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RESEARCH **Open Access**

Predicting the establishment of *Diaphorina citri* and *Tamarixia radiata* on *Citrus x aurantiifolia* orchards based on the plant–psyllid–parasitoid interaction on *Murraya paniculata*

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Abstract

Background: The insect vector of Huanglongbing, *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Lividae) was detected in Ecuador in 2013 and its main parasitoid *Tamarixia radiata* (Waterston, 1922) (Hymenoptera: Eulophidae) was reported for the first time in 2017. In the citrus production region of Manabí province, Ecuador, *D. citri* and *T. radiata* were reported for the first time on *Murraya paniculata* L. in 2016 and 2018, respectively. *D. citri* was first found infesting *Citrus x aurantiifolia* (Christm.) Swingle in Manabí province at the end of 2018. The present study was conducted between August 2018 and May 2021 to: (1) monitor *D. citri* populations on *M. paniculata* and *C.* x *aurantiifolia* and determine the parasitism rates of *T. radiata* on *D. citri* nymphs on both host plants, (2) establish the occurrence of *T. radiata* parasitizing *D. citri* on *C.* x *aurantiifolia*, and (3) calculate a predictive model for estimating the number of parasitized nymphs on a planting lot of *M. paniculata* and a *C. aurantiifolia* orchard.

Results: *Diaphorina citri* populations on *M. paniculata* decreased from 11 nymphs (2018–2019) to approximately 2 nymphs per flush (2020). This was associated with a natural increase in parasitism rates of *T. radiata* from 20% (2018) to 96% in 2020. The regression equation ($Y = 2.049\mathrm{Ln}(x) + 5.88$) was able to estimate the number of parasitized *D. citri* nymphs based on parasitism on *M. paniculata* (R^2: 0.8315). *Tamarixia radiata* was first detected on *C. x aurantiifolia* in July 2020. Populations of *D. citri* reached 55 nymphs per flush (no parasitism) and subsequently decreased to the minimum level of 14 nymphs per flush (parasitism rates of up to 31%). The model allowed estimating the number of parasitized nymphs by *T. radiata* on *M. paniculata* and *C.* x *aurantiifolia*, with a maximum deviation of approximately 2 nymphs.

Conclusions: Based on the colonization and establishment of the psyllid–parasitoid interaction on *M. paniculata*, it is estimated that approximately by the end of 2022, populations of *D. citri* on *C. x aurantiifolia* would decline due to the highest percentages of parasitism by *T. radiata*. High parasitism rates may indicate the potential of *T. radiata* in conservation biological control and integrated pest management programs.

Keywords: *Diaphorina citri*, Parasitism, *Tamarixia radiata*, Pest management

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Background

In Ecuador, citrus agriculture represents an important agricultural activity, which occurs mainly in the continental zone. Citrus are commercially grown in six of the 24 provinces of Ecuador, both in the Pacific coastal region and in the highlands of the country (Cañarte-Bermudez and Navarrete-Cedeño 2019). Approximately 29,721 ha of key limes, oranges, mandarins, among other citrus species are harvested in Ecuador, with an annual production of 17,544 tons (FAOSTAT 2019). One of the potential threats to the Ecuadorian citrus industry is Huanglongbing, considered the most destructive disease of citrus worldwide, caused by the bacteria *Candidatus* Liberibacter spp. that obstruct the phloem and can cause the eventual death of the plant (Bové 2006).

Although this disease has not yet been reported in Ecuador, in 2013, its known insect vector in the Americas, the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera, Liviidae) was detected in the coastal province of Guayas on both, *Citrus* spp. (Rutaceae) as well as on the ornamental plant host, orange jasmine, *Murraya paniculata* (L.) Jack (Rutaceae) (Cornejo and Chica 2014). From there, it spread to different citrus regions on Ecuador (Cuadros et al. 2020). After the detection of *D. citri*, its parasitoid, *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) was reported in the province of Guayas, following the same initial dispersal of its insect host (Portalanza et al. 2017). Subsequently, *T. radiata* was reported in other provinces of Ecuador, in the coast (Cuadros et al. 2020) and the highlands (Erraez et al. 2020).

Manabí constitutes one of the main citrus provinces of the coast where *D. citri* was observed for the first time on *M. paniculata* shrubs in Portoviejo 2016 (Navarrete et al. 2016). In 2018, *T. radiata* was found parasitizing *D. citri* on *M. paniculata* and by the end of that same year, *D. citri* began to infest key lime trees (Cuadros et al. 2020).

Diaphorina citri has a wide host range that includes 25 genera within the family Rutaceae (Halbert and Manjunath 2004). The preference of *D. citri* for *M. paniculata* over other citrus species was reported both in early observations (Aubert 1987) and in later studies (Teck et al. 2011), which probably explains that its colonization in Manabí occurred first on *M. paniculata* before colonizing *Citrus x aurantiifolia* (Christm,) Swingle. Then, starting from the establishment of the plant–psyllid–parasitoid interaction on *M. paniculata* in the studied area the complete establishment of the same interaction on citrus that began by the end of 2018 was predicted. .

Mathematical models have been proposed to explain psyllid–parasitoid interactions (Miksanek and Heimpel 2019). Likewise, several studies have been conducted on the population dynamics of *D. citri* resulting from interactions with density-dependent and density-independent processes (Milosavljević et al. 2021). This study aimed to explain the importance of parasitism by *T. radiata* on *D. citri*, as well as the colonization and establishment of this psyllid–parasitoid interaction on *M. paniculata* and *C.* x *aurantiifolia* (Rutaceae) in the province of Manabí, Ecuador.

Methods

The study was carried out during the period August 2018–May 2021 on the host plants, orange jasmine, *Murraya paniculata* and key lime, *Citrus x aurantiifolia*. In Ecuador, *M. paniculata*, a shrub planted as an ornamental plant, is commonly used as hedges in parks, commercial establishments and in house gardens in urban areas. One hundred and fifty plants of *M. paniculata* were planted in the Portoviejo city (Coordinates: 01°03′17″S, 80°27′16″W, 53 m a.s.l.), which were sampled weekly from August 2018 to December of 2020 when the parasitism reached more than 90%. At the same time, a survey began at a key lime, *C.* x *aurantiifolia* orchard in an area of 2 ha, consisted of 200 4-year-old trees, located in the town of Mejía, via Crucita, Portoviejo (00°59′22.4″S 80°27′57.1″W, 53 m a.s.l.). The distance between the key lime orchards to the planting lot of orange jasmine was about 8 km. The life zone corresponds to a tropical dry forest. Precipitation data (mm) obtained from the National Institute of Meteorology and Hydrology of Ecuador are included.

Forty flushes (young shoots), each 10 cm long, were randomly sampled within the lots established for each of the host plant. These flushes were placed in plastic bags and transported to the Entomology Laboratory, Faculty of Agronomic Engineering, Technical University of Manabí. The number of non-parasitized nymphs of *D. citri* and the number of nymphs parasitized by *T. radiata* were counted. Parasitized nymphs were initially identified based on their dark brown coloration. These nymphs were placed in a Petri dish and dissected to confirm the presence of parasitoid larvae or pupae. Counts were performed, using a Carl-Zeiss® stereoscope (magnification: 10–40×).

The percentage of parasitism was calculated as follows:

$$\frac{\text{No. of parasitized nymphs}}{\text{No. of nymphs(parasitized + non - parasitized)}} \times 100$$

Data analysis

For each of the host plants, *i.e., C. x aurantiifolia* and *M. paniculata*, the number of non-parasitized *D. citri* nymphs, number of parasitized *D. citri* nymphs per week were averaged. Monthly averages of *D. citri* nymphs and rainfall were plotted, including a correlation analysis between both variables ($P < 0.05$). A correlation analysis was carried out between the non-parasitized *D. citri* nymphs (X) and the parasitized *D. citri* nymphs (Y)

($P < 0.01$) observed on *M. paniculata*. From these observations, an equation was subsequently obtained to estimate the number of parasitized *D. citri* nymphs ($P < 0.01$). With the calculated equation, the parasitized nymphs on both host plants were estimated.

Results

Rainfall

The plant–psyllid–parasitoid interaction was analysed to plot the population dynamics in relation to rainfall. In the province of Manabí, each year the rainy period begins approximately from January until April (Fig. 1). The torrential rains that occur in the region are associated with the decrease in population densities of *D. citri*. Thus, when rainfall ranged between 140 and 280 mm, the populations were practically nil (Fig. 1). However, as rainfall decreases, the rutaceous plants start to produce young shoots, which are ideal for the development of *D. citri* nymphs, resulting in a population increase. This is corroborated by the highly significant inverse correlation between populations of *D. citri* and rainfall, on *M. paniculata* (r: −0.5202, $P < 0.05$) and on *C. x aurantiifolia* (r: −0.5215, $P < 0.05$).

Host plant-*Diaphorina citri*–*Tamarixia radiata* interactions

Orange jasmine, Murraya paniculata

The populations of *D. citri* nymphs and *T. radiata* parasitism rates varied from the first year of evaluations (Fig. 2a). From August to December 2018, the population densities of *D. citri* ranged 3–9 nymphs per flush (average: 4.9 ± 0.5), while the natural parasitism rate increased from 20 to 80% (average: 38 ± 4.2). In 2019, the number of *D. citri* nymphs per flush increased from June and reached the maximum peak between August and October (range 9–11 nymphs per flush) (average: 3.7 ± 0.5). Parasitism rates ranged from 12 to 82% (2018–2019) (average: 37.2 ± 3.2), with the highest parasitism rates associated with low population densities of *D. citri*. In 2020, *D. citri* populations fell to their lowest values (range 0.2–2.3 nymphs) (average: 0.9 ± 0.1) coupled with higher rates of parasitism (57–96%) (average: 81.9 ± 1.8).

The calculated logarithmic regression model showed a high and significant percentage of determination (R^2: 0.8315, $P < 0.01$) for estimating the parasitism rates (Fig. 3a). The residual analysis showed that the equation could have a maximum deviation of approximately 2 nymphs (4% of the cases) (Fig. 3b). The estimated number of parasitized *D. citri* nymphs were plotted together with the non-parasitized *D. citri* nymphs and observed parasitized nymphs (Fig. 4a). It was observed that when there was a greater number of parasitized nymphs, there were fewer non-parasitized nymphs and vice versa, indicating an inverse association (r: −0.8064, $P < 0.01$). Likewise, the close relationship between the observed parasitized *D. citri* nymphs and the estimated parasitized *D. citri* nymphs had the greatest variation in

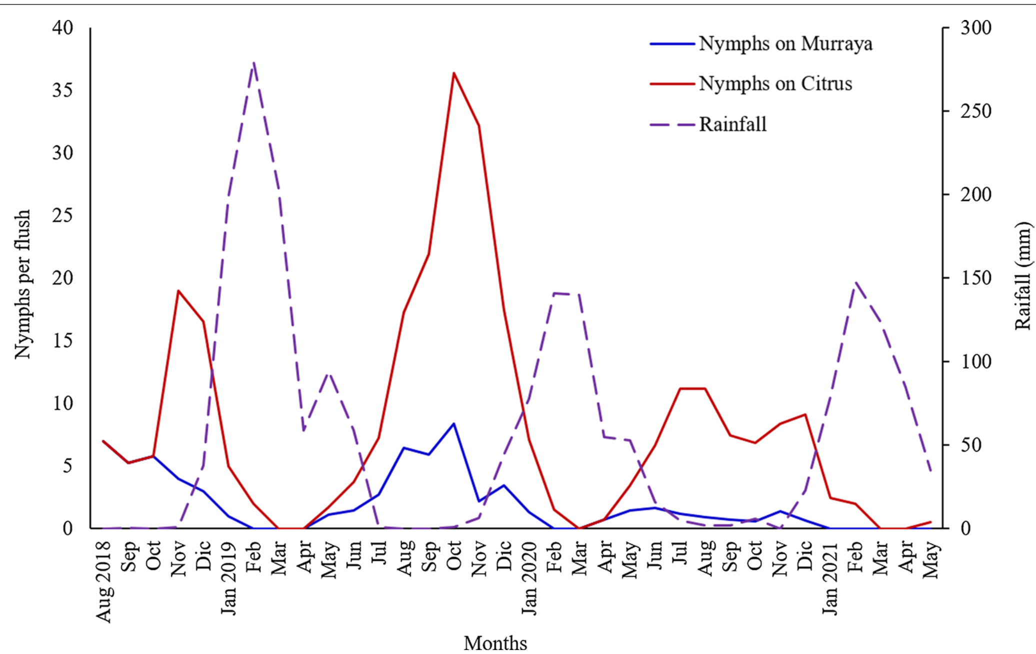

Fig. 1 Fluctuation of *Diaphorina citri* nymphs on both host plants and rainfall. Period August 2018–May 2021

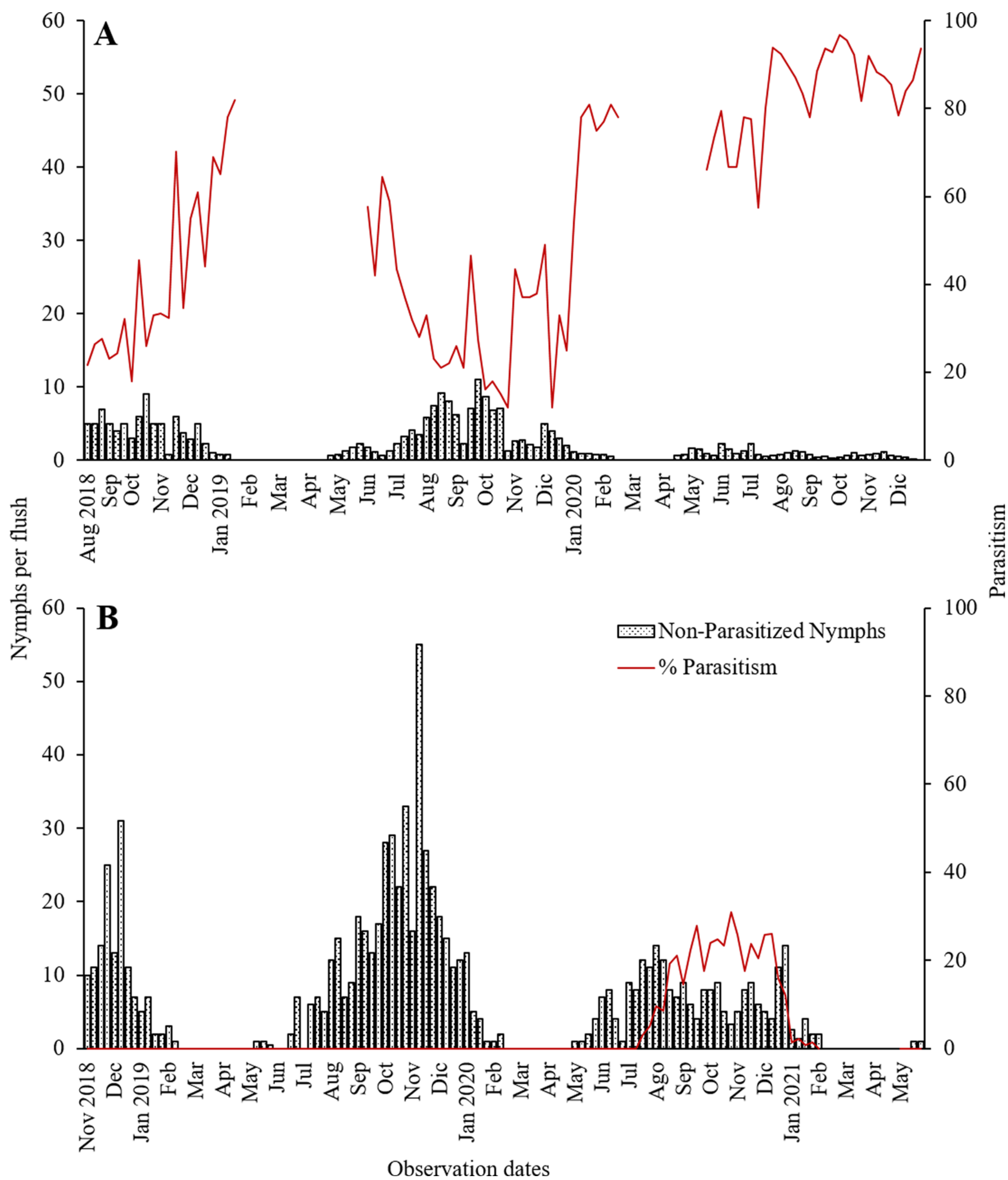

Fig. 2 Population fluctuation of non-parasitized nymphs of *Diaphorina citri* and the percentage of parasitism by *Tamarixia radiata*. **a** *Murraya paniculata*, **b** *Citrus x aurantiifolia*. Period August 2018–May 2021

the first observations (1–20) and stabilized in posterior observations (Fig. 4a).

Key lime, Citrus x aurantiifolia

In 2018, when *D. citri* was detected on *C.* x *aurantiifolia*, populations increased with maximum peaks of 25–31 *D. citri* nymphs per flush (Fig. 2b) (average: 15.3 ± 2.9). However, in 2019, after the rainy season, the highest levels of 55 *D. citri* nymphs per flush were recorded (Fig. 5a) (average: 12.1 ± 2.0). When *D. citri* nymphs' parasitized by *T. radiata* were first detected (Fig. 5b) in July 2020, the parasitism rates were very low (3%, Fig. 2b) and by the end of October 2020, it reached the maximum parasitism rates of 30% (average: 8.7 ± 1.8). Although during this period the populations continued to be high (maximum of 14 nymphs per flush), these were much lower than those reached in previous years, especially in 2019 when parasitism with *T. radiata* was absent (average: 6.5 ± 0.6).

Number of non-parasitized *D. citri* nymphs, the observed parasitized *D. citri* nymphs and the estimated

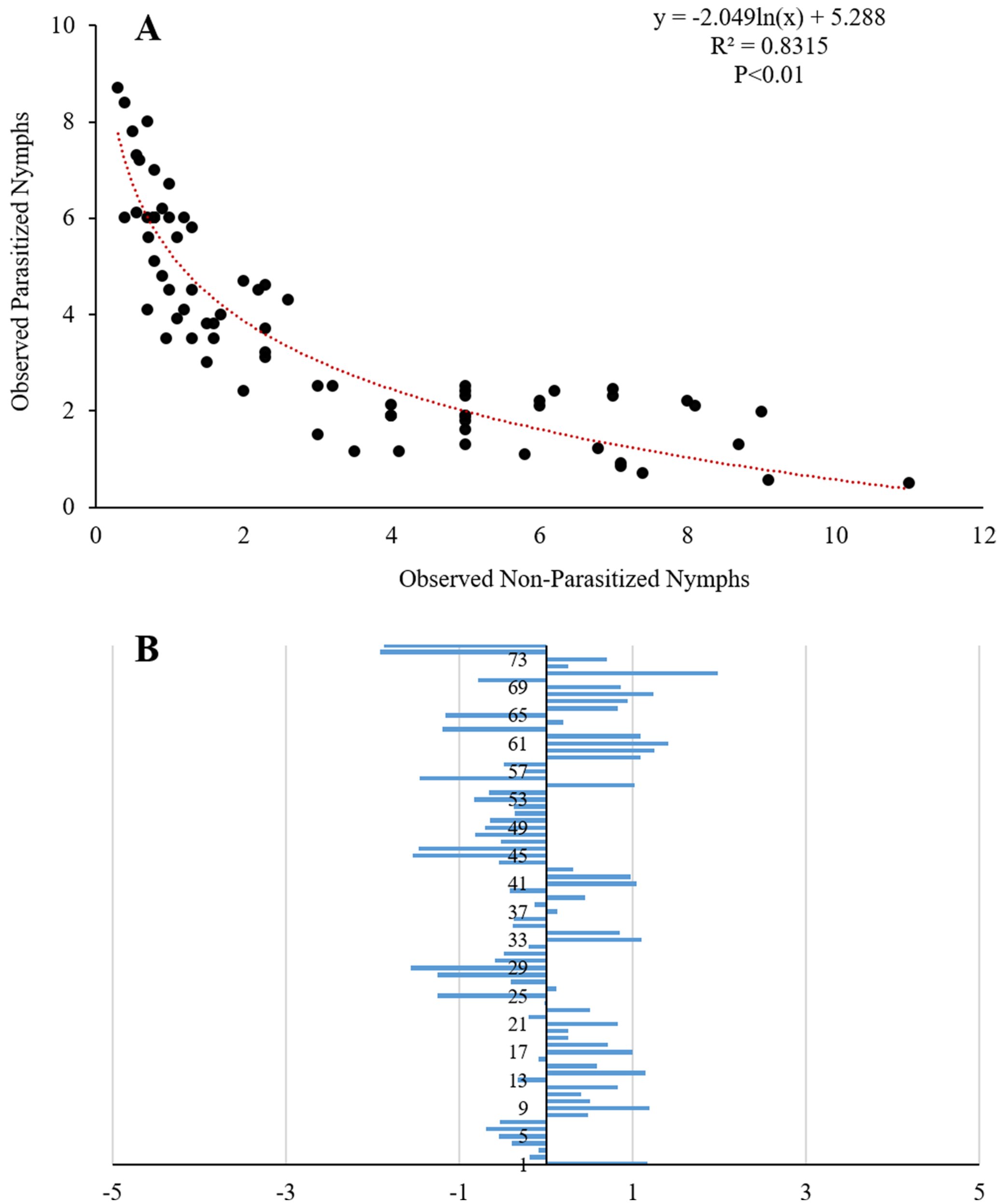

Fig. 3 **a** Regression analysis between parasitized and non-parasitized nymphs of *Diaphorina citri* observed in the study on *Murraya paniculata*. **b** Residuals in the nymph estimation

parasitized *D. citri* nymphs on *C.* x *aurantiifolia* are shown in Fig. 4b. The variations found between the observed number of parasitized *D. citri* nymphs and the estimated number of parasitized *D. citri* nymphs in the 22 observations were similar to those found on *M. paniculata* in the 2nd half of 2018. The residue analysis between the observed number of parasitized *D. citri* nymphs and the estimated number of parasitized nymphs on key lime showed the same deviation trends (2 nymphs per flush) as the residue analysis estimated in *M. paniculata* (Fig. 3b).

Discussion

The highly significant inverse correlation between the numbers of *D. citri* nymphs versus rainfall indicated that this abiotic factor regulates the population densities of

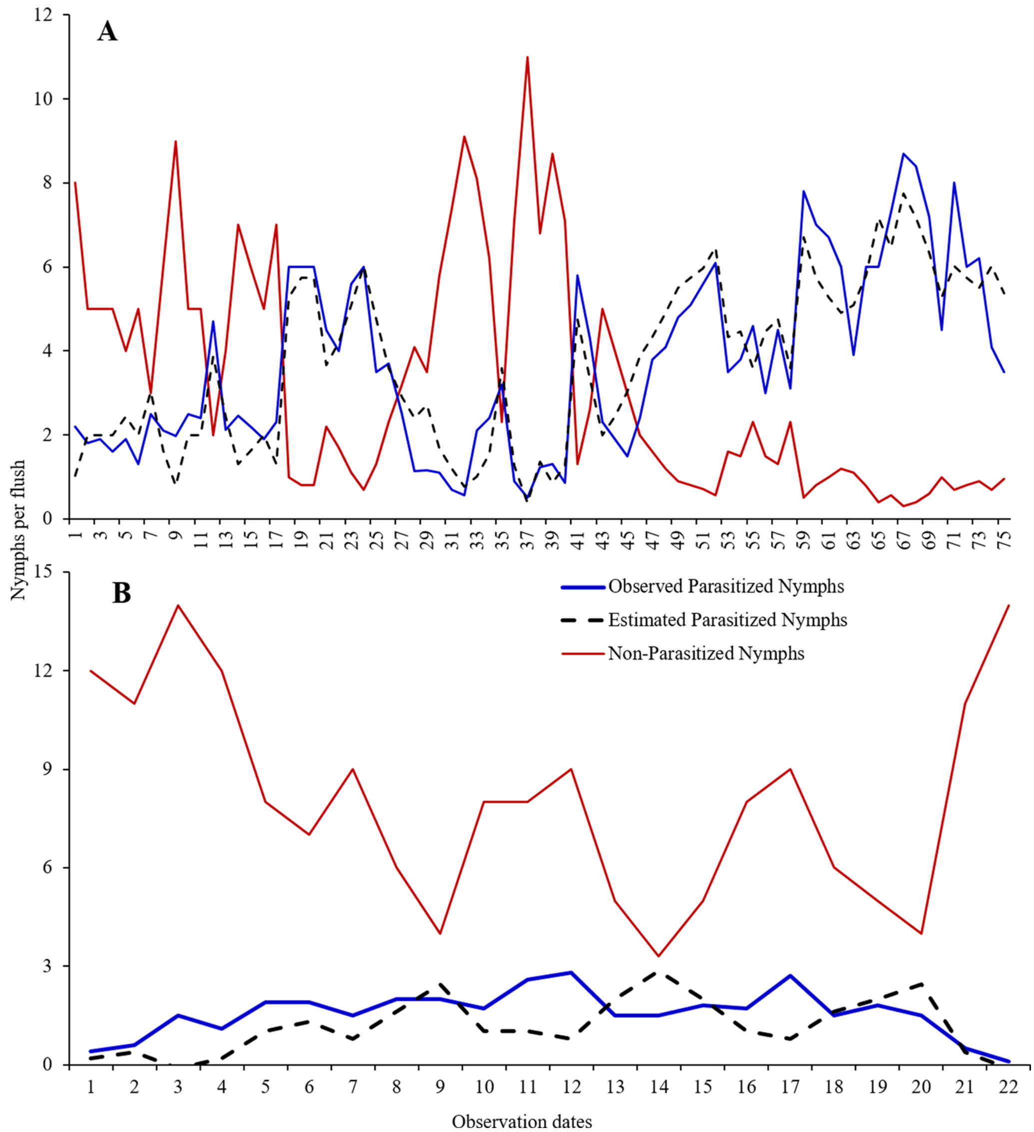

Fig. 4 Nymphs of *Diaphorina citri*: observed parasitized and non-parasitized, as well as estimated parasitized on: **a** *Murraya paniculata,* **b** *Citrus x aurantiifolia*

the pest in the rainy periods. Kiritani (2013) reported that, although density-dependent processes regulate the population density of any organism, density-independent processes also influence it, and its magnitude may vary. Studies have shown that rainfall can limit the population development of *D. citri* (Chavez-Medina et al. 2016). Furthermore, Aubert (1987) reported that monthly rainfall exceeding 150 mm is generally associated with low populations of *D. citri* due to the washing of eggs and nymphs from the plant surface.

At the end of the rainy season, the population densities of *D. citri* increased and within the interaction of the plant–psyllid system, another density-dependent process came into play, i.e., the parasitoid, *T. radiata*. The importance of *T. radiata* as a biocontrol agent of *D. citri* on *M. paniculata* was supported by the high inverse correlation (r: −0.9119, $P < 0.05$) between the number of parasitized and non-parasitized *D. citri* nymphs that resulted in high parasitism rates (Fig. 3a).

The importance of parasitism by *T. radiata* on *D. citri* has been previously established for *M. paniculata* and citrus species. Pluke et al. (2008) observed levels of parasitism, ranged between 70–100 and 48–70% for *Citrus* spp. and *M. paniculata*, respectively. Releases of *T. radiata* decreased the number of *D. citri* nymphs

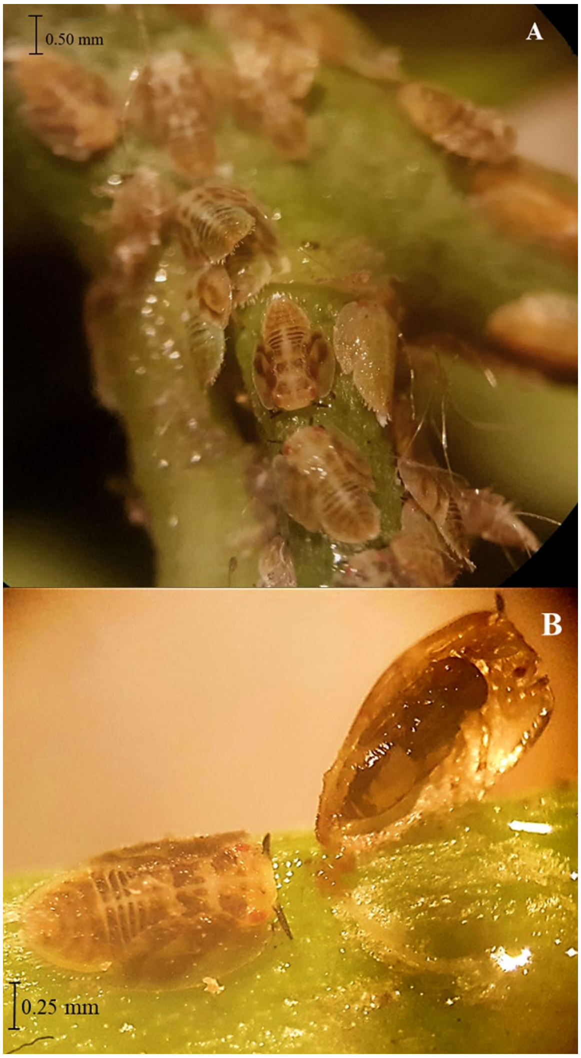

Fig. 5 **a** Population density of *Diaphorina citri* nymphs per flush of *Citrus x aurantiifolia* in the absence of parasitism. Years 2018 and 2019. **b** Nymphs of *Diaphorina citri* parasitized by *Tamarixia radiata* detected on *Citrus x aurantiifolia.* July 2020

per flush from 42 to 3.8, which represented (91.2%) of the population reduction (Flores and Ciomperlik 2017). Four years of study in different regions of Southern California indicated a significant mortality of *D. citri* due to high rates of parasitism by *T. radiata* in citrus plants (Milosavljević et al. 2021).

Parasitism rates of *T. radiata* on *D. citri* on *M. paniculata* and *C.* x *aurantiifolia* in Manabí province showed a colonization process of an exotic insect pest and the phenological desynchronization in the colonization of its parasitoid. Thus, the fieldwork showed that *M. paniculata* was colonized by *D. citri* in Manabí province approximately in August 2016 (Navarrete et al. 2016) and approximately 2 years later, in May 2018, *T. radiata* parasitized *D. citri* nymphs were observed (Cuadros et al. 2020).

Subsequently, *C.* x *aurantiifolia*, colonized by *D. citri* at the end of 2018 and this process, together with the absence of parasitism, may explain the high densities detected in that year and especially in the following year (2019). With an asynchrony of 2 years, in July 2020, in this agro-ecosystem, the parasitoid *T. radiata* became part of the interaction with very low rates of parasitism at the beginning, which increased over time.

A similar case of phenological desynchronization (insect host—parasitoid) was reported in Venezuela with the guava cottony scale, *Capulinia linarosae* Kondo and Gullan, 2016 (Hemiptera: Eriococcidae), a pest of the guava tree, *Psidium guajava* L. (Myrtaceae). In 1993, this invasive insect species of unknown origin appeared colonizing the guava crop in different guava producing regions of Venezuela (Cermeli and Geraud-Pouey 1997). With a difference of approximately 2 years (January 1996), the wasp parasitoid *Metaphycus marensis* Chirinos and Kondo, 2019 (Hymenoptera: Encyrtidae) was observed parasitizing *C. linarosae* on guava (Cermeli and Geraud-Pouey 1997). By 1999, the parasitoid, *M. marensis*, was fully established and interacting with its host, *C. linarosae* in the different regions of Venezuela where guava is grown (Geraud-Pouey et al. 2001).

Jeffs and Lewis (2013) reported that time is fundamental for many interspecific interactions that evolve to optimize temporal overlap and additionally mentioned that asynchrony can be part of the adaptive process. The same researchers indicated that few studies have observed the potential for phenological asynchrony between parasitoids and their insect hosts.

The colonization and establishment of *D. citri* and *T. radiata* in Manabí province likely occurred first on *M. paniculata*. *D. citri* was found for the first time on citrus trees and *M. paniculata* (=*M. exotica*) plants in Guayaquil, in the province of Guayas, where the highest population densities (approx. 20 nymphs per flush) were observed on the latter host (Cornejo and Chica 2014). Likewise, the parasitoid *T. radiata* was also found for the first-time parasitizing *D. citri* nymphs infesting *M. paniculata* in Guayas province (Portalanza et al. 2017). Thus, it is likely that *D. citri* and *T. radiata* were introduced to the city of Portoviejo, in Manabí province, from the province of Guayas through the retail trade of orange jasmine and other rutaceous plants. A similar situation occurred in Florida, U.S.A., where *D. citri* dispersed throughout the state through migration of the adult psyllids and the commercial trade of infested *M. paniculata* plants that were sold as ornamentals (Halbert et al. 2008).

On the other hand, the citrus growing region of Mejía is located 8 km from the city of Portoviejo and thus it is likely that the psyllid and its parasitoid were introduced on *D. citri* infested orange jasmine plants brought from Mejía city, and posteriorly colonized citrus orchards. Thus, the probable pathway, followed by *D. citri* and *T. radiata* in Manabí province, is as follows: orange jasmine (Guayas)—orange jasmine (Portoviejo city)—orange jasmine (Mejía)—key lime (Mejía).

Despite the short distance between Mejía and Portoviejo cities, the colonization of *C. x aurantiifolia* by the Asian citrus psyllid occurred 2 years later. Parasitization of *T. radiata* on *D. citri* nymphs in orange jasmine in Portoviejo city, probably delayed the colonization of the citrus growing region. The process of colonization and establishment of the plant–psyllid–parasitoid interaction observed in *M. paniculata* may be repeated in *C.* x *aurantiifolia*. The same pattern in the population dynamics of *D. citri* nymphs occurred on both host plants in terms of the effect of rainfall, the phenological desynchronization between colonization and the establishment of the plant–psyllid–parasitoid interaction. Based on the data gathered on the pattern of colonization of *D. citri* and *T. radiata* in *M. paniculata*, a model for estimating the number of *T. radiata* parasitized *D. citri* nymphs on *M. paniculata* and *C. x aurantiifolia* can be calculated.

Frequency of colonization and establishment events of the Asian citrus psyllid on *M. paniculata* and *C.* x *aurantiifolia* and subsequent appearance of the parasitoid and its establishment on *M. paniculata*, may be estimated by the end of 2022, populations of *D. citri* might fluctuate at low levels associated with high percentages of parasitism by *T. radiata* on *C.* x *aurantiifolia*. However, in Ecuador, a high percentage of citrus farmers use chemical insecticides to control insect pests (Sornoza-Robles et al. 2020), which would affect the levels of parasitism by *T. radiata* in commercial citrus orchards. Field and laboratory studies have demonstrated the lethal and sublethal effects of pesticides belonging to various chemical groups on *T. radiata* (Beloti et al. 2015). Therefore, it is important to establish biological control and/or integrated pest management programs for the conservation of *T. radiata* and other natural enemies.

Conclusions

Parasitoids are key regulators in the population fluctuations of their insect hosts. The present study showed the colonization of an invasive citrus pest, *D. citri* and its parasitoid, *T. radiata*, in a region, first on its ornamental host, *M. paniculata* and later on key lime, *C.* x *aurantiifolia*. The levels of parasitism indicated the importance of *T. radiata* as a biocontrol agent of *D. citri* that could be included in integrated pest management programs as a tool against the eventual arrival of Huanglongbing in Ecuador.

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Authors' contributions
DTC designed the study, DTC, IMC, JV, RC, GS conducted the field sampling and laboratory counts. All authors contributed equally to the analysis and interpretation of the results. DTC, TK wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
All data is included in the figures and are so clear.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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