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Field distribution patterns of pests are asymmetrically affected by the presence of other herbivores

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Abstract

Because plant phenotypes can change in response to attacks by herbivores in highly variable ways, the distribution of herbivores depends on the occurrence of other herbivore species on the same plant. We carried out a field study to evaluate the co-occurrence of three coconut pests, the mites *Aceria guerreronis* (Acari: Eriophyidae), *Steneotarsonemus concavuscutum* (Acari: Tarsonemidae) and the moth *Atheloca bondari* (Lepidoptera: Pyralidae). The eriophyid mite *Ac. guerreronis* is the most important coconut pest around the world, whereas *S. concavuscutum* and *At. bondari* are economically important only in some areas along the Brazilian coast. A previous study suggested that the necrosis caused by *Ac. guerreronis* facilitates the infestation of *At. bondari* larvae. Because all three species infest the area under the perianths on coconuts and *S. concavuscutum* also causes necrosis that could facilitate *At. bondari*, we evaluated the co-occurrence of all three species. We found that the occurrence of *At. bondari* was positively associated with *Ac. guerreronis*, but negatively associated with *S. concavuscutum*. In addition, the two mite species showed negative co-occurrence. *Atheloca bondari* was found on nuts of all ages, but more on nuts that had fallen than on those on the trees, suggesting that nuts infested by *At. bondari* tend to fall more frequently. We discuss the status of *At. bondari* as a pest and discuss experiments to test the causes of these co-occurrence patterns.

Introduction

Biotic interactions play an important role in the structure and stability of ecological communities (Ives and Carpenter, 2007; Thébault and Fontaine, 2010; Benkman, 2013). Food web interactions have been extensively investigated in ecological research (Williams and Martinez, 2000; Tang *et al.*, 2014; Allesina *et al.*, 2015), showing that direct trophic (feeding) interactions are only one of many mechanisms by which species can influence each other (Bertness and Callaway, 1994; Ings *et al.*, 2009; Mougi and Kondoh, 2012; Sanders *et al.*, 2014), and that non-trophic interactions can have important effects on the dynamic of insect populations (Schmitz, 1998; Anderson *et al.*, 2009; Utsumi, 2011). Both trophic and non-trophic interactions can change species distribution and abundance through trait- and density-mediated indirect effects (Ohgushi *et al.*, 2007; Bukovinszky *et al.*, 2008; Eubanks and Finke, 2014). Indirect effects occur when the effect of one species on another is mediated by changes to a third species (Wootton, 1994).

Trait-mediated indirect interactions are important in plant–insect communities (Ohgushi, 2008; Karban, 2011; Giron *et al.*, 2018) because herbivory leads to phenotypic changes affecting physiology, chemistry and morphology of the plant (Karbon and Baldwin, 1997; Kant *et al.*, 2015; Ohgushi and Hambäck, 2015), which affect the performance of other herbivores. These herbivore-induced plant traits have the potential to affect whole host plant communities (Dicke *et al.*, 2009; Soler *et al.*, 2012; Poelman and Kessler, 2016; Stam *et al.*, 2018; Vaello *et al.*, 2018), and they may facilitate or impede the performance of subsequent herbivores (Stam *et al.*, 2014; Harvey *et al.*, 2015; Cornelissen *et al.*, 2016; Uesugi *et al.*, 2016; Lee *et al.*, 2017; Li *et al.*, 2018). Changes caused by herbivory can create new habitats within a plant that can be used by opportunistic herbivores (Ohgushi, 2008). Plants are often attacked by multiple herbivores and they respond specifically to single or dual herbivory (Kessler and Halitschke, 2007; Poelman *et al.*, 2008), which differentially affects the interactions with a third herbivore (Kroes *et al.*, 2016). Here, we studied a special case of interaction among herbivores, wherein the natural distribution of the moth *Atheloca bondari* Heinrich

(Lepidoptera: Pyralidae) is influenced by the co-occurrence with the mites *Aceria guerreronis* Keifer (Acari: Eriophyidae) and *Steneotarsonemus concavuscutum* Lofego and Gondim (Acari: Tarsonemidae). Assessing this co-occurrence is a first step in assessing the pest status of this moth as a coconut pest in natural fields.

The coconut palm is a perennial plant native to Southeast Asia but is currently distributed throughout the pantropics (Chan and Elevitch, 2006; Gunn et al., 2011; Ahuja et al., 2014) and considered a crop of economic importance in many countries (Hoe, 2018). Mites and moths are considered important coconut pests around the world, usually related to decreasing production of coconut fruits due to damage and abortion of the reproductive structure (Bondar, 1940; Moore, 2001; Fernando and Aratchige, 2010; Navia et al., 2013; Rezende et al., 2016). Larvae of different species of moths feed on the male and female flowers of coconuts (Bondar, 1940; Moore, 2001; Cock and Burris, 2013). The moths can complete their life cycle in developing nuts (Bento et al., 2006; Santana et al., 2010), but their occurrence in nuts is very low. This suggests that the larvae of moths are not able to bore the exocarp of the nuts.

The exterior of the nut is formed by a fibrous exocarp and an arranged set of tepals (perianths) covering the meristematic region (Smit, 1970; Howard and Rodriguez, 1991). Herbivores that can access the meristematic region can feed on nutritional tissues, but only very small organisms such as mites are able to enter the space between the exocarp and perianth (Moore, 2001; Navia et al., 2005; Lawson-Balagbo et al., 2008). For example, the mites *Ac. guerreronis* and *S. concavuscutum* are often found feeding on the meristematic region of the nuts under the perianth (Lofego and Gondim, 2006; Lawson-Balagbo et al., 2007; Lima et al., 2017). Coconuts infested by mites show necrotic lesions extending from the meristematic region to the surface of the nut not covered by the perianth (Navia et al., 2005; Lofego and Gondim, 2006).

A previous study shows that the moth *At. bondari* is an opportunistic species that uses necrosis of *Ac. guerreronis* to access the meristematic region of the nut (Santana et al., 2009). Although *At. bondari* is associated with economic loss in coconut crops (Bondar, 1940; Ferreira et al., 2002), the study of Santana et al. (2009) reveals that this species may be a secondary pest. However, Santana et al. (2009) did not evaluate fallen nuts, and if nuts infested only by *At. bondari* have a higher probability of falling, the co-occurrence between *At. bondari* and *Ac. guerreronis* may have been overestimated.

In the laboratory, larvae of *At. bondari* were better able to access the meristematic region of nuts that had necrosis of *Ac. guerreronis* or had received mechanical damage (Santana et al., 2009), reinforcing the idea that morphological changes of the exocarp of the coconut facilitate the infestation of the larva of *At. bondari*. *Aceria guerreronis* and *S. concavuscutum* cause similar necrotic lesion patterns (Navia et al., 2005), so it is expected that *At. bondari* also co-occurs with *S. concavuscutum*. This is what we set out to test in this manuscript by sampling coconuts in the field and assessing co-occurrence of the moth and the two mite species.

Since the space between the perianth and the exocarp increases as fruits ages (Lima et al., 2012), we collected nuts with different ages to analyse if age influenced the occurrence of *At. bondari* larvae. In addition, as both mite species and the moth occupy the same feeding sites, each could in theory influence the distribution of the other species (Capitán et al., 2015; Segre et al., 2016), we also evaluated the co-occurrence of the mites and how this influenced the presence of *At. bondari*.

Materials and methods

We randomly collected bunches from the tree and fallen nuts of coconut palms (*Cocos nucifera* L.). According to coconut tree phyllotaxis (Sobral, 1994), we collected the bunches corresponding to leaves 12–16, which refers to bunches of 2–6 months old, respectively. The fallen nuts under the palm trees were collected, the age of fallen nuts was determined by comparing their size with nuts removed from bunches of the palm tree, and fallen nuts were subsequently grouped by age. Fallen nuts that did not have the perianths or that were damaged by humans were not evaluated. Nuts were harvested from trees every 15 days in the state of Pernambuco, Brazil, between March and July of 2016 in the following fields: Itamaracá (Sossego) (7°43'S, 34°49'W), Itamaracá (Pilar) (7°47'S, 34°51'W), Itamaracá (Coroa do Avião) (7°48'S, 34°50'W) and Igarassú (Mangue Seco) (7°49'S, 34°50'W). Fallen nuts were collected only from Igarassú (Mangue Seco). In total, 1194 nuts (967 collected from coconut palms and 227 fallen nuts) were brought to the laboratory for evaluation, where we carefully removed the perianths and observed the meristematic region under them with a stereomicroscope (Zeiss Stemi DV4), and we scored the presence of *Ac. guerreronis*, *S. concavuscutum* and larvae of *At. bondari*.

The probability of co-occurrence was calculated following Griffith et al. (2016), assuming a hypergeometric distribution:

$$P_j = \frac{\binom{N_1}{j} \times \binom{N - N_1}{N_2 - j}}{\binom{N}{N_2}},$$

with N_i the number of nuts with species i ($= 1, 2$) and N the total number of plants sampled, and j ranging from 1 to N_1 (Griffith et al., 2016). This probability shows whether the species are positively, negatively or randomly associated. We analysed all co-occurrence combinations among species and discuss the results with a focus on *At. bondari* infestations. A positive association could be the result of attraction of *At. bondari* and the mites to the same nuts, independent of the presence of the other species or of facilitation of the caterpillars entering the area under the perianth due to mite damage. The absence of a positive or negative association would show that the moths and mites are not attracted to the same nuts, and that the infestation of mites does not facilitate the infestation by moths. The proportions of nuts infested by the different herbivores were compared between fallen nuts and nuts on trees and among nuts of different ages with a generalized linear model (GLM) with a binomial error distribution (Crawley, 2013). All statistical analyses were performed in R (R Development Core Team, 2014).

Results

The presence of *At. bondari* larvae in nuts not infested by mites was lower than expected in both fallen fruits and fruit from trees (fig. 1a, b). We observed a significant positive co-occurrence between *At. bondari* and *Ac. guerreronis* in both nuts collected from coconut palms and in fallen nuts (fig. 1a, b). The moth occurred significantly less than expected when the nuts on trees were infested by *S. concavuscutum* (fig. 1a), but the numbers of fallen fruits coinfecting with *At. bondari* and *S. concavuscutum* did not differ from expected under a random distribution (fig. 1b). The observed distribution of *At. bondari* also did not

Figure 1. Occurrence of *At. bondari*, *Ac. guerreronis* and *Steneotarsonemus concavuscutum* and their co-occurrence in the field. (a) Nuts collected from trees; (b) fallen nuts. The grey bars correspond to the total number of nuts collected for each category and the black bars represent the number expected. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test, Griffith et al., 2016): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

differ from expected for nuts infested by both species of mites, both in nuts from trees and in fallen nuts (fig. 1a, b). Furthermore, we found that *Ac. guerreronis* and *S. concavuscutum* co-occur less than expected in nuts from trees and fallen nuts (fig. 1a, b).

The distance between the edge of the perianth of coconut and the subjacent nut surface increases with nut age (Lima et al., 2012) and may therefore become more accessible to the moth caterpillars. We therefore first analysed the occurrence of *At. bondari* in nuts of different ages both in fallen nuts and nuts from trees. The proportion of *At. bondari* did not differ among nuts of different ages ($P = 0.32$), but the proportion of infested nuts was higher in fallen nuts than from trees ($P < 0.0001$) (fig. 2).

Third, we analysed the co-occurrence of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* in nuts of different ages. The proportion of *At. bondari* was higher than expected in nuts

infested by *Ac. guerreronis* of all ages sampled from the coconut palm (fig. 3a). The proportion of fallen nuts infested by *At. bondari* and *Ac. guerreronis* was also higher than expected at all ages sampled; however, this difference was not always significant (fig. 3b).

The proportion of nuts infested by *At. bondari* and *S. concavuscutum* varied between different ages. In nuts collected from palm trees, the co-occurrence of these two species was lower than expected at age 3, age 4 and age 5 (fig. 3c). The co-occurrence of *At. bondari* and *S. concavuscutum* did not differ from expected on fallen fruits of any age (fig. 3d).

Co-occurrence of the three species did not differ from random in nuts of different ages. In nuts collected from trees, *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* co-occurred more often than expected only in nuts of age 2 (fig. 3e). There was no difference in occurrence in fallen nuts of any age (fig. 3f).

Co-occurrence of the two mites was significantly lower than expected for all nut ages both on nuts collected from coconut palm and on fallen nuts. In nuts from trees, the proportion of nuts infested by *Ac. guerreronis* and *S. concavuscutum* did not differ from expected at age 2 (fig. 3g). In fallen nuts, the co-occurrence of mites was significantly lower than expected at age 3, age 4 and age 6 (fig. 3h).

Finally, we compared the occurrence and co-occurrence of species between fruits collected from trees and fallen fruits. The proportion of fruits with *At. bondari* was always higher in fallen fruits than fruits from trees, but the proportion of fruits infested by *At. bondari* together with *S. concavuscutum* did not differ between fruit origins (fig. 4a, b, c). The proportion of fruits infested by *At. bondari* and *Ac. guerreronis* was significantly higher in fallen fruits than in fruits from trees, but the proportion of fruits infested by *Ac. guerreronis* without *At. bondari* was higher in fruits from trees than in fallen fruits (fig. 4a). The proportion of fruits infested by *At. bondari* without *Ac. guerreronis* was higher in fallen fruits (fig. 4a). The highest proportion of fruits without these two species was found in fruits collected from the palm trees (fig. 4a).

Steneotarsonemus concavuscutum occurred more in fruits collected from trees than in fallen fruits when not co-occurring with *At. bondari* (fig. 4b). In contrast, without *S. concavuscutum*, *At. bondari* occurred significantly more in fallen fruits. The proportion of fruits without these two species was higher in fruits collected from the trees (fig. 4b).

The proportion of fruits infested by both mites without *At. bondari* was higher in fruits from trees than in fallen fruits, the same was found for fruits without any of the three species (fig. 4c). The occurrence of *At. bondari* in fruits not infested by mites was higher in fallen fruits than fruits from coconut palms (fig. 4c).

Without *S. concavuscutum*, *Ac. guerreronis* was observed in higher proportions in fallen fruits than in fruits from trees, this is probably due to the higher co-occurrence of *At. bondari* with *Ac. guerreronis* (fig. 4d).

Discussion

We show positive and negative co-occurrence among three species that use coconuts as a resource. The occurrence of larvae of the moth *At. bondari* under the perianths of coconuts on palm trees was higher than expected when the nuts were infested by *Ac. guerreronis*, whereas it was lower than expected for nuts that were infested by the other mite species *S. concavuscutum*

Figure 2. Proportion of *At. bondari* in fallen coconuts and nuts from trees of different ages. Bars below the dashed line represent the proportion of fallen nuts; these above the dashed line represent the proportion of nuts collected from trees. Asterisks indicate significant overall difference between fallen and trees nuts (GLM): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(fig. 1a). Santana *et al.* (2009) suggest that the co-occurrence of *At. bondari* and *Ac. guerreronis* is mainly due to a change in nut shape caused by the necrotic lesions of the mite, which allow the larvae of the moth access to the meristematic region under the perianths. However, the patterns of necrotic lesions caused by *S. concavuscutum* are similar to those caused by *Ac. guerreronis* (Navia *et al.*, 2005), thus positive co-occurrence would also be expected between *S. concavuscutum* and *At. bondari*. Thus, our results show that the co-occurrence among these species seems not to be related only to the necrotic lesions caused by the mites.

The simplest explanation for the co-occurrence, or lack thereof, is that the mites and the moths prefer the same, or different fruits, independent of the presence of the other species. For example, if *At. bondari* and *Ac. guerreronis* prefer to infest coconuts with the same quality inside a bunch, the positive co-occurrence between these species may be caused by similar preferences of the two species for nuts with a certain quality. Likewise, the lack of co-occurrence between *At. bondari* and *S. concavuscutum* may be caused by these two herbivores having different preferences.

Another explanation for the co-occurrence, or lack thereof, is the effects of the herbivores on each other through induced plant defences. Changes of plant traits induced by herbivory (Karban and Baldwin, 1997; Kessler and Baldwin, 2002; Kant *et al.*, 2015) are known to affect the interactions in herbivore-plant communities (Gouinguéné and Turlings, 2002; Heil, 2008; Ohgushi, 2008; Ali and Agrawal, 2014; Stam *et al.*, 2014; Ohgushi and Hamback, 2015; Poelman and Kessler, 2016; Howard *et al.*, 2018; Rusman *et al.*, 2018; Vries *et al.*, 2018). These changes may be a simple loss of plant tissue, resulting in resource competition between herbivores, but may also be of chemical origin, through the induction of herbivore-induced plant defences (Kessler and Halitschke, 2007; Ohgushi *et al.*, 2007; Poelman *et al.*, 2008; Poelman and Kessler, 2016). Attacks of herbivores can activate induced defences of plants through the jasmonic acid and salicylic acid (SA) phytohormonal signalling networks (Pieterse *et al.*, 2012; Glas *et al.*, 2014;

Grinberg-Yaari *et al.*, 2015), and different herbivore species can induce different defences. Due to cross-talk between these two phytohormonal pathways, induction of defences by one species may have positive, neutral or negative effects on the performance and occurrence of other species (Rodríguez-Soana *et al.*, 2010; Mathur *et al.*, 2013; Kant *et al.*, 2015), resulting in positive, negative or no effects of herbivores on each other's performance (Thaler *et al.*, 2002). If *Ac. guerreronis* and *S. concavuscutum* induce different plant defence responses, coconuts with different induced defences may not only influence the occurrence of *At. bondari* larvae but also the co-occurrence of both mites, as was found in this study (fig. 1a).

Furthermore, changes induced by herbivory may be physical, for example, the habitat construction by species of leaf-rolling caterpillars (Lill and Marquis, 2004). In our study system, physical changes as a result of herbivore attacks do occur, for example, the damage caused by the mites may increase the size of the opening between the perianth and the nut, allowing access to other herbivores. Thus, the co-occurrence of the three herbivores studied here may well be the consequence of all such changes induced by the mites on the coconuts. Clearly, to disentangle these different mechanisms, studies of the performance of *At. bondari* larvae on nuts that are both naturally or artificially infested with *Ac. guerreronis*, *S. concavuscutum* or not infested, as well as studies on the preference of larvae and oviposition of females for such nuts are needed.

Atheloca bondari larvae were not totally incapable to access the meristematic region of nuts that were not infested by mites (fig. 1a). Attacks by other herbivores or natural increases of the perianth opening may also facilitate the access of *At. bondari* larvae to nuts without mites. However, the distribution of *At. bondari* did not differ among coconuts of distinct ages (fig. 2), suggesting that the natural increase of the opening to the meristematic region in older nuts (Howard and Rodríguez, 1991; Lima *et al.*, 2012) is not sufficient to allow larval infestation. We recommend a study to measure the size of access to the meristematic region in nuts either infested by *Ac. guerreronis* or *S. concavuscutum*, and not infested by mites.

Figure 3. Proportion of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their co-occurrence on coconut fruits of different ages for different combinations of these three species (a–h). Left-hand panels represent the nuts collected from trees; right-hand panels fallen nuts. The red dash indicates the expected proportion of fruits infested by both species. The total numbers of fruits sampled per age show below the ages along the horizontal axis. Asterisks indicate significant differences between observed and expected (hypergeometric distribution test; Griffith et al., 2016): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 4. Proportion of *At. bondari*, *Ac. guerreronis* and *S. concavuscutum* and their interactions in fruits collected from tree and fallen fruits for different combinations of these three species (a-d). Bars below the dashed line represent the proportion of fallen fruits, above the dashed line the proportion of fruits collected from trees. Asterisks indicate significance with a GLM test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The presence of *At. bondari* larvae in coconuts seems mostly positively related to infestations by *Ac. guerreronis* (fig. 1a, b; fig. 3a, b). In nuts collected from palm trees, *At. bondari* larvae co-occur with *Ac. guerreronis* more frequently than expected at all ages of nuts, whereas the co-occurrence of these species was higher than expected only in fallen nuts of ages 2 and 3 (fig. 3a, b). The lack of significant co-occurrence between *At. bondari* and *Ac. guerreronis* in older fallen fruits may be due to the low number of these nuts found (fig. 3b, d, f, h). Apparently, older coconuts tend to fall less than the younger ones, in agreement with observations that the nuts typically fall 3–8 weeks after the spathe opens (Lever, 1969; Cock *et al.*, 1985), where younger nuts are more likely to fall after the herbivore attack (Vanderplank, 1959; McKinlay, 1965; Williams, 1974).

Aceria guerreronis is considered the main pest of the coconut palm, where the attack of this mite results in copra yield loss (Mathews *et al.*, 2004; Navia *et al.*, 2013). In some cases, it has been reported that *Ac. guerreronis* infestations cause significant premature coconut drop (Nair, 2002; Rezende *et al.*, 2016). If *Ac. guerreronis* reduces the vigour and germination of coconut seeds, premature drop of nuts infested by the mite may be advantageous for the coconut palm, because it might reduce the risk of infection of the other nuts in the bunch and reduce the investment in nuts of lower quality. However, many nuts infested with *Ac. guerreronis* produce vigorous seedlings (Haq *et al.*, 2002; Regi and Mathews, 2004; Beevi *et al.*, 2006), hence, the question remains whether feeding by *Ac. guerreronis* is also detrimental for the coconut trees, and not just for commercial production of coconuts. Here we show that infestations by *At. bondari* are correlated with the fall of coconuts (fig. 4a, b, c), whereas infestations with *Ac. guerreronis* are less so (fig. 4a, c). Thus, the presence of *Ac. guerreronis* in nuts can increase production losses not due to herbivory of this mite, but due to the facilitation of nut attack by other herbivores. Clearly, further study is needed into the causes of prematurely fallen coconuts.

The co-occurrence of *At. bondari* and *S. concavuscutum* was exceptionally low in nuts of age 3, 4 and 5 harvested from trees (fig. 3c), and the proportion of fallen nuts with *At. bondari* and *S. concavuscutum* did not differ from that of nuts collected from the trees (fig. 4b). It is not clear to us why *At. bondari* and *S. concavuscutum* co-occur less in nuts of intermediate age, but this may be due to the low quality of the nuts of these ages. We emphasize again the importance of studying the performance of *At. bondari* in nuts that are artificially infested with mites.

In nuts from trees, there is a tendency of *Ac. guerreronis* and *S. concavuscutum* to co-occur less frequently as coconut nuts become older (fig. 3g), and this tendency cannot be explained by the larger number of old fallen nuts infested by both mites (fig. 3h). Measurements of non-infested coconuts show that the opening between the perianth and the nut surface of nuts of age 2 is 20–40 µm (Lima *et al.*, 2012). The tiny adult females of *Ac. guerreronis* (36–52 µm thick) (Keifer, 1965) can colonize these young nuts; however, adult females of *S. concavuscutum* (110–125 µm wide) (Lofego and Gondim, 2006) may have difficulties to enter the microhabitat of non-infested young nuts. Lima *et al.* (2012) show that infestation by *Ac. guerreronis* increases the opening between the perianth and the meristematic region. The co-occurrence of *Ac. guerreronis* and *S. concavuscutum* in younger nuts may thus be due to facilitation of *S. concavuscutum* by *Ac. guerreronis*, and the less frequent co-occurrence in older fruits may be due to competitive exclusion.

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Conflict of interest. The authors declare that they have no conflict of interest.

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