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Article

Article

Florivory by the occupants of phytotelmata in flower parts can decrease host plant fecundity

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Abstract

Some types of plant accumulate liquid in their inflorescences creating phytotelmata. These environments protect the flowers against florivory, although they may be colonized by aquatic or semi-aquatic florivorous insect larvae, whose effects on the fitness of the plants remain unclear. We tested the hypothesis of floral antagonism by the occupants of phytotelmata, which predicts that florivory by the occupants of the phytotelmata represents a cost to the female fitness of the plant, reducing its fecundity. We manipulated experimentally the infestation by 3 florivores larvae species occupants of phytotelmata in inflorescences of *Heliconia spathocircinata* (Heliconiaceae) to test for negative direct trophic effects on the fecundity of the flowering and fruiting bracts. We found that the foraging of the hoverfly (Syrphidae) and moth (Lepidoptera) larvae in the inflorescences contributed to a decline in the fecundity of the plant. While the lepidopteran impacted fecundity when foraging in both flowering and fruiting bracts, the syrphid only affected the fruiting bracts, which indicates that the nectar and floral tissue are the principal resource exploited by the hoverfly. By contrast, soldier fly (Stratiomyidae) had a neutral effect on fecundity, while foraging in flowering or fruiting bracts. These findings corroborate our hypothesis, that herbivory by the larval occupants represents cost to the host plant having phytotelmata. The negative influence of this foraging on plant fecundity will nevertheless depend on the consequences of the exploitation of resources, which vary considerably in ephemeral habitats such as the phytotalmanta of flower parts.

Key words: Atlantic forest, Brazil, florivory, frugivory, Heliconia, water-held plants

Trophic interactions between plants and animals are fundamental to the maintenance of natural ecosystems and community structure (Albrecht et al. 2014; Céréghino et al. 2020). Many of the interactions are being lost as biodiversity declines (Valiente-Banuet et al. 2015), which can lead to knowledge gaps, given that macro-scale scientific research in this field is still incipient (Rosas-Guerrero et al. 2014; Turcotte et al. 2014; Bartomeus et al. 2016; Katz 2016; Rojas-Nossa et al. 2016; Bello et al. 2017; Moreira et al. 2019; Dellinger 2020; Haas and Lortie 2020; Herrera 2020). In this context, the exploitation of resource and the implications of this phenomenon for the ecosystem processes mediated by animal–plant interactions (i.e., antagonism, mutualism, and commensalism) have become core topics in ecological and evolutionary research (Galetti et al. 2013; Maruyama et al. 2016).

Trophic plant–animal interactions are predominantly antagonistic (e.g., herbivory) or mutualistic (e.g., pollination and seed dispersal), although the type of interaction involving some plant visitors remains undefined (Chamberlain et al. 2014). Florivory, that is, herbivory of flower parts (revised in McCall and Irwin, 2006) is typically an antagonistic interaction in which the animal feeds on the floral tissue or other pre-fruit reproductive structures of the plant. Florivory is widespread in plant species, and is probably at least as frequent as folivory (Soper Gorden and Adler 2016). However, the evidence on resource exploitation behavior and its implications for

the ecosystem processes mediated by florivory are scarce in comparison with other types of animal–plant trophic interaction (Haas and Lortie 2020), despite its relevance to the understanding of animal–plant coevolution (Strauss 1997; Sõber et al. 2009; Soper Gorden and Adler 2016).

Most ecological studies are either observational or experimental, and only a few have combined these 2 types of approach, which is necessary to advance our understanding of the phenomenon (Alves-Silva and Del-Claro 2016; Tsuji et al. 2016). Most of the interactions between plants and herbivores (folivory, florivory, nectarivory, and frugivory) involve multiple species (Bacher and Friedli 2002; Irwin et al. 2010; Rosas-Guerrero et al. 2014), and are influenced by the interactions among these species (Assunção et al. 2014; Nunes et al. 2016; Missagia and Alves 2017; Robinson et al. 2017; Start et al. 2019). However, most studies of florivory are restricted to the consumption of the flowers, and overlook the other interactions between the florivore and the host plant. These interactions include the predation of developing fruits and seeds (post-zygotic, pre-seed reproductive structures) and frugivory by non-dispersers (post-seed reproductive structures) (Borchert and DeFalco 2016; van den Bosch et al. 2019).

Florivory combines aspects of both herbivory and pollination (McCall and Irwin 2006). Florivory may have a direct effect on the female fitness of the plant when it interferes with the seed set (Cascante-Marín et al. 2009; Botha and Pauw 2017), impacting fecundity (McCall 2008; West and Louda 2018). Alternatively, florivory may have an indirect effect on the reproductive success of both male and female fitness when it interferes with other interactions of the host plant, such as pollination (Ikemoto et al. 2017). In particular, a damaged flower may be unattractive to a potential pollinator, which will interfere with the reproductive capacity of the host plant (Sõber et al. 2009; Cardel and Koptur 2010; Ferreira and Torezan-Silingardi 2013; Moreira et al. 2019). This indirect influence on pollinator behavior corresponds to an indirect, non-trophic effect on plant reproduction (McCall and Irwin 2006).

However, the negative effects of florivory on host fitness are not a rule (Moreira et al. 2019), and in fact, some authors have speculated that the florivores associated with certain types of flower may have neutral effects (Tsuji et al. 2016) or even benefit the host plant (Wootton and Sun 1990; Carper et al. 2016). Positive effects of herbivores on host plants have been reported primarily in cases where these animals establish an indirect mutualism with the host plant by stimulating either growth or the development of the plant's defenses against herbivory (Belsky 1986; Liu et al. 2012). The positive effects of florivory may also include an increase in the male fitness by interfering with the behavior of pollinators (Carper et al. 2016) and increasing the intraspecific transfer of pollen (Blüthgen and Klein 2011). In addition, florivory may not only affect floral structure, but also the interaction between herbivores and leaves (Soper Gorden and Adler 2016). Given this, florivory may have both ecological and evolutionary implications in relation to the interactions with the host plant (Nakano et al. 2020; Vega-Polanco et al. 2020).

Many plant species have developed physical and chemical defense mechanisms against florivory (Haas and Lortie 2020). Physical defenses include the accumulation of liquids in the flower buds, as seen in plants of the families Heliconiaceae, Bromeliaceae, and Marantaceae (Richardson et al. 2000; Meskens et al. 2011; Jalinsky et al. 2014; Buosi et al. 2015). This results in the formation of a particular type of phytotelma, composed of the flower parts (*sensu* Greeney 2001), which are small bodies of water, in the reproductive structures of the plant, which shelter a characteristic insect community. In some plants, the phytotelmata of the flower parts may protect buds, flowers, and fruits from herbivory (Wootton and Sun 1990) and are secreted actively by the plant (Bronstein 1986). However, a number of florivorous arthropod species are able to occupy this potential anti-florivory defense system, and the effects of the presence of these animals on the fecundity of the host plant remain unclear (Wootton and Sun 1990; Missagia and Alves 2017).

The phytotelmata support characteristic communities of small organisms (Seifert 1981, 1982; Naeem 1990; Richardson et al. 2000; Jalinsky et al. 2014). These environments are colonized by a range of both micro- and macro-organisms (Kitching 2001; Benítez-Malvido et al. 2016; Céréghino et al. 2020), many of which depend exclusively on phytotelmata as a breeding or feeding substrate (Seifert and Seifert 1976a, 1976b; Fish 1977; Thompson 1997). The microorganisms include fungi (Barbosa et al. 2012), bacteria (Giongo et al. 2019), protozoa (Dunthorn et al. 2012; Mendes et al. 2019), and a number of micro-arthropods (Naeem 1990). Macroinvertebrates are primarily arthropods (e.g., insects, myriads, crustaceans, and arachnids), as well as gastropods and flatworms (Maguire 1971; Seifert 1981; Naeem 1990; Greeney 2001; Campos 2016). Vertebrates, such as frogs, may often colonize the phytotelmata of bromeliads (Romero et al. 2010). The most common inhabitants of the phytotelmata found in *Heliconia* (Heliconiaceae) inflorescences are dipterans (flies and mosquitoes), which oviposit inside the bracts or in wounds in the plant tissues, where their herbivorous larvae develop (Fontenelle et al. 2012). These larvae feed on debris, plant tissue (including flower*s*), and nectar, and can be found inside either the flowers or other parts of the plant (Seifert and Seifert 1976a; Fontenelle et al. 2012). Seifert (1982) introduced the hypothesis of floral antagonism by the occupants of phytotelmata, predicting that the larvae of the family Syrphidae reduce the fecundity of *Heliconia* plants, although no quantitative evidence was provided to support it. Up to now, we have found no evidence in the literature on the role of the inhabitants of phytotelmata in the system, from a phytocentric perspective.

In a recent study, Missagia and Alves (2017) showed that hummingbirds avoided the flowers of *Heliconia spathocircinata* (Heliconiaceae) when the flowers were infested with stratiomyid (Diptera) larvae, which may represent an indirect, non-trophic pre-zygotic effect (McCall and Irwin 2006; Haas and Lortie 2020) of the presence of the larvae in the phytotelmata on pollinator behavior. However, these authors did not measure the fecundity of the host plants in this previous study. In the present study, we investigated the host plant fecundity in the context of the post-zygotic effects caused by the occupants of the phytotelmata, by evaluating the pre- and post-seed effects of herbivory (both florivory and frugivory), which are direct trophic effects (McCall and Irwin 2006; Haas and Lortie 2020). Using *Heliconia* inflorescences as a model, we conducted a field survey and developed an experimental procedure to quantify larvae infestation and evaluate the implications of the florivorous occupants of the phytotelmata on the female fitness of host plants.

We focused on the question: does herbivory by the larvae inhabiting the phytotelmata of flower parts influence the fecundity of the host plant? We tested the hypothesis of floral antagonism by occupants of the phytotelmata (Seifert 1982), which predicts that florivory by these occupants represents a cost to the female fitness of the plant, by reducing fecundity. We also evaluated the effects of herbivory on post-seed reproductive structures, to investigate the possible differential effects of the foraging behavior of the larvae in the bracts on the flowering (pre-zygotic) and fruiting (post-zygotic) stages.

Materials and Methods

Study sites

We studied the populations of *H. spathocircinata* at 3 localities in the state of Rio de Janeiro, Brazil. One study site was the 12,500 ha Pedra Branca State Park (PEPB: *Parque Estadual da Pedra Branca*) a large fragment of Atlantic forest on the Pedra Branca Massif (22°56′ S, 43°28′ W) located within the urban zone of the city of Rio de Janeiro. The second site was the 7,000 ha Guapiaçu Ecological Reserve (REGUA: *Reserva Ecológica de Guapiaçu*), a private ecological reserve in the municipality of Cachoeiras de Macacu (22°24′ S, 42°44′ W), in the Rio de Janeiro highlands, at the foot of the Três Picos State Park. The third site was the União Biological Reserve (REBIO: *Reserva Biológica União*) a 7,700 ha federal conservation unit in the municipality of Rio das Ostras (22°25′ S, 42°02′ W), in the state's lake district. The vegetation of the REBIO is typical lowland Atlantic forest, and the local climate is of the Aw type in the Köppen classification system (Alvares et al. 2013), with a cooler dry season between May and August (Cruz et al. 2006). The vegetation of the PEPB and REGUA is typical montane Atlantic forest, and the local climate of both sites is of the tropical Af type in the Köppen classification system, characterized by high temperatures and rainfall throughout the year (Alvares et al. 2013). As it is located within the metropolitan area of Rio de Janeiro, the PEPB suffers a certain amount of anthropogenic pressure, whereas the REGUA and REBIO are located in rural areas.

Study plant

Heliconia spathocircinata (Figure 1) is an herbaceous plant found in a number of South American countries. In Brazil, the species can be found in the biogeographic domains of the Atlantic and Amazon forests, the Caatinga dry forest, and the Pantanal wetlands (Braga 2015). In Rio do Janeiro, *H. spathocircinata* flourishes between November and March. The bracts of the developing inflorescences open sequentially at intervals of approximately 1 week. As the bract opens, it exposes the hummingbird-pollinated flowers to visitors and colonizing insects. Each flower lasts 1 day, so normally, only 1 receptive flower is found in a bract on a given day (Missagia and Verçoza 2011). The *H. spathocircinata* flower buds develop submerged in the phytotelma, where they are sheltered by the bracts (Figure 2) and the protection offered by the bract persists as the flowers mature and the fruits form, as observed in other *Heliconia* species (Seifert 1982; Richardson and Hull 2000). The *Heliconia* fruits contain 1–3 seeds (Kress 1990). The bracts of *H. spathocircinata* may host the larvae of a number of different insect taxa (Figure 2), including dipterans of the families Syrphidae and Stratiomyidae (Fontenelle et al. 2012; Missagia and Alves 2017). In southeastern Brazil, hummingbird pollinators have been observed visiting *H. spathocircinata* flowers (Buzato et al. 2000; Cruz et al. 2006; Missagia and Verçoza 2011; Missagia and Alves 2017), and in some cases, the birds defend patches of inflorescences as territories (Missagia and Alves 2016).

Figure 1. Inflorescences of *H. spathocircinata* (Heliconiaceae) photographed at the Atlantic forest of Rio de Janeiro state, Brazil. The flowers are sheltered within the bracts of the inflorescences.

Florivore species

Our initial field surveys of the phytotelmata of the flower parts (conducted prior to the present study) at all 3 study sites revealed that the *H. spathocircinata* inflorescences are occupied primarily by the florivorous larvae of 3 insect taxa (Figure 3). Two of these taxa belong to dipteran families, that is, soldier flies (Stratiomyidae) and hoverflies (Syrphidae), while the other is a member the order Lepidoptera (a moth). We observed that the larvae remain hidden within the bracts of the inflorescence beyond the flowering period, when the structure of the bract can be considered an infructescence, within which the fruit develops. Given this, these herbivores (initially identified as florivores) may also act as frugivores or seed predators.

Procedures

We conducted field surveys to evaluate the intensity of the larval infestation of the inflorescences (Johnson et al. 2016) at the 3 study sites and in 2 *H. spathocircinata* flowering seasons. We also conducted experimental manipulations of the resource availability (i.e., receptive flowers) and infestation rates within the bracts at the PEPB to evaluate their effects on plant fecundity. We analyzed the foraging of the larvae in the presence of receptive flowers (flowering bracts) or developing fruits (fruiting bracts), and the implications of this foraging for the female fitness of the host plants. We thus evaluated the impact of the florivorous larvae of the 3 insect taxa on both pre- and post-seed reproductive structures.

Field survey to quantify larval infestation

Over 2 consecutive flowering seasons, from December to February (in 2015–2016 and 2016–2017), we sampled a total of 144 inflorescences to evaluate larval infestation rates in the bracts of *H. spathocircinata*. We calculated the infestation rate for each of the 3 insect taxa at each study site (infestation rate = number of larvae collected in all bracts divided by the number of bracts sampled). Considering that *Heliconia* inflorescence bracts accumulate rainwater in their bracts, the effect of precipitation on larvae infestation was also investigated. During each season, we collected 8 inflorescences per month from each study site, with a total of 24 inflorescences per site per season. We selected inflorescences with exactly 5 open flowering bracts, for the evaluation of a total of 720 bracts (240 per site). The inflorescences were selected haphazardly at each study site in riparian forest under relatively similar conditions, including stream width (approximately 2–5 m), elevation (approximately 30–250 m a.s.l.), and phytophysiognomy (ombrophilous forest), with a minimum distance of 100 m being maintained between the inflorescences.

We collected and dissected each bract to quantify the density of the larvae of each target insect taxon, and also investigated the internal parts of the flowers and other soft tissues. To prevent the

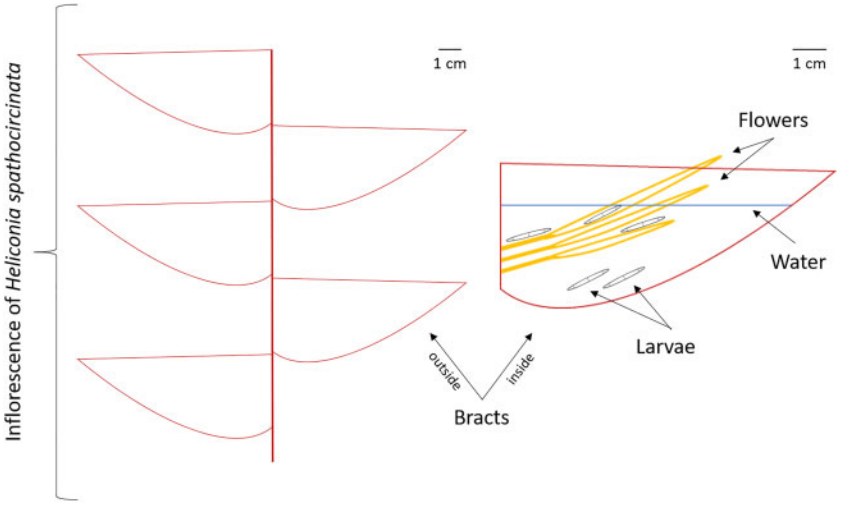

Figure 2. Illustration of an inflorescence of *H. spathocircinata* (Heliconiaceae). The flower buds are formed inside the bracts, in the water of the phytotelmata.

Figure 3. Plant–insect trophic interactions in *H. spathocircinata* (Heliconiaceae) at 3 Atlantic forest sites in Rio de Janeiro State, Brazil. The bracts of the plant have been partially removed to reveal the reproductive structures and larvae within. (A, B) Examples of the sequential development stages of the inflorescences of *H. spathocircinata* within the bract. (A) The left arrow indicates the ovary of the first receptive flower in the bract and the right arrow, the liquid accumulated inside the bract (phytotelma), which is poor in organic matter at this stage of development. (B) The left arrow indicates a nearly fully developed fruit, and the right arrow, an accumulation of organic matter inside the bract, which is formed by senescent flowers 15–20 days after the opening of the bract. (C) Herbivory on a bract of an inflorescence. The arrow shows the debris formed after the total destruction of the reproductive structures. (D) The arrow indicates a moth caterpillar (Lepidoptera). (E) The arrows indicate soldier fly larvae (Stratiomyidae). (F) The arrows indicate hoverfly larvae (Syrphidae).

larvae from escaping or moving between bracts, we collected each of the bracts and stored them individually in plastic bags until arriving at the laboratory for analysis. We dissected the bracts on the same days as they were collected. The stage of development of the inflorescences was determined based on the classification system proposed by Richardson and Hull (2000).

Experimental manipulations of florivory

We conducted the experimental procedures in January and February 2017 at the PEPB, concomitantly with the field surveys. To evaluate the effects of foraging (in flowering and fruiting bracts) by the larvae on the fecundity of the host plant, we compared infested (treatment) and uninfested (control) bracts in 30 inflorescences exposed to the same manual pollination procedure. We used 2 bracts from each inflorescence, one bract as the treatment and the other as the control. Each inflorescence belonged to a different individual plant. As *H. spathocircinata* inflorescences usually have only 1 receptive flower per bract per day (Missagia and Verçoza 2011), we controlled the availability of receptive flowers to the larvae per day. We used the fruiting bracts (i.e., bracts that have finished flowering) as the treatment without flowers.

In both treatments (flowering and fruiting bracts), we inserted either 4 same-size soldier fly larvae, 1 hoverfly larva or 1 lepidopteran larva per bract (only 1 species per bract). These larvae were collected at the same site 1 day before the insertion of the larvae inside the bracts. We used a larger number of soldier fly larvae because they are smaller and are typically more abundant in the flowers (Missagia and Alves 2017). We inserted the larvae in the treatment bracts (infested group) using tweezers and manipulated the control bracts (uninfested group) in exactly the same way, but without inserting any insect larvae. To exclude the spontaneous colonization of the bracts by insects (i.e., insects colonizing the bract naturally), in both treatments, we bagged the inflorescences at the beginning of their development when the bracts were still closed. Once the inflorescences had matured and the bracts had opened, each bract used in the experiment was bagged individually, to avoid the transfer of larvae between bracts (Missagia and Alves 2017). To ensure that no larvae moved between bracts, we coated the bract with a layer of non-toxic sticky (*TangleFoot*®) resin (Missagia and Alves 2015; Alves-Silva and Del-Claro 2016). The bracts used in the experiment thus had physical and chemical barriers to proven the larvae from escaping. In both treatments and their respective controls, we bagged the inflorescences in their initial stage of development, when no flower had developed (closed bracts). The treatment group consisted of bracts infested with larvae, while the control group consisted of non-infested bracts.

For the florivory experiment, we selected inflorescences with bracts in which the first receptive flower had opened approximately 10 days prior to the insertion of the larvae. Bracts of this age allow for the presence of receptive flowers throughout the period of experimental manipulation (up to 15 days). In the fruiting experiment, we used bracts in which the flowers no longer existed.

Manipulation of the pollination

We ensured the pollination of the flowers in both the treatments (infested) or control (uninfested) group. For this, following the preparation of the experimental bracts (treatments and controls), we conducted daily cross-pollination, by hand, of the receptive flowers of both groups until each bract contained 12 fertilized flowers (after around 15 days). In the fruiting bracts, we hand-pollinated the flowers in the same way, but approximately 15 days before we infested the bracts with larvae to ensure that the 12 developing fruits considered in each bract were cross-pollinated. We pollinated each flower included in the experiment with an anther obtained from a pre-anthetic flower collected from a different individual, located at a minimum distance of 10 m from the flower to be pollinated. A distance of 10 m was adopted here to ensure that the flower that was the source of the pollen belonged to a different *H. spathocircinata* individual. Each pollinated flower received 1 pollen load and each anther was used only once.

In the treatment group (i.e., infested) we used one bract per inflorescence ($n = 30$ plants), with 10 bracts for each insect taxon. To provide a paired sample, we selected one more bract per inflorescence to use as a control group (i.e., uninfested) for comparison with the treatment groups. In each of the 30 study plants, then, there was one treatment bract and one control bract.

Foraging of the larvae

We then evaluated the substrate in which the larva foraged (i.e., flowers and bracts) in relation to the availability of receptive flowers inside the bracts. We classified the substrates used by the larvae according to the examination of the interior of the bract at the end of the experiment. We examined each bract for signs of florivory in the different tissues and the position of the larvae within the bract (i.e., inside the flower or nectaries, or among the petioles). We thus dissected the bracts to obtain clues on the consumption of the different types of flower tissue, including reproductive structures, bracts, other tissue, or debris. Information on the manipulation of the senescent flowers that accumulate inside the bracts is available for other *Heliconia* species from Central America (Naeem 1990; Yee and Willing 2007).

Data analysis

The data analysis was performed according to the premises of the tests (Gotelli 2009; Legendre and Legendre 2012) using the software PAST v.4.03 (Hammer et al. 2001). We tested the data for normality using Lilliefors' test ($P < 0.05$). We tested for differences in the density of the 3 larvae in the inflorescences of the REGUA, PEPB, and REBIO populations between larvae species and reproductive seasons and among sites using the Kruskal–Wallis test for equal medians ($P < 0.05$) with Bonferroni–Dunn's *post hoc* test. We checked for correlations between larvae densities using the Spearman's correlation coefficient (rs, $P < 0.05$) and used a multivariate analysis of variance (MANOVA) to evaluate the potential relation among infestation by the 3 larvae species (dependent variables) and the respective local accumulated precipitation (independent variable). As *Heliconia* bracts tend to accumulate rainwater (Bronstein 1986), which increases the volume of the habitat (phytotelma) available for the study species of larvae, we also investigated the relationship between precipitation and infestation. For this, we tested the data on larval density against the climatological data obtained from the Brazilian Institute of Meteorology—INMET (https://portal.inmet.gov.br/). We obtained these data from the meteorological stations located closest to the study sites. These stations were at Marambaia (approximately 15 km from the PEPB), Macaé (20 km from the REBIO), and Nova Friburgo (approximately 10 km from the REGUA). We tested the hypothesis of floral antagonism by the occupants of the phytotelmata using Student's t-test with Bonferroni's correction ($P < 0.05$), comparing the mean seed set of treatment

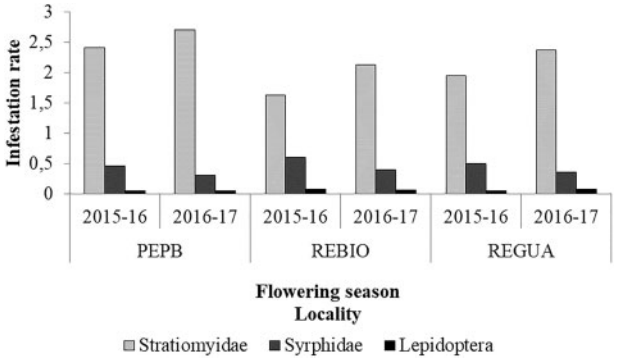

Figure 4. Infestation rates of herbivorous insect larvae of the Stratiomyidae and Syrphidae (Diptera) and Lepidoptera in the bracts ($n = 720$) of 144 inflorescences of *H. spathocircinata* (Heliconiaceae) collected at 3 Atlantic forest sites in Rio de Janeiro state, Brazil. REBIO, União Biological Reserve; REGUA, Guapiaçu Ecological Reserve. Infestation rate = number of larvae collected divided by the number of bracts sampled.

(infested bracts) and control (uninfested bracts) groups, in both flowering and fruiting bracts.

Results

Each of the inflorescences collected to quantify infestation contained larvae of at least one of the 3 study taxa. The density of each larval species in the inflorescences did not vary intraspecifically between breeding seasons or the 3 study populations, although significant interspecific variation was observed (Supplementary Table S1). Considering the whole study period (2 flowering seasons: Figure 4), the highest infestation rates (larvae per bract) were recorded for the soldier fly larvae, ranging from 1.87 (REBIO), through 2.16 (REGUA) to 2.55 (PEPB). The second highest rates were recorded for the hoverfly larvae, but were much lower, varying from 0.38 (PEPB), through 0.43 (REGUA) to 0.50 (REBIO). The lowest rates were recorded for the lepidopteran larvae, that is, 0.05 (PEPB), 0.06 (REGUA), and 0.07 (REBIO).

Considering all the data collected at the 3 sample sites (density of all larvae species in all the sites together), the values of soldier fly and hoverfly larvae density were negatively correlated ($rs = 1448.5$; $P = 0.0397$), as well as the density of soldier fly larvae and the precipitation ($rs = 1684.5$; $P = 0.0023$). The density of the larvae infestation was dependent on the precipitation (MANOVA, Wilks' lambda = 0.537; $F = 4.008$; $R^2 = 0.392$; $P = 0.029$). When analyzing the data collected per sample site (density of all larvae species per each site), only in REGUA the larvae density was associated with the precipitation (MANOVA, Wilks' lambda = 0.022; $F = 29.6$; $R^2 = 0.674$; $P = 0.032$). Finally, when analyzing the effects per species per site (density of each larvae species per each site), the models generated by MANOVA revealed that soldier fly showed a negative relationship with precipitation in the 3 sample sites and that hoverfly presented a positive relationship with the precipitation in the PEPB (Table 1). In the flowering bracts, only the lepidopteran larvae reduced the seed set significantly. In these bracts, the larvae of neither type of fly (hoverfly or soldier fly) reduced the seed set of *H. spathocircinata*. In the fruiting bracts, the larvae of both lepidopterans and hoverflies reduced the seed set (Figure 5), while soldier fly larvae had a neutral effect (Table 2 and Figure 6).

During the examination of the interior of the bracts used in the experiment, we realized that the larvae of both dipterans apparently fed on the nectar and abraded the tube of the corolla, damaging the flower, although this did not affect the seed set of the hand-pollinated flowers. The lepidopteran larvae fed on flowers and on the tissue to which the flowers were attached within the bract (Figure 5A). In the absence of receptive flowers, the soldier fly larvae apparently fed on the debris found in the bract (Figure 3), while the hoverfly and lepidopteran larvae excavated the tissue of the flowers themselves (Figure 5C and D). This excavation causes extensive damage to the flower tissue, disrupting the development of the flower buds and the fruits. This was the main cause of the decline in seed set in the treatment group in comparison with the control group (Figure 5B).

Table 1. Evaluation of the dependence of larval infestation on precipitation

Site	Variable	Slope	Error	Intercept	Error	r^2	P
PEPB	**ST**	**−0.233**	**0.077**	**124.27**	**82.473**	**−0.833**	**0.039**
	SY	**0.106**	**0.019**	**54.258**	**20.674**	**0.939**	**0.005**
	LP	−0.013	0.011	34.522	1.275	−0.493	0.319
REBIO	**ST**	**−0.215**	**0.075**	**104.3**	**11.742**	**−0.818**	**0.046**
	SY	0.072	0.031	10.166	48.618	0.757	0.081
	LP	−0.003	0.010	33.319	15.778	−0.178	0.735
REGUA	**ST**	**−0.133**	**0.032**	**120.53**	**93.922**	**−0.896**	**0.015**
	SY	−0.015	0.032	21.339	92.693	−0.234	0.654
	LP	−0.009	0.007	51.119	20.567	−0.553	0.254

The slopes, intercepts, regression coefficients, and *P*-values of the models of the density of the 3 larval taxa in the inflorescences of *H. spathocircinata* (Heliconiaceae) are shown as a function of local precipitation at the 3 study sites (REGUA, REBIO, and PEPB) in Rio De Janeiro, Brazil. The models were calculated using the MANOVA. REGUA = Guapiaçu Ecological Reserve; REBIO = União Biological Reserve; ST = soldierfly larvae (Diptera: Stratiomyidae); SY = hover fly larvae (Diptera: Syrphidae). LP = lepidopteran larvae (Lepidoptera).

Discussion

The similarities in the intraspecific infestation rates of each florivore taxon (Figure 4 and Supplementary Table S1) among the study areas (PEPB, REGUA, and REBIO) and between flowering seasons (2015–2016 and 2016–2017) indicate that these insects associate systematically with *H. spathocircinata* (Seifert 1981, 1982). We also confirmed that the 3 most common inquilines of *H. spathocircinata* inflorescences in southeastern Brazil were present in the majority of the inflorescences in each study population.

Our results showed that precipitation affected the larval infestation rate in the phytotelmata of flower parts (Table 1), that is, a system in which the flowers develop in water accumulated by the plant (Greeney 2001). The significant increase in the infestation of the *H. spathocircinata* inflorescence bracts by soldier fly larvae during the driest weather (Table 1) contrasts with the decrease in the abundance of hoverfly larvae during the same period ($rs = 1448.5$; $P = 0.0397$). The hoverfly larvae, which are more sensitive to dryness, probably find a limitation in the driest periods to colonize bracts, or even the eggs left in the bracts should not be successful. Then, with increased precipitation, colonization should be more successful for the hoverfly. In this context, fluctuations in the density of florivores should follow those in rainfall, which implies changes in the intensity of the negative pressures exerted by the florivores on the fecundity of the host plant.

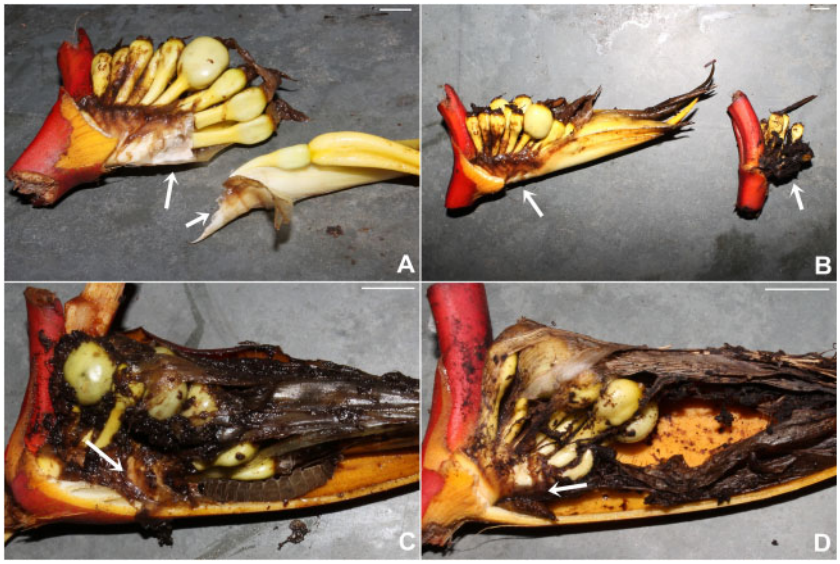

Figure 5. Only Figure 4. Herbivory in the bracts of the inflorescences of *H. spathocircinata* (Heliconiaceae) in the Brazilian Atlantic forest. The bracts were removed completely (A, B) or partially (C, D) to reveal the reproductive structures within. (A) The arrows indicate the tissue which the larvae ingested, together with the flowers. (B) Normal bract with no herbivory (left) and bract following intense herbivory by the caterpillar (right). The arrows indicate the sites at which tissue was consumed. (C) The arrow indicates the tissue (see panel A) ingested by the caterpillar (to the right). (D) The arrow indicates the hoverfly larvae feeding on the tissue highlighted in A.

Table 2. Results of the *t*-tests with Bonferroni's correction for the comparison of the mean seed set in the bracts of inflorescences of *H. spathocircinata* (Heliconiaceae) infested ($n = 30$) and uninfested ($n = 30$) with herbivorous larvae (see Figure 5)

	T		Degrees of freedom		*P*	
	Flowers	Fruits	Flowers	Fruits	Flowers	Fruits
Stratiomyidae	−0.09	−1.09	18	18	0.81	0.34
Syrphidae	−0.59	−2.81	18	18	0.82	0.01
Lepidoptera	−17.11	−5.65	18	18	<0.001	<0.001

Column flowers refer to flowering bracts (receptive flowers available), and column fruits to the results of fruiting bracts (receptive flowers unavailable).

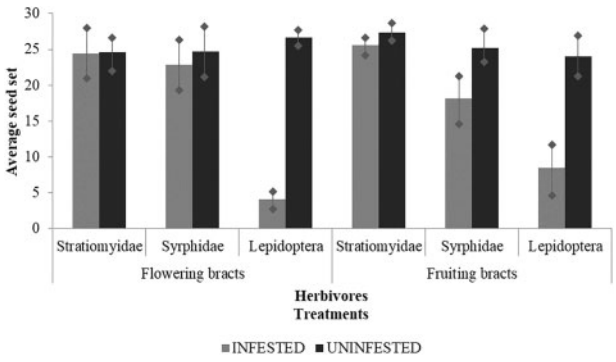

Figure 6. Number of seeds produced per bract in the inflorescences of *H. spathocircinata* (Heliconiaceae) used in 2 experimental procedures at the PEPB in Rio de Janeiro, Brazil. Flowering bracts = bracts with receptive flowers available; fruiting bracts = bracts with only developing fruits available; Soldier fly = Stratiomyidae (Diptera); Hoverfly = Syrphidae (Diptera); Moth = Lepidoptera; infested bracts = bracts infested experimentally with the insect larvae; uninfested bracts = bracts with no larvae. Bars indicate standard error.

We corroborate the hypothesis of floral antagonism in the phytotelmata of the flower parts (Table 2), which we believe to be an unprecedented finding. However, not all the species acted as antagonists in the system. Resource availability defined the role played by the hoverfly (Figure 5), although it did not influence the effect of the soldier flies (neutral) or that of the lepidoptera (negative). In the flowering bracts, only the lepidopteran larvae acted as floral antagonists, inducing a reduction in the production of seeds in the bracts. In the fruiting bracts (no flowers), the lepidopteran and hoverfly larvae acted as floral antagonists (Figure 6). While the lepidopteran larvae were the least abundant herbivores in *H. spathorcircinata* inflorescences, they impacted the fecundity of the plant more than the hoverfly larvae. These 2 taxa fed on most of the tissue of the inflorescence, including the flowers, fruits, and rachis, and the base of the flowers, in the vicinity of the nectar chamber, and the tissue in which the flowers are inserted (Figure 5A). This tissue is viscous and has a sweet fragrance, and is probably rich in sugars, which are transferred to the developing flowers, fruits, and seeds. The lepidopteran larvae did not appear to feed on the tissue of the bract itself, but only on other structures found inside the bract, which may reflect the nutritional value of the different structures (McCoy 1985; Colasurdo et al. 2009; Silva et al. 2020). During the surveys, we did not observe lepidopteran larvae feeding on leaves or even moving outside the inflorescence, although they did appear to take refuge inside the bracts when they were being collected, possibly as a defense against visually orientated predators (Heinrich 1979; Greeney et al. 2012). Based on our results, we can classify the lepidopteran and hoverfly larvae as floral antagonists in the phytotelmata of the bracts of *H. spathocircinata*. The soldier fly larvae acted commensally in the system. It is important to note here that this conclusion does not take the flower–pollinator interaction of *H. spathocircinata* into consideration (Missagia and Alves 2017), given that this relationship was not included in the focus of the present study.

Our findings also indicate that both the dipterans are able to forage in different plant parts, according to resource availability,

apparently alternating from one substrate (e.g., nectar) to another (e.g., debris and soft tissue) according to availability of flowers, although this implies further impacts on plant fecundity (Table 2). In the absence of receptive flowers (i.e., fruiting bracts), the hoverfly larvae decreased plant fecundity by foraging on the soft tissue inside the inflorescences, in a manner similar to that of the lepidopteran larvae, that is, by excavating the tissue (Figure 5), whereas the soldier fly larvae appear to forage on the debris found inside the bract (Figure 3), which does not affect plant fecundity (Table 2). We were unable to define the most important resource for these dipteran larvae, given that both appeared to feed on nectar and the soft tissue of the flower. Given this, the availability of floral resources within the bract proved to be a determining factor, which defined the role of the florivorous larvae that inhabit the phytotelmata of the inflorescences of *H. spathocircinata* (Table 2 and Figure 6).

The density of hoverflies was correlated negatively with that of soldier flies ($rs = 1448.5$; $P = 0.0397$). In some samples, the density of both types of fly was correlated with precipitation (Table 1). From a zoocentric perspective, the reduction in resource availability (i.e., receptive flowers) may cause the dipteran larvae to forage on items other than nectar or flower tissue, which may provide the potential for resource partitioning between the soldier fly (debris) and hoverfly (soft tissue). The hoverfly larvae may have been searching for sugars within the tissue, thus producing debris in the system. In fact, scavenger larvae (e.g., soldier flies in fruiting bracts) may benefit from their coexistence with excavating larvae (i.e., hoverfly larvae in the fruiting bracts) in the bracts of *H. spathocircinata*, as the foraging activities of other herbivores may result in an increase in the availability of debris inside the bract (Seifert and Seifert 1976b). However, this hypothetical partitioning of bract resources by the dipteran larvae has yet to be tested experimentally.

As the organic matter found in phytotelmata is immersed in a humid substrate (Figure 3), we suspect that the liquid that accumulates in the bracts during flowering may contain nutritional components for the larvae, such as the debris or even micro-invertebrates (see Seifert and Seifert, 1976a; Seifert, 1982). Indeed, the phytotelmata contain a number of microorganisms and even micro-invertebrates (Giongo et al. 2019; Céréghino et al. 2020), which can provide the basis of the food web in this system (Kitching 2001). However, as the amount of this liquid decreases during the development of the fruit (Wootton and Sun 1990), this shift in resource availability may have trigged the excavating behavior of the hoverfly we recorded in *H. spathocircinata* (Figure 5). We would recommend further studies on the natural history and ecology of the inhabitants of these phytotelmata to better understand their ecological role. In particular, studies of the diet (the exact items consumed by each species) and the behavioral ecology of the larvae found in the phytotelmata (in the context of resources partitioning) will be especially important. These data will be essential for the interpretation (from a phytocentric perspective) of the costs and benefits of the trophic interactions established by each animal species that inhabits this host plant.

One other important aspect of our results is the knock-on effects of the florivores on pollination ecology. Even though flower–pollinator interactions were not considered experimentally in the present study (we used only manual pollination), we cannot overlook the potential effects of damaged or infested corollas on the attractiveness of the flower to pollinators, as discussed in *H. spathocircinata* by Missagia and Alves (2017). The ecological and evolutionary implications of floral antagonism for ornithophilous pollination systems (Gélvez-Zúñiga et al. 2018) are thus an additional question that should be considered in future studies. The interaction between pollinating hummingbirds and *Heliconia* inflorescences has received much attention in studies of ecology and evolution (Linhart 1973; Stiles 1975; Gill 1987; Temeles et al. 2000, 2013; Martén-Rodríguez et al. 2011; Missagia and Verçoza 2011; Betts et al. 2015; Missagia and Alves 2016, 2017), although the results of our study indicate that this previous research has greatly underestimated the effects of florivory by the larval occupants of the inflorescence on both pollination (pre-seed stage) and the development of the fruits and seeds (post-seed stage). This is despite the fact that a large body of zoocentric data exists on insect communities of the phytotelmata of *Heliconia* inflorescences (Skutch 1933; Seifert and Seifert 1976a, 1976b; Seifert 1981; Lounibos et al. 1987; Naeem 1988, 1990; Richardson et al. 2000; Richardson and Hull 2000; Meskens et al. 2011; Benítez-Malvido et al. 2016). We suggest that these herbivores must impose selective pressures on the morphology of the inflorescences and flowers of *Heliconia* (Irwin et al. 2010), given the effects of florivory on the reproductive structures, as observed here in *H. spathocircinata* (Table 2), may be antagonistic (Gélvez-Zúñiga et al. 2018) to the selective pressures exerted by pollinating hummingbirds (Temeles et al. 2000, 2013). We thus propose that the presence of both herbivores and pollinators in the inflorescences of *H. spathocircinata* phytotelmata may contribute to the shaping of the floral morphology of *Heliconia*, an interaction that we are currently investigating.

In the present study, we showed that herbivory by the florivorous insect larval occupants of the phytotelmata of flower parts on the pre- and post-zygotic reproductive structures of the plant can have negative effects on the fecundity of the host plant, corroborating the hypothesis of floral antagonism by the occupants of the phytotelmata. However, the antagonistic effects of the foraging of some types of larvae may depend on resource availability, which varies continuously in the ephemeral environment of the bracts of *Heliconia*. Our results are novel because they have revealed a previously unknown perspective on the pollination ecology of plants that form phytotelmata in their inflorescences: the effects on female fitness of host plants provoked by the florivorous occupants of these environments. Cleary, a multi-species, multiple interaction approach will provide insights into the adaptive relationships of the organisms involved in this association.

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Conflict of interest

The authors declare no conflict of interest.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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