which females were exposed: **(a)** female longevity (day), **(b)** number of eggs laid during the lifespan of females. C: current, F: future, U: untreated, BM: Bordeaux mixture, BMB: Bordeaux mixture sprayed before laying, BMA: Bordeaux mixture sprayed after laying. The horizontal edges of the rectangles represent the first and third quartiles, the horizontal line inside the box indicates the median, the black circle represents the mean, and the vertical lines extend to the minimum and maximum values within the data range. Asterisks highlight significant differences (\*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05, n.s. non-significant). Numbers associated with boxes correspond to the number of fertilized females tested. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

differences, as the concentration used in the study by Prophetou-Athanasiadou et al. (1991) (1%) was higher than the concentration applied in our study (0.4%). Furthermore, the deterrent effect of copper-based fungicides may be species-specific, as Lepidoptera and Diptera are likely to have different sensitivities to copper-based compounds. However, we can also hypothesize that the toxicity of the substance is partly responsible for the repellent effect of the fungicide. For example, Tacoli et al. (2020) reported that sulfur dust, another fungicide widely used in viticulture, had a repellent effect on L. botrana oviposition while also showing significant toxicity to eggs. The minimal effect of the Bordeaux mixture on oviposition and the absence of any effect on egg development likely also explain the limited selectivity observed in our experiments. Another factor that could explain the slight preference for untreated grapes is the number of eggs laid by females prior to their contact with the grapes, a design feature intended to confirm female fecundity. Indeed, analysis showed that the reduction in oviposition on grapes was influenced by the number of eggs already laid before the females encountered the grapes. This suggests that prior egg deposition may influence the results by reducing the remaining egg-laying capacity of the females, which in turn may influence their choice of grapes for oviposition. To minimize this potential bias, females should be placed directly with the grapes to ensure that the grapes are the first oviposition substrate they encounter.

Although this study revealed that Bordeaux mixture exerts moderate side effects on the oviposition behavior of L. botrana, climatic conditions were found to have a substantial influence on the female's life history traits. Female longevity was significantly reduced under future climatic conditions, leading to a shorter egg-laying period compared to current climatic conditions. Consistent with findings in previous Lepidoptera studies (Geng and Jung, 2017; Liang et al., 2021; Sampaio et al., 2024), in our study, rising temperatures were found to reduce the lifespan of L. botrana, thereby shortening their oviposition period and decreasing fecundity over their lifespan (-18% eggs under future climatic conditions). Despite this decline in fecundity under future climatic conditions, the number of larvae hatching remained high, with an average of 95 larvae under future conditions compared to 116 under current conditions. Interestingly, studies by Iltis et al. (2022) and Nusillard et al. (2024b) have shown that L. botrana larvae develop more rapidly under future climatic scenarios, potentially increasing the number of pest generations per year. This accelerated development heightens the risk of pest damage in viticulture, as faster population growth and elevated pest pressure are likely outcomes. While our study focused on the unintended effects of Bordeaux mixture on oviposition behavior, it did not evaluate the fungicide's toxicity to newly hatched larvae. Future research should assess the potential toxic effects on larvae to fully understand the implications of Bordeaux mixture on insect development. A previous study

on *L. botrana* under constant temperature conditions (22°C) showed that larval ingestion of Bordeaux mixture reduced survival rates and slowed their development (Garinie et al., 2024). In contrast, Iltis et al. (2022), found that under fluctuating temperatures, larvae of L. botrana ingesting low concentrations of Bordeaux mixture exhibited improved survival and enhanced immune activity under future climatic conditions. However, they also showed that the fungicide continued to slow larval development, even as the developmental period was shortened by approximately 10 days under future compared to current conditions. Further research is needed to fully understand the implications of Bordeaux mixture on L. botrana in the context of climate change. Future studies should explore not only the combined effects of Bordeaux mixture and temperature on larval development and survival but also the potential long-term impacts on adult fitness, reproduction, and population dynamics. A comprehensive assessment of these factors will be crucial for evaluating the broader consequences of Bordeaux mixture use on pest populations and viticultural sustainability under changing climatic conditions.

# 5. Conclusion

This study provides valuable insights into the oviposition behavior of Lobesia botrana in the context of copper-based fungicide (Bordeaux mixture) applications and climate change. Our results showed that Bordeaux mixture had no effect on egg survival or the overall reproductive output of L. botrana, indicating that the copper-based fungicide does not influence L. botrana oviposition in viticultural practice. Moreover, these findings provide insights into potential pest dynamics in vineyards under future climatic change scenarios. Under both current and future climatic conditions, L. botrana exhibited only a marginal inclination toward laying eggs on untreated grapes as opposed to those treated with Bordeaux mixture. However, while warmer temperatures were associated with a reduction in reproductive output, this initially lower pest pressure can be offset by other factors. Previous studies reported that shorter lifespans due to higher temperatures could accelerate generation turnover and increase the number of L. botrana generations per year (i.e., increased voltinism), thereby intensifying pest pressure (Iltis et al., 2019; Martín-Vertedor et al., 2010; Reineke and Thiéry, 2016). Moreover, our results revealed that temperature did not negatively affect egg survival, indicating that L. botrana can maintain high survival rates even under future environmental conditions. This combination of factors could exacerbate the threat posed by L. botrana in the future, emphasizing the urgent need for adaptive management strategies in viticulture.

## CRediT authorship contribution statement

Tessie Garinie: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Yann Lelièvre: Writing – review & editing, Methodology, Conceptualization. William Nusillard: Writing – review & editing. Sébastien Zito: Writing – review & editing, Formal analysis, Conceptualization. Denis Thiéry: Writing – review & editing, Resources, Conceptualization. Jérôme Moreau: Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

# **Ethics approval**

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

# Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments and funding

We thank Lionel Delbac and Louis Gross from "UMR 1065 Santé et Agroécologie du Vignoble" who maintained and managed the insect stock. This work was supported by the *Conseil Régional de Bourgogne Franche-Comté* through the "Project ESITE BFC PESTICLIM – LOUAPRE".

#### Data availability

Data will be made available on request.

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