

Florivorous caterpillars act as ecosystem engineers and provide a cool microhabitat for thrips in *Peixotoa tomentosa* (Malpighiaceae)

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Abstract: We investigated the role of florivorous lycaenid butterflies in creating microhabitats available to occupation by thrips (*Pseudophilothrips*) in *Peixotoa tomentosa* (Malpighiaceae). Both insects feed on flower buds, but thrips are suckers, whereas caterpillars chew the internal part of flower buds, leaving only the external bud surface (bud-shells). We hypothesised that thrips inhabit bud-shells as protection from high temperatures. The study was conducted in a Brazilian savanna (18°59'S, 48°18'W). The results revealed that thrips indeed remained in bud-shells when temperatures were high and returned to their foraging behaviour outside the buds when temperatures lowered. *Pseudophilothrips* depend on intact buds for feeding, whereas bud-shells act as shelter against the environment, so lycaenid caterpillars provide a complementary resource for thrips. To our knowledge, this is the first record of a free-living caterpillar as an ecosystem engineer, as examples to date are based mostly on leaf-rolling and shelter-living butterflies.

Key words: *Allosmaitia strophius*, Cerrado, Lycaenidae, *Pseudophilothrips*, *Peixotoa*, Malpighiaceae.

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In general, animals interact with their habitat both temporally and spatially, and the consequent effects can either positively or negatively influence the occurrence of other animals (Jones *et al.* 1997; Kupika *et al.* 2014). The term “ecosystem engineer” is used for organisms that provoke and induce changes in the physical state or condition (e.g. creation, modification and maintenance) of their habitats, and consequently, either facilitate or prevent the occurrence of other organisms in the new environment that is created (Crooks *et al.* 2002; Gutiérrez *et al.* 2003; Jones *et al.* 1994).

This study examined the role of florivorous lycaenid butterflies (Lepidoptera) in creating

microhabitats available to thrips (Thysanoptera) occupation in *Peixotoa tomentosa* A. Juss. (Malpighiaceae). In the Cerrado biome (Brazilian savannah), lycaenids co-occur with herbivore thrips in Malpighiaceae and both feed on flower buds, but thrips are suckers (Alves-Silva & Del-Claro 2014), whereas lycaenid caterpillars feed on the whole content of buds (Kaminski & Freitas 2010), leaving only their shells (external surface), hereafter referred to as “bud-shells”. Thrips forage throughout the whole day in *P. tomentosa*, but during field surveys, we noted that at around midday, these insects were predominantly found inside the bud shells, presumably as protection

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against high temperature (see Mound & Terry 2001). During the reproductive season of *P. tomentosa* (June–July), temperatures in the Cerrado are high and rains are scarce (see Réu & Del-Claro 2005). Studies have demonstrated that high temperatures are a cause of mortality in thrips (McDonald *et al.* 1998, 1999). Thus, any type of shelter that is available to thrips occupation in *P. tomentosa* might benefit their maintenance in the plant. As shown by Mound & Terry (2001), thrips seek refuges within the plants to escape from high temperatures. In this context, we hypothesised that bud-shells created by lycaenids might provide a cool microhabitat for thrips during the hottest part of the day.

We examined a possible spatial segregation of thrips in relation to daily temperature. We hypothesised that thrips would be predominantly found outside bud-shells in the morning and the evening, when the temperature is cooler, but that around midday, when the temperature in the Cerrado may reach up to 40 °C, thrips would remain in the bud-shells. This might indicate that bud-shells are important as a refuge from the environment. Lycaenid–thrips interactions in the laboratory and the rate of shell occupation by thrips were also examined. If a positive relationship between thrips abundance in bud-shells and temperature exists, it might be evidence that lycaenid caterpillars act as ecosystem engineers by creating a microhabitat for thrips.

Fieldwork was performed in a Cerrado reserve (18°59'S, 48°18'W; 230 ha) in Uberlândia, Brazil. The study area is characterised by a tropical climate with well-defined dry (April to September) and wet (October to March) seasons (Réu & Del-Claro 2005). *Peixotoa tomentosa* is an extrafloral nectaried shrub (~1.5 m in height), occurring in

open areas; its reproductive season takes place from June to late July; flower buds are round and grow in clusters of four buds at the apex of branches (Fig. 1a). Each flower bud is surrounded by eight elliptical and green oil-glands (Del-Claro *et al.* 1997). Adults and larvae of *Pseudophilothrips* (Phlaeothripidae) are roughly 2 mm and 1 mm long, respectively, and feed constantly on flower buds. Adults are black and winged, whereas larvae are wingless and reddish in colour (Alves-Silva & Del-Claro 2014). To avoid ambiguity in this study, lycaenid and immature thrips are referred to as ‘caterpillars’ and ‘larvae’, respectively.

As a preliminary evaluation of the daytime variation of thrips in flower buds (intact buds and bud-shells), we observed five shells and five intact buds from two *P. tomentosa* individuals (N = 20 flower buds) on one sunny day from 08:00 h to 17:00 h. Each plant was examined for two minutes in each hourly interval and we registered the number of thrips in both shells and intact buds. The temperature (°C) during the daytime was measured with a thermometer placed in the soil near the plants. The relationship between thrips abundance in bud-shells (Fig. 1b, c), intact buds and temperature was examined using linear regression (assuming $\alpha = 0.025$ as corrected *P* value), as the original data was normally distributed. The temperature in and out of the shells was measured with an infrared thermometer at around midday.

To investigate the interactions between thrips and lycaenids in the laboratory, and the occupation of bud-shells by thrips, we used 4th instar caterpillars. In this stage, caterpillars feed extensively on flower buds, allowing us to rapidly examine the relationship between bud consumption (shell creation) and shell occupation by thrips. Our study focussed on the species *Allosmaitia strophius* (Godart 1824) (Fig. 1d), which is a frequent caterpillar on *P. tomentosa* (*pers. obs.*). Caterpillars collected in the field (N = 13) were reared until the 4th instar in the laboratory (following Bachtold *et al.* 2013).

Lycaenid–thrips interactions were observed in transparent plastic pots (200 ml). At the base of each pot (N = 13 pots) we placed a cluster of flower buds and carefully added an *A. strophius* caterpillar. Then six *Pseudophilothrips* individuals (N = 3 adults and 3 larvae) were placed at the lid of the pot, using a fine brush. Each pot was closed and we waited 15 minutes for insect accommodation. Observations were subsequently

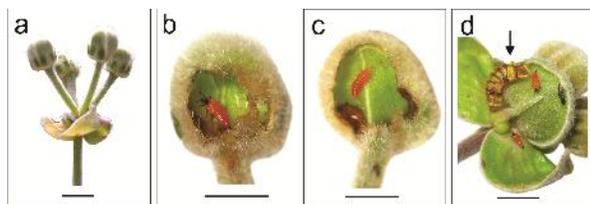


Fig. 1. (a) Cluster with four flower buds of *Peixotoa tomentosa*; (b) Lycaenids consume the internal tissues of buds, leaving an empty space where thrips dwell; a bud-shell containing a *Pseudophilothrips* larva is shown here; (c) a thrips pre-pupa inside a bud-shell; (d) *Allosmaitia strophius* (arrow), together with two larvae (red) and one adult (black) of thrips. Scale bars: a, c, d–5 mm; b–3 mm.

performed each 30 minutes for 300 minutes and at each interval, we registered the number of buds consumed by caterpillars and the number of *Pseudophilothrips* (adult and larvae) inside shells. The relationship between the number of buds eaten by lycaenids (bud-shells), and occupation by thrips (adults and larvae) was examined using linear regression.

In the morning, thrips were more abundant in intact buds, but in the afternoon when the temperature was higher (peaking above 40 °C), thrips were mostly found inside bud-shells. In the evening, thrips left the bud-shells and returned to their foraging behaviour on intact buds (Fig. 2a). There was a negative relationship between the abundance of thrips on intact buds and temperature ($F_8 = 13.09$, $R^2 = -0.62$, $P = 0.01$), and a positive, though only marginally significant, relationship between thrips in shells and temperature ($F_8 = 7.39$, $R^2 = 0.48$, $P = 0.03$) (Fig. 2b). At midday, the interior of the shells was cooler (28 °C) than the external surface (31 °C).

During the observations, we found a pre-pupa

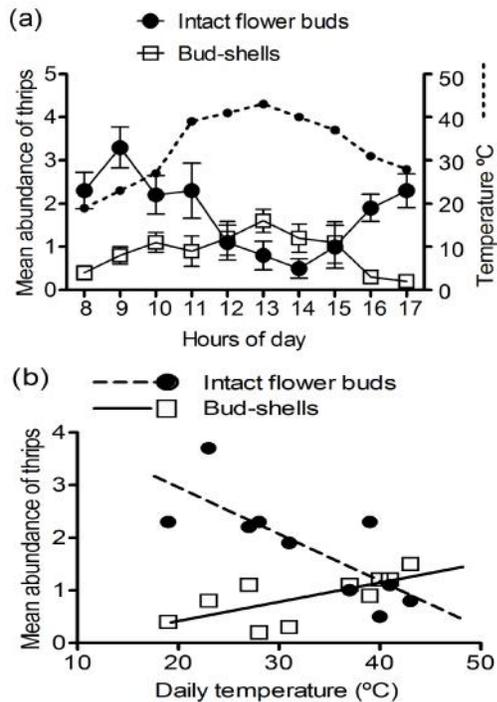


Fig. 2. (a) Daytime variation (mean \pm SE) in the number of *Pseudophilothrips* in intact buds and bud-shells of *Peixotoa tomentosa* (b) Relationship between thrips abundance in buds and temperature. During the hotter parts of the day, thrips moved to bud-shells.

in one shell (Fig. 1c) and three eggs of *Pseudophilothrips* in other shells. Apart from *Pseudophilothrips*, some florivore thrips species were also noted in bud-shells, such as *Heterothrips peixotoa* (Del-Claro *et al.* 1997) ($N = 4$ bud-shells), *Scutothrips nudus* (Moulton 1932) ($N = 3$ bud-shells) and one species of *Heterothrips* sp. ($N = 1$ bud-shell).

In the laboratory, thrips were observed to walk over or remain on the *A. strophius* body very often, apparently without provoking disturbances in lycaenid behaviour (Fig. 1d). Adult *Pseudophilothrips* moved rapidly from flower buds, whereas larvae were less mobile. Thrips entered the bud-shells as soon as lycaenids consumed the internal tissues of flower buds. Thrips abandoned the shells very often, visiting intact buds and then returning to the shells. A positive and significant relationship between the abundance of buds consumed by *A. strophius* and the number of thrips that occupied the bud-shells was found (adult: $F_9 = 33.13$, $R^2 = 0.89$, $P < 0.001$; larvae: $F_9 = 52.28$, $R^2 = 0.92$, $P < 0.0001$). At the end of the experiment, when all buds had been consumed by lycaenid caterpillars, 38% of the thrips were inside shells; the other thrips were wandering or immobile inside the pot.

Our hypothesis that caterpillars might act as an ecosystem engineer by modifying the architecture of flower buds in *P. tomentosa* and making them attractive to thrips was supported. Thrips are well known for their habit of entering small cracks (Crespi *et al.* 1997; Sakai 2001), including the shelters of other thrips species (kleptoparasitism) or other insects (Bächtold & Alves-Silva 2013; Cavalleri *et al.* 2013; Crespi & Abbot 1999). To the best of our knowledge, the present study is the first to demonstrate that thrips benefit from a habitat created by another animal in the context of ecosystem engineering. According to Fukui (2001), shelter inquilines (such as thrips) have a series of advantages (e.g. favourable microclimate, protection from natural enemies), without incurring costs related to the construction and maintenance of the habitat (see also Lill & Marquis 2007). The occupation of bud-shells by thrips is therefore advantageous, as they find a cool microhabitat, which protects them against the environment.

In *P. tomentosa*, both intact buds and bud-shells play a complementary role in thrips life history. Thrips depend on intact buds for feeding, whereas shells act specifically as shelters, as the external layer of bud-shells is crispy and the oil

glands are dry, offering no food for thrips. High temperature was related to the migration of thrips from intact buds to shells, as most thrips were found within shells around midday. The temperature inside shells was also cooler in comparison to that outside. The flower buds of *P. tomentosa* grow at the apex of branches and are exposed to direct sunlight all day long. Thrips are small insects with a thin cuticle, therefore, direct sunlight and high temperatures might interfere with their metabolism and increase the risk of desiccation. In Australia, for instance, thrips seek shelter during the hottest period of the day in cones of cycads (Mound & Terry 2001), as thrips mortality is high at temperatures above 35 °C (McDonald *et al.* 1998, 1999; Tsai *et al.* 1995; Wiesenborn 2000). In the laboratory, thrips moved to shells as soon as lycaenids fed on buds, but many thrips continued to wander inside the pot. These results can be explained by the mobility of *Pseudophilothrips*, which move very often from plant structures in the field, eventually stopping on buds to feed. In the laboratory the temperature was cooler (~24 °C), and as shown in Fig. 2, thrips sought shells as the temperature rose.

In this study lycaenids were shown to be able to physically manipulate flower buds and turn them into a microhabitat appropriate to thrips. Other herbivores, such as endophytic beetles also feed on the content of buds (Alves-Silva *et al.* 2013), but abandoned buds are wide open and contain the waste and faeces of beetles, and are thus not favourable to occupation by thrips. To conclude, we assume that *A. strophius* can be considered an ecosystem engineer, by creating a microhabitat that can be used by thrips when temperatures are high.

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