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Avocado Sustains a Complex of *Neosilba* spp. (Diptera: Lonchaeidae) in Veracruz, Mexico

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Abstract

Avocado (*Persea americana* Miller), a crop of major economic importance in Mexico, is threatened by several quarantine pests, and recent reports have suggested that the lance fly *Neosilba batesi* (Diptera: Lonchaeidae) may be responsible for significant yield losses. To clarify the role of this species, we surveyed avocados from six localities in Veracruz State on the Gulf coast of Mexico and identified lance flies using both morphological and molecular tools. None of the symptoms previously attributed to *N. batesi* infestation in Hass avocado were observed in any of the fruits inspected across the six localities. However, 90 fruits displayed clear signs of borer attack by *Conotrachelus* spp. or other primary pests, and 64 of these damaged fruits (60%) yielded lance flies. Hass avocados were rarely infested and hosted only *N. batesi*, whereas creole avocados (*P. americana* var. drymifolia) were hosts to *N. batesi*, *N. glaberrima*, *N. recurva*, and *N. flavitarsis* and an undescribed species (*Neosilba* sp.3) that was detected by analysis of the COI gene sequences of males. Additionally, *Lonchaea cristula* was reported for the first time emerging from creole avocado. Each avocado yielded an average of between 2.3 and 21.0 adult lance flies. Infestation was more frequent and numerous in fruits collected from the ground than in those harvested directly from trees, supporting the idea that lance flies preferentially exploit pre-damaged or fallen fruits. Indeed, lonchaeid eggs were frequently observed deposited on the periphery or inside oviposition holes created by other pests. Overall, our results indicate that *Neosilba* spp. act as secondary invaders in Veracruz, with no evidence of *N. batesi* behaving as a primary pest in this region. None of the avocados were infested by species of Tephritidae and none of the *Neosilba* species we identified appear to pose a threat to avocado production in Mexico. This study highlights the value of combining morphological and molecular tools for species identification and underscores the importance of differentiating between primary and secondary invaders in the context of avocado pest management.

Keywords: lance flies; Hass; creole; secondary pest; *Lonchaea cristula*; new host records

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1. Introduction

Avocado (*Persea americana* Miller) is a member of the flowering plant family Lauraceae native to Mexico and Central America. Mexico is the world's leading producer of avocado, with an annual production of 2.7 million tonnes in 2023, half of which was exported to the United States [1]. Several species and varieties of *Persea* are cultivated in Mexico, with *P. americana* var. Hass being of particular commercial importance. However, the ancestral variety *P. americana* var.

drymifolia, known as creole avocado, is also grown widely in Mexico and is highly appreciated by local consumers. Several fruit-boring pests of quarantine significance infest avocado in this region, including *Conotrachelus aguacatae* (Barber), *Conotrachelus perseae* (Barber) (Coleoptera: Curculionidae), *Helipus lauri* Boheman (Coleoptera: Curculionidae), and *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae) [2].

Lance flies of the genus *Neosilba* Waddill & Weems are native to the Neotropics and are usually considered to be a polyphagous secondary invader of fruits that had previously been infested by tephritid fruit flies (Diptera, Tephritidae), or other primary pests [3–5]. However, *Neosilba batesi* (Curran, 1932) (Diptera: Lonchaeidae) has been identified as a potential pest of economic concern for avocado production in Colombia [6]. Recently, this pest was reported to be responsible for 30% crop losses in avocado in the central Mexican state of Michoacan [7,8], although this estimate was made in the absence of a rigorous assessment of the insect's phytosanitary status. The genetic identity of this pest in central Mexico has now been confirmed by amplification and sequencing of the mitochondrial cytochrome c oxidase subunit I (COI) gene [9]. The main sign of *N. batesi* infestation in avocado in Michoacan was described as a ring of reddish discoloration around the peduncle or reddish spots, presumably caused by larval development following female oviposition in the junction of the pedicel with the fruit. According to Lemus-Soriano et al. [9], infestation accelerates ripening and leads to premature fruit drop.

Given the enormous economic importance of avocado production in Mexico and the paucity of published information on avocado infestations by *N. batesi* and other lance flies, this study surveyed avocado fruits across six localities in the state of Veracruz, Mexico, that borders the Gulf of Mexico. The aim of the study was to document the occurrence of lonchaeid fly infestations of avocado in this region using morphological and genetic techniques.

2. Materials and Methods

2.1. Fruit Collection

Avocado fruits were inspected in the central region of Veracruz state, between 16 May and 6 June 2024, and between 27 March, and 16 May in 2025. Fruits of the creole or Hass varieties were inspected and collected from isolated avocado trees in the localities of Tatatila, Tenexpanoya, Tlanehuayocan and Xalapa and from two orchards in Altotonga and Huatusco (Figure 1A,B).

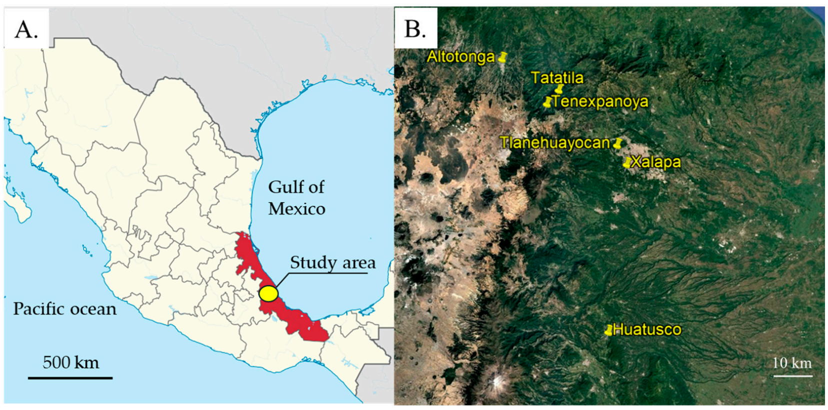

Figure 1. Location of the study area (yellow circle) in Veracruz State (red fill) on the Gulf coast of Mexico (**A**). The sample locations of the study (yellow pins) were located close to the villages of Altotonga, Tatatila, Tenexpanoya, Tlanehuayocan, Xalapa and Huatusco (**B**). Image (**A**) was adapted from https://commons.wikimedia.org/wiki/File:Veracruz_in_Mexico_(location_map_scheme).svg (accessed on 15 August 2025) under the Creative Commons Attribution (CC BY-SA 3.0) (accessed on 15 August 2025). Image (**B**) was adapted from Google Earth (image date 12 December 2020), used under Google's policies for non-commercial academic use.

Avocado fruits were collected directly from the tree or from the ground after shaking the branches with a stick to induce premature fruit drop. The five fruits collected in Tlanehuayocan were gathered from the ground as no fruits were present on trees.

2.2. Fruit Classification and Insect Rearing

All avocado fruits were carefully inspected for signs of damage. Fruits with no evident damage (intact fruits) and those showing signs of infestation by insect pests were separated. Avocados with signs of infestation were transported to the laboratory for a detailed inspection. The presence of eggs or larvae was assessed at 35× magnification using a stereomicroscope (Leica EZ4, Wetzlar, Germany). A slice was cut from the apical section of the fruit to detect signs of larval feeding damage (Figure 2A,D). Fruits with holes that presumably indicated the presence of a borer pest (Figure 2B,C,E,F), were taken to the laboratory, weighed, measured for equatorial diameter, and individually placed in a 470 mL plastic cup with a 5 mm layer of vermiculite as a pupation substrate. The cups were maintained at 24 ± 1 °C, 65 ± 10% relative humidity, and a 12:12 h L:D photoperiod in a climate-controlled laboratory. Adult lonchaeid emergence was recorded daily for 48 days following fruit collection. Emerged flies were euthanized by freezing at −20 °C and preserved in 70% ethanol for subsequent identification.

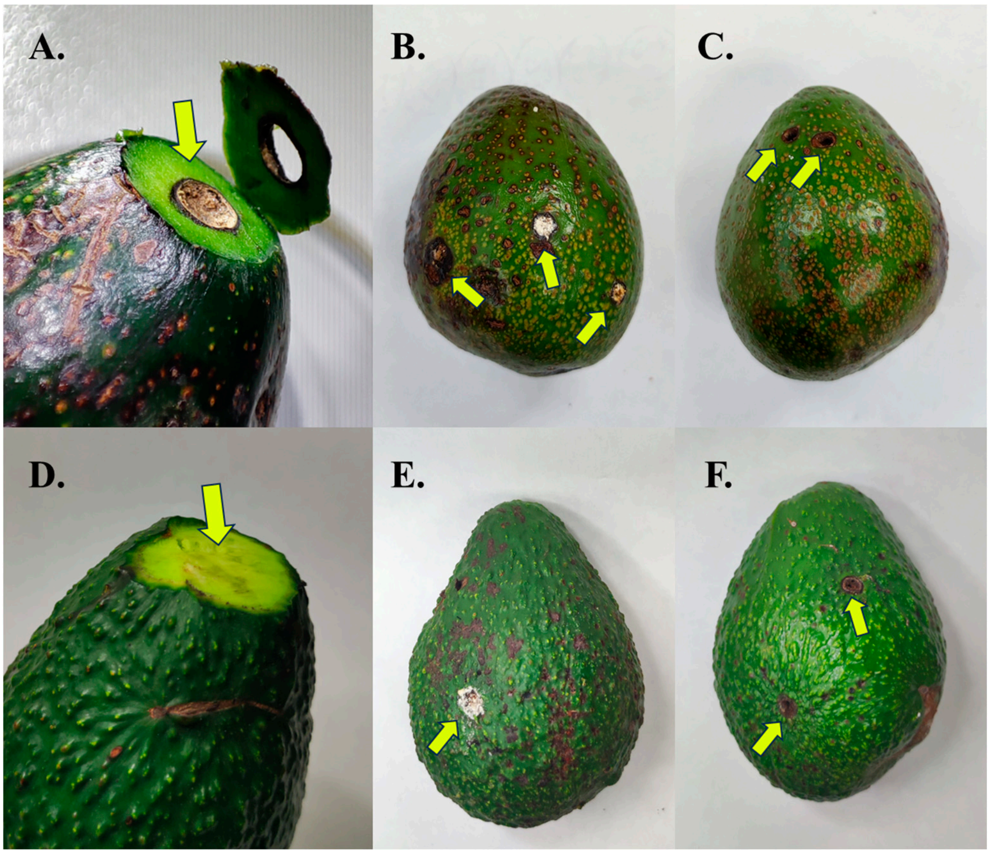

Figure 2. Inspection of damaged and undamaged avocado fruits. The apical section at the peduncle insertion point was dissected for the presence of lonchaeid eggs and larvae in non-damaged fruits of the creole variety (**A**–**C**) and Hass variety (**D**–**F**). Avocado fruits with borer pest holes in the creole variety (**B**,**C**) and the Hass variety (**E**,**F**). The apical section around the pedicel (**A**,**D**) and the lateral borer holes of damaged fruits (**B**,**C**,**E**,**F**) are indicated by yellow arrows.

2.3. Species Identification, Sequencing and Phylogenic Analysis

Lonchaeid flies that emerged from avocados were examined under a stereomicroscope to determine species and sex [3,4,10]. Females were not identified due to the absence of taxonomic keys for *Neosilba*. Male identification was initially based on the morphological characteristics of the genitalia [11–13]. A subset of the specimens was sent to the National Museum of Scotland to confirm species-level identifications.

Nine males and one female of *Neosilba* spp. and two females of *Lonchaea cristula* McAlpine, 1964 were subjected to COI gene sequence analysis. For this, DNA extraction, PCR amplification, sequencing and sequence assembly were performed as described previously [5,13]. Briefly, DNA extraction was performed using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. COI gene amplification was performed using primers C1-J-1718 and C1-N-2191 [14] on a SureCycler 8800 thermocycler (Agilent Technologies, Santa Clara, CA, USA). The resulting amplicons (525 bp in length) were purified using the Wizard SV Gel and PCR System Clean-Up kit (Promega, Madison, WI, USA), and were sequenced at the Labsergen Langebio laboratory (Irapuato, Mexico). The sequences were assembled and edited using BioEdit v.7.0.5 software in line with previous studies [5,13].

For the phylogenetic analysis, COI gene sequences obtained in this study and those of the related species present in GenBank were aligned in MAFFT v.7 [15] and MEGA 7.0.26 software [16]. The best nucleotide substitution model was identified using the Akaike Information Criterion (AIC) within jModelTest 2.1.10 software [17]. The phylogenetic tree was generated by applying the maximum likelihood (ML) method in raxmlGUI 2.0.16 with the GTR + I + G evolutionary model [18]. Bootstrap analysis was performed on 1000 repetitions. Finally, a phylogenetic analysis was performed by Bayesian inference with the MrBayes v.3.2.6 software [19] for five million generations. The resulting phylogenetic tree was edited in FigTree v.1.4.3 [20]. Numbers at branch nodes indicate bootstrap values (BS $\geq$ 70) and Bayesian Posterior Probabilities (BPP $\geq$ 0.9). *Silba fumosa* (Egger, 1862), collected in Germany [21], was used as an outgroup for the phylogenetic tree, as it had previously been employed in the genetic identification of *N. batesi* from Mexican avocados [9].

2.4. Statistical Analysis

The mean diameter and weight of infested avocados, and the mean number of flies that developed in each infested fruit, were analyzed by fitting generalized linear models (GLM) with a quasi-Poisson distribution to account for overdispersion. The results of GLM analyses are presented as χ^2 statistics. Means were compared using the Bonferroni test. Pairwise comparisons of the number of flies that emerged per fruit were subjected to the Holm-Bonferroni *p*-value adjustment in order to control the risk of a type I error. The prevalence (%) of fruits from which two or more *Neosilba* species emerged was analyzed using Fisher's exact test. The median time elapsed for adults to emerge from field-collected avocados was determined by Kaplan–Meier analysis and compared by log-rank test. All analyses were performed using the R-based package Jamovi, version 2.3.28 [22].

3. Results

3.1. Fruit Inspection and Global Fly Emergence

A total of 181 avocado fruits were inspected across the six locations of which 90 (50%) showed clear signs of external damage (Table 1). Samples were obtained at six sites with elevations of 1608–2286 m.

The external reddish ring discoloration at the peduncle, or the presence of eggs, larvae, or other signs of damage previously described for *N. batesi* in the pedicel region [9], were not observed in any of the inspected fruits. However, the 90 damaged fruits from Tatatila, Tenexpanoya, Tlanehuayocan, and Xalapa all showed external lateral damage, characterized by boring holes, likely caused by *Conotrachelus* spp. Examination of the lateral holes at 35× magnification revealed unhatched eggs or post-hatching egg chorion around and inside the pest borer holes (Figure 3A–C).

Table 1. Location of inspected creole and Hass avocados across various localities in Veracruz state. A different number of fruits were examined in each locality and categorized as either intact (no visible external damage) or damaged (showing clear signs of boring pest damage).

Locality	Variety	Month and Year of Sample	Intact Fruits	Damaged Fruits	Coordinates; Elevation
Tatatila	creole	May–June 2024, March 2025	22	32	19°41′28″ N; 97°06′39″ W; 2047 m
Tenexpanoya	creole	May 2025	22	34	19°39′34″ N; 97°08′26″ W; 2208 m
Tlanehuayocan	creole	May 2025	0	5	19°33′30″ N; 96°58′04″ W; 1608 m
Huatusco	Hass	May 2025	15	0	19°07′32″ N; 96°59′51″ W; 1915 m
Altotonga	Hass	May 2025	15	0	19°46′05″ N; 97°15′06″ W; 2286 m
Xalapa	Hass	May 2025	17	19	19°30′46″ N; 96°56′41″ W; 1667 m

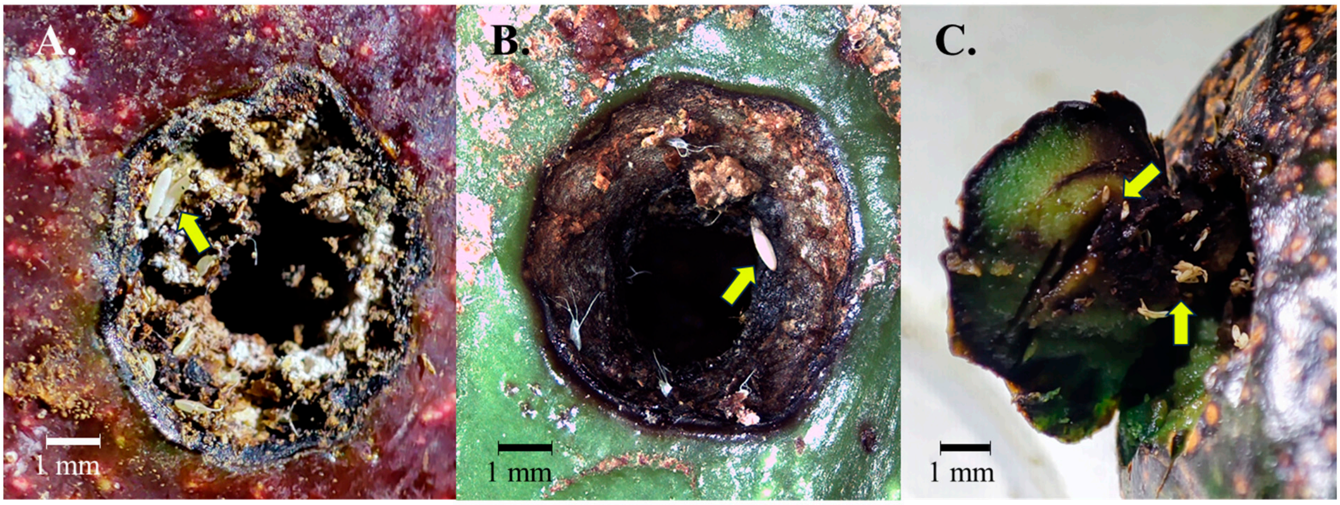

Figure 3. Magnified images of boring insect damage to avocados with the presence of *Neosilba* eggs on the periphery of the hole (**A**,**B**) or inside the hole when the hole was lightly excavated and inspected (**C**). *Neosilba* eggs were easily visible when magnified and are indicated by yellow arrows. No eggs were observed in undamaged avocados.

3.2. Emergence of Lonchaeid Flies

A total of 355 *Neosilba* spp. adults (195 females and 160 males) emerged from 90 damaged avocado fruits collected in Veracruz, including 86 infested fruits of the creole variety and 4 of the Hass variety (Table 2). Additionally, 11 adults of *Lonchaea cristula* (5 females and 6 males) emerged exclusively from six creole avocados collected in Tatatila in 2024. No infestation by *L. cristula* was recorded in 2025 at any location.

The diameter and weight of avocados differed significantly among localities, with fruits from Tatatila showing the smallest average diameter (GLM, χ^2 = 59.1, df = 3, $p < 0.001$) and weight (GLM, χ^2 = 138, df = 3, $p < 0.001$), followed by those from Tenexpanoya (Table 2). The largest fruits were collected from the ground at Tlanehuayocan, although their diameter and weight did not differ significantly from those of Hass avocados collected in Xalapa.

The mean percentage of damaged fruits from which at least one *Neosilba* adult emerged differed significantly among localities (GLM χ^2 = 15.6, df = 3, $p < 0.001$). Hass avocados from Xalapa exhibited a significantly lower prevalence of infestation (21%) compared to creole avocados collected in Tatatila, Tenexpanoya, and Tlanehuayocan (68–80%) (Table 2).

Table 2. Number, mean diameter, and mean weight of damaged avocados collected from different localities and the mean number of *Neosilba* spp. adults that emerged per fruit with the median emergence time and 95% confidence interval (CI) under laboratory conditions.

Locality (Avocado Var.)	Damaged Fruits	Fruit Diameter (±SE) (mm)	Fruit Weight (±SE) (g)	Infested Fruits (%)	*Neosilba* spp. Adults Emerged per Fruit	Emergence Time (95% CI) (Days)
Tatatila (creole)	32	32.4 ± 0.7 a	23.0 ± 1.3 a	23 (72%) a	6.7 ± 2.4 ab	29 (29–30) a
Tenexpanoya (creole)	34	41.0 ± 1.3 b	64.9 ± 5.4 b	23 (68%) a	4.7 ± 0.4 a	33 (32–35) c
Tlanehuayocan (creole)	5	58.4 ± 2.5 c	165.6 ± 25.4 c	4 (80%) a	21.0 ± 7.9 b	31 (33–35) b
Xalapa (Hass)	19	49.6 ± 2.1 bc	105.1 ± 8.7 bc	4 (21%) b	2.3 ± 0.5 ab	41 (40–?) [1] c

Values followed by different letters differ significantly for comparisons within each column (GLM, Bonferroni $p < 0.05$). [1] undefined upper limit to 95% CI.

Despite differences in fruit size, no correlation was found between the number of emerging flies and fruit diameter (Spearman's R = −0.180, df = 52, $p = 0.193$) or weight (Spearman's R = 0.175, df = 52, $p = 0.205$).

The mean number of *Neosilba* flies that emerged from fruits was highly variable and was higher for the creole avocados collected directly from the ground in Tlanehuayocan ($\chi^2 = 8.74$, df = 3, $p = 0.033$) than the damaged avocados fruits collected in Xalapa (Table 2). A maximum of 58 *Neosilba* spp. adults emerged from a single small creole avocado (30 cm diameter, 22 g) collected in Tatatila. Interestingly, *L. cristula* emerged from 19% of the fruits with a mean (±SE) of 1.8 ± 0.5 flies per fruit and a maximum of 4 adults emerging from a single creole fruit. This is the first record of *L. cristula* infestation of [creole] avocado. Of the six creole avocados that produced adults of *L. cristula*, five (83%) were also infested by *Neosilba* spp.

The median (95% CI) time from fruit collection to *Neosilba* spp. emergence in the laboratory was similar for males and females of fruits collected in all localities; Tatatila (log-rank test, $p = 0.076$), Tenexpanoya (log-rank test, $p = 0.86$), Tlanehuayocan (log-rank test, $p = 0.63$) and Xalapa (log-rank test, $p = 0.23$). However, the median emergence time of adults (both sexes) differed significantly among localities (log-rank test, $p < 0.001$), being shortest for Tatatila, longest for Tenexpanoya and Xalapa, and intermediate in samples from Tlanehuayocan (Table 2). The median emergence time of all *Neosilba* spp. (32 days) (all individuals pooled) was similar to that of *L. cristula* (31 days) (log-rank test, $p = 0.54$).

3.3. Species Identification, Sequencing and Phylogenic Analysis

Males of *Neosilba* spp. were identified based on examination of the genitalia. Four males from Tatatila were lost during handling, so a total of 156 males from the 160 males that emerged were examined. Among the emerged males, *N. batesi*, *N. glaberrima* (Wiedemann, 1830), *N. recurva* MacGowan & Lasa, 2025 and *N. flavitarsis* MacGowan & Lasa, 2025 were identified (Table 3). *Neosilba batesi* was the most abundant species, comprising 65% of the emerged males, followed by *N. glaberrima* (28%). Both species were present in samples from all four localities. A smaller number of males corresponded to *N. recurva* (6%) and *N. flavitarsis* (1%), which were only recorded in samples from Tatatila and Tenexpanoya.

Based on the identification of males, the prevalence of creole avocados containing two or more *Neosilba* species was similar among localities ($\chi^2 = 3.83$, df = 3, $p = 0.280$) (Table 3). Half of the fruits from Tlanehuayocan were co-infested, and it is worth bearing in mind that these fruits were collected from the ground. More importantly, the prevalence of co-infestation may be underestimated, as only males were used for species identification.

Taxonomic identification was confirmed through COI sequencing of males from each species group and a single female (INECOL_24/20F) that could not be identified from morphological characteristics (Table 4).

Table 3. Total number of *Neosilba* males identified by genital dissection and the species composition and prevalence of co-infestation by two or more species across the different localities.

Locality [1]	Number of Males Disected	*N. batesi*	*N. glaberrima*	*N. recurva*	*N. flavitarsis*	Prevalence of Co-Infested Avocados (%)
Tatatila	68	46	17	5	-	13%
Tenexpanoya	44	30	8	4	2	17%
Tlanehuayocan	41	22	19	-	-	50%
Xalapa	3	3	-	-	-	0%
Total (%)	156	101 (65%)	44 (28%)	9 (6%)	2 (1%)	24%

[1] All samples were obtained from creole avocados, except for the samples from Xalapa (var. Hass).

Table 4. Species and host plant, specimen number, origin and GenBank accession numbers for COI gene nucleotide sequences obtained from *Neosilba* spp., *Lonchaea cristula* in the present and previous studies, which were used in the phylogenetic analysis. Bold text indicates individuals that were reared from avocado in the present study.

Species (Host Plant)	Voucher	State, Country	GenBank Number
Neosilba batesi (fig)	INECOL_24/21	Veracruz, Mexico	PV504763
Neosilba batesi (fig)	INECOL_24/22	Veracruz, Mexico	PV504764
Neosilba batesi (fig)	INECOL_24/30	Veracruz, Mexico	PV504765
Neosilba batesi (avocado)	Mx-CIQA-Mich01	Michoacan, Mexico	PV243309
Neosilba batesi (avocado)	Mx-CIQA-Mich02	Michoacan, Mexico	PV243310
Neosilba batesi (avocado)	Mx-CIQA-Mich01	Michoacan, Mexico	PV243311
Neosilba batesi (avocado)	CSCA_17X541	Florida, USA	MW283302
***Neosilba batesi* (avocado)**	**INECOL_24/48**	**Veracruz, Mexico**	**Sequence [3]**
***Neosilba batesi* (avocado)**	**INECOL_24/23**	**Veracruz, Mexico**	**Sequence [3]**
Neosilba glaberrima (fig)	INECOL_24/43	Veracruz, Mexico	PV504766
Neosilba glaberrima (fig)	INECOL_24/52	Veracruz, Mexico	PV504767
***Neosilba glaberrima* (avocado)**	**INECOL_24/50**	**Veracruz, Mexico**	**Sequence [3]**
***Neosilba glaberrima* (avocado)**	**INECOL_25/57**	**Veracruz, Mexico**	**Sequence [3]**
***Neosilba glaberrima* (avocado)**	**INECOL_24/20F**	**Veracruz, Mexico**	**Sequence [3]**
Neosilba recurva (fig)	INECOL_24/40	Veracruz, Mexico	PV522076
Neosilba recurva (fig)	INECOL_24/46	Veracruz, Mexico	PV522077
Neosilba recurva (fig)	INECOL_24/51	Veracruz, Mexico	PV522078
***Neosilba recurva* (avocado)**	**INECOL_24/47**	**Veracruz, Mexico**	**Sequence [3]**
***Neosilba recurva* (avocado)**	**INECOL_25/58**	**Veracruz, Mexico**	**Sequence [3]**
Neosilba flavitarsis (fig)	INECOL24/1M	Veracruz, Mexico	PQ834830
Neosilba flavitarsis (fig)	INECOL24/2F	Veracruz, Mexico	PQ834831
Neosilba flavitarsis (fig)	INECOL24/3M	Veracruz, Mexico	PQ834832
***Neosilba flavitarsis* (avocado)**	**INECOL_25/55**	**Veracruz, Mexico**	**Sequence [3]**
***Neosilba flavitarsis* (avocado)**	**INECOL_25/56**	**Veracruz, Mexico**	**Sequence [3]**
Neosilba sp.1 (fig)	INECOL_24/41	Veracruz, Mexico	PV504769
Neosilba sp.1 (fig)	INECOL_24/42	Veracruz, Mexico	PV504770
Neosilba sp.2 (fig)	INECOL_24/44	Veracruz, Mexico	PV504772
***Neosilba* sp.3 (avocado)**	**INECOL_24/49**	**Veracruz, Mexico**	**Sequence [3]**
Neosilba pendula (*Inga vera*)	IV18-A	Minas Gerais, Brazil	OQ160349
Neosilba zadolicha (*Passiflora alata*) [1]	YSUW02121210	Rio de Janeiro, Brazil	KR262649
Lonchaea cristula (*Passiflora edulis*) [1]	LCR11-2	Antioquia, Colombia	MZ189772
Lonchaea cristula (*Passiflora edulis*) [1]	LCR5-1	Antioquia, Colombia	MZ189773
***Lonchaea cristula* (avocado)**	**INECOL_24/53**	**Veracruz, Mexico**	**Sequence [3]**
***Lonchaea cristula* (avocado)**	**INECOL_24/54**	**Veracruz, Mexico**	**Sequence [3]**
Lonchaea aculeata (*Passiflora edulis*) [1]	LCU20-2A	Antioquia, Colombia	MZ189778
Silba fumosa [2]	ZFMK-TIS-2574287	Ahrweiler, Germany	OP831869

[1] Host plant uncertain; specimen was collected from a trap placed in *Passiflora alata* or *P. edulis* crops. [2] Specimen of *Silba fumosa* was collected in a Malaise trap. [3] Sequences are available at https://data.mendeley.com/datasets/tr4zf7kzxz/1 (accessed on 13 October 2025).

Two *N. batesi* males (INECOL_24/48, INECOL_24/23) showed clear genetic similarity to the specimens of *N. batesi* previously recorded from Hass avocados from Michoacan state in Mexico [9] and from figs in Veracruz state [5] (Figure 4). As noted previously [5,9], *N. batesi* specimens clustered into a clade that did not correspond to the *N. batesi* sequence reported from Florida (CSCA-17X541) (Figure 4). The sequences from two pairs of males identified morphologically as *N. recurva* (INECOL_24/47, INECOL_25/58) and *N. flavitarsis* (INECOL_25/55, INECOL_25/56) matched with their respective species. As these species had been previously reared from figs in Veracruz State [5,13], these records from avocado represent new host records for each of these species. Two males morphologically identified as *N. glaberrima* (INECOL_24/50, INECOL_25/57) clustered with *N. glaberrima* specimens from figs (INECOL_24/43 and INECOL_24/52) in Veracruz state [5] (Table 4, Figure 4). The sequenced female (INECOL_24/20F) also belonged to the *N. glaberrima* cluster. In contrast, another glaberrima-like male (INECOL_24/49) exhibited genetic divergence and formed a separate branch of the phylogenetic tree, suggesting the presence of an additional cryptic species in avocado (*Neosilba* sp.3) that was different from the unknown species reported previously in figs, which we previously named *Neosilba* sp.1 (INECOL_24/41, INECOL_24/42) and *Neosilba* sp.2? (INECOL_24/44) [5] (Figure 4). Neither *Neosilba* sp.1 or *Neosilba* sp.2? were detected infesting avocados in our study area.

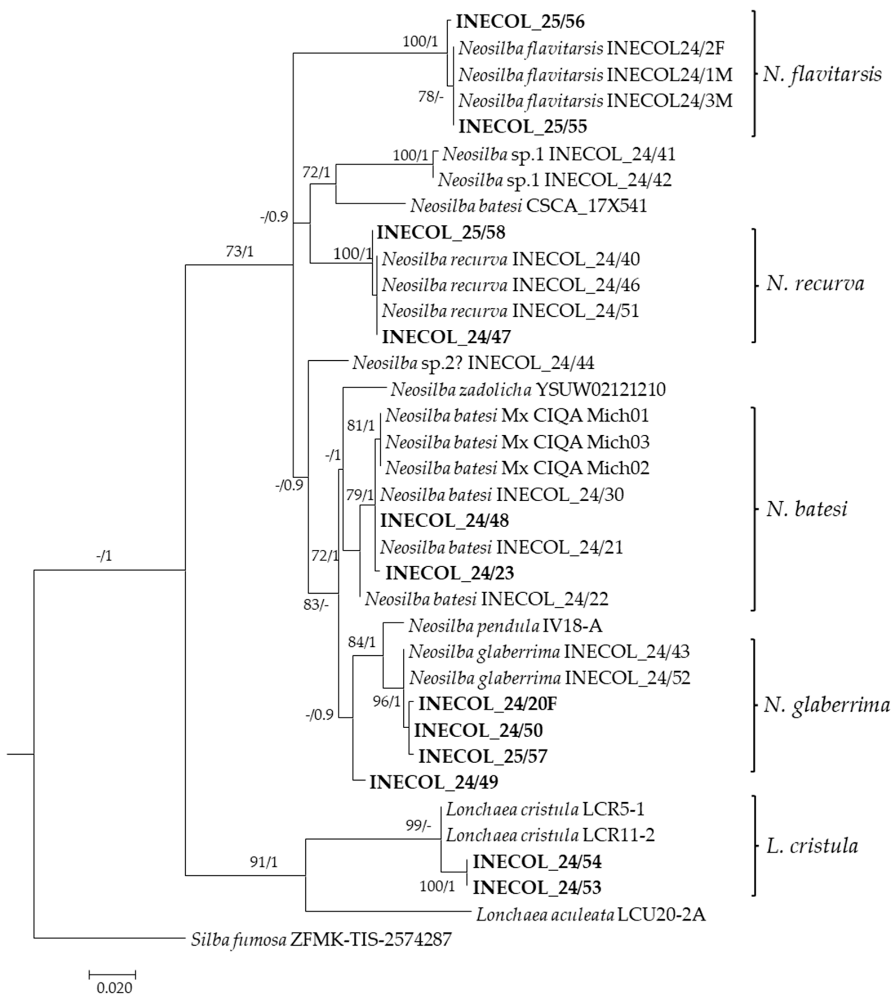

Figure 4. Maximum likelihood phylogenetic tree based on COI gene partial sequences illustrating the evolutionary relationships among lonchaeid flies. Specimens sequenced in the present study are shown in bold text. The tree was reconstructed using raxmlGUI and GTR + I + G evolutionary model with 1000 rapid bootstrap replicates. The numbers at the nodes indicate bootstrap values for 1000 replicates (BS $\geq$ 70%)/Bayesian Posterior Probabilities (BPP $\geq$ 0.9).

The identity of *L. cristula* specimens that developed in avocado (INECOL_24/53, INECOL_24/54), was confirmed by one of us (I.M.) at the National Museum of Scotland. The amplified sequences of these individuals clustered (98.9% sequence identity), with two specimens of *L. cristula* from Colombia [23] (Figure 4). The presence of this species in the study area had been detected earlier in torula yeast baited traps used for monitoring the invasive pest *Silba adipata* McAlpine, 1956 in fig orchards in this region [5].

4. Discussion

Lonchaeid flies were reared from 86 creole and 4 Hass avocados collected from different sites in central Veracruz State, Mexico. The characteristic reddish ring discoloration around the peduncle, or reddish partial spots previously reported as symptoms of larval development following *N. batesi* oviposition in Hass avocado [9], were not observed in any of the avocados inspected during this study across any of the localities sampled in Veracruz State. In the neighboring state of Puebla, producers associate the reddish avocado symptomatology with a natural abortion of the fruits (R. Lasa, pers. obs.). A total of 90 of the inspected fruits in Veracruz exhibited damage caused by borer pests. The holes observed on the lateral surface of the avocados (Figure 2), sometimes accompanied by a white residue, resembled the signs of damage caused by the curculionid pests *C. aguacatae* and *C. perseae* [24]. Some additional weevil and lepidopteran pests also attack avocado in this region [25–28]. However, no emergence of *Conotrachelus* spp. or other insects was recorded from the collected avocados, with the exception of an unidentified moth that emerged from a single fruit from Tatatila in 2025. Overall, 64 of the damaged fruits (60%) were infested by lance flies (*Neosilba* spp.). During fruit inspections, lonchaeid eggs or egg chorions were frequently observed on the external surface and within the borer holes, indicating that *Neosilba* spp. act as secondary invaders in avocados in this region.

A recent study conducted in Michoacan State in central Mexico postulated that *N. batesi* females exhibit opportunistic oviposition behavior by exploiting existing wounds or openings at the pedicel-fruit junction that result from pathogen infection or other types of damage [9]. This idea aligns with earlier observations suggesting that *N. batesi* prefers to oviposit on damaged or fallen fruits rather than on healthy, intact fruits [29,30]. Our findings are consistent with these observations, as *N. batesi* and other *Neosilba* species only emerged from fruits exhibiting signs of physical damage. In this respect, it seems unlikely that differences in lonchaeid infestation would be related to differences in exocarp (skin) thickness or toughness between Hass and creole avocados, as the use of wounds for oviposition immediately bypasses the exocarp barrier. The finding that infestation was not correlated with fruit size or weight further indicates that physical damage is more important than fruit development, which contrasts markedly with the oviposition preferences of tephritid flies in which fruit phenology is highly influential [31]. Although based on a limited number of samples, it appears that creole avocados are a better quality of host than the Hass variety, as the mean number of *N. batesi* adults that developed in each Hass avocado (2.3 adults/fruit in the present study, or 1.7–3.8 adults/fruit reported in Michoacán state [9]) was lower than the number of *Neosilba* spp. flies that emerged from creole avocados (4.7–21.0 adults/fruit) (Table 2). Also, the development time in creole avocado was approximately 10 days shorter (29–31 days) than observed in the Hass variety (41 days).

Hass avocados were infested exclusively by *N. batesi*, whereas *N. glaberrima*, *N. recurva*, *N. flavitarsis*, and *N. batesi* emerged from creole avocados. The identity of all the species detected in our study was confirmed by sequencing of the COI gene. This procedure also detected the presence of an unidentified species (*Neosilba* sp.3) which resembled *N. glaberrima* (based on the apical segment of the male abdomen [5]) but which remains to be described and named.

Among the emerged flies, *N. batesi* was the most prevalent species (65%) at all surveyed localities. *Neosilba batesi* has been reared from avocado, mango (*Mangifera indica* L.), orange (*Citrus sinensis* L.), tabog (*Swinglea glutinosa* Blanco), papaya (*Carica papaya* L.), peach palm (*Guilielma gasipaes* Kunth), guava (*Psidium guajava* L.), passion fruit (*Passiflora* spp.), miconia (*Miconia* sp.), fig (*Ficus carica* L.) and various pawpaw species in the genus *Annona* [3,5,11,32–34]. This species has been recorded from Florida (USA), Mexico, Guatemala, El Salvador, Costa Rica, Panama, Colombia and Peru [4].

Neosilba glaberrima was the second most abundant species in avocado in our study. This fly is recognized as a polyphagous species in Brazil, where it has been recorded emerging from avocado and from fruits of sixteen other species across different families [35]. In Veracruz, *N. glaberrima* also develops in fig [5] and various *Annona* species [11].

The emergence of *N. recurva* and *N. flavitarsis* was only observed in creole avocados collected in the Tatatila locality. Both species have been reported emerging from figs that were previously used for oviposition by the black fig fly *Silba adipata* [5,13]. This study identifies creole avocado as a new host for both *N. recurva* and *N. flavitarsis*.

Most of the avocados collected directly from trees were infested by a single *Neosilba* species, although a fraction harbored two or more lonchaeid species. While the co-occurrence of Tephritidae and Lonchaeidae has been documented, in which lonchaeids exploit oviposition wounds created by tephritids, the coexistence of multiple lonchaeid species within a single fruit has been less studied. Given the saprophagous behavior of most lonchaeids, it is reasonable to expect that fruits collected from the ground have a higher probability of being co-infested by multiple species compared to fruits attached to the tree. In our study, half of the damaged fruits collected from the ground in Tlanehuayocan were co-infested by *N. batesi* and *N. glaberrima*, whereas 0–17% were co-infested by these species in fruits collected from trees.

The occurrence of multiple *Neosilba* species within the same fruit was previously noted in Colombia [32], although this was not quantified. A few avocados in our study were co-infested with *Neosilba* spp. and *L. cristula*. Members of the genus *Lonchaea*, especially in the Nearctic and Palearctic, have traditionally been considered saproxylic, the larvae being found under the bark of dead or dying trees, often in association with other insects [36]. However, some members of this genus infest the fruit of various plant species in Colombia [32,37,38]. To our knowledge, this is the first report of *L. cristula* emerging from avocado. In contrast, members of the tephritid genus *Anastrepha* Schiner 1868 fail to develop in avocado as the eggs are rapidly encapsulated [30], a plant response that we never observed when dissecting the apical region of avocados in the present study.

In general, lance flies exhibit diverse larval feeding behaviors, including saprophagy, zoophagy, and phytophagy, and are associated with a wide range of ecological niches, though they are primarily linked to forested environments [39]. Within this family, the genera *Neosilba* and *Lonchaea* Fallen, 1820 are notable for developing in fruits of commercial importance [32,40–42]. Although there is some evidence suggesting that certain species can oviposit in apparently healthy fruits [40,43–45], most species within these genera are associated with fruits that have been damaged by other primary pests [5,46,47].

Our study faced several limitations in the small number of avocados that could be sampled at some sites and the inability to identify female flies to species given the lack of taxonomic keys for females, an issue that affects the majority of studies on lonchaeids. It should also be noted that the damaged avocados appeared to have been infested by *Conotrachelus* spp., which are recognized avocado pests in this region, although no weevils were reared from our samples. Consequently, the relationship between *Conotrachelus* spp. and lonchaeid infestation could not be established with absolute certainty. One possibility is that the weevils responsible for the original infestation had completed their development and exited the fruit prior to our sampling, or alternatively that lonchaeid infestation made the avocado unsuitable for the development of *Conotrachelus* spp. progeny; an issue that merits future study.

The results of this study indicate that *N. batesi* and *N. glaberrima* act as secondary invaders of avocados in Veracruz State. We present the first evidence that *N. recurva*, *N. flavitarsis* and *L. cristula* also function as secondary pests of this crop. As none of the undamaged avocados produced lonchaeids, we found no evidence of *N. batesi* acting as a primary pest, which has been reported in central Mexico.

Our findings have several practical implications. First, it appears that *N. batesi* is not a major threat to avocado production in Mexico but rather an opportunistic species that exploits damaged or diseased avocados or those in the process of abortion, which is likely the reason why this fly has attracted the attention of plant protection workers in central Mexico and Colombia. The risks to the avocado export industry appear to be low as the *Neosilba* and *Lonchaea* species that we identified are not primary pests and damaged avocados are destroyed in packaging plants before they can be exported.

5. Conclusions

This study provides novel evidence on the diversity and infestation patterns of lonchaeid flies associated with avocados in central Veracruz, Mexico. *Neosilba batesi* and *N. glaberrima* were the most prevalent species, both functioning as secondary invaders by exploiting wounds or borer damage in fruits. In contrast, *N. recurva*, *N. flavitarsis*, and *Lonchaea cristula* were recovered at lower frequencies but are reported here for the first time as secondary colonizers of avocado, whereas an additional unidentified species (*Neosilba* sp.3) was detected by COI gene sequencing and remains to be described.

Overall, these findings highlight the value of integrating morphological and molecular tools for species identification and underscore the importance of differentiating between primary and secondary invaders in the context of avocado pest management. Given the paucity of studies on the diversity and host-plant relationships for the Lonchaeidae in North America, future studies should involve surveys over a wider geographic range, across different types of natural and agricultural ecosystems to identify areas of particular interest in which seasonal variation in lonchaeid populations and the phytosanitary status of this family could be better understood.

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