ORIGINAL PAPER



Potential side effects of the interaction between *Phthorimaea absoluta* parasitoids: the exotic *Dolichogenidea gelechiidivoris* and the native *Bracon nigricans*

Sahadatou Mama Sambo^{1,2} · Shepard Ndlela¹ · Hannalene du Plessis² · Esther Awuor Owino¹ · Samira Abuelgasim Mohamed¹

Accepted: 20 April 2023 / Published online: 6 November 2023 © The Author(s) 2023

Abstract

The coexistence and efficiency in pest control of introduced and native parasitoids can be challenging. Continuous observations of the cohabitation of parasitoid species could confirm the persistence of the introduced parasitoid in the ecosystem under co-existence scenarios. This study provides an example of such a co-existence for biocontrol of the invasive pest, *Phthorimaea absoluta* (Meyrick) (Lepidoptera: Gelechiidae). Two parasitoids, the introduced endoparasitoid *Dolichogenidea gelechiidivoris* (Marsh) (Hymenoptera: Braconidae) and the native ectoparasitoid *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae) were released in cages containing a tomato plant infested with *P. absoluta*. Parasitism and killing rate of *P. absoluta* by both parasitoid species, and the parasitoid and *P. absoluta* population were monitored weekly. The parasitoid species coexisted for seven weeks in the experimental units. Parasitism by *D. gelechiidivoris* was significantly affected by the presence of *B. nigricans*, with 73% and 22% parasitism in the absence and presence of *B. nigricans*, respectively. Parasitism by *B. nigricans* was not affected by its co-existence with *D. gelechiidivoris*. The number of *D. gelechiidivoris* adults increased eight-fold in five weeks in the absence of *B. nigricans*, while less than the initial number of adults were present in co-existence with *B. nigricans*. The *P. absoluta* infestation declined from the fifth week to 98% lesser than the control in all the treatments, either *D. gelechiidivoris* or *B. nigricans* as standalone treatments, as well as in combination. Since *B. nigricans* negatively affected *D. gelechiidivoris* population growth, releases of this introduced parasitoid should be considered with caution in areas where *B. nigricans* occurs.

Keywords Population dynamics · Co-existence · Ectoparasitoid · Endoparasitoid · Pest control

Introduction

Interferences between species occurs when more than one species attack the same host species, affecting the distribution and population dynamics of the same (Xu et al. 2013; Holt and Bonsall 2017). These interferences between species arise during adult host searching or during the development

of the immature stages of the parasitoids inside the same host (Bográn et al. 2002; Cusumano et al. 2013, 2016; Xu et al. 2013). The outcomes of such interference can affect the ecosystem in different ways such as the reduction or extinction of a specific species, which affects pest control in terms of the depletion, displacement, or extinction of natural enemies (Reitz and Trumble 2002; Wang et al. 2008; Feng et al. 2015; Tan et al. 2016). For example, the ectoparasitoid, Spathius agrili Yang (Hymenoptera: Braconidae) eggs do not develop on Agrilus planipennis (Fairmaire) (Coleoptera: Buprestidae) larvae earlier parasitised by the endoparasitoid, Tetrastichus planipennisi Yang (Hymenoptera: Eulophidae) (Ulyshen et al. 2010). On that same pulse beetle, the endoparasitoid, Dinarmus basalis (Rond.) (Hymenoptera: Pteromalidae) differentiated larvae previously parasitised by the ectoparasitoid, Eupelmus vuilleti Crawford (Hymenoptera: Eupelmidae) (van Alebeek et al. 1993). It is therefore

Sahadatou Mama Sambo sahadatou.mamasambo@gmail.com

Samira Abuelgasim Mohamed sfaris@icipe.org

¹ International Centre of Insect Physiology and Ecology (icipe), P.O. Box 30772-00100, Nairobi, Kenya

² Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

important to understand the possible effects that different parasitoids can have when planning a biological control program that involves more than one parasitoid species (Mills 1992; Cusumano et al. 2016).

Since the invasion of *P. absoluta*, numerous parasitoids associated with this pest were discovered in invaded countries (Tropea Garzia et al. 2012; Zappalà et al. 2012, 2013; Naselli et al. 2017; Mansour et al. 2018; Ferracini et al. 2019; Salas Gervassio et al. 2019). A combination of natural enemies for control of this pest has been reported in various studies. The parasitoid Stenomesius japonicus Ashamed (Hymenoptera: Eulophidae) released together with the predator Macrolophus pygmaeus Rambur (Hemiptera: Miridae) improved control of *P. absoluta* Chailleux et al. (2017). The predator Nesidiocoris tenuis (Reuter) (Hemiptera: Miridae) in combination with the egg parasitoid, Trichogramma brassicae Bezdenko (Hymenoptera: Trichogrammatidae) showed the highest tomato yield in a trial compared to where each of the natural enemies was alone (Mirhosseini et al. 2019). When evaluated in combination, females of both the ectoparasitoid, Dineulophus phthorimaeae De Santis (Hymenoptera: Eulophidae) and the endoparasitoid, Pseudapanteles dignus (Muesebeck) (Hymenoptera: Braconidae) changed their searching behaviour for P. absoluta in the presence of the competing species. The efficacy of P. dignus was, however, not affected by the presence of the ectoparasitoid and it achieved the same parasitism rate whether the competitor was present or absent (Savino et al. 2016).

Bracon nigricans Szépligeti (Hymenoptera: Braconidae) is a gregarious, generalist idiobiont larval ectoparasitoid (Yu and Actherberg 2010), recorded in *P. absoluta* in several invaded areas. For example, its association with P. absoluta was recorded in Italy (Zappalà et al. 2012), Jordan (Al-Jboory et al. 2012), Spain (Gabarra et al. 2013) and Sudan (Idriss et al. 2018). This parasitoid was amongst the three most abundant parasitoids recorded in Italy. Bracon nigricans was reported to co-occur with other larval parasitoid species such as Diadegma pulchripes (Hymenoptera: Ichneumonidae), Elachertus inunctus Nees, Necremnus sp., Neochrysocharis formosa (Hymenoptera: Eulophidae) and Elasmus sp. (Hymenoptera: Elasmidae). In Spain, B. nigricans was reported to co-occur with Hockeria unicolor Walker (Hymenoptera: Chalcididae), Pnigalio cristatus (Ratzeburg), and Neochrysocharis formosa (Westwood) (Hymenoptera: Braconidae), while a Cotesia sp., and Dolichogenidea litae (Nixon, 1972) (Hymenoptera: Braconidae) has also been recorded in a nearby locality two years before (Gabarra et al. 2013). Bracon nigricans has also recently been recorded in Kenya, and several areas in Africa are suitable for the persistence of this parasitoid (Mama Sambo et al. 2022b). Approximately 21% parasitism of T. absoluta by B. nigricans was reported from open field tomatoes in central Kirinyaga county, Kenya where the exotic D.

gelechiidivoris was released (Shiraku 2020; Mama Sambo et al. 2022b).

Dolichogenidea gelechiidivoris is a specialist solitary endoparasitoid of some Gelechiidae species, including P. absoluta (Bajonero et al. 2008; Mujica and Kroschel 2017; Aigbedion-Atalor et al. 2020; Mama Sambo et al. 2022c). The parasitism rate by this parasitoid under laboratory conditions varied between 55 and 87% (Bajonero et al. 2008; Aigbedion-Atalor et al. 2020; Mama Sambo et al. 2022a, c), depending on the host and parasitoid density, as well as P. absoluta larval stage. Dolichogenidea gelechiidivoris was established in Chile 10 years after its release (Desneux et al. 2010). In Kenya, less than 5% parasitism by D. gelechiidivoris on P. absoluta larvae were recorded in open fields, five months after the release of D. gelechiidivoris (Mama Sambo et al. unpublished data). However, D. gelechiidivoris has also been recovered from non-release areas in Europe and Africa (Krache et al. 2021; Denis et al. 2022).

Bracon nigricans hasa very high ability to kill its host (Biondi et al. 2013; Becchimanzi et al. 2017, 2020). This parasitoid prefers 4th-instar *P. absoluta* larvae (Idriss et al. 2018), while *D. gelechiidivoris* prefers 1st and 2nd-instar larvae of this host (Aigbedion-Atalor et al. 2020). Parasitism by *D. gelechiidivoris* in Kenya was reported to be very low in the release area, where *B. nigricans* was recovered (Shiraku 2020; Mama Sambo et al. 2022b). The aim of this study was to investigate the population dynamics of *P. absoluta* and two of its parasitoid species, *D. gelechiidivoris* and *B. nigricans* in laboratory bioassays, when present alone or in combination.

Materials and methods

Host plants

Tomato (cv. Moneymaker) seedlings were planted in plastic pots ($14 \text{ cm} \times 14 \text{ cm} \times 9 \text{ cm}$) containing soil mixed with goat manure. The seedlings were grown in a greenhouse following the procedures described by Mama Sambo et al. (2022c).

Insects rearing

Phthorimaea absoluta

Tomato plants with *P. absoluta* larvae and eggs were collected from farmers' plots in the Kirinyaga County $(00^{\circ}37'196'' \text{ S}, 37^{\circ}22'615'' \text{ E}, \text{ Elevation} \approx 1200 \text{ msl}$ and $00^{\circ}37'922'' \text{ S}, 37^{\circ}22'794'' \text{ E}$, Elevation ≈ 1200), Kenya to initiate a colony. The infested plants were incubated and *P. absoluta* obtained from these plants was reared on healthy tomato plants following the procedure described by Mama Sambo et al. (2022c).

Dolichogenidea gelechiidivoris

Dolichogenidea gelechiidivoris cocoons were kept in a Perspex cage (40 cm \times 20 cm \times 40 cm) with 80% honey solution droplets provided on the inside of the top of the cage for the emerged parasitoids to feed on. The adults were kept isolated in the Animal Rearing and Containment Unit (ARCU) at *icipe* and reared on *P. absoluta* larvae according to the protocol described by Mama Sambo et al. (2022c).

Bracon nigricans

The B. nigricans colony was initiated from parasitoids that emerged from infested tomato plant material collected from Mwea (00°37′196" S, 37°22′615" E, Elevation ≈ 1200 msl and $00^{\circ}37'922''$ S, $37^{\circ}22'794''$ E, Elevation ≈ 1200 msl), Kirinyaga, Kenya. The infested leaves were kept in a transparent plastic lunch box. Upon adult parasitoid emergence, insects were aspirated into a clean Perspex cage $(40 \text{ cm} \times 20 \text{ cm} \times 50 \text{ cm})$ and provided with 80% honey solution droplets applied on the top of the cage. The insects were maintained under ambient laboratory conditions $(25 \pm 1 \, ^{\circ}C)$ 70 ± 5 RH, and 12:12 L:D of photoperiod) in the Animal Rearing and Containment Unit (ARCU) at icipe. Third instar *P. absoluta* larvae in tomato plant leaves were exposed to *B*. *nigricans* adults for 48 h. Thereafter, the tomato leaves were transferred to another Perspex cage until B. nigricans and P. absoluta emerged. Two days-old females (F3) were used in this experiment.

Experimental setup

The interaction between *D. gelechiidivoris* and *B. nigricans* was investigated under laboratory conditions $(25 \pm 1 \,^{\circ}C, 70 \pm 5 \,\text{RH}, \text{ and } 12:12 \,\text{L:D}$ of photoperiod). The experiment was conducted in cages (30 cm × 30 cm × 30 cm) and consisted of four treatments. Initially, one uninfested potted tomato plant (3 weeks old) was placed in each cage. Ten newly emerged naïve *P. absoluta* male–female moth pairs were released per cage. Drops of an 80% honey solution were streaked onto the inner top part of the cage as food for the moths. Four treatments were applied (Table 1). Each

treatment was replicated ten times. For each treatment, an additional potted plant was placed into each cage at threeday intervals for the entire duration of the study and supplemented daily with fresh tomato leaves to ensure that enough food was available for *P. absoluta* larvae.

Data collection

Parasitism by the two species

To determine the level of parasitism, ten *P. absoluta* larvae were removed from plants in each cage, two weeks after release of *B. nigricans* and dissected under a stereomicroscope (Leica EZ4D digital stereomicroscope; Leica Microsystems, Heerbrugg, Switzerland). Additionally, dead *P. absoluta* larvae inside mines were recorded in each of the treatments.

Population dynamics of the different insect species

The number of *P. absoluta* mines and eggs was determined by counting the number of eggs and mines in each leaflet on the plant every week from the third-week of monitoring. In addition, the number of *D. gelechiidivoris* and *B. nigricans* parasitoids that emerged were counted. The experiment was conducted over a period of 10 weeks.

Data analysis

A Generalised Linear Model (GLM) with a negative binomial was used to determine the difference in percentage parasitism by *D. gelechiidivoris* and *B. nigricans*, of dissected larvae, as well as the number of larvae killed by *B. nigricans*. The numbers of *D. gelechiidivoris* and *B. nigricans* adults and mines per treatment were analysed using a mixed-effects model with repeated measures, using *lmer* function under the lme4 package. All the data were analysed in R (R Core Team 2018).

Table 1 Experimental scenarios used to assess the effect of the co-occurrence of D. gelechiidivoris and B. nigricans

Treatments	Description
D. gelechiidivoris	Release of 10 D. gelechiidivoris pairs into a cage where P. absoluta moths were released five days previously
B. nigricans	Release of 10 B. nigricans pairs into a cage where P. absoluta moths were released 10 days previously
D. gelechiidivoris & B. nigricans	Release of five pairs of <i>D. gelechiidivoris</i> pairs into a cage where <i>P. absoluta</i> moths were released five days previously, followed by the release of five <i>B. nigricans</i> pairs into the same cage, five days after release of <i>D. gelechiidivoris</i>
Control	a control treatment with a cage containing only P. absoluta with no parasitoids released into the cage

Results

Parasitism by the two species

The level of *D. gelechiidivoris* parasitism varied significantly, depending on the presence or the absence of *B. nigricans* ($F_{1,18}=26.69, P < 0.001$). Significantly more larvae were parasitised by *D. gelechiidivoris*, when it was present alone, compared to the level of parasitism when *P. absoluta* larvae were exposed to both *D. gelechiidivoris* and *B. nigricans* (Fig. 1a). However, no difference in parasitism by *B. nigricans* was observed regardless of the presence or absence of *D. gelechiidivoris* ($F_{1,18}=1, P=0.33$). Similarly, the release of *B. nigricans* after *D. gelechiidivoris* was already present did not increase *P. absoluta* larval mortality ($F_{1,18}=0.35, P=0.56$). Although the maximum parasitism by *B. nigricans* (10%) (Fig. 1b) was lower than that by *D. gelechiidivoris* (73%) (Fig. 1a), its parasitism was not affected by the presence of *D. gelechiidivoris* (Fig. 1b).

Population dynamics of the different insect species

The treatments with an absolute t-value > 2 affected the parameters significantly (Table 2). The *D. gelechiidivoris* population was negatively affected by the association with *B. nigricans* (t = 5.70) while no significant effect on the *B. nigricans* population was observed by the cooccurrence of the two parasitoids species (Table 2). Where the *D. gelechiidivoris* population was kept separate, the number of adults present was high, with an average of 156 parasitoids five weeks after introduction. In co-occurrence with *B. nigricans* only 8 *D. gelechiidivoris* individuals survived at week 5 (Fig. 2). The number of *P. absoluta* progeny expressed as the number of mines and eggs, was significantly higher compared to all other treatments with parasitoids present in the respective combinations, five weeks after release of the

Fig. 1 a Mean percentage $(\pm SE)$ *P. absoluta* larvae parasitised by *D. gelechiidivoris* and **b** Mean percentage *P. absoluta* larvae parasitised and killed by *B. nigricans*, when released as a standalone treatment as well as in combination with a competitor. Bars capped with different upper or lower letters are not significantly different (Tukey's HSD, p < 0.05)

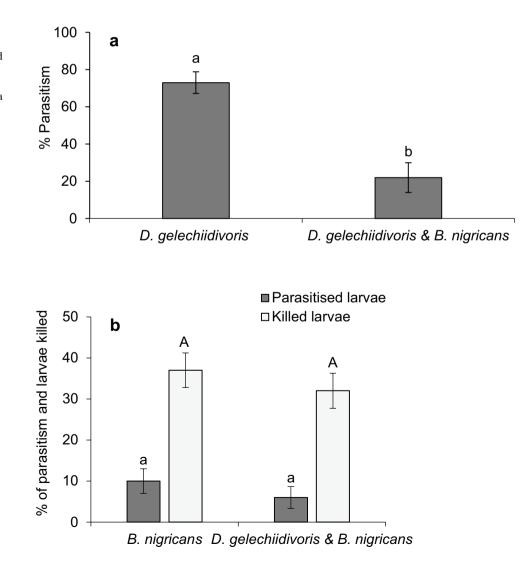
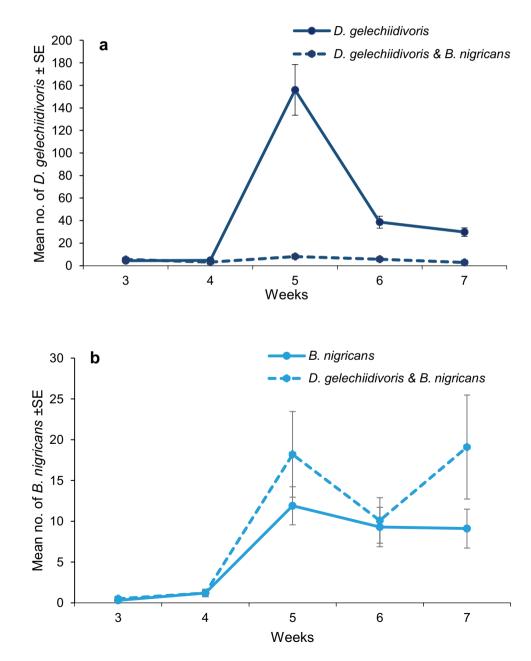
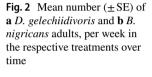
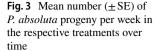


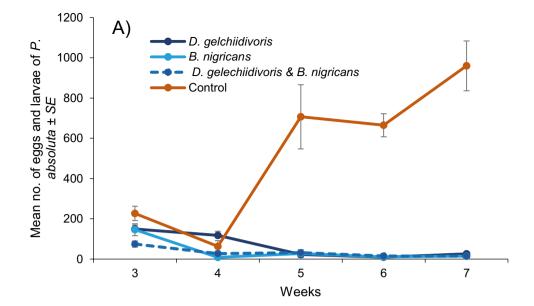
Table 2 Parameter estimatesfor the effect of parasitoidcombinations in terms of <i>D.</i> gelechiidivoris and <i>B. nigricans</i> population growth and <i>P.</i> absoluta infestation			Estimate	Std. Error	t-value
	Number of D. gelechiidivoris	(Intercept)	5.08	14.91	0.34
		D. gelechiidivoris	41.62	7.31	5.70
	Number of <i>B. nigricans</i>	(Intercept)	6.36	3.26	1.95
		D. gelechiidivoris & B. nigricans	3.46	1.94	1.79
	Number of <i>P. absoluta</i> progenies (eggs and larvae)	(Intercept)	41.80	28.47	1.47
		D. gelechiidivoris & B. nigricans	-8.66	32.45	-0.27
		D. gelechiidivoris	23.44	34.72	0.67
		Control (no parasitoids)	482.66	177.39	2.72

P. absoluta moths (t = 2.72) (Table 2). At week four, the pest level significantly decreased where both B. nigricans occurred alone and where the combination of D. gelechiidivoris and B. nigricans occurred (Fig. 3). From week 5, significantly lower pest levels occurred in all treatments, except for the control (Fig. 3).









Discussion

The efficacy of control of *P. absoluta* by two parasitoids, viz. the imported endoparasitoid, D. gelechiidivoris, and the endogenous ectoparasitoid, B. nigricans was confirmed in this laboratory study. The negative impact of the co-occurrence of these two species on D. gelechiidivoris was also demonstrated. Multiple parasitism by parasitoid species frequently occur in the absence of interspecific host discrimination (van Alphen and Visser 1990; Hassell and Godfray 1994), and cause competition by the offspring of parasitoid species within a host. It also affects the population growth of a specific parasitoid if, as in most cases with ectoparasitoids, the female kills the host (Biondi et al. 2013; Chailleux et al. 2014; Idriss et al. 2018). Consequently, the chances of survival of a host are low when initially parasitized by an endoparasitoid and subsequently by an ectoparasitic, resulting in the larvae of the endoparasitoid being instantly killed together with the host (Rosenheim et al. 1995). This might be the case with B. nigricans, an ectoparasitoid (Biondi et al. 2013; Becchimanzi et al. 2017) when present in co-occurrence with the endoparasitoid, D. gelechiidivoris (Fernandez-Triana et al. 2020). Bracon nigricans is abundant in Kenya (Mama Sambo et al. 2022b), where D. gelechiidivoris was also released (Shiraku 2020). The level of parasitism by D. gelechiidivoris in the area investigated in this study, was low in comparison to parasitism levels when released in a greenhouse in the absence of B. nigricans (Mama Sambo et al. Unpublished data).

Phthorimaea absoluta larvae were effectively controlled by *D. gelechiidivoris* when exposed to this species alone (parasitism level of 73%). It was in contrast to the level of parasitism by *B. nigricans* of only 10%, when exposed under the same conditions. Previously, parasitism levels of 87% (Mama Sambo et al. 2022a), 58% (Mama Sambo et al. 2022c), and 55% Aigbedion-Atalor et al. (2020) were reported when 1st -instar P. absoluta larvae were exposed to female D. gelechiidivoris for 24 h. Biondi et al. (2013) and Idriss et al. (2018) reported that B. nigricans parasitised 4th-instar P. absoluta larvae and that only one or two parasitoids emerged from these larvae per day. Parasitism by B. nigricans, therefore, appears to be insignificant compared to parasitism by D. gelechiidivoris. However, Idriss et al. (2018), reported 54% parasitism of 4th instar larvae under laboratory conditions, and Mama Sambo et al. (2022b), up to 21% parasitism of P. absoluta larvae by this parasitoid species, in recent field studies. It emphasises the effect of other factors such as the host: parasitoid ratio and host stage available that can significantly affect the level of parasitism. A reduction of approximately 50% in D. gelechiidivoris parasitism was recorded in this study when this species cooccurred with B. nigricans. A highly negative impact on the population growth and resultant parasitism level and control of P. absoluta larvae by D. gelechiidivoris can therefore be expected in areas where B. nigricans is abundant.

Bracon nigricans did not discriminate the larvae already parasitised by the endoparasitoid, *D. gelechiidivoris*. Ectoparasitoids are in general also better competitors than endoparasitoids, and the venom from the females often paralyze the immature stages of the endoparasitoid already present in the host, as well as the host itself (Harvey et al. 2013). However, Savino et al. (2016) reported that the ectoparasitoid, *D. phthorimaeae* spent more time in general host searching for *P. absoluta* when in competition with the endoparasitoid *P. dignus*, while the presence of the ectoparasite did not have any effect in this regard on *P. dignus*. From the perspective of insect biological control, a superior parasitoid species must have a shorter developmental time, greater searching capability, high host specificity, a positive correlation with host density, good synchronization between the populations of the host and parasitoid as well as a good dispersal ability (Haye et al. 2008). The approximate female developmental time and longevity of B. nigricans are 12 days and between 13-24 at 25 °C respectively (Biondi et al. 2013; Idriss et al. 2018) while at the same temperature, the developmental time of D. gelechiidivoris is approximately between 19-25 days and its longevity, between to 59 days (Bajonero et al. 2008; Aigbedion-Atalor et al. 2020; Mama Sambo et al. 2022c).) The development time of B. nigricans is therefore shorter than that of D. gelechiidivoris, but it lives longer than D. gelechiidivoris. The number of B. nigricans progeny per day was reported to be fewer than five per female (Biondi et al. 2013; Idriss et al. 2018) while the number of D. gelechiidivoris progeny was reported to be host-density dependent (Mama Sambo et al. 2022c). Bracon nigricans is a generalist parasitoid, known to attack different lepidopteran families (Loni et al. 2016; Becchimanzi et al. 2017; Aigbedion-Atalor et al. 2019; Mama Sambo et al. 2022b), while the only family known to be attacked by D. gelechiidivoris to date, is Gelechiidae (Bajonero et al. 2008; Mujica and Kroschel 2017; Aigbedion-Atalor et al. 2020, 2021; Mama Sambo et al. 2022c).

It should, however, be noted that 32% killing of host larvae could have interfered with the population growth of a competing parasitoid as well as with that of the pest population. Several studies documented the performance of *B. nigricans* on host larval killing. For example, Biondi et al. (2013) reported the killing of approximately 50% of mature *P. absoluta* larvae by *B. nigricans*, while Idriss et al. (2018) found 55% mortality of 3rd-and 40% of 4th-instar *P. absoluta* larvae. The parasitism rates by *D. gelechiidivoris* might have been consequently affected by the population size of *B. nigricans*. However, predation by *N. tenuis* of 1st-instar *P. absoluta* larvae was not found to affect the progeny production and adult emergence of *D. gelechiidivoris* (Aigbedion-Atalor et al. 2021), although *N. tenuis* prefers the egg stage of *P. absoluta* (Sylla et al. 2016).

The number of P. absoluta mines drastically decreased from the second week after the parasitoids were introduced into the cages where P. absoluta larvae were present, both as standalone treatments as well as in combination, to represent the co-occurrence of the two species. Several studies reported an additional effect of more than one natural enemy on the control of P. absoluta. For example, P. absoluta larval parasitism by the parasitoids D. phthorimaeae and P. dignus resulted in high *P. absoluta* mortality in the field (Luna et al. 2015). A complementary effect in control of P. absoluta was also reported for the specialist, S. japonicus, and omnivorous natural enemy *M. pygmaeus* (Chailleux et al. 2017). Combined use of N. tenuis and T. achaeae also resulted in better control compared to N. tenuis alone (Calvo et al. 2012). The combined use of the parasitoid T. achaeae, and the predator *M. caliginosus* also increased *P. absoluta* control (Kortam et al. 2014). However, an antagonistic effect has been reported between *Spathius agrili* Yang (Hymenoptera: Braconidae) and *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) with larvae from the latter being paralyzed after parasitisation. It served as an indicator to *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae) to discriminate between *S. agrili* parasitized and non-parasitized larvae (Yang et al. 2013). *Spathius agrili* cannot detect larvae parasitised by *T. planipennisi*, which is disadvantageous to the parasitoid, since its progeny cannot survive on a host previously parasitized by *T. planipennisi* (Ulyshen et al. 2010).

Conclusion

The endoparasitoid D. gelechiidivoris and the ectoparasitoid, B. nigricans can co-exist by exploiting the same P. absoluta larvae differently. However, the presence of B. nigricans negatively affected the population growth of D. gelechiidivoris while the presence of D. gelechiidivoris did not affect B. nigricans population growth. Ecological niche differences created by biotic factors such as host plant, host preference, and abiotic factors, specifically climate, may drive the augmentation of these two parasitoids for control of P. absoluta. Additionally, since B. nigricans is a generalist parasitoid of several lepidopteran species such as Spodoptera littoralis Boisduval (Lepidoptera Noctuidae) (Becchimanzi et al. 2017) and Lobesia botrana (Denis & Schiffermüller) (Lepidoptera, Tortricidae) (Loni et al. 2016), a minimal effect is expected on the introduced D. gelechiidivoris under field conditions. However, the host plant species and host pest species preferences of B. nigricans should be studied to determine the optimal conditions for the co-existence of the two P. absoluta parasitoids.

Fundings

This research was supported by the following organizations: Biovision Foundation grant number BV DPP-012/2019-2022, Norwegian Agency for Development Cooperation-(NORAD), the section for research, innovation and higher education grant number RAF-3058 KEN-18/0005, Scaling-up Climate-Smart Pest Management Approaches for Enhanced Maize and Tomato Systems Productivity in Eastern Africa (SCLAMP) grant number 81250394, the Swedish International Development Cooperation Agency (Sida); the Swiss Agency for Development and Cooperation (SDC); the Federal Democratic Republic of Ethiopia; and the Government of the Republic of Kenva. The first author was supported by the German Academic Exchange Service (DAAD) through the African Regional Postgraduate Programme in Insect Science (ARP-PIS) tenable at *icipe*. The views expressed herein do not necessarily reflect the official opinion of the donors.

Acknowledgements The authors acknowledge Alex Muthembwa, Omar Jimali Ibrahim, Peterson Nderitu, Patrick Kipkorir Koech, Francis Obala, John Macharia, and all the African Fruit Fly Program (AFFP) colleagues for their technical support.

Data availability The data of these results is available on the International Centre of Insect Physiology and Ecology (icipe) data repository and can be accessed if requested.

Declarations

Competing interests We declare that this study has no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Aigbedion-Atalor PO, Abuelgasim S, Hill MP et al (2020) Host stage preference and performance of *Dolichogenidea gelechiidivoris* (Hymenoptera: Braconidae), a candidate for classical biological control of *Tuta absoluta* in Africa. Biol Control 144:104215. https://doi.org/10.1016/j.biocontrol.2020.104215
- Aigbedion-Atalor PO, Hill MP, Ayelo PM et al (2021) Can the combined use of the mirid predator *Nesidiocoris tenuis* and a braconid larval endoparasitoid *Dolichogenidea gelechiidivoris* improve the biological control of *Tuta absoluta*? InSects 12:1–12. https://doi.org/10.3390/insects12111004
- Aigbedion-Atalor PO, Hill MP, Zalucki MP et al (2019) The South America tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), spreads its wings in Eastern Africa: distribution and socioeconomic impacts. J Econ Entomol 112:2797–2807. https://doi.org/10.1093/jee/toz220
- Al-Jboory IJ, Katbeh-Bader A, Shakir AZ (2012) First observation and identification of some natural enemies collected from heavily infested tomato by *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Jordan. World Appl Sci J 17:589–592
- Bajonero J, Córdoba N, Cantor F et al (2008) Biology and life cicle of Apanteles gelechiidivoris (Hymenoptera: Braconidae) parasitoid of Tuta absoluta. Agron Colomb 26:417–426
- Becchimanzi A, Avolio M, Bostan H et al (2020) Venomics of the ectoparasitoid wasp *Bracon nigricans*. BMC Genomics 21:1– 15. https://doi.org/10.1186/s12864-019-6396-4
- Becchimanzi A, Avolio M, Di LI et al (2017) Host regulation by the ectophagous parasitoid wasp Bracon nigricans. J Insect Physiol. https://doi.org/10.1016/j.jinsphys.2017.07.002
- Biondi A, Desneux N, Amiens-Desneux E et al (2013) Biology and developmental strategies of the Palaearctic parasitoid *Bracon nigricans* (Hymenoptera: Braconidae) on the Neotropical moth *Tuta absoluta* (Lepidoptera: Gelechiidae). J Econ Entomol 106:1638–1647. https://doi.org/10.1603/EC12518

- Bográn CE, Heinz KM, Ciomperlik MA (2002) Interspecific competition among insect parasitoids: field experiments with whiteflies as hosts in cotton. Ecol Soc Am 83:653–668
- Calvo FJ, Lorente MJ, Stansly PA, Belda JE (2012) Preplant release of Nesidiocoris tenuis and supplementary tactics for control of Tuta absoluta and Bemisa tabaci in greenhouse tomato. Entomol Exp Appl 1:111–119. https://doi.org/10.1111/j.1570-7458.2012.01238.x
- Chailleux A, Desneux N, Arnó J, Gabarra R (2014) Biology of two key Palaearctic larval ectoparasitoids when parasitizing the invasive pest *Tuta absoluta*. J Pest Sci 87:441–448. https://doi.org/10.1007/ s10340-014-0557-7
- Chailleux A, Droui A, Bearez P, Desneux N (2017) Survival of a specialist natural enemy experiencing resource competition with an omnivorous predator when sharing the invasive prey *Tuta absoluta*. Ecol Evol 7:8329–8337. https://doi.org/10.1002/ece3.3396
- Cusumano A, Peri E, Amodeo V et al (2013) Intraguild interactions between egg parasitoids: the window of opportunity and fitness costs for a facultative hyperparasitoid. PLoS ONE 8:1–7. https:// doi.org/10.1371/journal.pone.0064768
- Cusumano A, Peri E, Colazza S (2016) Interspecific competition/facilitation among insect parasitoids. Curr Opin Insect Sci 14:12–16. https://doi.org/10.1016/j.cois.2015.11.006
- Denis C, Riudavets J, Alomar O et al (2022) Naturalized *Dolichogenidea gelechiidivoris* complement the resident parasitoid complex of *Tuta absoluta* in North-eastern Spain. J Appl Entomol 146:461–464. https://doi.org/10.1111/jen.12994
- Desneux N, Wajnberg E, Kris WAG et al (2010) Biological invasion of European tomato crops by *Tuta absoluta*: Ecology, geographic expansion and prospects for biological control. J Pest Sci 83:197– 215. https://doi.org/10.1007/s10340-010-0321-6
- Feng Y, Wratten S, Sandhu H, Keller M (2015) Interspecific competition between two generalist parasitoids that attack the leafroller *Epiphyas postvittana* (Lepidoptera: Tortricidae). Bull Entomol Res 105:426–433. https://doi.org/10.1017/S0007485314000923
- Fernandez-Triana J, Shaw MR, Boudreault C et al (2020) Annotated and illustrated world checklist of Microgastrinae parasitoid wasps (Hymenoptera, Braconidae). Zookeys 920:1–1089. https://doi.org/ 10.3897/zookeys.920.39128
- Ferracini C, Bueno VHP, Dindo ML et al (2019) Natural enemies of *Tuta absoluta* in the Mediterranean basin, Europe and South America. Biocontrol Sci Technol 29:1–32. https://doi.org/10. 1080/09583157.2019.1572711
- Gabarra R, Arnó J, Lara L et al (2013) Native parasitoids associated with *Tuta absoluta* in the tomato production areas of the Spanish Mediterranean Coast. Biocontrol 59:45–54. https://doi.org/10. 1007/s10526-013-9545-8
- Harvey JA, Poelman EH, Tanaka T (2013) Intrinsic inter- and intraspecific competition in parasitoid wasps. Annu Rev Entomol 58:333– 351. https://doi.org/10.1146/annurev-ento-120811-153622
- Hassell MP, Godfray HCJ (1994) Natural enemies: The population biology of predators, parasites and diseases. Michael J Crawley Q Rev Biol 69:256–257. https://doi.org/10.1086/418554
- Haye T, Mason P, Kuhlmann U (2008) Predictive value of biological control agent's attributes for introduction: *Peristenus digoneutis* as a case study. In: Third International Symposium on Biological Control of Arthropods, Christchurch, New Zealand. pp 403–415
- Holt RD, Bonsall MB (2017) Apparent competition. Annu Rev Ecol Evol Syst 48:447–471. https://doi.org/10.1146/annurevecolsys-110316-022628
- Idriss GEA, Mohamed SA, Khamis F et al (2018) Biology and performance of two indigenous larval parasitoids on *Tuta absoluta* (Lepidoptera: Gelechiidae) in Sudan. Biocontrol Sci Technol 28:614–628. https://doi.org/10.1080/09583157.2018.1477117
- Kortam MN, El Arnaouty SA, Afifi AI, Heikal IH (2014) Efficacy of different biological methods for controlling the tomato leaf miner,

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) on tomato in greenhouse in egypt. Egypt J Biol Pest Control 24:523–528

- Krache F, Boualem M, Fernandez-Triana J et al (2021) First record in Africa of the parasitoid *Dolichogenidea gelechiidivoris* (Hymenoptera: Braconidae) on tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) from tomato fields in Algeria. J Hymenopt Res 88:115–131. https://doi.org/10.3897/jhr.88.75279
- Loni A, Samartsev KG, Scaramozzino PL et al (2016) Braconinae parasitoids (Hymenoptera, Braconidae) emerged from larvae of *Lobe*sia Botrana (Denis & Schiffermüller) (Lepidoptera, Tortricidae) feeding on Daphne gnidium L. Zookeys 587:125–150. https://doi. org/10.3897/zookeys.587.8478
- Luna MG, Pereyra PC, Coviella CE et al (2015) Potential of biological control agents against *Tuta absoluta* (Lepidoptera: Gelechiidae): current knowledge in Argentina. Florida Entomol 98:489–494. https://doi.org/10.1653/024.098.0215
- Mama Sambo S, Akutse KS, du Plessis H et al (2022a) Interactions between the Entomopathogenic fungus *Metarhizium anisopliae* ICIPE 20 and the endoparasitoid *Dolichogenidea gelechiidivoris*, and implications for combined biocontrol of *Tuta absoluta*. Biology (basel) 11:1323. https://doi.org/10.3390/biology11091323
- Mama Sambo S, Ndlela S, Plessis H et al (2022b) Identification, microhabitat, and ecological niche prediction of two promising native parasitoids of *Tuta absoluta* in Kenya. InSect 16:496. https://doi. org/10.3390/insects13060496
- Mama Sambo S, Ndlela S, Plessis H et al (2022c) Ratio dependence effects of the parasitoid *Dolichogenidea gelechiidivoris* on its associated host *Tuta absoluta*. Biocontrol Sci Technol 32:497– 510. https://doi.org/10.1080/09583157.2022.2033702
- Mansour R, Brévault T, Chailleux A et al (2018) Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. Entomol Gen 38:83–112. https://doi.org/10.1127/entomologia/2018/0749
- Mills NJ (1992) Parasitoid guilds: depning the structure of the parasitoid communities of endopterigote insect hosts. Environ Entomol 23:1066–1083
- Mirhosseini MA, Fathipour Y, Soufbaf M, Reddy GVP (2019) Implications of using two natural enemies of *Tuta absoluta* (Lepidoptera: Gelechiidae) toward tomato yield enhancement. Bull Entomol Res 109:617–625. https://doi.org/10.1017/S0007485318000998
- Mujica N, Kroschel J (2017) Host preference of *Dolichogenidea gelechiidivoris* (Marsh) (Hymenoptera: Braconidae) for *Tuta absoluta* (Meyrick) or *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae). In: 15 Siconbiol, Resumo: 385–44. p 423 p
- Naselli M, Biondi A, Tropea-Garzia G et al (2017) Insights into food webs associated with the South American tomato pinworm. Pest Manag Sci 73:1352–1357. https://doi.org/10.1002/ps.4562
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL https://www.R-project.org/. Accessed 25 July 2022
- Reitz SR, Trumble JT (2002) Competitive displacement among insects and arachnids. Annu Rev Entomol 47:435–465
- Rosenheim JA, Kaya HK, Ehler LE et al (1995) Intraguild predation among biological-control agents: Theory and evidence. Biol Control 5:303–335. https://doi.org/10.1006/bcon.1995.1038
- Salas Gervassio NG, Aquino D, Vallina C et al (2019) A re-examination of *Tuta absoluta* parasitoids in South America for optimized biological control. J Pest Sci 92:1343–1357. https://doi.org/10.1007/ s10340-018-01078-1
- Savino V, Luna MG, Gervassio NGS, Coviella CE (2016) Interspecific interactions between two *Tuta absoluta* (Lepidoptera: Gelechiidae) larval parasitoids with contrasting life histories. Bull Entomol Res 107:32–38. https://doi.org/10.1017/S0007485316000547

- Shiraku H (2020) ICIPE Makes the first release of parasitoids into the farm in fight against *Tuta absoluta*. Infonet-Biovision. Available online: https://infonet-biovision.org/News/ ICIPE-Makes-first-release-parasitoids-farm-fight-against-Tuta-Absoluta. Accessed 14 Nov 2020
- Sylla S, Brévault T, Streito J, Diarra K (2016) First record of *Nesidiocoris tenuis* (Reuter) (Heteroptera: Miridae), as a predator of the Tomato Leaf Miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), in Senegal. Egypt J Biol Pest Control 26:851–853
- Tan X, Hu N, Zhang F et al (2016) Mixed release of two parasitoids and a polyphagous ladybird as a potential strategy to control the tobacco whitefly *Bemisia tabaci*. Sci Rep 6:1–9. https://doi.org/ 10.1038/srep28245
- Tropea Garzia G, Siscaro G, Biondi A et al (2012) Tuta absoluta, a South American pest of tomato now in the EPPO region: Biology, distribution and damage. EPPO Bull 42:205–210. https://doi.org/ 10.1111/epp.2556
- Ulyshen MD, Duan JJ, Bauer LS (2010) Interactions between Spathius agrili (Hymenoptera: Braconidae) and Tetrastichus planipennisi (Hymenoptera: Eulophidae), larval parasitoids of Agrilus planipennis (Coleoptera: Buprestidae). Biol Control 52:188–193. https://doi.org/10.1016/j.biocontrol.2009.10.017
- van Alebeek FAN, Rojas-Rousse D, Leveque L (1993) Interspecific competition between Eupelmus vuilleti and Dinarmus basalis, two solitary ectoparasitoids of Bruchidae larvae and pupae Interspecific competition between Eupelmus vuilleti and Dinarmus basalis, two solitary ectoparasitoids of Bruchidae larvae. Entomol Exp Appl 69:21–31. https://doi.org/10.1111/j.1570-7458. 1993.tb01724.x
- van Alphen JJM, Visser ME (1990) Superparasitism as an adaptive strategy for insect parasitoids. Annu Rev Entomol 35:59–79. https://doi.org/10.1146/annurev.en.35.010190.000423
- Wang XG, Bokonon-Ganta AH, Messing RH (2008) Intrinsic interspecific competition in a guild of tephritid fruit fly parasitoids: Effect of co-evolutionary history on competitive superiority. Biol Control 44:312–320. https://doi.org/10.1016/j.biocontrol. 2007.10.012
- Xu H, Yang N, Wan F (2013) Competitive interactions between parasitoids provide new insight into host suppression. PLoS ONE 8:16–21. https://doi.org/10.1371/journal.pone.0082003
- Yang S, Duan JJ, Lelito J, Van DR (2013) Multiparasitism by *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) and *Spathius agrili* (Hymenoptera : Braconidae): implication for biological control of the emerald ash borer (Coleoptera : Buprestidae). Biol Control 65:118–123. https://doi.org/10.1016/j.biocontrol.2012.09.010
- Yu DSK, Actherberg C (2010) Taxapad Ichneumonoidea. In Bisby FA, Roskov YR, Orrell TM, Nicolson D, Paglinawan LE, Bailly N, Kirk PM, Bourgoin T, Baillargeon G (eds), Species 2000 & IT IS. Cat life 2010 Annu checklist DVD, Species 2000, Reading, United Kingdom
- Zappalà L, Bernardo U, Biondi A et al (2012) Recruitment of native parasitoids by the exotic pest *Tuta absoluta* in southern Italy. Bull Insectology 65:51–61
- Zappalà L, Biondi A, Alma A et al (2013) Natural enemies of the South American moth, *Tuta absoluta*, in Europe, North Africa and Middle East, and their potential use in pest control strategies. J Pest Sci 86:635–647. https://doi.org/10.1007/s10340-013-0531-9

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.