

Trade-offs underlying polyphagy in a facultative ant-tended florivorous butterfly: the role of host plant quality and enemy-free space

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Abstract The underlying mechanisms mediating the use of multiple host plants were investigated in *Parrhasius polibetes* (Lycaenidae), a florivorous and facultative myrmecophilous butterfly. Plant traits such as presence of ant–treehopper associations as a source of enemy-free space, flower bud dimensions, toughness, thickness, trichomes, and the corresponding performance and wear of *P. polibetes* mandibles were examined for three natural hosts: *Schefflera vinosa* (Araliaceae), *Pyrostegia venusta* (Bignoniaceae) and *Luehea grandiflora* (Malvaceae). Parasitism levels of larvae found on the three hosts were also determined. Almost all *Luehea* had ant–treehopper associations, and all larvae found on this host were non-parasitized. Parasitism was low in larvae found on *Schefflera*, half of which hosted ant–treehopper associations. No ant–treehopper association was found on *Pyrostegia*, where parasitism was significantly higher compared to other hosts. In the laboratory, *P. polibetes* performed well on *Schefflera*, followed by *Pyrostegia*. No larvae survived when fed with *Luehea*. Flower buds of *Luehea* were thicker and tougher than those of *Schefflera* and *Pyrostegia*. Indeed, mandibles of larvae reared on *Luehea* showed substantial wear, whereas those

reared either on *Schefflera* or *Pyrostegia* presented no significant damage. Additionally, we suggest that co-occurrence with ant–treehopper associations on a plant provides parasitoid-free space for *P. polibetes* larvae. Our results support the hypothesis that ecological trade-offs among host plants (i.e., food quality and enemy-free space) promote polyphagy in natural populations of *P. polibetes*. Host morphological traits seem to play a relevant role in *P. polibetes* performance. To our knowledge, this is the first report showing the costs of polyphagy in a myrmecophilous butterfly.

Keywords Insect performance · Mandibular wearing · Enemy-free space · Myrmecophilous lycaenid · *Parrhasius polibetes*

Introduction

Although equally important for understanding community structure and dynamics, polyphagy in herbivorous insects has historically received less attention in ecological and evolutionary studies than oligophagy (see Janz and Nylin 2008; Singer 2008, and references therein). From a bi-trophic perspective (i.e. host plants and the herbivore), it is expected that the use of multiple hosts in nature entails trade-offs between components of herbivore performance on different hosts. That is, while a certain host can provide an herbivore the best outcome regarding a given performance component (e.g., survivorship), the same may not be true for some other parameters (e.g., growth rate) (Janz et al. 1994; Agosta 2008). In addition, performance outcomes on plants that are both phylogenetically and structurally (i.e. physically and/or chemically) different can be quite distinct (e.g., Janz and Nylin 2009). In such cases, the

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underlying factors that determine such differences are poorly known.

Singer (2008) pointed out some hypotheses to explain how polyphagy could arise and be maintained in nature. Several of these hypotheses involve differences in enemy-free space among different host plants (see Singer 2008, and references therein). For example, a herbivore might experience trade-offs between food quality and enemy-free space among hosts (Singer et al. 2004). According to this hypothesis, some hosts support superior performance due to favorable chemical or physical characteristics, whereas others may confer protection against natural enemies despite poor food quality. Although this hypothesis has been tested with several different study systems in temperate regions, it has rarely been tested in the tropics, where insect and plant diversity are greatest.

The myrmecophily (symbiotic association with ants) present in some lycaenid and riodinid butterflies offers an unusual opportunity to examine how enemy-free space influences the evolution of host plant use (Atsatt 1981a). Several studies have shown that ant-tended lycaenid caterpillars gain an advantage in enemy-free space over untended caterpillars (e.g., Pierce and Eastal 1986; Weeks 2003). This observation suggests that the quality of enemy-free space conferred by ants could be as important as host plant characteristics for the performance of myrmecophilous caterpillars (Pierce and Elgar 1985; Oliveira and Del-Claro 2005). It has been proposed that obligate myrmecophily may be associated with the rise and maintenance of polyphagy (e.g., Pierce and Elgar 1985; Fiedler 1994; DeVries et al. 1994; Kaminski 2008), where the presence of ants is one of the main factors leading to the use of a given host plant. The known cases of association between polyphagy and myrmecophily in riodinid and lycaenid larvae (e.g., Pierce and Elgar 1985; Kaminski 2008) suggest two testable hypotheses. First, myrmecophilous butterflies might use a set of host plants on which ants are present, regardless of host plant quality. Alternatively, there might be a trade-off between enemy-free space and food quality among different host plants, with each of these factors contributing to host plant use.

The presence of ants on host plants as a source of enemy-free space for myrmecophilous caterpillars could result from host plant characteristics, such as extrafloral nectar, or from ants drawn to plants by sap-feeding insects (Carroll and Janzen 1973; Atsatt 1981a). Indeed, ants tending trophobiont insects such as honeydew-producing treehoppers (Del-Claro and Oliveira 2000) can extend their protective services to nearby myrmecophilous lycaenids (Oliveira and Del-Claro 2005). Moreover, although ant presence and plant quality can mediate both oviposition and larval survival in obligate ant-tended oligophagous lycaenids (Atsatt 1981b; Baylis and Pierce 1991), there is no

information on whether host plant morphological and ecological attributes can influence larval and adult life-history in polyphagous butterflies that are facultatively tended by ants.

This study investigates how characteristics of different host plants influence the performance of *Parrhasius polibetes* (Stoll) (mentioned as *Panthiades polibetes* in Oliveira and Del-Claro 2005), a florivorous lycaenid facultatively associated with ants (Fig. 1a). Through experimental manipulations of ant–treehopper associations, *P. polibetes* has been shown to infest preferentially *Schefflera vinosa* (Cham. and Schldl.) (Araliaceae) (hereafter *Schefflera*) plants hosting ant-tended treehoppers compared to plants without such associations (Oliveira and Del-Claro 2005). More recently, presence of ant–treehopper associations on *Schefflera* plants has been shown to mediate *P. polibetes* oviposition, positively affecting larval survival (L.A. Kaminski, A.V.L. Freitas and P.S. Oliveira, submitted data). The enemy-free space provided by ant–hemipteran associations, together with the quantification of the quality of different hosts that may harbor such associations, can help distinguish between the two hypotheses for polyphagy in facultative myrmecophilous butterflies described above. Although monophagous at the individual level, *P. polibetes* larvae have been found on over 20 plant species from several families (Beccaloni et al. 2008; Kaminski 2010). We examine some ecological and morphological traits of three common host plants that vary in enemy-free space and/or host suitability. More specifically, because host plants differ remarkably in morphology and size (Fig. 1), we investigate how plant traits can affect *P. polibetes* performance, mandibular wear, and thus life-history traits and associated trade-offs.

Materials and methods

Study sites, insects, and host plants

Parrhasius polibetes eggs, larvae and host plants were collected in the cerrado area of the Laboratório Síncrotron in Campinas (22°48'S, 47°03'W) and in the Reserva Biológica e Estação Experimental de Mogi Guaçu (22°18'S, 47°13'W), both in the State of São Paulo (southeastern Brazil), during May–June 2008, which corresponds to the dry season (fall–winter). The vegetation in both areas consisted of a cerrado sensu stricto, the typical fire-prone savanna growing on sandy nutrient-poor soils covered by a grass layer, small palms, bushes, and trees (Oliveira-Filho and Ratter 2002). A survey for *P. polibetes* eggs on the three host plant species was carried out at the Síncrotron site on 27 May 2008: 63, 96, and 150 eggs were recorded on *Schefflera*, *Pyrostegia venusta* (Ker-Gawler) Miers (Bignoniaceae) (hereafter

Fig. 1 Flower buds of **a** *Schefflera*, **b** *Pyrostegia*, **c** *Luehea* and **d** *P. polibetes* eggs near ant–treehopper associations on *Luehea* stems. Arrows indicate the oviposition site selected by *P. polibetes* on *Schefflera* (**a**) as well as eggs on *Luehea* (**c,d**). Bars 10 mm



Pyrostegia), and *Luehea grandiflora* Mart (Malvaceae) (hereafter *Luehea*), respectively. These hosts are native to the region and commonly occur in the cerrado (see references below).

Schefflera (Fig. 1a) is a shrub frequently hosting aggregations of the honeydew-producing treehopper *Guayaquila xiphias* Fabr. (Hemiptera: Membracidae), which are regularly tended by ants in the cerrado. Prospective tending ants are attracted to treehoppers after finding scattered droplets of flicked honeydew on the ground and lower leaves (Del-Claro and Oliveira 1996). Increased aggression by tending ants wards off predators and parasitoids from nearby foliage, and positively affects treehopper survival (Del-Claro and Oliveira 2000). The plant flowers from May to October and treehoppers usually aggregate close to the inflorescence (Del-Claro and Oliveira 1999).

Pyrostegia (Fig. 1b) is an evergreen, climbing woody vine that flowers from April to September (Lorenzi and Souza 2001; Polatto et al. 2007).

Luehea (Fig. 1c) can be found either as large shrubs or trees, with a blooming season from May to July (Lorenzi 2002; Milward-de-Azevedo and Valente 2005). *Guaya-*

quila xiphias and other treehopper species, as well as honeydew-gathering ants, are commonly found on reproductive branches of *Luehea* at the Sincrotron site (Fig. 1d).

Ant–treehopper associations and larval parasitism in the field

Occurrence of a supposed enemy-free space for *P. polibetes* through the presence of ant–treehopper associations was investigated for all individuals of each host plant species found in a 908-m-long trail. Because *Pyrostegia* is a climbing vine, branches were considered as belonging to different individuals when displaced at least 1 m apart. This survey was carried out at the cerrado area of Laboratório Sincrotron on 13 June 2008. The three hosts were also examined with respect to presence of *P. polibetes* larvae, which were collected and brought to the laboratory to assess parasitism rates. In the laboratory, larvae were kept individually in covered, transparent plastic pots (250 ml) and fed with the hosts used in the field. Larvae were followed until pupation or death. Unopened flower buds were offered ad libitum by inserting their peduncles in 1.5-ml Eppendorf tubes, and rearing pots were checked

daily, with food replacement and cleaning when necessary. This survey was carried out on 27 May 2008.

Performance on three host plants

Larvae used in this experiment came from eggs laid in the field on the three hosts mentioned above. In order to avoid biased results, newly-hatched larvae were assigned to the same host species where the corresponding eggs were found in the field. A total of 60 larvae ($n = 20/\text{host plant}$) were individually reared following the procedure described in the previous section under controlled conditions ($25 \pm 2^\circ\text{C}$; 12L:12D). The experiment was run simultaneously, in a completely randomized design (Peterson 1985). Traits chosen for determining performance included larval development time, survivorship until the adult stage, pupal mass and forewing length (Thompson 1988). Pupal mass was obtained by weighing 8-day-old pupae using an AB 104-S Mettler Toledo® Balance; forewing length was assessed by using Etalon® calipers.

Mandibular wear

After molting, head capsules were collected from the individuals reared on each of the three hosts by using a thin dissecting pin ($n = 10/\text{instar}$). Both right and left mandibles were then detached from the corresponding head capsules under a Zeiss Stemi SV6® stereomicroscope. The right mandible was immersed in glycerin jelly, mounted using slide/cover slip and its length (from the mandibular basis to the tip of the longest incisor, which is the third tooth) taken using a Zeiss Axioskop 2 plus® microscope (see Raupp 1985; Dockter 1993). In order to assess the length of intact mandibles as a control, additional larvae reared on *Schefflera* ($n = 10/\text{instar}$) were fixed in Dietrich's fluid just after molting (that is, without feeding) and measurements were taken as described above.

Because no larvae reached the third instar when reared in the laboratory with flower buds of *Luehea*, the mandibular length of *P. polibetes* was compared among the three hosts and control only for the first and the second instars. In addition, we photographed the mandibles of fourth instar larvae found on the three host plants in the field in order to illustrate mandibular wear in nature. Mandibles were photographed through scanning electron microscopy (see Rodrigues and Moreira 2005), and procedures were done at Centro de Microscopia Eletrônica of Universidade Federal do Rio Grande do Sul.

Flower bud traits

Flower buds from the three hosts ($n = 15/\text{plant species}$) were collected in the Síncrotron site and measured in rela-

tion to the following traits: length (enclosed sepals or calyx length for some *Pyrostegia* individuals when necessary), width, thickness (sepal width) and toughness. Metric data were taken under MZ 75 Leica® stereomicroscope equipped with a micrometric ruler. Toughness was assessed with a TA-TX2® texturometer at Laboratório Central of Faculdade de Engenharia de Alimentos/Universidade Estadual de Campinas. Trichome characterization and structural details were obtained through scanning electron microscopy of five flower buds per host plant fixed in 50% FAA (see above).

Statistical analysis

Frequencies of ant–treehopper associations and parasitized larvae of *Parrhasius polibetes* among host plants were analyzed through Chi-Square test (Sokal and Rohlf 1995). To assess whether frequency of parasitized larvae were dependent on the corresponding frequency of ant–treehopper association across hosts, a 3×2 *G* test of independence with Williams correction was performed (Sokal and Rohlf 1995). *Parrhasius polibetes* survivorship on each host plant was compared through Fisher's exact tests. Larval development time, pupal mass and forewing length, as well as data on host plant traits showed a normal distribution (D'Agostino and Pearson tests) and were analyzed using unpaired *t* tests and one-way ANOVA followed by Tukey's Multiple Comparison tests. Data on *P. polibetes* mandibular length were not normally distributed, and were analyzed through a non parametric ANOVA (Kruskal–Wallis tests) followed by Dunn's Multiple Comparison tests. All tests were performed using Biostat 3® and GraphPad® Softwares (Motulsky 1999; Ayres et al. 2003).

Results

Ant–treehopper associations and larval parasitism in the field

A total of 51 individuals of *Pyrostegia*, 26 of *Schefflera* and 22 of *Luehea* were recorded. Frequency of the honeydew-producing treehoppers and associated ants differed markedly among the three hosts of *P. polibetes* (Chi-square test, $\chi^2 = 182.90$, $df = 2$, $P < 0.0001$). Whereas no ant–treehopper interaction was found on *Pyrostegia*, ant–treehopper associations were present on 57.3 and 95.5% of the *Schefflera* and *Luehea* individuals recorded, respectively (Fig. 2).

We found 38 larvae of *P. polibetes* on *Schefflera*, 9 on *Pyrostegia* and 13 on *Luehea*. In all hosts, larvae ranged from early to late instars. Parasitoids came out of three larvae found on *Schefflera* (two 2nd and one 4th instar) and two on *Pyrostegia* (one 1st and one 3rd instar), respectively.

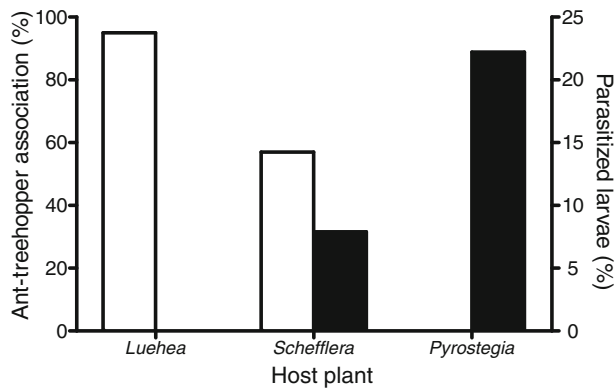


Fig. 2 Relative frequency of ant–treehopper associations on *Schefflera*, *Pyrostegia* and *Luehea* branches (white bars) and parasitized larvae of *P. polibetes* collected on the same host plants (black bars). Surveys carried out in May–June 2008

No larvae collected on *Luehea* were parasitized (Fig. 2). Frequency of parasitized larvae of *P. polibetes* differed significantly among hosts (Chi-square test, $\chi^2 = 25.42$, $df = 2$, $P < 0.0001$). Parasitoids consisted of four unidentified species of Hymenoptera and one species of Diptera (Tachinidae).

Across the three hosts, frequency of parasitized larvae was significantly affected by the corresponding frequency of ant–treehopper associations (3×2 G test of independence with William’s correction, $G = 111.50$; $df = 2$; $P < 0.01$).

Performance on three host plants

All the 20 newly-hatched larvae survived until the adult stage when fed with *Schefflera* flower buds; 14 larvae reached the pupal stage when feeding on *Pyrostegia*, from which ten adults emerged. No larvae reached the third instar when reared on *Luehea* (Table 1). Survivorship was significantly different between *Schefflera* versus *Luehea* (Fisher’s exact test, $P < 0.0001$), *Schefflera* versus *Pyrostegia* (Fisher’s exact test, $P = 0.0004$), and *Pyrostegia* versus *Luehea* (Fisher’s exact test, $P = 0.0004$). Larvae reached the pupal stage faster when reared on *Schefflera* compared to *Pyrostegia* flower buds (unpaired two-tailed t test, $t = 6.05$, $P < 0.0001$). Pupae and adults were also significantly heavier and larger when larvae were fed with *Schefflera* compared to *Pyrostegia* (unpaired two-tailed t test, $t = 6.80$ for pupal mass and $t = 4.90$ for forewing length, $P < 0.0001$).

Mandibular wear

There was a significant difference in mandibular length among treatments and control larvae, a pattern that was consistent across instars (Kruskall–Wallis test, $P = 0.001$

Table 1 Survivorship, larval development time, pupal mass and forewing length of *P. polibetes* individuals reared on *Schefflera*, *Pyrostegia* and *Luehea* under controlled abiotic conditions (mean \pm SD)

Host plant/ performance trait	<i>Schefflera</i>	<i>Pyrostegia</i>	<i>Luehea</i>	P
Survivorship (%)	100	50	0	See text
Development time (days)	17.45 ± 0.60	19.57 ± 1.40	–	<0.0001
Pupal mass (g)	0.29 ± 0.42	0.19 ± 0.02	–	<0.0001
Forewing length (mm)	19.92 ± 1.07	17.88 ± 1.08	–	<0.0001

For each performance trait, results differed significantly between/ among hosts (Fisher’s exact test for survivorship and Tukey’s multiple comparison tests for the remaining performance traits)

and $P = 0.01$ for first and second instars, respectively). Mandibles of larvae reared on *Schefflera* did not differ in length from those reared on *Pyrostegia*, or from control larvae (Dunn’s Multiple Comparison tests, $P > 0.05$ for all comparisons) (Fig. 3a). Mandibles of larvae reared on *Luehea* differed significantly from those reared on *Schefflera* and also from control larvae (Dunn’s Multiple Comparison tests, $P < 0.05$ for all comparisons) (Fig. 3b). Broken teeth were found only when larvae were fed with *Luehea* (Fig. 4h, i for first and fourth instars, respectively). On the other hand, mandibles remained intact when larvae were fed with *Schefflera* and *Pyrostegia* (Fig. 4b, c, e, f).

Flower bud traits

Pyrostegia possessed the largest flower buds (Tukey’s Multiple Comparison test, $P < 0.05$), while *Luehea* had the widest ones (Tukey’s Multiple Comparison test, $P < 0.05$) (Fig. 5a, b). With respect to physical barriers to herbivores, *Luehea* flower buds were significantly tougher and thicker than those of *Schefflera* and *Pyrostegia* (Tukey’s Multiple Comparison test, $P < 0.05$ for both traits). The latter two species did not differ significantly in bud toughness or thickness (Tukey’s Multiple Comparison test, $P > 0.05$) (Fig. 5c, d).

Flower buds of *Schefflera* were densely covered by simple trichomes (Fig. 4a). In contrast, those of *Pyrostegia* had an almost glabrous surface with both simple and glandular trichomes (Fig. 4d). *Luehea* flower buds were densely covered by both simple and stellate trichomes (Fig. 4g).

Discussion

Our data clearly demonstrate that the three natural host plants provide contrasting performance outcomes in *P. polibetes*. *Schefflera* confers superior performance, followed by *Pyrostegia*, whereas no late instar larvae were obtained

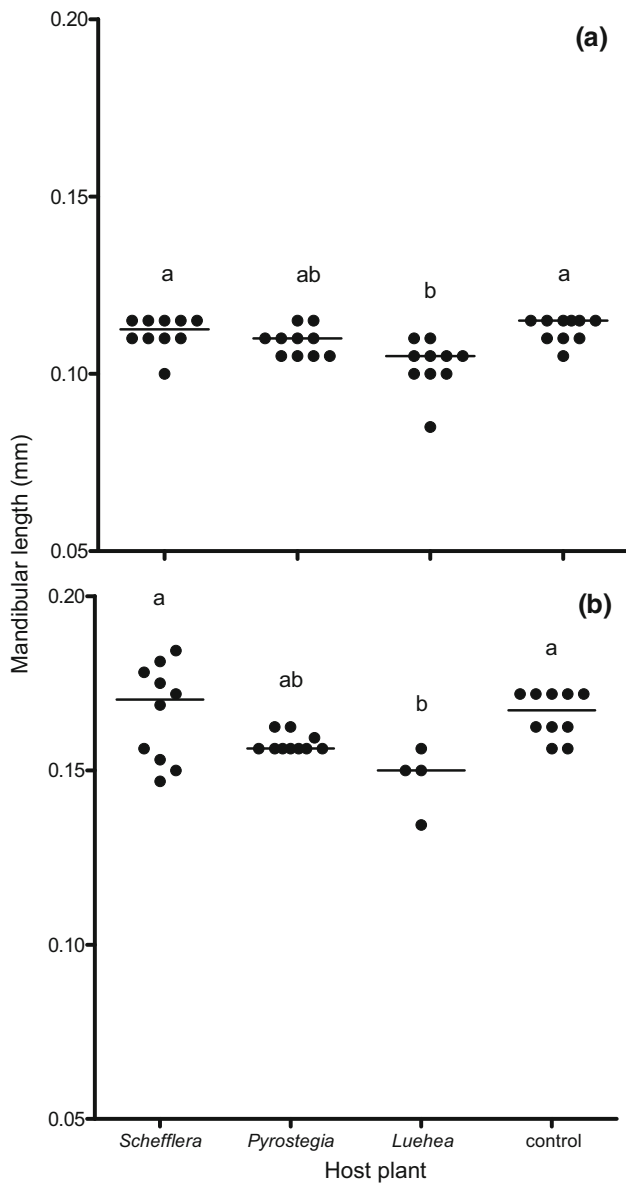


Fig. 3 Mandibular wear of **a** first and **b** second instar larvae of *P. polibetes* reared on *Schefflera*, *Pyrostegia* and *Luehea*, as well as control (=intact mandibles detached just after molting). Each circle represents individual measures; medians are represented by horizontal lines

when newly-hatched ones were reared on *Luehea*. According to our data, the total failure of *P. polibetes* when fed with *Luehea* flower buds is probably due to the physical characteristics of this plant. As compared to the other hosts, flower buds of *Luehea* are more difficult to chew and ingest due to their high degree of toughness and thickness. The broken mandibular teeth recorded in both early and late instar larvae feeding on *Luehea* confirm these physical constraints. In addition, the mandibles of larvae fed with *Luehea* whose teeth were unbroken are smaller than those reared on *Schefflera* or *Pyrostegia*. This indicates that the few *P. polibetes* able to survive despite the physical barriers

imposed by *Luehea* in nature will probably be smaller adults. High mortality of first instar Lepidoptera larvae due to physical plant traits has already been reported for several species (see a review in Zalucki et al. 2002). Unsuitability of *Luehea* cuttings is not an issue for explaining the total failure of *P. polibetes* on these hosts, given that other lycaenid species (e.g., *Panhiades hebraeus*) have successfully been reared under laboratory conditions with such cuttings (Kaminski et al., unpublished data). Moreover, considering the sample size of the performance experiment (20 larvae per host plant) and the low proportion of *P. polibetes* larvae relative to eggs on *Luehea* in the field (13–150), one might expect that about one larva or even less would reach the pupal stage when fed with this host in the laboratory, which agrees with our results.

From a bi-trophic perspective, *Schefflera* confers performance advantages to *P. polibetes* regarding all traits, which reflects a lack of trade-off between host use and performance components. These results contrast with data from other polyphagous species such as *Polygonia c-album* (Janz et al. 1994), suggesting that the existence of trade-offs between use of multiple hosts and performance traits are system-dependent. As a consequence, additional explanations are needed to clarify why this butterfly species commonly lays eggs on *Pyrostegia* and even on *Luehea* in nature. Three non-exclusive factors likely account for *P. polibetes* oviposition behavior, and consequently the maintenance of a polyphagous habit.

First, *P. polibetes* may use flower bud morphology as a cue for oviposition site selection, which can explain the use of not only *Schefflera* but also *Pyrostegia* and *Luehea* in the field. The population peak of *P. polibetes* matches the blooming period of these three hosts (L.A. Kaminski, personal observation), so both insect and host phenology may matter. Since *P. polibetes* density reaches its highest level in the winter (L.A. Kaminski, personal observation; see Brown 1992), laying eggs on the plants that present flower buds might be advantageous for this polyphagous species. Indeed, ovipositing females occasionally use other blooming species in the same period, such as *Miconia ferruginea* (Melastomataceae) and *Serjania caracasana* (Sapindaceae) (Kaminski 2010). Flower bud morphology (rather than chemistry or phylogeny) has been already suggested as a strong visual cue for egg-laying in polyphagous flower-feeding butterflies (Robbins and Aiello 1982; Chew and Robbins 1984), which may lead to host range expansion. A lycaenid species has recently been reported as expanding its host range by using flowers as cues, with the apparent cost of poor performance on its novel host (Forister et al. 2009; see Janz and Nylin 2008). Flower bud size may also be an issue given that *Luehea* and *Pyrostegia* presented the largest ones, which can also explain a high proportion of eggs found on these hosts compared to *Schefflera*.

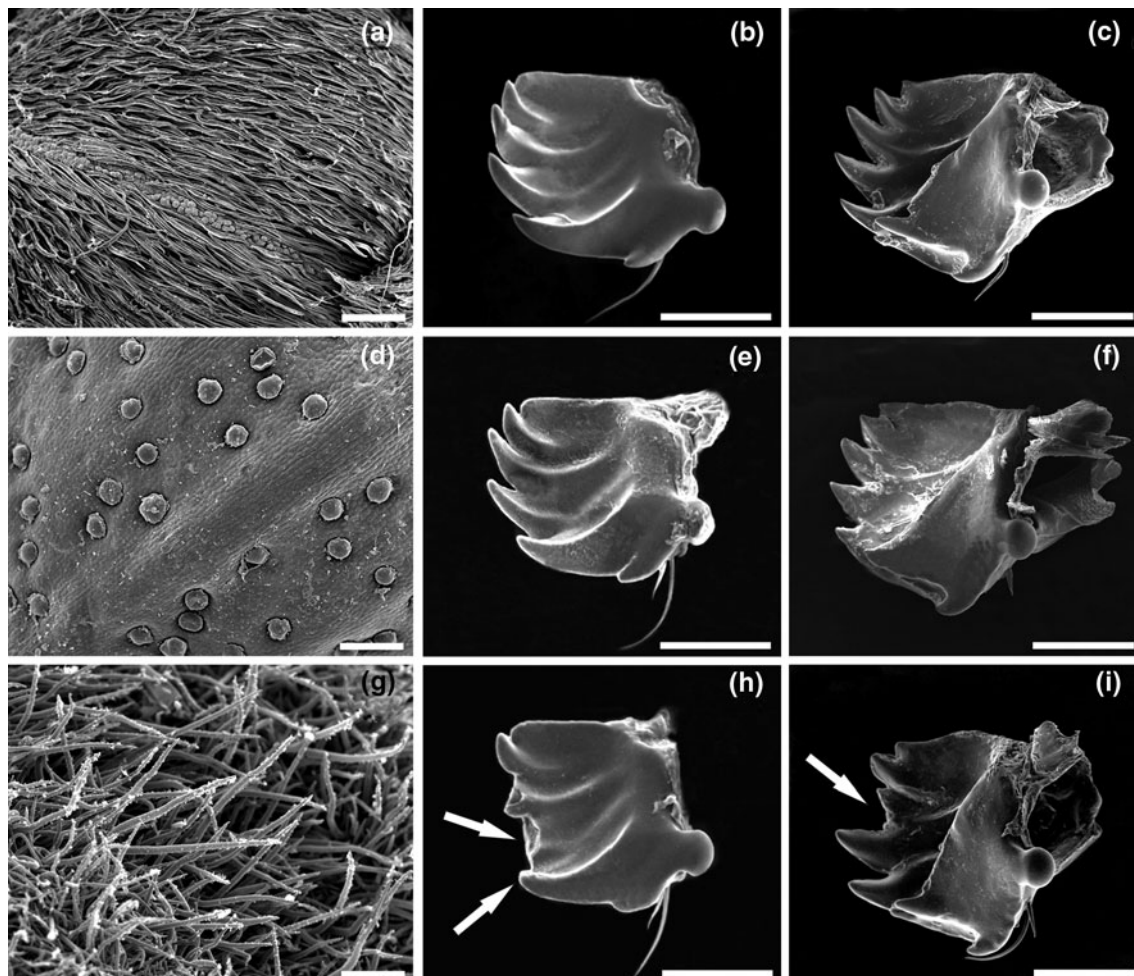


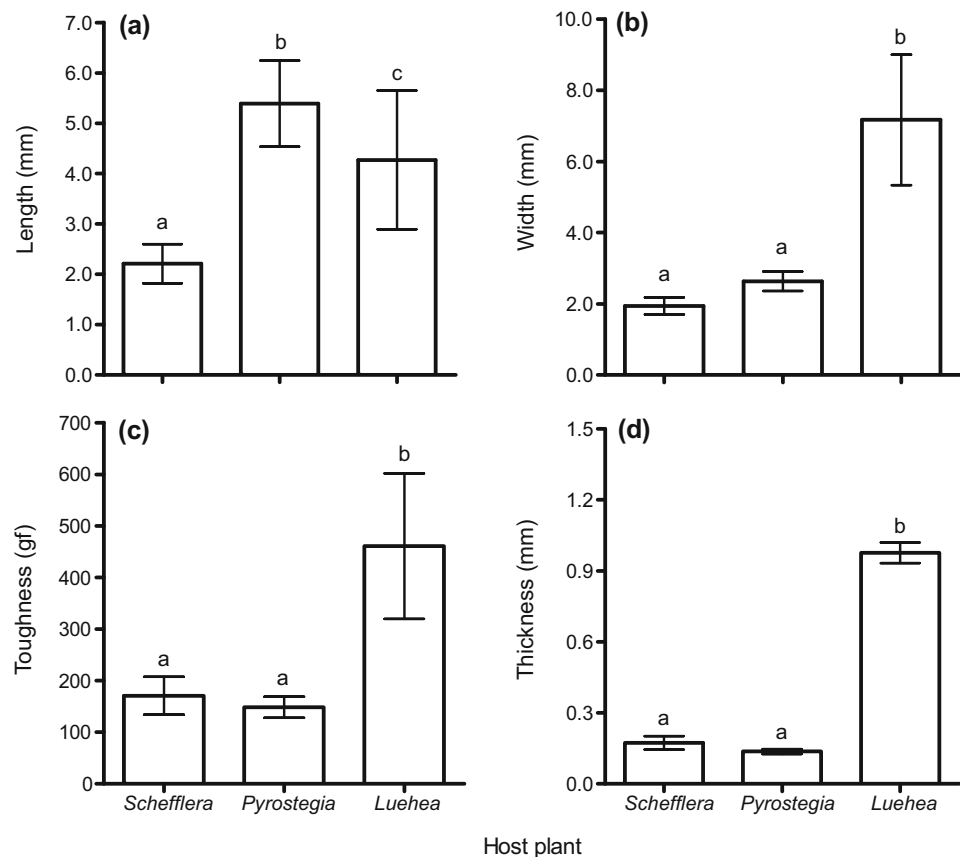
Fig. 4 Scanning electron microscopy of flower bud surfaces of **a** *Schefflera*, **d** *Pyrostegia* and **g** *Luehea* showing the corresponding trichomes (bars 200 μm). Mandibular wear of first (**b**, **e**, **h**; bars

50 μm) and fourth (**c**, **f**, **i**; bars 100 μm) instar larvae reared on *Schefflera*, *Pyrostegia* and *Luehea*, respectively. Arrows indicate sites where *P. polibetes* teeth are missing or broken

Second, the search for an enemy-free space by *P. polibetes* also partially explains our results. Ant presence can be used by lycaenid butterflies as oviposition cues, leading sometimes to lycaenid diversification and/or oviposition mistakes (see Pierce 1984; Fiedler 1994). Several lycaenid species were already reported to use ants as cues for oviposition (e.g., Atsatt 1981b; Pierce and Elgar 1985; Fiedler and Maschwitz 1989), and a nymphalid species has been recently shown to visually avoid ovipositing on plant locations occupied by predaceous ants (Sendoya et al. 2009). In addition, some authors have suggested that not only ants but ant–treehopper associations as a whole can provide oviposition cues for ant-tended butterflies (Atsatt 1981a, b; Pierce and Elgar 1985), including *P. polibetes* (Oliveira and Del-Claro 2005). This behavior explains the high number of *P. polibetes* eggs found on *Luehea*, a host plant that consistently harbors ants and treehoppers in the field. The large number of eggs and the larvae from all instars recorded on *Luehea* in our surveys rules out the

possibility that *P. polibetes* is making oviposition mistakes when laying eggs on this plant species, a pattern that has been consistently observed across the years (L.A. Kaminski and D. Rodrigues, personal observation). Given that ant–treehopper interactions provide enemy-free space for *P. polibetes*, we would expect that *P. polibetes* larvae would be less parasitized when using *Schefflera* and *Luehea*, which commonly hosted ant–treehopper associations. Our results confirm this tendency: use of *Schefflera* and *Luehea* by *P. polibetes* larvae confers a low probability of attack by parasitoids or no parasitism at all, respectively, compared to *Pyrostegia*. In other words, the few *P. polibetes* larvae that overcome the physical barriers of *Luehea* under natural conditions may benefit from ant-derived protection against natural enemies. Ants preventing parasitoid attack in facultative myrmecophilous larvae had already been documented for other lycaenid species (e.g., Pierce and Mead 1981; Weeks 2003), thus giving support to our findings.

Fig. 5 Flower bud traits of *Schefflera*, *Pyrostegia* and *Luehea*: **a** length; **b** width; **c** hardness; **d** toughness (mean \pm SD). Letters above bars indicate significant differences among host plants on each trait (Tukey's Multiple Comparison tests, $\alpha = 0.05$)



Third, by using different hosts *P. polibetes* may avoid both intra- and interspecific competition. In the same period, eight other lycaenid species (genera *Chalybs*, *Cyanophrys*, *Kolana*, *Parrhasius*, *Rekoa* and one unidentified species) were also recorded on *Schefflera* flower buds. In contrast, three other species (genera *Michaelus* and *Rekoa*) were seen on *Pyrostegia*, and two on *Luehea* (genera *Cyanophrys* and *Panhiades*) (L.A. Kaminski, unpublished data). This seems to indicate a more intense use of *Schefflera* by several lycaenid species. Such an intense use of *Schefflera* by this butterfly family may reflect a superior suitability of this plant for this herbivore assemblage as a whole.

It is also interesting to note that the total number of larvae found in the field on each host plant corroborates our laboratory findings: 38 larvae were found on *Schefflera* and only 2 of them were parasitized. *Schefflera* not only confers the best performance but also consistently provides enemy-free space via the presence of ant–treehopper associations. In contrast, 13 non-parasitized larvae were found on *Luehea*, a plant hosting an impressive number of *P. polibetes* eggs and which is normally free from natural enemies. This indicates that the high mortality of *P. polibetes* larvae fed on *Luehea* was due mostly to the plant's physical barriers rather than natural enemies. The nine larvae found on

Pyrostegia, from which 22% were parasitized, seem to reflect a combination between an intermediate suitability of this host and no protection against natural enemies.

Although flower bud morphology and the corresponding physical properties of the hosts likely explain the performance outcomes in this system, chemical properties may also play a role in host plant selection and performance. Apart from *Pyrostegia*, we have no information on the chemical compounds present in the other host plants. Sugars, flavonoids and hydrocarbons were recorded for *Pyrostegia* flowers (Dubey and Misra 1976) and for stem bark (Dinda et al. 2000), but there is no indication that they can reduce herbivory or herbivore performance. The way polyphagous species deal with plant secondary compounds may vary among species. For instance, some tiger moths (Arctiidae) use more than 50 plant species, a few of which contain pyrrolizidine alkaloids that are sequestered for caterpillar self-medication and adult reproduction (see Hartmann et al. 2005; Singer et al. 2009). In contrast, other polyphagous lepidopterans are able to partially or completely eliminate secondary compounds ingested from some of their host plants (Wink and Schneider 1990; Fiedler et al. 1993).

In summary, our results support the hypothesis that ecological trade-offs among host plants promote polyphagy in

natural populations of *P. polibetes*. Our current evidence is most consistent with the trade-off between enemy-free space and food quality among hosts. Further research on *P. polibetes* oviposition and feeding preferences on these host plants would help clarify the selective pressures favoring polyphagy in this species.

This study underscores the pervasiveness of ant–plant–herbivore interactions in the cerrado savanna, and its relevance for the behavioral ecology of insect herbivores (Oliveira and Freitas 2004). The dominance of ants on cerrado foliage derives mostly from the high occurrence of predictable liquid food sources in the form of extrafloral nectaries and insect-derived exudates, which act as efficient promoters of ant activity on vegetation (Rico-Gray and Oliveira 2007). Depending on their impact on herbivores (negative or positive), dominant foliage-dwelling ants can produce contrasting effects on host plant selection and oviposition decisions by butterflies, as shown for ant-deterred *Eunica bechina* (Sendoya et al. 2009) and ant-tended *P. polibetes* (current study). Behavioral ecology at the ant–plant–herbivore interface is thus a promising research area that remains largely unexplored, especially in tropical environments where ants abound.

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