



# Biological control in a changing climate: plant-mediated impact of elevated CO<sub>2</sub> concentration on *Lobesia botrana* eggs and egg parasitism by *Trichogramma cacoeciae*

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## Abstract

Climate change can affect biological pest control by altering trophic interactions. Elevated carbon dioxide (CO<sub>2</sub>) concentrations can reduce host plant quality and, in turn, alter herbivore and natural enemy preference and performance. Using the Geisenheim VineyardFACE (free-air carbon dioxide enrichment) facility, we studied plant- and herbivore-mediated bottom-up effects of elevated CO<sub>2</sub> concentration on the European grapevine moth, *Lobesia botrana*, and the parasitoid *Trichogramma cacoeciae*. Grapevine inflorescences of two cultivars cultivated at ambient or elevated CO<sub>2</sub> (aCO<sub>2</sub> and eCO<sub>2</sub>: 400 and 480 ppm) in the VineyardFACE were incorporated into *L. botrana* artificial diet. Eggs laid by the respective adults were parasitized by *T. cacoeciae*. Egg size and emergence rate of *L. botrana* as well as parasitism rate, parasitoid emergence rate and egg size preference of *T. cacoeciae* were evaluated. We observed an indirect grapevine cultivar-dependent bottom-up effect of CO<sub>2</sub> on both herbivore and egg parasitoid. Compared to aCO<sub>2</sub>, eCO<sub>2</sub> resulted in larger host eggs and higher parasitism rates regarding Riesling-feeding but not regarding Cabernet Sauvignon-feeding *L. botrana* larvae. Parasitoid emergence rate was higher when *L. botrana* had fed on Riesling compared to Cabernet Sauvignon-diet. Egg size preference depended on the host's diet: *T. cacoeciae* preferred larger *L. botrana* eggs when the larvae had fed on grapevine-containing diet but not when they fed on standard artificial diet. Our results highlight the importance of the host's diet for the parasitoid's preference and performance. They furthermore suggest that the future efficiency of *L. botrana*-biocontrol by *T. cacoeciae* will not decrease under elevated CO<sub>2</sub> concentrations.

**Keywords** Tritrophic system · FACE · Egg parasitoid · Climate change · Carbon dioxide · Bottom-up effects

## Introduction

The Anthropocene is accompanied by drastic changes in our climate, caused by increasing emissions of greenhouse gases leading to rising temperatures (IPCC 2022). Rising temperatures, increasing carbon dioxide (CO<sub>2</sub>) concentrations, and changing precipitation patterns can severely affect food security (Hoegh-Guldberg, Jacob et al. 2018). Climate change has also the potential to affect food webs through bottom-up effects: abiotic factors that induce changes on the plant level can affect preference and performance of

herbivores and, as a result, of natural enemies (Rosenblatt and Schmitz 2016; Han et al. 2019).

In this regard, elevated CO<sub>2</sub> concentrations can affect plant nutritional quality and defense compounds (Denno et al. 2002; Bidart-Bouzat and Imeh-Nathaniel 2008). A higher carbon (C) to nitrogen (N) ratio due to elevated atmospheric CO<sub>2</sub> concentrations generally reduces the nutritional value of plant tissue to the second trophic level: herbivores (Facey et al. 2014). They depend on plant-derived nitrogen, among other nutrients, and lower concentrations of nitrogen can lead to compensatory feeding and/or negatively impact herbivore performance (Stiling and Cornelissen 2007). At the same time, plant defense compounds, notably carbon-based phenolic compounds, can be present in higher concentrations in response to elevated CO<sub>2</sub> (Stiling and Cornelissen 2007). In consequence, herbivorous insects themselves can be of lower host quality to the third trophic level, e.g., natural enemies like parasitoids, due to

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higher C:N ratio and the accumulation of plant defense compounds they ingested with their diet (Hilker and Meiners 2002; Facey et al. 2014; Rosenblatt and Schmitz 2016). This can affect the natural enemies' performance as biocontrol agents (Han et al. 2019).

While elevated CO<sub>2</sub> concentrations definitely have the potential to trigger bottom-up effects on the third trophic level, reports have been mixed so far, including positive effects on parasitoid abundance (Hillstrom and Lindroth 2008), no effects on parasitoid performance (Schulze-Sylvester and Reineke 2019; Moreno-Delafuente et al. 2021), or negative effects on parasitoid performance and fitness (Klaiber et al. 2013).

Studying such tritrophic interactions can yield important insight into underlying mechanisms of pest management (Castex et al. 2018) and on the future efficacy of biological control programs. However, not much research has been undertaken so far on the host plant-mediated effects of elevated CO<sub>2</sub> on higher trophic levels and the experimental setup of realistic scenarios is technically challenging. Free-Air Carbon dioxide Enrichment (FACE) facilities with cultivated crop plants present a very interesting setting to study the effect of elevated CO<sub>2</sub> on such tritrophic interactions of relevance for biological pest control.

The European grapevine moth, *Lobesia botrana* (Denis & Schiffmüller; Lepidoptera: Tortricidae), is the major insect pest in vineyards in Europe and has demonstrated its invasive potential in wine-growing regions worldwide (Ioriatti et al. 2011; Gutierrez et al. 2012). The larvae of this polyphagous, multivoltine pest feed on different phenological stages of grapevine reproductive organs, often accompanied by the necrotrophic fungus *Botrytis cinerea*, potentially inflicting severe economic damage on grapevine harvests (Moschos 2005; Ioriatti et al. 2011). The parasitic wasp *Trichogramma cacoeciae* (Marchal; Hymenoptera: Trichogrammatidae) is an egg endoparasitoid of *L. botrana*, naturally occurring in vineyards (Barnay et al. 2001). It is employed as a biocontrol agent in vineyards, using an inundative approach (Thiéry et al. 2018).

In grapevine, higher photosynthetic assimilation rates under elevated CO<sub>2</sub> have been documented (Wohlfahrt et al. 2018) alongside changes in berry chemical composition due to elevated CO<sub>2</sub> concentrations, especially in the unripe developmental stages which are of highest relevance to *L. botrana* larval feeding in Central Europe (Bindi et al. 2001; Wohlfahrt et al. 2021). Declining plant nutritional quality due to potentially higher C:N ratio and concentrations of phenolic defense compounds is very likely to affect *L. botrana* feeding on grapevine (Castex et al. 2018).

Since adults of *L. botrana* rarely feed, the nutrients taken up with the larval diet are crucial for all subsequent development stages and are the basis for the nutrient content of their eggs, i.e., the development of the next generation. This has been

demonstrated for *Amphion floridensis* (Hübner; Lepidoptera: Sphingidae) (O'Brien et al. 2002). Offspring of egg parasitoids such as *T. cacoeciae* are confined to the egg their mother chose for oviposition until they emerge as adults. Hence, they are dependent on the nutrients present in the egg at the moment of oviposition and, at the same time, potentially challenged by plant defense compounds that may have been carried along from one trophic level to the next or even have been enriched in this process (Hilker and Meiners 2002; Castex et al. 2018). Egg size has been suggested as one of the parameters used by egg parasitoids to judge the egg's quality for their offspring's development (Vinson 1994; Moreau et al. 2009).

It is well documented that *Trichogramma*-egg parasitism can be affected by the larval diet of *L. botrana* when feeding on different grapevine cultivars or different host plant species (Moreau et al. 2009; Thiéry and Desneux 2018). Yet, the question remains if CO<sub>2</sub>-induced changes in plant quality will propagate up to higher trophic levels and affect the parasitism preference and/or success of *T. cacoeciae* on *L. botrana* eggs which could have consequences of future biological control programs.

To elucidate if elevated atmospheric CO<sub>2</sub> concentration has an indirect effect on *T. cacoeciae* parasitism on *L. botrana* eggs, we investigated the following hypotheses:

- (1) The size of *L. botrana* eggs is affected by the grapevine cultivar of their larval diet and the CO<sub>2</sub> concentration during cultivation of those plants.
- (2) Parasitism preference of *T. cacoeciae* depends on the size of *L. botrana* eggs.
- (3) The parasitism rate of *T. cacoeciae* on *L. botrana* eggs and the parasitoid emergence rate are affected by the grapevine cultivar of the *L. botrana*-larval diet and the CO<sub>2</sub> concentration during cultivation of those plants.

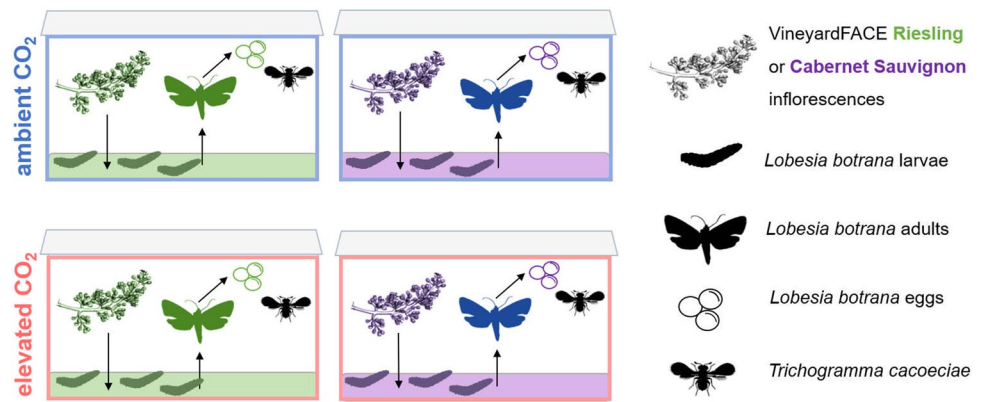
In order to address these hypotheses, we collected grapevine reproductive organs in a VineyardFACE facility where two different grapevine cultivars (Riesling and Cabernet Sauvignon) are cultivated under current (ca. 400 ppm) and elevated CO<sub>2</sub> concentrations (ca. 480 ppm) that are expected in the near future. We incorporated the plant material into the artificial diet of *L. botrana*. Eggs laid by adults after larval feeding on these diets for one generation were subjected to parasitism by *T. cacoeciae*. This experimental procedure is summarized in Fig. 1.

## Material and methods

### Plant material

Grapevine inflorescences were obtained from the Geisenheim VineyardFACE facility which was established in 2011

**Fig. 1** Visual summary of the experimental procedure. Grapevine inflorescences from the Geisenheim VineyardFACE were incorporated into artificial diet. *Lobesia botrana* larvae were raised on the respective diets and standard artificial diet as control. Eggs produced by the respective adults were then parasitized by *Trichogramma cacoeciae*



at Geisenheim University, Germany (49°59'N, 7°57'E; 96 m above sea level) and consists of six ring-frame structures each with an inner diameter of 12 m, of which three are under elevated CO<sub>2</sub> (eCO<sub>2</sub>, ca. 480 ppm) and three under ambient CO<sub>2</sub> (aCO<sub>2</sub>, ca. 400 ppm) concentration. Each ring contains seven rows of grapevine *Vitis vinifera* L. 'Riesling' and 'Cabernet Sauvignon' plants, with a total of 32 grapevine plants per ring and variety. For a detailed description of the Geisenheim VineyardFACE facility, see publications by Reineke and Selim (2019) and Wohlfahrt et al. (2018). The vineyard is managed according to the principles of good agricultural practice and integrated pest management in viticulture. Inflorescences of both grapevine cultivars and CO<sub>2</sub> concentrations were harvested from three plants per cultivar and FACE ring in early summer 2018, at BBCH code 60 ("beginning of flowering" according to Lorenz et al. (1995)). Inflorescences were pooled per cultivar and FACE ring and stored at -20 °C until they were lyophilized and ground to a fine powder.

## Insects

The *L. botrana* colony was maintained at Geisenheim University, Geisenheim, Germany, that is regularly supplemented with additional *L. botrana* genotypes either collected in vineyards or received from other laboratory strains outside Geisenheim. Larvae were cultured in groups in plastic boxes (20 × 15 cm and 9 cm high) in an insect rearing room (24 ± 1 °C; 40 ± 12% relative humidity; light/dark photoperiod: 16:8 h) and were fed ad libitum with a modified semi-synthetic diet according to the general-purpose diet of Singh and Moore (1985) that will in the following be referred to as "standard artificial diet" (SAD; for ingredients see Table 1). Eggs from this colony were maximum 24 h old when used in the experiment.

The *T. cacoeciae* colony was kept in a climate cabinet at 25 °C, 70% RH, light/dark photoperiod 12:12 h, representing optimal conditions for this species. A starter set of parasitoids was obtained from a commercial supplier of

**Table 1** Ingredients of the different artificial diets *L. botrana* larvae were raised on

Standard artificial diet (SAD)		Grapevine-based artificial diet (GAD)	
		Freeze-dried grapevine inflorescences	10.05 g
Water	100 ml	Water	100 ml
Agar	3.30 g	Agar	2.50 g
Lucerne	4.17 g		
Wheat germ	15.59 g	Wheat germ	0.83 g
Yeast	3.17 g	Yeast	4.55 g
Wesson's salt	2.04 g	Wesson's salt	0.34 g
Sugar	6.17 g		
Casein	7.34 g		
Sunflower oil	1.67 ml		
Cholesterol	0.21 g		
Sorbic acid	0.34 g	Sorbic acid	0.37 g
Vitamine C	0.04 g	Vitamin C	0.61 g
Multivitamins	0.47 g		
Nipagin	0.21 g	Nipagin	0.28 g
Ethanol 70%	1 ml	Ethanol 70%	1 ml
Propionic acid	1 ml		
		Maize flour	1.69 g

biological control agents (AMW Nützlinge, Pfungstadt, Germany). The thelytokous *T. cacoeciae* strain was reared for at least 14 generations on eggs from the laboratory colonies of *L. botrana*. A subsection of parasitized eggs was set aside in empty glass tubes. They were checked daily and hatched adults were removed into new glass tubes, separated by day of emergence, to obtain parasitoids of defined age (max. 24 h) for the experiment.

## Parasitism experiment

Eggs from the *L. botrana* lab colony, max. 24 h old, were transferred into boxes containing a modified version of the standard artificial diet in which the freeze-dried and ground

plant material was incorporated (plant samples were pooled per cultivar and CO<sub>2</sub> concentration; for ingredients, see Table 1). The diet was developed based on the recipe published by Muller et al. (2015). In the following, this will be referred to as “grapevine-based artificial diet” (GAD). For each cultivar and CO<sub>2</sub> concentration, a separate box was prepared, resulting in four experimental diets (Table 1). Larvae of *L. botrana* were raised on the respective GAD and treated like the lab colony for the remaining development, including pupation, hatching, mating, and oviposition. Eggs were laid on a plastic film covering the large container in which the adults hatched and mated.

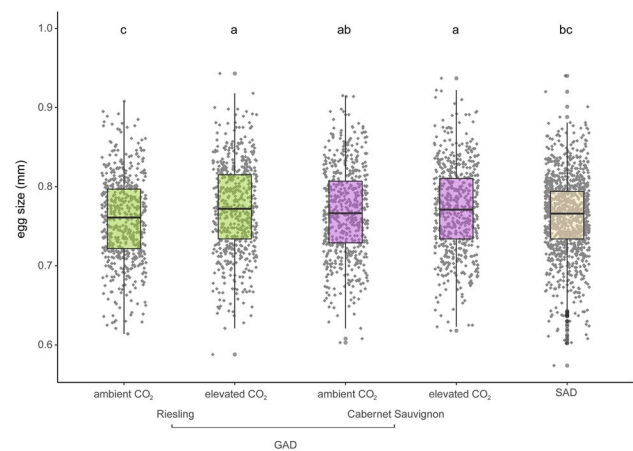
Pieces of plastic film carrying 30 freshly laid (max. 24 h old) eggs were cut and transferred into glass vials (70×30 mm) that were covered with a thin fabric allowing air exchange. Per vial, a single *T. cacoeciae* individual was added for 24 h, together with a droplet of honey agar to prevent host feeding. Only vials in which the parasitoid was still alive after 24 h were included in the experiment. To separate parasitized from non-parasitized eggs and to avoid cannibalism, eggs were transferred into boxes containing artificial diet for six days, which lured hatching larvae away from the eggs. Afterward, apparently parasitized eggs were transferred into boxes with water agar (300 ml water, 6 g agar, 0.75 g nipagin, and 1.5 ml ethanol 70%) to improve the microclimate. For 16–19 days we counted the number of emerging *L. botrana* larvae, the number of black (i.e., parasitized) eggs, and the number of emerged *T. cacoeciae* parasitoids. As a control, we observed how many larvae hatched from *L. botrana* eggs treated the same way but without parasitoids. This was repeated until 80 replicates per experimental diet were obtained, both with and without parasitism. The same setup was used to evaluate *T. cacoeciae* parasitism on *L. botrana* eggs after larvae were reared on SAD, however with a reduced number of replicates ( $N=40$ ).

## Egg size

Before being transferred into the vials for parasitism, the length of 600 eggs per experimental diet was measured under the microscope (EZ4W, Leica Microsystems AG, Switzerland) using the LAS 3.4.0 software. After parasitism, eggs were checked again under the microscope to assess which of the differentially sized eggs had been parasitized.

## Statistics

For statistical analyses, we used RStudio version 1.4.1717 (RStudioTeam 2020). One-factorial generalized linear models (GLM) from the Gamma family with inverse-link were used to investigate if the size differed between those eggs that were parasitized and those that were not. One-factorial GLM from the binomial family with logit-link were used to



**Fig. 2** Size of eggs (length in mm) laid by *Lobesia botrana* adults that were raised on standard artificial diet (SAD) or grapevine-based artificial diet (GAD) containing inflorescences of the cultivar Riesling or Cabernet Sauvignon, cultivated at ambient (ca. 400 ppm) or elevated (ca. 480 ppm) CO<sub>2</sub> concentrations in the Geisenheim Vineyard-FACE. Identical letters indicate that no significant differences were detected (GLM, Tukey contrasts;  $N=600$ )

investigate if the *L. botrana* larval emergence rate with and without parasitism, *T. cacoeciae* parasitism rate and parasitoid emergence rate differed between GAD diets and SAD. Two-factorial GLM from the binomial family with logit-link were used to investigate the effect of CO<sub>2</sub> concentration and cultivar on *L. botrana* larval emergence rate with and without parasitism, *T. cacoeciae* parasitism rate and parasitoid emergence rate. Two-factorial GLM from the Gamma family with inverse-link were used to investigate their effect on *L. botrana* egg size. For multiple comparisons of means, Tukey contrasts were used. A significance level of  $\alpha=0.05$  was assumed.

## Results

### Effects of larval diet on insect host

**Egg size.** After feeding on GAD containing eCO<sub>2</sub>-Riesling inflorescences (GAD + eCO<sub>2</sub>-Riesling) in the larval developmental stage, *L. botrana* eggs were larger than after larval feeding on GAD + aCO<sub>2</sub>-Riesling, whereas egg size did not differ significantly after larval feeding on GAD containing Cabernet Sauvignon cultivated under ambient or elevated CO<sub>2</sub> concentration ( $\chi^2_4=0.13$ ,  $p<0.0001$ ; Fig. 2). The two-factorial evaluation did not reveal further details (CO<sub>2</sub>:  $\chi^2_1=0.06$ ,  $p=0.0005$ ; cultivar:  $\chi^2_1=0.02$ ,  $p=0.06$ ; cultivar \* CO<sub>2</sub>:  $\chi^2_1=0.02$ ,  $p=0.03$ ). Eggs laid by adults after larval feeding on SAD had approximately the same size as those produced after feeding on GAD + aCO<sub>2</sub>-grapevine inflorescences but were smaller than those laid after larval



feeding on GAD + eCO<sub>2</sub>-grapevine ( $\chi^2_4 = 0.13$ ,  $p < 0.0001$ ; Fig. 2).

**Larval emergence rate.** Without parasitoids, the emergence rate of *L. botrana* larvae from eggs laid by adults after larval feeding on different GAD did not differ significantly due to grapevine cultivar or CO<sub>2</sub> concentration but were mostly larger than eggs laid after feeding on SAD (except for eggs laid after feeding on GAD + aCO<sub>2</sub>-Cabernet Sauvignon;  $\chi^2_4 = 37.6$ ,  $p = 0.0006$ ; Fig. 3A). The two-factorial evaluation additionally showed a tendency toward a slightly higher emergence rate after larval feeding on GAD + Riesling than on GAD + Cabernet Sauvignon (on average 87.8 and 86.4%, respectively, cultivar:  $\chi^2_1 = 3.7$ ,  $p = 0.06$ , CO<sub>2</sub>:  $\chi^2_1 = 0.41$ ,  $p = 0.52$ ; cultivar \* CO<sub>2</sub>:  $\chi^2_1 = 2.5$ ,  $p = 0.11$ ). Without parasitoids, the average larval emergence rate from eggs laid by adults after larval feeding on different GAD was  $87 \pm 0\%$  and, therefore, the egg abortion rate was  $13 \pm 0\%$  (mean  $\pm$  standard error).

With parasitoids present, the emergence rate of *L. botrana* larvae from eggs produced after larval feeding on different GAD was higher on GAD + aCO<sub>2</sub>-Riesling than on GAD + eCO<sub>2</sub>-Riesling; whereas it was not significantly different after feeding on GAD containing Cabernet Sauvignon cultivated under ambient or elevated CO<sub>2</sub> concentration (56, 47, 42, 43%;  $\chi^2_4 = 127.8$ ,  $p < 0.0001$ ; Fig. 3B). The larval emergence rate from eggs laid after feeding on SAD was as high as from eggs laid after feeding on GAD + aCO<sub>2</sub>-Riesling ( $\chi^2_4 = 127.8$ ,  $p < 0.0001$ ; Fig. 3B). The two-factorial evaluation did not reveal further details (CO<sub>2</sub>:  $\chi^2_1 = 14.9$ ,  $p = 0.0001$ ; cultivar:  $\chi^2_1 = 75.0$ ,  $p < 0.0001$ ; cultivar \* CO<sub>2</sub>:  $\chi^2_1 = 28.3$ ,  $p < 0.0001$ ). In GAD-replicates where no successful parasitism was observed, the *L. botrana* larval

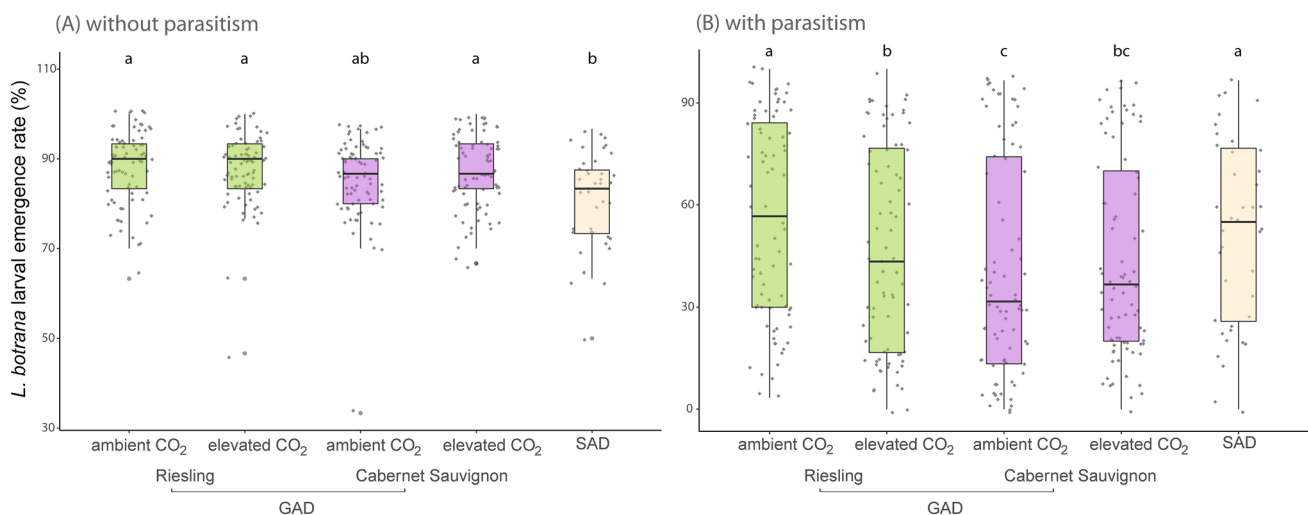
emergence rate was  $87 \pm 1\%$ . With parasitoids present, the larval emergence rate of *L. botrana* larvae from eggs laid by adults after larval feeding on SAD was  $52 \pm 4\%$  and the egg abortion rate was  $16 \pm 2\%$ .

### Effect of host larval diet on parasitism

**Parasitism rate.** When exposed to *L. botrana* eggs laid by adults after larval feeding on GAD, *T. cacoeciae* successfully parasitized eggs in 72% of the samples with a mean parasitism rate of  $38 \pm 2\%$ . When exposed to eggs produced after feeding on SAD, *T. cacoeciae* successfully parasitized eggs in 70% of the samples with a mean parasitism rate of  $32 \pm 5\%$ . Only considering the samples where at least one egg was successfully parasitized, the parasitism rate was  $53 \pm 1\%$ .

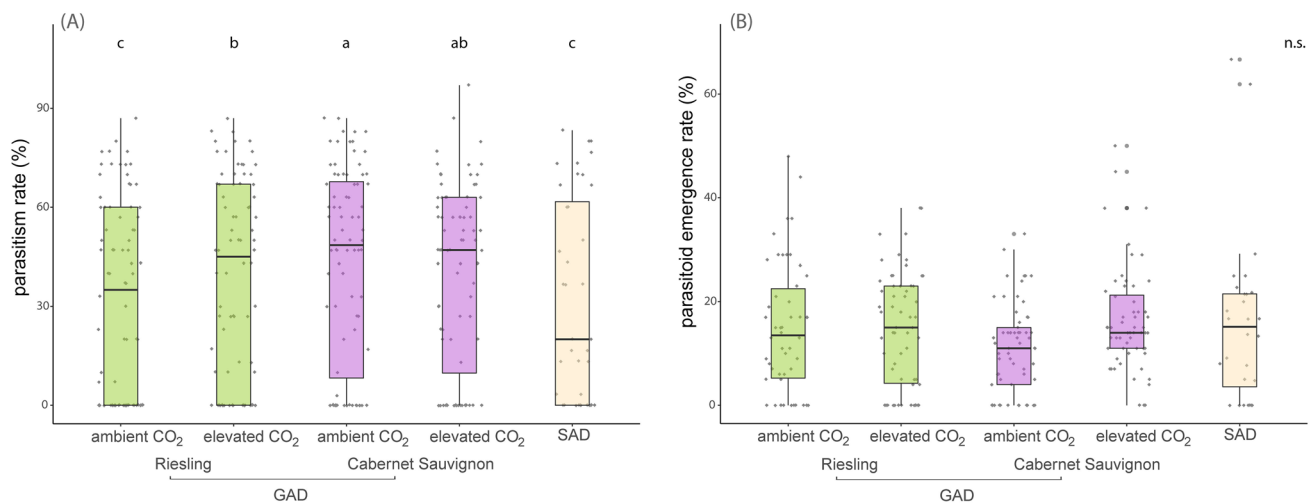
Parasitism rate was lower on eggs produced by *L. botrana* after feeding on GAD + aCO<sub>2</sub>-Riesling than on GAD + eCO<sub>2</sub>-Riesling but not significantly different on GAD + aCO<sub>2</sub>-Cabernet Sauvignon or GAD + eCO<sub>2</sub>-Cabernet Sauvignon (32, 38, 43, and 40%, respectively;  $\chi^2_4 = 82.8$ ,  $p < 0.0001$ ; Fig. 4A). The parasitism rate on eggs laid after feeding on SAD was as low as on eggs laid after feeding on GAD + aCO<sub>2</sub>-Riesling ( $\chi^2_4 = 82.8$ ,  $p < 0.0001$ ; Fig. 4A). The two-factorial evaluation did not reveal further details (CO<sub>2</sub>:  $\chi^2_1 = 2.7$ ,  $p = 0.10$ ; cultivar:  $\chi^2_1 = 38.5$ ,  $p < 0.0001$ ; CO<sub>2</sub> \* cultivar:  $\chi^2_1 = 23.85$ ,  $p < 0.0001$ ).

**Parasitoid emergence rate.** One-factorial evaluation detected significant differences regarding parasitoid emergence rate from eggs laid after feeding on the different diets but they were not detected in the multiple comparison ( $\chi^2_4 = 11.1$ ,  $p = 0.03$ ; Fig. 4B). However, the two-factorial



**Fig. 3** *Lobesia botrana* larval emergence rate from eggs **A** without or **B** with parasitoids present. Eggs were produced after feeding on standard artificial diet (SAD) or grapevine-based artificial diet (GAD) containing inflorescences of the cultivar Riesling or Cabernet Sauvignon, cultivated at ambient (ca. 400 ppm) or elevated (ca. 480 ppm) CO<sub>2</sub> concentrations in the Geisenheim VineyardFACE. Identical letters indicate that no significant differences were detected. ns: not significant (GLM, Tukey contrasts; N=80)

gnon, cultivated at ambient (ca. 400 ppm) or elevated (ca. 480 ppm) CO<sub>2</sub> concentrations in the Geisenheim VineyardFACE. Identical letters indicate that no significant differences were detected. ns: not significant (GLM, Tukey contrasts; N=80)



**Fig. 4** Parasitism rate **A** and emergence rate **B** of *Trichogramma cacoeciae* on *Lobesia botrana* eggs produced after larval feeding on standard artificial diet (SAD) or grapevine-based artificial diet (GAD) containing inflorescences of the cultivar Riesling or Cabernet Sauvignon, cultivated at ambient (ca. 400 ppm) or elevated (ca. 480 ppm) CO<sub>2</sub> concentrations in the Geisenheim VineyardFACE. Different letters indicate that significant differences were detected (GLM, Tukey contrasts;  $N=80$ )

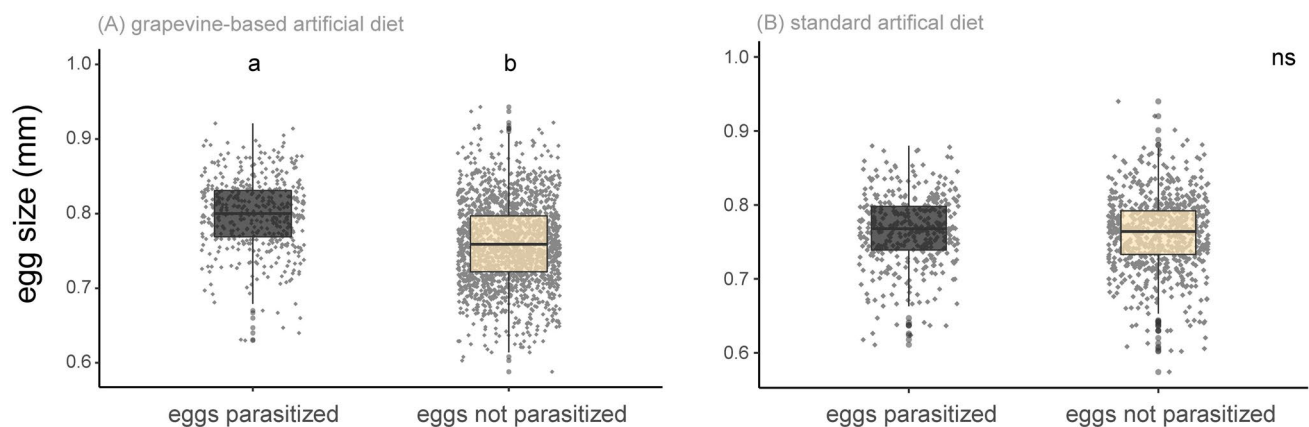
evaluation detected a higher parasitoid emergence rate from *L. botrana* eggs produced after larval feeding on GAD + Riesling than on GAD + Cabernet Sauvignon inflorescences, which was not affected by the CO<sub>2</sub> concentration at which the plant had been cultivated (15 and 13.5%, respectively; cultivar:  $\chi^2_1 = 8.0$ ,  $p = 0.005$ ; CO<sub>2</sub>:  $\chi^2_1 = 2.9$ ,  $p = 0.09$ ; CO<sub>2</sub> \* cultivar:  $\chi^2_1 = 0.001$ ,  $p = 0.98$ ). Parasitoid emergence rate on eggs produced after feeding on SAD was  $16 \pm 3\%$  (Fig. 4B).

**Egg size preference.** When *L. botrana* eggs were produced after larval feeding on GAD the size of eggs that were parasitized by *T. cacoeciae* was larger than the size of

non-parasitized eggs ( $\chi^2_1 = 0.96$ ,  $p < 0.0001$ ; Fig. 5A). When eggs were produced after feeding on SAD, the size between parasitized and non-parasitized eggs did not differ significantly ( $\chi^2_1 = 0.006$ ,  $p = 0.25$ ; Fig. 5B).

## Discussion

Rising CO<sub>2</sub> concentrations can affect all levels in food webs and thereby alter trophic interactions in a complex manner (Facey et al. 2014; Rosenblatt and Schmitz 2014). Changes to the chemical composition of the host plant can



**Fig. 5** Size of *Lobesia botrana* eggs (length in mm), parasitized or not parasitized by *Trichogramma cacoeciae*, that were produced after larval feeding on either **A** grapevine-based artificial diet containing inflorescences from the Geisenheim VineyardFACE (data were pooled over the two cultivars and CO<sub>2</sub> concentrations) or on **B** standard artificial diet. For details on diets, see Table 1. Different letters indicate that significant differences were detected. (GLM, Tukey contrasts; on grapevine-containing diet: eggs parasitized=465, not parasitized=1965, on standard artificial diet: eggs parasitized=381, not parasitized=740)

lead to changes in the chemical composition of the insect host which can alter their host quality for parasitoids (Han, Lavoit et al. 2022). For egg parasitoids like *Trichogramma*, the quality and size of host eggs are particularly important as their development is restricted to this confined space and the resources stored within (Vinson 1994).

Our results illustrate a grapevine cultivar-dependent, plant- and insect host-mediated bottom-up effect of elevated atmospheric CO<sub>2</sub> concentration on *L. botrana* egg parasitism by *T. cacoeciae*.

In brief, the different CO<sub>2</sub> concentrations during plant cultivation affected the size of *L. botrana* eggs when feeding on a Riesling-based diet whereas no such effect was observed for the Cabernet Sauvignon-based diet. This finding partly confirms our hypothesis 1. The parasitoids preferentially parasitized larger *L. botrana* eggs that were produced after feeding on GAD but not after feeding on SAD. In turn, this partly confirms our hypothesis 2. Parasitism rates were higher on eggs produced after *L. botrana* larvae feeding on elevated CO<sub>2</sub>-Riesling than on ambient CO<sub>2</sub>-Riesling diet but there was no CO<sub>2</sub>-effect on parasitism rates after feeding on Cabernet Sauvignon-diet. Emergence rates of parasitoids were not affected by the CO<sub>2</sub> concentration their host plant was cultivated at. Again, this partly confirms our hypothesis 3.

To the best of our knowledge, this is the first study investigating the bottom-up effect of elevated CO<sub>2</sub> on an egg parasitoid. A few studies have been conducted on the effect of eCO<sub>2</sub> on herbivorous larvae, with varying results. Studying the impact of CO<sub>2</sub> concentrations on the attack rates of parasitoids on leaf mining larvae in a scrub-oak community, Stiling et al. (1999) found higher rates under elevated CO<sub>2</sub> concentrations. This agrees with our findings regarding GAD + Riesling. In contrast, studying the impact of CO<sub>2</sub> concentrations on parasitism of *Microplitis mediator* (Haldy; Hymenoptera: Braconidae) on *Helicoverpa armigera* larvae (Hübner; Lepidoptera: Noctuidae), (Yin et al. 2009) found no effect. Similarly, (Holton et al. 2003) found no effect of elevated CO<sub>2</sub> concentrations on parasitism of the tachinid fly *Comptosia concinnata* (Meigen; Diptera: Tachinidae) on *Malacosoma disstria* larvae (Hübner; Lepidoptera: Lasiocampidae) in their Aspen FACE. This agrees with our findings regarding GAD + Cabernet Sauvignon.

Studies on the indirect bottom-up effect of elevated CO<sub>2</sub> on parasitoids of pests that feed on plant sap likewise came to varying results (Klaiber et al. 2013; Schulze-Sylvester and Reineke 2019; Moreno-Delafuente et al. 2021). Klaiber et al. (2013) found a negative impact of elevated CO<sub>2</sub> on the parasitoid *Diaretiella rapae* (M'Intosh; Hymenoptera: Braconidae) parasitizing the aphid *Brevicoryne brassicae* (Linnaeus; Hemiptera: Aphididae) feeding on *Brassica oleraceae* plants. Moreno-Delafuente et al. (2021) found no effect on the parasitoid *Aphidius colemani* (Dalman;

Hymenoptera: Braconidae) parasitizing the aphid *Aphis gossypii* (Glover; Hemiptera: Aphididae) feeding on *Cucumis melo* plants. They were studying pest species with different life cycles, feeding on shorter-lived plants in the vegetative state, exposed to elevated CO<sub>2</sub> for several weeks whereas we were studying the reproductive organs of perennial plants, that had been exposed to elevated CO<sub>2</sub> for 7 years. In our study, the whole plant organ was consumed by the pest species while the mentioned sap feeders are only exposed to plant sap that is quite different chemically. Accordingly, this variation in the bottom-up effects of eCO<sub>2</sub> emphasizes the influence of degree of elevation and duration of the CO<sub>2</sub> treatment as well as plant species—in our case even cultivar—considered. Studies on the bottom-up effect of CO<sub>2</sub> in the grapevine-pest-natural enemy agroecosystem are scarce (Reineke and Thiéry 2016). A report investigating the impact of elevated CO<sub>2</sub> concentrations on the grapevine pest vine mealybug *Planococcus ficus* (Signoret; Hemiptera: Pseudococcidae) and their natural enemy, the parasitic wasp *Leptomastix dactylopii* (Howard; Hymenoptera: Encyrtidae), did not detect bottom-up effects on the parasitoid (Schulze-Sylvester and Reineke 2019). The reason for these different results might again be the different herbivore and parasitoid species studied. Additionally, they could be due to the different experimental settings: harvested inflorescences from long-term CO<sub>2</sub>-exposed grapevine plants compared to living, short-term-exposed grapevine plants in the vegetative state.

Since our experimental setting included freeze-dried, ground plant material, it focused on the chemical composition of the grapevine inflorescences and excluded other changes, e.g., those related to plant morphology. In a previous study, we measured significant differences in sugar and phenolic compound concentrations between grapevine inflorescences of the cultivars Riesling and Cabernet Sauvignon and due to cultivation at ambient and elevated CO<sub>2</sub> concentration in the Geisenheim VineyardFACE facility (Becker et al. *in preparation*). Plant defense compounds consumed by herbivores can be incorporated into their eggs and can have an impact on the performance of parasitoids (Hilker and Meiners 2002; Hunter 2003; Desneux et al. 2009; Becker et al. 2021) and the offspring of idiobiont endoparasitoids like *T. cacoeciae* can only access the nutrients found in the one egg that they have been oviposited into, at the moment of oviposition.

Our previous analysis of plant compounds under aCO<sub>2</sub> and eCO<sub>2</sub> revealed that inflorescences of the cultivar Riesling contained higher concentrations of glucose and fructose than Cabernet Sauvignon (Becker et al. *in preparation*). Putatively higher sugar concentrations in *L. botrana* eggs produced after feeding on GAD + Riesling than on GAD + Cabernet Sauvignon may have promoted the development of *T. cacoeciae* larvae inside these eggs and resulted in the observed higher parasitoid emergence rates, even if

the respective differences were small. Riesling inflorescences additionally contained lower concentrations of 2-S-gluthathionyl caftaric acid, coumaroyl glucose, caftaric acid, coumaric acid, quercetin derivative 2, and unknown phenolic compound 4 than Cabernet Sauvignon (Becker et al. *in preparation*). These plant toxins may have been passed on from the *L. botrana* larval diet to the eggs, and may have impacted the developing *T. cacoeciae* larvae, contributing to the lower parasitoid emergence rates from eggs produced after feeding on GAD + Cabernet Sauvignon than on GAD + Riesling.

The parasitism rate of 38% that we observed in our experiment is slightly higher than the 15–33% reported by Pease et al. (2016) but lower than the 50% reported by Thiéry and Desneux (2018) or the 47–76% reported by Moreno et al. (2009). Successful parasitism occurred in 72% of the replicates where females were alive after 24 h. This is a much lower rate than the roughly 98% reported by Thiéry and Desneux (2018). Furthermore, the parasitoid emergence rate that we observed (14%) was much lower than the 55% reported by Pease et al. (2016). This indicates that our *T. cacoeciae* strain may have been less efficient in parasitizing *L. botrana* eggs than those used in other experiments. A switch of insect host species can affect parasitism efficiency (Henry et al. 2010). However, since our lab colony of *T. cacoeciae* was reared on *L. botrana* eggs for at least 14 generations prior to the experiments to achieve maximum host adaptation, we discard this as a reason for the comparably low oviposition rates. However, due to this long period of isolated inbreeding overall parasitoid performance might be reduced (Bertin et al. 2017). In samples where no successful parasitism occurred, the egg abortion rate was very close to the naturally occurring egg abortion rate in our *L. botrana* colony. This suggests that some individuals of *T. cacoeciae* did not attempt to parasitize at all.

While previous studies did report an effect of grapevine cultivar on *L. botrana* larval development time and female reproductive performance (Moreau et al. 2006; Moreau, Thiéry et al. 2007), we only observed a very weak effect on the second trophic level. Still, the fact that there was a bottom-up effect of cultivar on larval emergence on the third but not the second trophic level is remarkable. It suggests that *L. botrana* may be tolerant to whatever factor was mediating the effect. Both altered nutritional value and levels of defense can be underlying mechanisms of bottom-up effects triggered by abiotic factors (Han et al. 2019; Becker et al. 2021). With parasitoids present, larval emergence rates of *L. botrana* can be reduced by successful parasitism of *T. cacoeciae* but also by host feeding or host probing of the wasps. By providing them with honey agar, we tried to minimize host feeding. Furthermore, the host egg immune system might be affected by larval diet, as has been demonstrated for the larvae themselves (Muller et al. 2015). Hence, some

host eggs and/or developing embryos may have been able to kill the parasitoid's egg while others may not have been able to, shaping the observed host larval emergence rate.

On *L. botrana* eggs produced after larval feeding on GAD, *T. cacoeciae* parasitism rates were higher in treatments where egg size was larger (GAD + eCO<sub>2</sub>-Riesling) than in those where they were smaller (GAD + aCO<sub>2</sub>-Riesling) and, when studied directly, parasitized eggs were larger than non-parasitized ones—when eggs were produced after feeding on GAD. This is in-line with previous results (Moreau et al. 2009). Yet, interestingly, this size preference of *T. cacoeciae* appears to be host-diet-dependent since it was not detectable when *L. botrana* eggs produced after larval feeding on SAD were parasitized. Egg size is often assumed to be an indicator of egg nutrient content because larger eggs supposedly contain more nutrients than smaller ones (Moreau et al. 2009). Indeed, larger eggs of *L. botrana* and other insect species are associated with a higher fitness of the emerging larvae (Fox and Czesak 2000; Torres-Vila and Rodríguez-Molina 2002) and egg size has been related to egg composition in *Bicyclus anyana* (Butler; Lepidoptera: Nymphalidae) (Karl et al. 2007). Overall, SAD is richer in nutrients than GAD. The latter contains only a small fraction of the amount of wheat germ incorporated in SAD and contrary to SAD, GAD contains no sugar, casein, cholesterol, sunflower oil, and lucerne (Table 1). Based on our results, we hypothesize that egg size is an important criterion for *T. cacoeciae* as long as the insect host diet is limited in its nutrient content. However, when the insect host diet is rich, even small eggs may contain enough nutrients to sustain parasitoid offspring development and the importance of size may then fade in comparison to other information gathered from the egg. In order to verify this interpretation, nutrient contents of eggs of varying sizes and produced by insect hosts fed with varying diets need to be analyzed. This should be an interesting albeit technically challenging route of investigation.

Our results show an interesting mismatch between parasitism preference and parasitoid emergence rate: parasitism rates were significantly higher on *L. botrana* eggs obtained after larval feeding on Cabernet Sauvignon-diet but parasitoid emergence rates were higher on eggs from Riesling-diet. A similar discrepancy has been reported for *T. evanescens* parasitizing eggs from *L. botrana* produced after feeding on different grapevine cultivars (Moreau et al. 2009). The preference-performance hypothesis predicts a positive relationship between the host preference of adult females and the successful development, *i.e.*, performance, of the offspring. While it has originally been postulated to describe the relationship between herbivores and host plants (Jaenike 1978), it was then extended to parasitoids and their insect hosts (Driessen et al. 1990; Brodeur et al. 1998; Desneux et al. 2009). A close preference-performance relationship has been found in oligophagous rather than polyphagous herbivorous



insects (Gripenberg et al. 2010) and has been proposed to indicate the degree of dietary specialization in parasitoids (Monticelli et al. 2019). Since *T. cacoeciae* is considered a generalist (Thiéry and Desneux 2018), this might explain the preference-performance-mismatch we observed.

Looking at the absolute numbers of emerging offspring in each replicate, the detected differences may seem small: on average, 1.55 and 1.70 parasitoids emerged from 30 eggs produced after feeding on Riesling- and Cabernet Sauvignon-diet, respectively. However, on a vineyard scale, this may well result in biologically relevant differences in population size and establishment in the field. Studying the insect community in a forest FACE experiment, Hillstrom and Lindroth (2008) found higher numbers of several parasitoid species. Studying the insect community in the Geisenheim VineyardFACE should be an interesting next step.

In conclusion, our laboratory trials have shown for the first time that the grapevine cultivar incorporated into semi-artificial diet can affect egg parasitism and thus biological pest control under future elevated CO<sub>2</sub> concentrations. Our data indicate a grapevine cultivar-dependent effect on *Trichogramma* parasitism under future elevated CO<sub>2</sub> concentrations, which might be relevant for future biological pest control programs. They suggest that future bottom-up effects of elevated CO<sub>2</sub> will not reduce the efficiency of classical biocontrol programs using *T. cacoeciae* against *L. botrana* feeding on the grapevine cultivar Cabernet Sauvignon and might improve on Riesling. However, since climate change will alter many abiotic and biotic factors simultaneously, our study is but one piece of the puzzle. Multifactorial studies involving several abiotic factors and several trophic levels in the vineyard are necessary to broaden our understanding of the efficacy of future biological control involving parasitoids.

## Author's contributions

CB, KH, and AR designed the experiment, KH conducted the experiment, CB and KH evaluated the data. CB, KH, and AR wrote and approved the manuscript.

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## Declarations

**Conflict of interest** The authors declare that they have no relevant financial or non-financial interests to disclose.

**Ethics approval** Not applicable.

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