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ORIGINAL CONTRIBUTION

Mite damage provides refuges and affects preference and performance of a subsequent herbivorous moth

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Abstract

Damage by herbivores often modifies plant structure and physiology, which may change the behaviour and performance of future herbivores. Here, we studied such interactions among the major coconut pest, the mite *Aceria guerreronis* (Acari: Eriophyidae), and two minor pests, the mite *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) and the moth *Atheloca bondari* (Lepidoptera: Pyralidae). All these species develop in the meristematic zone of coconuts, which is difficult to access because of the small opening between the epicarp and perianth. Both mites cause necrosis on the epicarp of the nuts, which may facilitate access to the meristematic zone by caterpillars of the moth. However, the caterpillars co-occur predominantly with *A. guerreronis* and not with *S. concavuscutum*. We show that caterpillars did not colonize nuts without mites and colonized nuts with *A. guerreronis* most frequently, in agreement with the openings caused by this mite and caterpillar size. When the opening between epicarp and perianth was artificially increased, caterpillars also colonized nuts without mites and nuts with *S. concavuscutum*. When offered a choice, caterpillars preferred nuts with easy access to the meristematic region, regardless of the presence of mites. Caterpillars performed better on the *A. guerreronis*-infested nuts than on other nuts, but moth females did not preferentially oviposit in coconut bunches infested with mites. Hence, caterpillars, not adults, select suitable feeding sites within a bunch of coconuts, and *A. guerreronis* facilitates the infestation of coconuts by *A. bondari*. We discuss how damage by mites affects the relevance of *A. bondari* as a coconut pest.

KEYWORDS
acari, *Atheloca bondari*, caterpillar dispersal, coconut, herbivore interactions, oviposition choice, premature fruit drop

1 | INTRODUCTION

Herbivore attacks trigger a cascade of responses in plants, modifying their chemical, physiological, morphological and architectural traits (Karban & Baldwin, 1997; Ohgushi, 2005; Stam et al., 2014). Herbivory affects the photosynthetic rates and resource allocation from and to storage tissues, which can impact their palatability through altered availability of basic nutrients (Poveda et al., 2012; Stowe et al., 2000). Thus, changes in plant traits caused by herbivores may have negative or positive effects on other members of the herbivore community on the shared host plant (Ali & Agrawal, 2014; Kessler & Halitschke, 2007; Mathur et al., 2013; Ohgushi, 2008). For example, shelter building by caterpillars results in increased species diversity within a plant (Lill

& Marquis, 2003), and leaf-rolling caterpillars can improve leaf quality and improve the performance of other herbivores that use the leaf roll as shelter (Fukui, 2001). Moreover, plant responses to herbivory can indicate the presence of potential competitors to subsequently arriving herbivore species (Dicke, 2000; Kessler & Baldwin, 2001; Stam et al., 2018), altering their recruitment to damaged plants (Kroes et al., 2016; Pallini et al., 1997; Poelman et al., 2008).

Some herbivores are adapted to use specific plant structures that provide not only food but also refuge (Berryman & Hawkins, 2006; Jeffries & Lawton, 1984), allowing them to develop in sites with low interspecific competition, high protection from predators and favourable climatic factors (Langellotto & Denno, 2004). However, herbivory can alter these plant structures, thereby modulating the occurrence of opportunistic herbivores (Lill & Marquis, 2003; Ohgushi, 2005; Uesugi et al., 2016). Here, we evaluated how the presence of the mites *Aceria guerreronis* (Acari: Eriophyidae) (Keifer) and *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) Lofego & Gondin Jr. on coconuts affects the preference and performance of the moth *Atheloca bondari* (Lepidoptera: Pyralidae) Heinrich. All three species feed on the meristematic zone of the coconut.

Aceria guerreronis is considered the main pest of coconut palms worldwide (Navia et al., 2013), and the attack of this mite is related to premature coconut fall (Doreste, 1968; Rezende et al., 2016). In the field, the occurrence of *A. bondari* is positively associated with *A. guerreronis*, and negatively with *S. concavuscutum* (Paz-Neto et al., 2020). Feeding by *A. guerreronis* causes necrotic lesions that modify the epicarp of nuts (Aratchige et al., 2007; Lima et al., 2012), enlarging the opening between the surface of the nut and the perianth. Santana et al., (2009) stated that *A. bondari* caterpillars use these lesions to infest nuts and reach the meristematic zone. Thus, *A. guerreronis* modulates the availability of resources for *A. bondari*. However, *S. concavuscutum* causes similar necrotic patterns on the epicarp of the nuts (Lofego & Gondim, 2006; Navia et al., 2005); therefore, necrosis caused by *S. concavuscutum* could also facilitate infestation of nuts by *A. bondari* caterpillars, which is in contrast to the negative association between these species. Morphological changes caused by herbivory often coincide with plant defence responses (Agrawal, 1999; Uesugi et al., 2016) and nutritional changes (Lou & Baldwin, 2004), and nuts attacked by *A. guerreronis* or *S. concavuscutum* may differ in quality and therefore have positive or negative effects on the preference and performance of *A. bondari*.

To further investigate the host plant-mediated interactions among these species, we first assessed the size of the opening of the meristematic zone in nuts that were either uninfested or infested by the mite species and compared it with the size of the caterpillars. In addition, the infestation of nuts by the caterpillars, the selection of clean and mite-infested nuts and bunches by both adult females and caterpillars of *A. bondari*, and the performance of *A. bondari* on infested and clean nuts were analysed.

2 | MATERIALS AND METHODS

2.1 | Moth rearing

Nuts showing signs of the presence of *A. bondari* caterpillars (hole with frass) were collected in Igarassú (Mangue Seco, state of Pernambuco, Brazil 7°49′S, 34°50′W) and transported to the laboratory. The caterpillars were removed and transferred to clean nuts collected at the campus of the Federal Rural University of Pernambuco (8°01′S, 34°94′W). We used the rearing method developed by Santana et al., (2011). In short, cuts were made in the epidermis of the three lateral sides of the nuts with a scalpel, forming a triangular opening (0.5 cm wide and deep) just below the bracts. One caterpillar of *A. bondari* was introduced on each side (i.e. three caterpillars per nut) and allowed to feed and develop. The artificially infested nuts were kept in a vertical position using a 10 × 10 cm styrofoam platform with a hole of approximately 5 cm wide in the middle in which the nut was placed. The platform was placed inside a 12 × 17 cm (diameter × height) plastic container. This container had a hole (12 × 8 cm in height and width) on the side, covered with a net (50 μm mesh) to allow ventilation. Three layers of paper towel were placed on the bottom of the container under the platform to collect the moist exudates from the nuts damaged by the caterpillar and to serve as a pupation substrate. The nuts rapidly decayed; therefore, caterpillars were transferred to a new nut after five days. Prepupae left the nut to pupate in the towels and were collected and incubated individually in 2.0 × 3.5 cm (diameter × height) acrylic vials until adult emergence. Newly emerged adults were sexed based on the shape of the tip of the abdomen (Santana et al., 2011) and paired in transparent plastic containers, as described above. They were fed a 10% honey solution in water, offered in a 3 cm (diameter) lid. Females oviposited in grooves on the sides of the lids. The lids with eggs were transferred daily to a new, similar container. Neonate caterpillars (~12 h old) were introduced to the nuts using the same method as above. The rearing units were kept at 27 ± 1.5°C, with a relative humidity of 70 ± 5% and a photoperiod of 12 h.

2.2 | Nut collection

We collected nuts infested with either *A. guerreronis*, *S. concavuscutum* or both from the coast of Igarassú. We discarded nuts with holes and frass, which are evidence of infestation by *A. bondari*. We also discarded nuts with changes in the perianth (e.g. raised or loose bracts) and nuts damaged by other herbivores. The mites cause similar necrosis on the surface of the nuts, but the shape of the necrotic spots caused by the two mite species differ markedly: *A. guerreronis* causes triangular yellow chlorotic spots, whereas *S. concavuscutum* causes longitudinal yellow stains close to the margin of the perianth, which become necrotic with nut growth. Nuts with an injury level from *A. guerreronis* of 16%–32% on the scale proposed by Galvão et al., (2008) were used. We

standardized the injury level of *S. concavuscutum* using the same scale. Based on these characteristic damage patterns, bunches corresponding to leaves 14 from the apex (4 months old) were collected and transported to the laboratory.

2.3 | Colonization of nuts by *Atheloca bondari* caterpillars

We tested whether damage caused by the two mites facilitated colonization of the meristematic zone by *A. bondari* caterpillars. Disposable plastic cups (200 mL) were filled with 100 mL of gypsum in water and a 6-cm nail was inserted with its head into the plaster, with the pointed end of the nail sticking out above the plaster (Silva et al., 2017). After the plaster had dried, the disposable plastic cup was removed, and the nail was inserted into the floral aperture of the nuts, resulting in the nut standing on a gypsum pedestal. A barrier of entomological glue (ISCA PEGA®) was applied 5 cm below the distal parts of the perianth to prevent escape of caterpillars.

Nuts infested by *A. guerreronis*, *S. concavuscutum* or both (same damage level), and clean nuts were used for this experiment. We performed 20 replicates (nuts) per treatment. Each experimental nut was placed in a separate tray with water, and two neonate caterpillars (<12 h old) were released on the external surface of the perianth with a brush (no. 000). After 96 h, we carefully removed the perianths with a staple remover and pruning shears to check for the presence of caterpillars in the meristematic zone using a stereomicroscope (Zeiss Stemi DV4). We also verified the infestation of the nuts by mites.

The previous experiment showed low colonization of uninfested nuts and nuts with *S. concavuscutum* by caterpillars. Thus, a similar experiment was performed but with manipulated openings between the perianth and epicarp of the nut to test whether the infestation by caterpillars was related to the size of the opening to the meristematic zone. We increased the size of access to the meristematic zone by partially inserting a 3-cm long and 3-mm thick wooden stick below the perianths (the natural opening size is given in Figure 3). Colonization of the meristematic tissue by caterpillars was evaluated using two different categories of nuts: (i) *S. concavuscutum*-infested nuts with access manipulation and (ii) non-infested nuts with access manipulation. In nuts infested with *S. concavuscutum*, the stick was placed on the side with necrosis caused by the mites. *Aceria guerreronis*-infested nuts were not used in this experiment because the previous experiment showed that many caterpillars settled under the perianth of such nuts without enlarged openings. After inserting the sticks, two neonate caterpillars (<12 h old) were released on the external surface of the perianth as above. We performed 20 replicates (nuts) per treatment. The infestation of nuts was analysed as described above.

For both experiments, the incidence of nuts infested by *A. bondari* caterpillars was compared among nuts with different treatments (infested by mites or not, enlarged openings) using a generalized linear model (GLM) with a binomial error distribution (logit link). Contrasts among treatments with mites were assessed with the Tukey method of the function emmeans of the package with the similar name (Lenth, 2019). Statistical analyses were performed using R (R Core Team, 2019).

2.4 | Caterpillar preference

We offered caterpillars a choice between two nuts, each of which had received a different treatment. We collected nuts that were either uninfested or infested by *A. guerreronis* or *S. concavuscutum* (see 'Collection of nuts'). We also used nuts in which the openings of the meristematic region were manipulated as described above.

Caterpillars and *A. guerreronis* may have the same preference for nuts with certain traits, independent of the presence of the other species, and this would result in a positive association between the caterpillars and the mites, independent of the presence of the other species. Therefore, we included a treatment in which nuts were artificially infested with *A. guerreronis*, thus eliminating the possible preferential infestation of certain types of nuts by these mites. For this purpose, *A. guerreronis*-infested nuts were collected from Igarassú (Mangue Seco) and transported to the laboratory. The bracts of these nuts were removed using a staple remover and pruning shears. Mites from these nuts were taken to trees with non-infested nuts on the campus, which were climbed using a ladder, and the mites were transferred to 2-month-old nuts with a brush (no. 000). When the nuts reached 4 months of age and had an injury level between 16 and 32% (see Galvão et al., 2008), they were collected and taken to the laboratory. Overall, this resulted in seven different nut treatments: 1 and 2: nuts naturally infested with *A. guerreronis* or *S. concavuscutum*, respectively; 3: uninfested nuts; 4: nuts artificially infested with *A. guerreronis*; 5: *A. guerreronis*-infested nuts with enlarged openings; 6: *S. concavuscutum*-infested nuts with enlarged openings; and 7: uninfested nuts with enlarged openingsn.

The floral aperture of each nut was pressed onto a nail and fixed in a block of plaster as above. Two nuts, each from a different treatment, were aligned with the spikelets pointing towards each other, and these were connected with modelling clay, thus forming a runway for the caterpillars. The position of the various nuts differed among replicates to correct for unforeseen asymmetries in the set-up or environment. The distance between the nuts was 20 cm (10 cm per spikelet). To prevent caterpillars from escaping from the nuts, each nut was provided with a barrier of entomological glue as described above.

We performed 20 replicates per treatment, where each replicate received eight neonate caterpillars (<12 h old), which were placed on the modelling clay with a brush (no. 000). The experimental units were covered with a glass dome to minimize the effects of the environment, and the caterpillars were allowed to choose a nut during 24 h. Subsequently, we checked the nuts as explained in the section 'Colonization of nuts by *Atheloca bondari* caterpillar'. The number of nuts infested with *A. bondari* caterpillars was assessed, and the preference was analysed using a binomial test (Siegel & Castellan, 1988).

2.5 | Measurement of the opening to the meristematic zone of nuts and cephalic capsule of caterpillars

Twenty nuts were collected according to the criteria described in the section 'Nut collection'. Cutting off the perianth may increase the natural size of the access to the meristematic region; therefore, we used the methods of Aratchige et al. (2007) and Lima et al. (2012). A scalpel was used to cut the mesocarp around the nuts just below the lower extremity of the perianth, and we removed the top of the nuts, leaving the perianth intact. The underside of the perianth of the nuts was photographed under a dissecting microscope (at 40×) using Fly capture software (v. 1.7, Point Grey Research). Subsequently, the distance between the edge of the bract and the subjacent surface of the nut was measured using Image Plus software (v. 2.0, Motic China Group, Xiamen, China). As the level of necrotic lesions caused by mites differs among the sides of the nuts, we photographed the side with the largest lesion, and if it was cracked, we measured the distance from the bottom of the slit to the edge of the bract. We also measured the height of the cephalic capsule of the caterpillars. This is the region of the caterpillar with the largest diameter and the only hard exoskeleton part, so its size determines through which opening sizes the caterpillars can enter the area under the perianth. To measure the cephalic capsule, we freeze-killed 20 neonate caterpillars (<12 h old), photographed their cephalic capsule and measured their heights using a dissecting microscope and the software described above. The variation in the size (access size or capsule size) was compared with nut treatment and caterpillars as one factor using a single GLM with a Gaussian error distribution (normal link). Contrasts among sizes and capsule size were assessed with the Tukey method as above.

2.6 | Oviposition

We performed a test to evaluate whether mated females oviposited more often in coconut bunches with mites than in non-infested bunches. Four-month-old mite-infested bunches were collected as described above. We selected 10 nuts and extracted the remaining nuts from the bunch. The spikelets of the selected nuts were cut to a length of 20 cm.

Oviposition of *A. bondari* was assessed in a cage (120 × 100 × 100 cm) constructed from PVC pipes and covered with a net (50 μm mesh). The cage was positioned in a greenhouse on the campus. Inside the cage, the bunches were kept vertically using a 10 L bucket full of plaster. A hole of 10 cm × 15 cm (diameter × height) in the middle of the plaster served to secure the base of the bunches. To feed the adult *A. bondari*, we provided 10 lids (5-cm diameter) filled with a 10% honey solution on the floor of the cage. Four mated females of *A. bondari* were released into the cage and allowed to oviposit for two days on

(i) *A. guerreronis*-infested bunches; (ii) *S. concavuscutum*-infested bunches; and (iii) non-infested bunches. The test was replicated five times for each treatment. The number of eggs on the bunches was compared using a GLM with a quasi-Poisson error distribution (log link). In addition, the numbers of eggs deposited on different parts of the bunches of the different treatments were analysed in a similar way.

We also performed an oviposition preference test. In this test, females were allowed to oviposit on two bunches of the following combinations: (i) *A. guerreronis*-infested bunches vs. *S. concavuscutum*-infested bunches; (ii) *A. guerreronis*-infested bunches vs. non-infested bunches; and (iii) *S. concavuscutum*-infested bunches vs. non-infested bunches. Five replicates were performed per combination. At the end of the test, the bunches were taken to the laboratory, and moth eggs were counted using a stereomicroscope (Zeiss Stemi DV4). The number of eggs on each bunch was analysed with a log-linear model for count data in contingency tables (GLM with a Poisson error distribution and log link, Crawley, 2013). Contrasts were assessed using Tukey's method.

2.7 | Caterpillar development

We evaluated the survival of caterpillars to pupae and adults, the duration of the development into adults, and the pupal weight on nuts with the following treatments: (i) *A. guerreronis*-infested; (ii) *S. concavuscutum*-infested; and (iii) non-infested nuts.

Coconut trees were climbed using a ladder and bunches that were either infested with *A. guerreronis*, *S. concavuscutum* or uninfested were selected using the criteria outlined above. A 3 cm long wooden stick (3-mm thick) was inserted below the perianth of the nuts to increase the access of caterpillars to the meristematic region. Nuts infested with mites received sticks at the site of necrosis caused by the mites. We released one neonate caterpillar (<12 h old) of *A. bondari* into the access created by the insertion of the stick. The artificially *A. bondari*-infested nuts were left on the trees and covered with a net (50 μm mesh) tied with a string to reduce caterpillar escape and further infestations.

To prevent the fall of nuts caused by phytophagous feeding (see Paz-Neto et al., 2020), all nuts were removed nine days after infestation with the caterpillars and transported to the laboratory. The nuts were kept in plastic containers as described above ('Moth rearing'). The nuts were observed daily until the beginning of pupation. Completely formed, brown pupae were collected, weighed and incubated individually in 2.0 × 3.5 cm (diameter × height) acrylic vials until emergence of the adults. The caterpillars were considered unviable when they started to feed but did not develop into pupae. We discarded replicates in which the nuts showed no sign of caterpillar feeding.

One caterpillar on one nut represented a replicate. For the analysis of the proportion of pupae and caterpillar-adult survival, the

number of replicates were 20, 30 and 28 for *A. guerreronis*-infested, *S. concavuscutum*-infested and non-infested nuts, respectively. As some caterpillars did not reach pupae, the number of replicates for the analysis of pupa weight were 19, 19 and 20 for *A. guerreronis*-infested, *S. concavuscutum*-infested and non-infested nuts, respectively. The proportion of individuals surviving to the pupal stage and pupal weight were analysed using a GLM with binomial and Gaussian error distributions (logit and normal link), respectively. Developmental rates were compared among treatments using a Cox proportional hazards model with the log-rank test.

3 | RESULTS

3.1 | Colonization of nuts by *Atheloca bondari* caterpillars

The infestation of nuts by different mite species affected the colonization of *A. bondari* caterpillars (Figure 1a; GLM: $\chi^2 = 45.8$, $df = 3$, $p < 0.001$). No caterpillars were found in the meristematic regions of nuts that were not infested by mites. The proportion of infested nuts was higher for *A. guerreronis* than for *S. concavuscutum* or for both mites (Figure 1a), whereas the latter two did not differ significantly (Figure 1a).

When access to the meristematic zone was manipulated, a larger proportion of nuts was colonized by caterpillars, and there was no significant difference between uninfested nuts and those infested with *S. concavuscutum* (Figure 1b, GLM: $\chi^2 = 0.41$, $df = 1$, $p = 0.52$).

3.2 | Caterpillar preference

When *A. bondari* caterpillars were offered a choice between nuts infested with *A. guerreronis*, either naturally or artificially, and nuts without mites, they significantly preferred nuts with *A. guerreronis* (Figure 2a, binomial test: $p < 0.001$ for both). In contrast, the caterpillars that could choose between *A. guerreronis*-infested and *S. concavuscutum*-infested nuts did not show a significant preference (Figure 2a, binomial test: $p = 0.194$). Furthermore, no caterpillar was found below the perianth when offered *S. concavuscutum*-infested and non-infested nuts (Figure 2a).

When we manipulated the access to the meristematic zone of the coconuts, the proportion of nuts colonized by caterpillars did not differ significantly for any of the combinations tested (*A. guerreronis*-infested nuts vs. *S. concavuscutum*-infested nuts, $p = 0.5$; *A. guerreronis*-infested nuts vs. non-infested nuts, $p = 0.108$), although the preference for *S. concavuscutum*-infested nuts when offered with non-infested nuts was bordering significance ($p = 0.05$) (Figure 2b).

A test with manipulation of the entrance of the meristematic zone against non-manipulated nuts showed that caterpillars preferred the nuts with the manipulated openings (Figure 2c), except for the combination of *A. guerreronis*-infested nuts and non-infested,
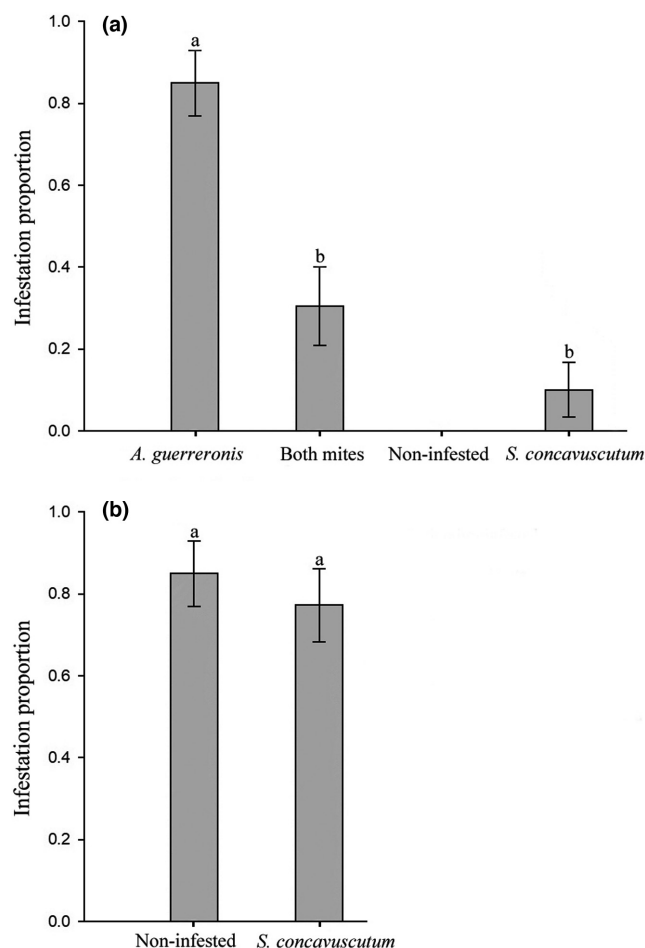

FIGURE 1 Proportions of nuts colonized by *Atheloca bondari* caterpillars. The caterpillars were offered a single nut that was either infested by *Aceria guerreronis*, by *Steneotarsonemus concavuscutum*, by both mites or uninfested. Nuts were considered as colonized when caterpillars were found feeding on the meristematic zone under the perianth. (a) Nuts without manipulation of the access to meristematic zone. (b) Nuts in which the opening between the perianth and the meristematic zone was artificially enlarged by inserting a wooden stick. Letters above bars indicate significance among different treatments (significance among treatments obtained through a contrast analysis after GLM with a Tukey correction for multiple comparisons: all significant p values < 0.003)

manipulated nuts, where no significant difference was observed (Figure 2c; $p = 0.151$).

3.3 | Size of the access to the meristematic zone of nuts and of the cephalic capsule of caterpillars

The opening of the meristematic region of non-infested nuts and nuts infested by mites and the cephalic capsule size of the caterpillars differed significantly (Figure 3, GLM, $F_{3,76} = 105.3$, $p < 0.0001$). Cephalic capsule size of neonate caterpillars was significantly smaller

FIGURE 2 Preference of *Atheloca bondari* caterpillars for coconuts that received various treatments. Coconuts were offered in pairs (d), the caterpillars were released in the middle. Nuts were either naturally infested by *Aceria guerreronis*, *Steneotarsonemus concavuscutum*, were uninfested or artificially infested with *A. guerreronis*. (a) Nuts without manipulation of entrance of meristematic zone. (b) Nuts with entrance manipulated. (c) Nuts with entrance manipulated (left) vs. non-manipulated nuts (right). Water: percentage of caterpillars that dropped into the water. Colonization was characterized by the caterpillar feeding on the meristematic zone. Asterisks indicate significance (binomial test: *p < 0.05; **p < 0.01; ***p < 0.001)
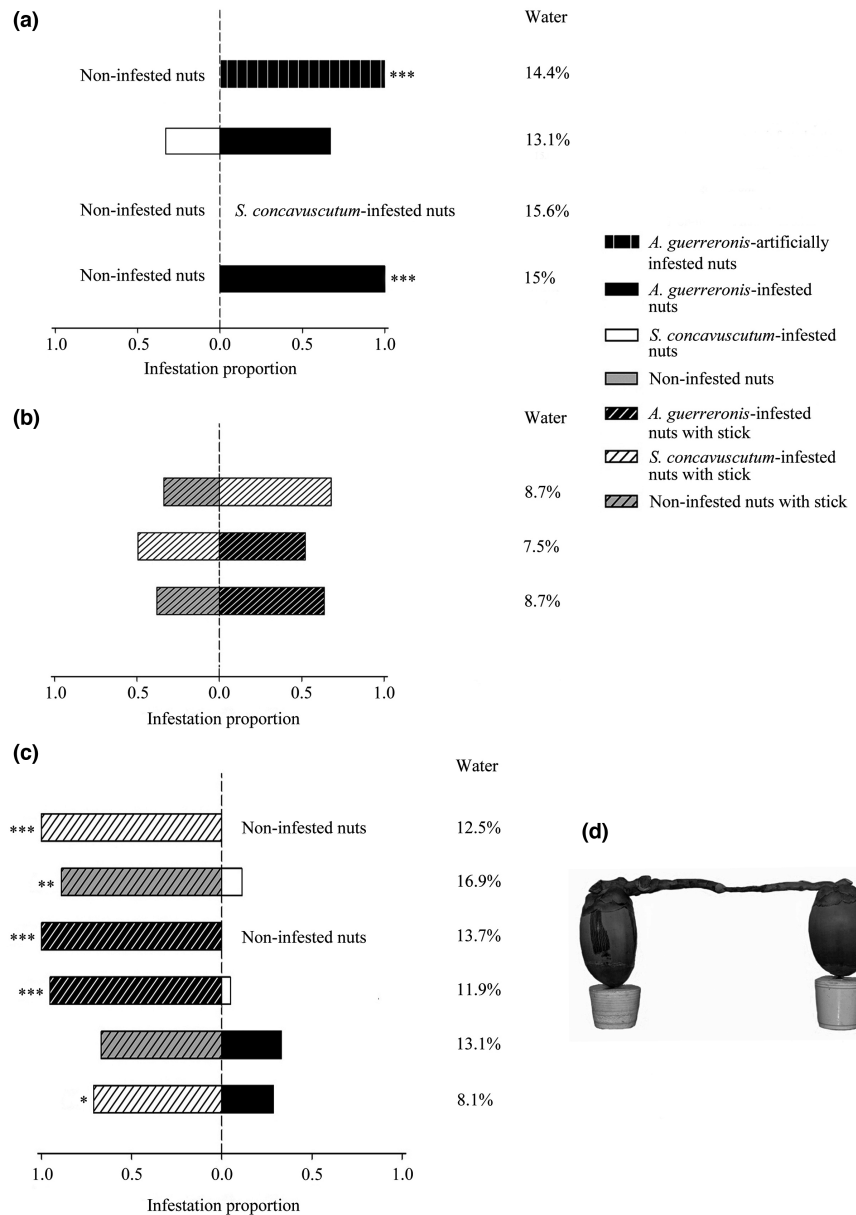
than the opening to the meristematic zone of *A. guerreronis*-infested nuts, significantly larger than the opening of non-infested nuts and did not differ significantly from the opening of *S. concavuscutum*-infested nuts (Figure 3).

When offered a choice, female *A. bondari* did not show a clear consistent preference; the variation among replicates was significant for all three combinations of coconut treatment (Figure 5, GLM: interaction between treatment and replicate, all $p < 0.001$).

3.4 | Oviposition

In the no-choice test, the average numbers of *A. bondari* eggs on nuts of the different treatments differed significantly (Figure 4, GLM: $F_{2,12} = 4.10$, $p = 0.044$). Females laid more eggs in bunches infested with *S. concavuscutum* than uninfested bunches. The distribution of eggs over the different parts of the bunches did not differ significantly among treatments (Figure 4; GLM: $F_{2,12} = 2.63$, $p = 0.11$).

3.5 | Caterpillar development

There was a significant effect of nut infestation on survival until pupa (Figure 6a GLM: $\chi^2 = 7.93$, $df = 2$, $p = 0.019$). Furthermore, the weight of caterpillars differed significantly with the treatment of the nuts (Figure 6b, GLM: $F_{2,55} = 8.17$, $p < 0.001$). Caterpillars from nuts previously uninfested or infested with *A. guerreronis* formed heavier pupae than caterpillars that developed on nuts infested by *S. concavuscutum* (Figure 6b). The developmental periods
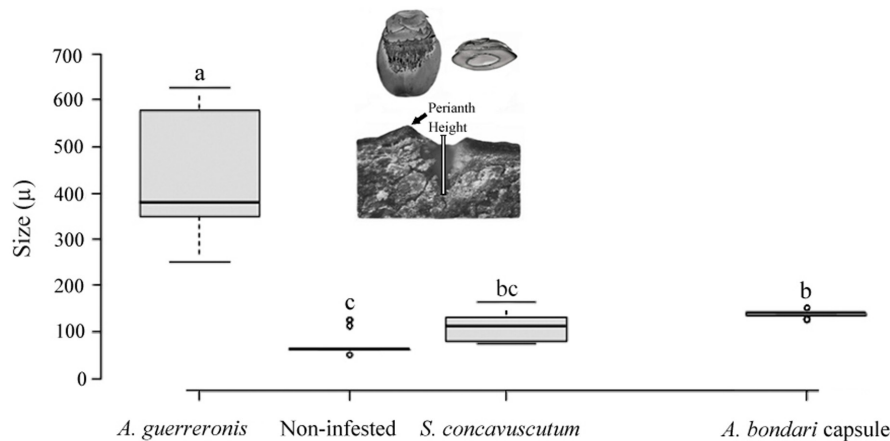
FIGURE 3 Comparison of the space between the perianth and epicarp of nuts infested by *Aceria guerreronis*, by *Steneotarsonemus concavuscutum* or uninfested and the height of the cephalic capsule of the *Atheloca bondari* caterpillar. Small letters indicate significance among measurements (contrast analysis after GLM with a Tukey correction for multiple comparisons: significant *p* values < 0.02) [Colour figure can be viewed at wileyonlinelibrary.com]
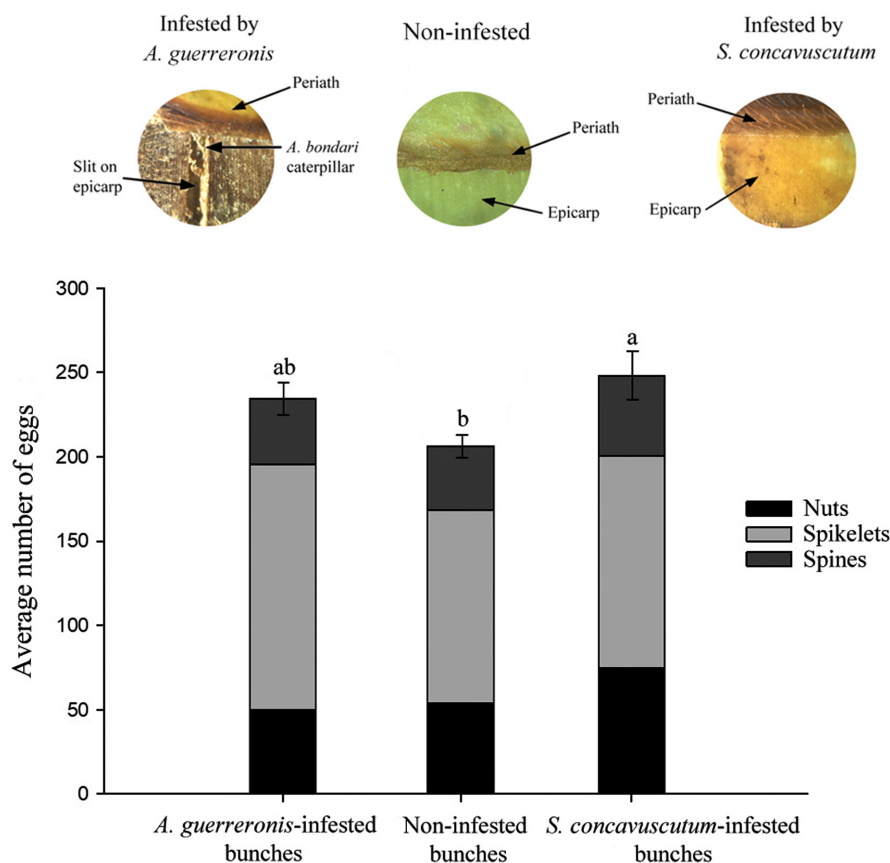

FIGURE 4 Average number of *Atheloca bondari* eggs in bunches infested by either *Aceria guerreronis*, *Steneotarsonemus concavuscutum* or uninfested. Female *A. bondari* were offered a bunch of coconuts of one treatment during two days. Different colours in the bars show where the eggs were found. Small letters indicate significance (contrast analysis after GLM with a Tukey correction for multiple comparisons, significant *p* value = 0.014)

of caterpillars into pupae differed significantly among treatments (Figure 6c, log-rank statistic: 8.45, *df* = 2, *p* = 0.015). Caterpillars that survived on nuts infested with *A. guerreronis* developed faster into pupae than those on uninfested nuts, while there was no significant difference in the development between caterpillars that survived on nuts infested by *S. concavuscutum* and the other treatments (Figure 6c).

4 | DISCUSSION

Taken together, our results suggest that *A. bondari* is an opportunistic herbivore that benefits from infestations of coconuts by mites, which increase the opening between the epicarp and the perianth,

thus facilitating access of caterpillars to the highly nutritious tissues under the perianth. Our conclusions are based on several observations. First, caterpillars did not colonize nuts that were not infested by mites and colonized a low proportion of nuts that were infested by *S. concavuscutum*, the mite species that causes smaller openings. Second, when the openings were experimentally enlarged, the caterpillars infested these nuts, irrespective of the presence of mites, suggesting that it is mainly the opening and not the presence of mites, which determines caterpillar preference. Third, compared with the height of the cephalic capsule of the caterpillars, only the openings of nuts infested with *A. guerreronis* were large enough to allow the entrance of the caterpillars. Although both mites cause similar injury patterns (Navia et al., 2005), our detailed analysis revealed minute differences between the necrotic patterns caused by

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FIGURE 5 Oviposition preference of *Atheloca bondari* for bunches infested either by *Aceria guerreronis*, *Steneotarsonemus concavuscutum* or uninfested. Each female was offered a choice between two bunches. (a) Choice between *A. guerreronis*-infested and *S. concavuscutum*-infested bunches. (b) Choice between *A. guerreronis*-infested and uninfested bunches. (c) Choice between *S. concavuscutum*-infested and uninfested bunches. The bars represent the percentage of *A. bondari* eggs in each replicate. Numbers inside the bars indicate the number of *A. bondari* eggs
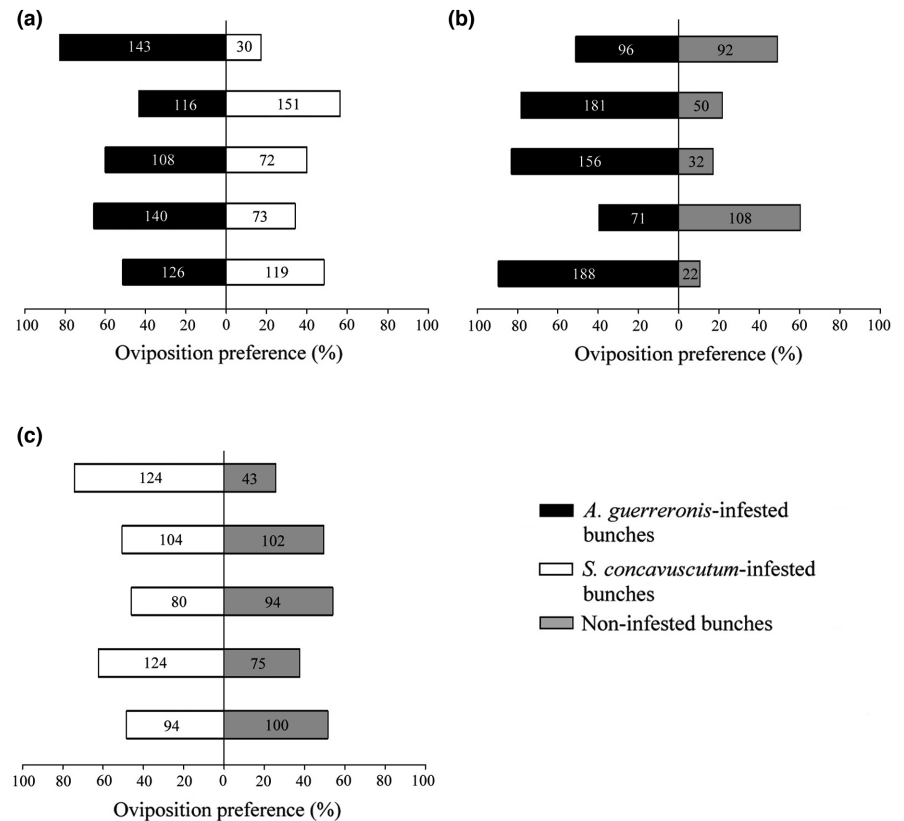
these two mites. Necrosis caused by *A. guerreronis* is often accompanied by deep slits in the epicarp, but these do not appear in necrotic spots caused by *S. concavuscutum* (Figure 3), and the resulting openings of the latter are only sometimes large enough to allow access by the caterpillars.

Other factors, such as attacks by other herbivores, drought and nutritional deficiency, can increase the access opening to the meristematic zone, allowing the colonization of *A. bondari* caterpillars. To carry out experiments here, we selected nuts in order to reduce the effect of these factors, as these could interfere with our results. In the field, we found caterpillars developing in coconuts infested by *S. concavuscutum* or without mites but in lower proportions than in nuts infested by *A. guerreronis* (Paz-Neto et al., 2020).

Nuts infested by both mites showed a low percentage of infestation of *A. bondari* caterpillars. In these nuts, the necrotic spots caused by the two mites often overlapped, and those caused by *S. concavuscutum* may modify the physical pattern of necrosis caused by *A. guerreronis*. Thus, while necrosis caused by *A. guerreronis* facilitated *A. bondari* caterpillars to reach the meristematic zone of coconuts (Santana et al., 2009), *S. concavuscutum* may impede the infestation of nuts by the caterpillars.

The infestation of *A. guerreronis* not only facilitated access to the meristematic zone of the nuts, but caterpillars also performed better on nuts infested by this mite than on uninfested nuts and on those infested with *S. concavuscutum*. Nut traits (e.g. colour, size and chemical composition) can vary within plants (Reschef et al., 2017; Zhang et al., 2015), and the simplest explanation for the association between *A. bondari* and *A. guerreronis* is that these species prefer

nuts with similar traits; thus, the preference for nuts with better nutritional quality results in better performance of *A. bondari*. In contrast, *A. bondari* caterpillars also showed a high preference for nuts that were artificially infested with *A. guerreronis* and not selected by the mites (Figure 2b), indicating that the association of these species is not related to preference for similar nut traits but to a preference for nuts with *A. guerreronis*. A possible explanation for the better performance of *A. bondari* on *A. guerreronis*-infested nuts is related to plant defences induced by mites. Different herbivore species can trigger distinct defence response pathways (e.g. the jasmonic or salicylic acid pathways) and cross-talk between these two defences (Kant et al., 2015; Stam et al., 2014). Possibly, *A. guerreronis* induces plant defences to which *A. bondari* is not sensitive, and the cross-talk between the two biochemical defence pathways prevents the induction of defences against the caterpillars. Alternatively, it is possible that *A. guerreronis* actively suppresses plant defences, as was found for several other phytophagous mites (Alba et al., 2015; Godinho et al., 2016; Kant et al., 2008; Sarmento et al., 2011) and *A. bondari* profits from this.

We previously observed that the nuts attacked by *A. bondari* started to fall nine days after caterpillar infestation, while nuts attacked by mites rarely fell until the harvest period (approximately 7 months of age) (Paz-Neto et al., 2020). Nevertheless, infestation by *A. guerreronis* is suggested as the main cause of coconut drop in several other studies (Doreste, 1968; Rezende et al., 2016; Wickramananda et al., 2007), but these studies did not consider co-infestation of the nuts with other organisms such as *A. bondari*. It is known that co-infestation with the fungus *Botryodiplodia*
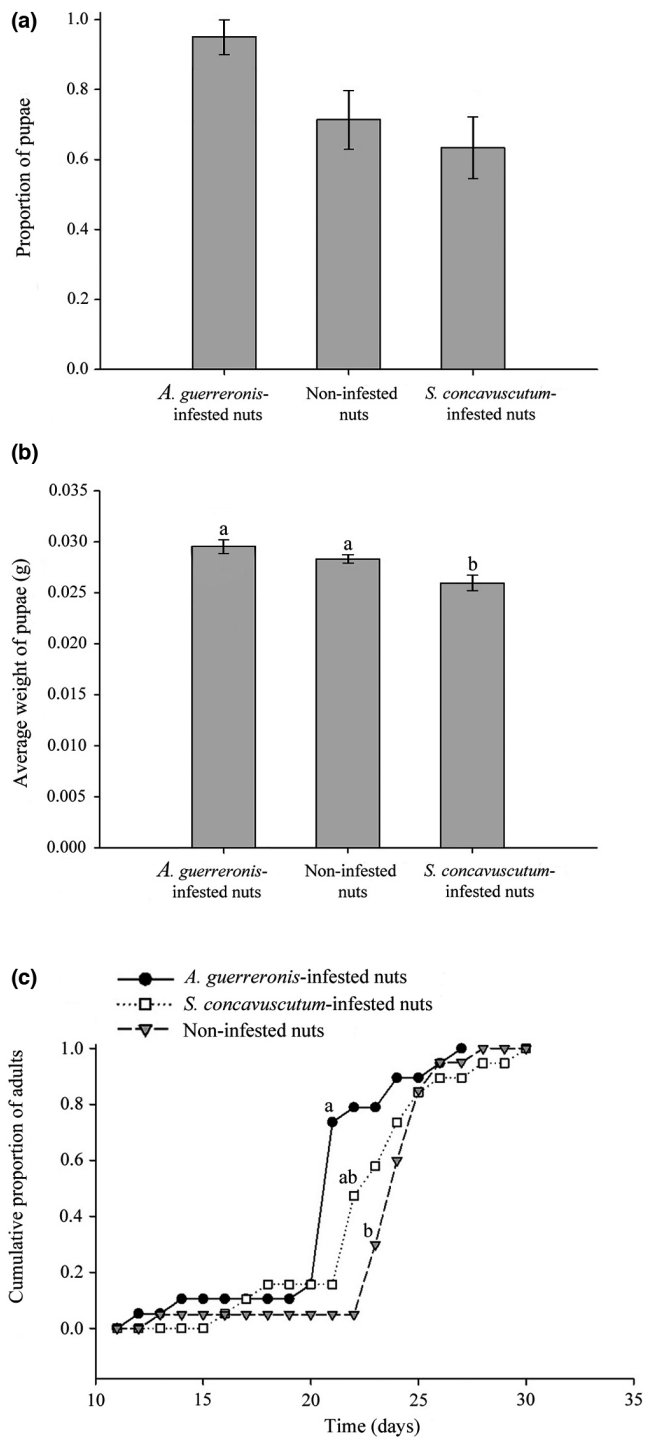
FIGURE 6 Performance of caterpillars on clean nuts or nuts infested by *Aceria guerreronis* or *Steneotarsonemus concavuscutum*. (a) Proportion of caterpillars becoming pupae. (b) Average weight of pupae Letters above bars indicate significance among treatments (contrast analysis after GLM with a Tukey correction for multiple comparisons, all significant $ps < 0.027$). (c) Survival of *Atheloca bondari* caterpillars until adulthood. Letters next to curves indicate significance, significant difference: $p = 0.02$

theobromae causes rotting of the nuts and higher immature nut fall than infestation by *A. guerreronis* alone (Lakshmanan & Jagadeesan, 2004). Along a similar vein, Dheepa et al. (2018) reported that the

fungus *Lasiodiplodia theobromae* was present in most rotten and fallen coconuts in India, and Venugopal and ChandraMohanan (2006) argued that the injury caused by *A. guerreronis* or other herbivores can allow infection of coconuts by this fungus. We observed that nuts fed upon by caterpillars rotted faster than those infested only by mites. Thus, the increase in nut dropping that is usually attributed to *A. guerreronis* may be more related to the facilitation of infestation by other organisms caused by this mite. Nevertheless, the control of *A. guerreronis* may decrease the number of fallen nuts (Rezende et al., 2016) because it may reduce subsequent colonization by *A. bondari* caterpillars or other organisms. The association between *A. guerreronis* and *A. bondari* may explain why *A. bondari* has not been reported as an important pest in coconut production areas where mites are controlled. However, *A. bondari* has been identified as a coconut pest along the coast of northeastern Brazil (Bondar, 1940; Paz-Neto et al., 2020), where mite control methods are not used in most areas and, consequently, more nuts are infested by *A. guerreronis* (Lawson-Balagbo et al., 2008). Obviously, there is a need for studies on the interactions of all these organisms and how this affects coconut production.

Plants can induce premature abscission of both vegetative and reproductive parts as a defence against pathogens and herbivores (Patharkar et al., 2017; Strauss & Zangerl, 2002), thus prioritizing physiological investments in healthy plant parts by eliminating those that are damaged. By inducing nut abscission, coconut palms may have the adaptive advantage of investing in coconuts with a higher probability of germination. Nuts infested by *A. guerreronis* produce vigorous seedlings (Beevi et al., 2006; Regi & Mathews, 2004); therefore, it does not appear to be advantageous for the coconut palm to induce the abscission of nuts infested by this mite. The effects of damage by *A. bondari* on the germination of coconuts is not known, but as the feeding of caterpillars deteriorates a large part of the nut meristem, a strong effect of this herbivore on seed vigour can be expected. If this is true, and abscission of nuts affects the fitness and survival of *A. bondari*, coconut palms will have an adaptive advantage by inducing a premature drop of coconuts attacked by *A. bondari*. However, a large number of caterpillars reached adulthood even in fallen nuts, so the moths seem to be adapted to nut abscission. Unlike the moth, mites on fallen nuts have little chance of infesting new coconuts because of the low active dispersal capacity of both mites (França et al., 2018; Galvão et al., 2012). Hence, *A. guerreronis* and *S. concavuscutum* appear to be more affected by nut abscission than *A. bondari*. However, it is necessary to study the co-occurrence of these species over time in more detail because the mites may escape from nuts colonized by *A. bondari* caterpillars, dispersing to other nuts of the bunch before abscission. *Aceria guerreronis* is known to avoid nuts previously infested by competing herbivores (Calvet et al., 2018), so attack of *A. bondari* possibly induces dispersal of the mites and thus increases the proportion of coconuts infested by mites within the bunch. The collection and disposal of fallen nuts may thus not only help to control the populations of *A. bondari* but also decrease the proportion of nuts infested by mites.

Atheloca bondari females did not show a preference for ovipositing on bunches infested with *A. guerreronis*; eggs were laid on all the bunches offered. However, analysing the oviposition preference of adult *A. bondari* in the field is essential to confirm the preferences found here. In our experiment, a large number of *A. bondari* eggs were found on spikelets and spines; thus, after hatching, the caterpillars had to move within a bunch to find a nut to infest. Thus, the behaviour of the caterpillars plays a central role in the selection of coconuts to infest. The caterpillars did not show a preference for *A. guerreronis*-infested nuts, and they used the opening of the meristematic zone as selection criterion (Figure 2). However, as the injury by *A. guerreronis* creates an opening to the meristematic zone (Figure 3), *A. bondari* caterpillars will mostly select nuts infested by this mite.

Summarizing, we demonstrate that *A. guerreronis* modifies the coconut structure, facilitating the access of *A. bondari* caterpillars to the feeding site, as stated by Santana et al. (2009), but the presence of another phytophagous mite, *S. concavuscutum*, interferes with this association between *A. bondari* and *A. guerreronis*. Furthermore, the presence of *A. guerreronis* also improved the performance of *A. bondari*, indicating that previous infestation of this mite modifies the chemical or nutritional traits of coconuts. Adult females of *A. bondari* did not show a preference for nuts infested with *A. guerreronis*, so the caterpillars, and not the adults, select suitable feeding sites within a bunch of coconuts. Considering all the issues discussed above, the interactions between these three species are likely to have a significant impact on coconut production and deserve further study.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Manoel Gondim Jr and Debora Lima were the supervisors of this research work and helped design the experiment. Antônio Paz-Neto and Érica Calvet conducted the experiments. José Melo and Arne Janssen did data curation and analysis. Antônio Paz-Neto and Arne Janssen wrote the manuscript.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.5874630.

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