RESEARCH ARTICLE

Effects of predation risk on invertebrate leaf-litter shredders in headwater streams in three Brazilian biomes

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Abstract

We evaluated the effect of predation risk for larvae of *Phylloicus* (Trichoptera: Calamoceratidae) on leaf-litter consumption and case-building in experimental microcosms performing three Brazilian biomes: Amazon Forest, Atlantic Rainforest, and Brazilian Savanna (*Cerrado*). We hypothesized the following: (1) predation risk by fish would decrease the feeding rate but increase the sheltering activities of *Phylloicus* larvae, mainly in a high-stimulus treatment (visual and chemical cues from predators' presence); and (2) when offered a resource with the same palatability, leaf consumption by *Phylloicus* larvae from Amazon Forest and Atlantic Rainforest will be higher than in those from the Savanna, independent of the predation risk. We found that larvae of *Phylloicus* species from the three biomes use the leaf disks in different proportions for case-building and consumption: Amazon Forest (case-building = 44% and consumption = 50%), Atlantic Rain Forest (60% and 36%), and Brazilian Savanna (32% and 26%). The larvae case-building and leaf consumption by *Phylloicus* were higher under predation than in the control treatment using data uncorrected by the biomass of the individual. On the other hand, case-building was not different among all treatments, and leaf consumption was lower under predation than in the control treatment when corrected by biomass. Our results indicate that predation risk can affect the behavior of *Phylloicus* due to a stress response to predator presence. Therefore, it might mean top-down effects on shredders during leaf-litter processing in Neotropical headwater streams. Besides, insectivorous fish could be the key group for functioning in these ecosystems.

Introduction

Trophic interactions between predator-consumers and prey resources can result in changes in the structure of biological communities (e.g., distribution of prey; Romero et al. 2021) and the functioning of terrestrial and aquatic ecosystems, for example, the decomposition of organic matter (Graça 2001; Li and Dudgeon 2008; Holt and Barfield 2009; Tank

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et al. 2010). Such trophic interactions influence the distribution and abundance of species, especially considering the influences of predators on prey (top-down effect; Leroux and Loreau 2015; Ripple et al. 2016). Therefore, knowledge about top-down mechanisms is essential to understanding the functioning of aquatic ecosystems (Tank et al. 2010; Raffard et al. 2021), including the role of invertebrate leaf-litter shredders (Wittmer et al. 2013; Navarro et al. 2013; Rezende et al. 2015).

Interactions between predators and invertebrate shredders may also affect the leaf-litter breakdown in aquatic ecosystems, thereby modifying the headwater streams' metabolism (Graça 2001; Li and Dudgeon 2008). These invertebrates reduce the size of leaf particles and make them available as fine particulate organic matter (*Fine Particulate Organic Matter*—FPOM) for other detritivorous organisms by shredding leaves (*Coarse Particulate Organic Matter*—CPOM) (Boyero et al. 2011). Shredders are also a food source for other consumers in aquatic food webs, including fish and predatory invertebrates (Dunoyer et al. 2014; Rodríguez-Lozano et al. 2016). Moreover, predation risk can result in behavioral changes among shredders, causing a reduction in the fragmentation of allochthonous organic matter and consequently negatively affecting its processing in headwater streams (Hawlena and Schmitz 2010; Rezende et al. 2015; Martins et al. 2017a).

Direct and indirect effects of predators on prey can occur through the following two mechanisms: (i) direct effect: consumptive interactions in which the predator kills and consumes the prey, and (ii) indirect effect: non-consumptive (non-lethal) interactions that result in the induction of phenotypic defense responses including reduced mobility, changes in feeding habits and escape by exhaustion (Hawlena and Schmitz 2010). Such non-consumptive interactions, therefore, may alter the activity of leaf-litter consumption by shredders. Consequently, this interaction can change the functioning of aquatic food chains (Ripple et al. 2016) and nutrient cycling by reducing the efficiency of assimilating consumed food (Schmitz et al. 2010). As a result, we have lower secondary production in the ecosystem due to the production of lower-quality biomass (e.g., change in body composition — low carbohydrate-to-protein ratio— C:N; Hawlena and Schmitz 2010).

The occurrence of a non-lethal mechanism allows prey activity to avoid predation risk to be evaluated (Boyero et al. 2006; Navarro et al. 2013), including changes in foraging activity (Lima 1998; Rezende et al. 2015; Navarro and Gonçalves 2017). Invertebrates escape predators by detecting the chemical cues they released (e.g., odors, pheromones) or by visualizing them. These signs are perceived by the larvae of aquatic insects and thus can affect their behavior (Boyero et al. 2008). Predation risk has been shown to adversely affect the time scrapers (e.g., Ephemeroptera: Baetidae, and

Trichoptera: Glossosomatidae) spend foraging on periphyton (Kohler and McPeek 1989). Moreover, it has also been observed that some nymphs of Ephemeroptera decrease drift during the day to avoid predation risk from fish that use vision to locate their prey (McIntosh and Peckarsky 1996).

Among shredders, larvae of *Phylloicus* (Trichoptera, Calamoceratidae) play an essential role in the entry of organic matter from riparian forests into the detritus food web of tropical headwater streams (Boyero et al. 2011). The genus is widely distributed from the southern USA to southern South America (Holzenthal and Calor 2017). Shredders are generally less abundant in tropical streams (Boyero et al. 2011; Ferreira et al. 2015; Aguiar et al. 2017). However, when we consider their biomass, they can play an important role in the process of leaf decomposition (Tonin et al. 2014; Aguiar et al. 2017; Martins et al. 2017b). Therefore, it is essential to know their relationship with the functioning of tropical aquatic ecosystems, especially given the increased risk to these ecosystems under projected global climate change and as a result of growing deforestation for agriculture and livestock (Strassburg et al. 2017; Boyero et al. 2021).

We tested the effects of predation risk on *Phylloicus* behavior and considered the potential consequences for tropical headwater metabolism. We assessed the non-lethal effects of predatory fish on leaf-litter consumption and case-building by *Phylloicus* larvae from the Amazon Forest, Atlantic Rainforest, and Brazilian Savanna (*Cerrado*) biomes in experimental microcosms. Based on the following premises: (i) predators directly affect their prey in a top-down manner (non-consumptive) in the food webs of streams; (ii) more significant exposure to predators should result in a high perception of predators by prey; and (iii) changing the prey's foraging behavior. The first hypothesis was that predation risk by fish would decrease the feeding rate but increase the sheltering activities of *Phylloicus* larvae, mainly in the high-stimulus treatment (both visual and chemical cues of the predators' presence). Also, based on other premises, there would be: (i) a higher abundance of shredders in the Amazon Forest and Atlantic Rainforest compared to the Savanna (Ferreira et al. 2011); (ii) greater diversity and availability of plant species (Tonin et al. 2017) with higher palatability (better nutritional quality, less secondary compounds, and softer leaves) in the Amazon Forest and Atlantic Rainforest biomes than in the Savanna biome (Gonçalves et al. 2012, 2017). Then, it could increase the necessity for high nutrition of *Phylloicus* spp. larvae from the Amazon Forest and Atlantic Rainforest biomes. Therefore, our second hypothesis was that even offering the same kind of resource, with the same palatability, leaf consumption by *Phylloicus* larvae from Amazon Forest and Atlantic Rainforest will be higher than in the Savanna, independent of the predation risk. The high leaf consumption (of more

palatable litters) by *Phylloicus* larvae in Rainforest zones compared to Savanna zones of the Neotropics has been shown by Rezende et al. (2021) and Sena et al. (2020).

Materials and methods

Sampling sites

Laboratory experiments were carried out concomitantly using specimens from three biomes in South America (Amazon Forest, Atlantic Rainforest, and Brazilian Savanna) that comprise a large part of the Neotropical Region and cover about 86% of Brazil (c. 7,400,000 km^2, IBGE, Fig. 1). In addition to having riparian zones with different plant species compositions, these biomes differ mainly in temperature, precipitation regime, and annual patterns of organic matter input into headwater streams (Tonin et al. 2017).

Three laboratory experiments were done using the following prey and predator combinations: *Phylloicus elektoros* Prather, 2003 larvae and the predatory fish *Hyphessobrycon* sp. (Characiforme: Characidae) collected in the Barro Branco stream (Amazon Forest stream); *Phylloicus angustior* Ulmer, 1905 and the fish *Astyanax rivularis* Lütken, 1875 (Characiforme: Characidae) collected in the Taboões stream (Atlantic Rainforest stream); and *Phylloicus* sp. and the fish *Astyanax* sp. collected in the Capetinga stream (Brazilian Savanna stream).

The Barro Branco stream (02°55′ S, 59°53′ W) is in Reserva Florestal Ducke in Manaus municipality (county), Amazonas State, Brazil, and encompasses ~10,000 ha of preserved upland (*terra firme*) forest. The climate is humid tropical equatorial, with a mean annual precipitation of 2286 mm and a mean annual temperature of 26.7 °C (Mendonça et al. 2005; Fig. 1). The Taboões stream (20°03′ S, 44°03′ W) is located in the Parque Estadual da Serra do Rola Moça (3941 ha) in Nova Lima, Minas Gerais State, Brazil. The climate is type Cwa (tropical of altitude) with dry winters and rainy summers, with a mean annual precipitation of 1700 mm and a mean annual temperature of 19.5 °C (Meyer et al. 2004; Guarçoni et al. 2010; Fig. 1). The Capetinga stream (15°57′ S, 47°56′ W) is in the Gama-Cabeça de Veado Protection Permanent Area in Brasília, Federal District. The climate is tropical, with two distinct
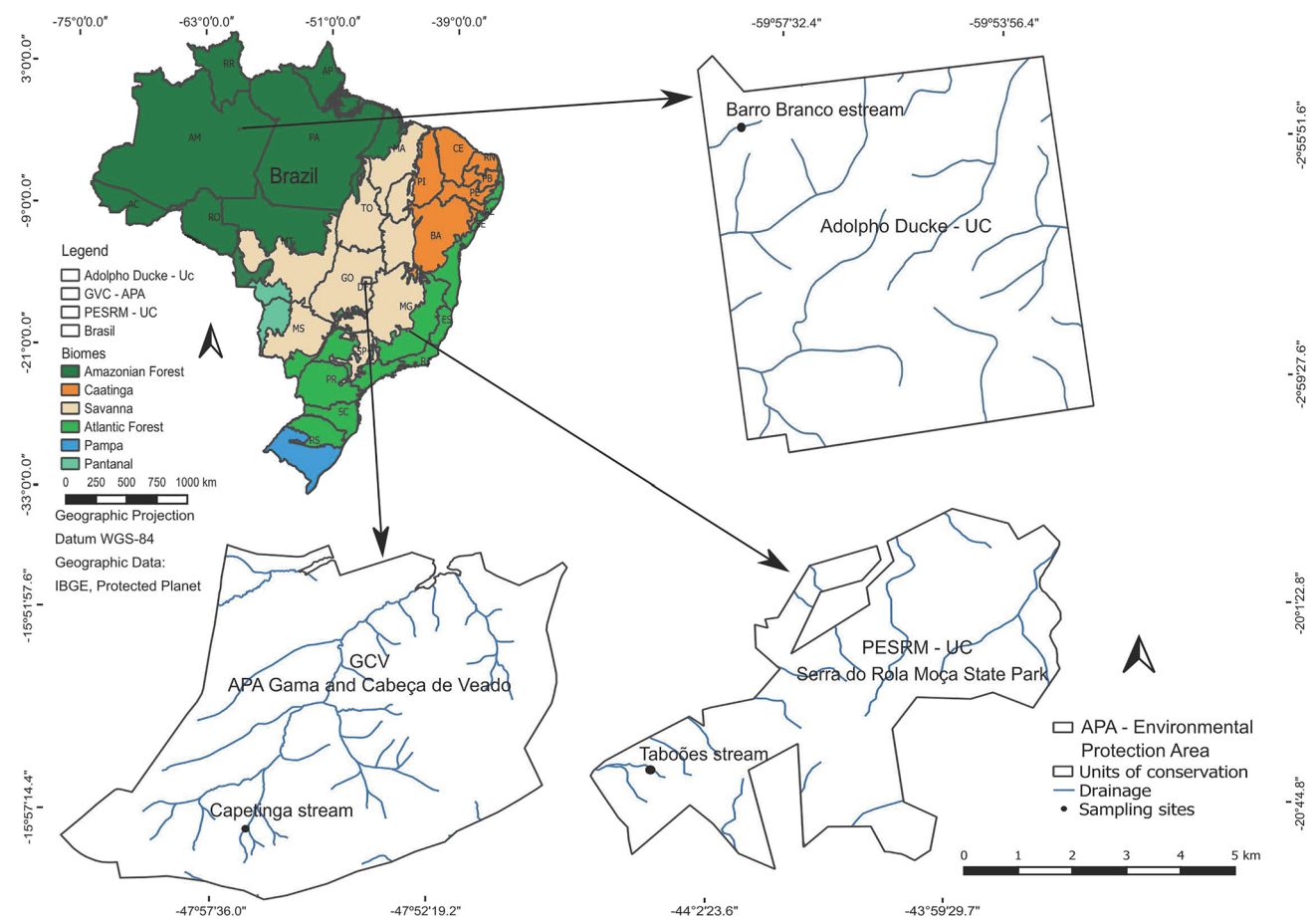

Fig. 1 Map the study area (biomes, conservation units, environmental protection areas, and sampling sites)

seasons (dry winter and rainy summer), with a mean annual precipitation of 1400 mm and a mean annual temperature of 20 °C (Rezende et al. 2014; Fig. 1).

Laboratory procedures

To perform the experiments on predation risk to *Phylloicus* in the presence of predatory fish, three treatments (chemical, visual and chemic-visual cues) were set up in the laboratory along with control without predatory fish. Larvae of *Phylloicus* were collected manually from the three streams/biomes cited above. They were taken to their respective laboratories in thermal boxes with water from the streams aerated with portable oxygen pumps. In the laboratory, larvae were placed in plastic microcosms (15 cm width × 20 cm length × 17 cm height) with water from the streams (2 L), which was aerated constantly with an air pump. The bottom was covered with approximately 2 cm of previously calcined sand in a muffle oven (500 °C, 4 h) for the total elimination of organic matter. The microcosms were maintained at the experimental sites at a constant temperature of 20 °C with a controlled 12/12-h light/darkness photoperiod. The cases of the *Phylloicus* larvae were removed before the beginning of the experiments to prevent the larvae from consuming the case instead of the disks offered as food or using the cases to build new ones (Rezende et al. 2015, 2021).

Leaves of *Maprounea guianensis* Aublet, 1775 (Euphorbiaceae) were used in all experiments because it is a widely distributed species with low lignin:N ratio (Gomes et al. 2016), and which occurs in the Amazon Forest, Atlantic Rainforest, and Brazilian Savanna biomes (Senna 1984). These leaves were collected in the Brazilian Savanna (15°57′ S, 47°56′ W). They were used in the experiments to ensure that the resource offered to *Phylloicus* larvae had the same nutritional value in all experiments. The leaves were cut into discs (diameter = 1.98 cm) and then were taken to conditioning (microbial communities) and to leach water-soluble compounds (e.g., polyphenols; Gomes et al. 2016) in streams in each biome. After conditioning, the leaf discs were oven-dried in the laboratory to constant mass. They were weighed on a precision scale (0.1/0.01 mg, model AUW220D, Shimadzu Corporation, Kyoto, Japan) to determine initial dry mass. At the end of the experiments, the remaining leaf discs and the discs used for case-building were removed, dried at 60 °C for 72 h, and weighed to determine the final dry mass. The leaf mass loss in each treatment and control was calculated as the difference between the initial and final dry mass. At the end of each experiment, the *Phylloicus* larvae without their cases were placed in pre-weighed aluminum crucibles on a Shimadzu precision balance and dried at 60 °C for 72 h until constant weight for determining individual biomass for later use in the evaluation of the relationship between consumption and case-building.

Design of the predation risk experiment

In total, we used 60 microcosms (sampling units) to test the non-lethal effects of fish predation risk. In each biome (Atlantic Rainforest, Amazon Forest, and Brazilian Savanna), 20 microcosms were distributed among four treatments (five replicates for each treatment, Fig. 2): (i) visual treatment: microcosms with *Phylloicus* + fish with visual contact; (ii) chemical treatment: microcosms with *Phylloicus* + fish with chemical contact; (iii) chemical + visual treatment: microcosms with *Phylloicus* + fish with visual and chemical contact; and (iv) control: microcosms with
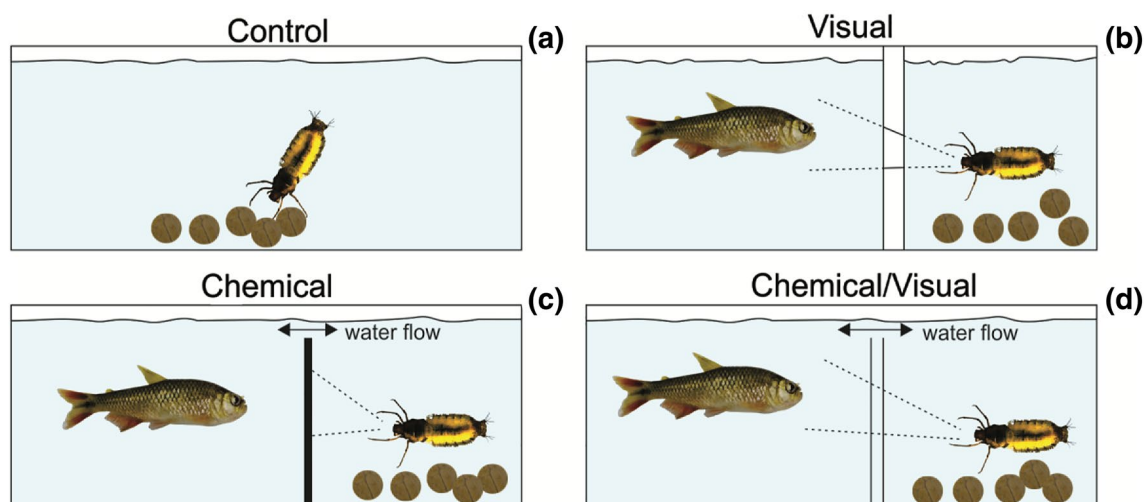

Fig. 2 Experimental design for the assessment of predation risk to *Phylloicus* (Trichoptera: Calamoceratidae) during leaf-litter consumption and case-building, with the treatments: **a** control (predator absent), **b** visual treatment, **c** chemical treatment, and **d** visual + chemical treatment

Phylloicus without fish. A single *Phylloicus* larvae was placed in each microcosm (to avoid competition) and offered five leaf discs of *M. guianensis.* Five replicates were performed for each treatment and the control in each biome. Each experiment was performed in seven days. For the visual treatment, a fish was placed as a potential predator in a clear glass vial (500 mL) to allow only visual contact between the *Phylloicus* larva and the fish. For the chemical treatment, a dark or opaque bottle with small holes was inserted into each microcosm to allow only water exchange between the microcosms without visual contact. In the chemical + visual treatment, a mesh microcosm allowed visual contact and water sharing between the predator and prey. The risks of predation in the visual, chemical, and combined treatments were evaluated under laboratory conditions in the three biomes.

Statistical analyses

We quantified consumption by *Phylloicus* and leaf-litter used for case-building as a percentage of the leaf-litter mass (LM; individually for each calculation, case, and food) in the microcosm, that is, the difference between initial and final leaf-litter DM (g) divided by the initial DM (g) $\times$ 100 provides the leaf-litter use in %. These values were corrected by the final larval biomass (g) to avoid potential effects due to differences in larval size (leaf-litter use/ biomass ratio). The microbial decomposition (mean LM in microcosms without larvae) was used as a control, and the values were used to correct the final percentage loss of leaf-litter mass. To assess differences between leaf-litter used for case-building

(biomass at the end of the experiment) and as a food resource (difference between initial biomass of the resource offered and biomass of the house + leaf remaining at the end of the experiment), we calculated the percentage of leaves used for each activity from the biomass of *Phylloicus* (independent variable). We assume that the resource used for case-building was not used as a food resource.

We analyzed these response variables in terms of biome (Amazon Forest, Atlantic Rainforest, and Brazilian Savanna) and predation risk by fish (visual, chemical, chemical + visual, and control; independent random variable), using as a random intercept the different microcosms nested by biome. We tested this model using a two-way factorial generalized linear mixed-effects analysis (glmer function of lme4 package) with a binomial (link=logit; test=F) and gaussian (link=identity; test=F) distribution for case-building and leaf consumption per invertebrate biomass (in g) and case-building and leaf consumption in percentage (%), respectively. The percentage data were corrected for overdispersion by quasi-binomial distribution. To further explore differences among levels of each treatment, we performed a contrast analysis (Crawley 2012). In the contrast analysis (orthogonal), biome and predation risk treatment (increasing) were tested pairwise (with the closest values) and sequentially in a stepwise model that was simplified by lumping each treatment´s levels that were not deemed significant and testing with the next (see Crawley 2012). Model fit and suitability of error distribution were always checked through analysis of the residuals. The analysis was performed in the R platform (R Core Team 2017, vegan package).

Table 1 Simplified two-way factorial generalized linear mixed-effects analysis (glmer function of lme4 package) and contrast analysis of the use of leaf litter for consumption and case-building by *Phylloicus* spp. larvae among three biomes (Amazon Forest, Atlantic Rainforest, and Brazilian Savanna) and three treatments (visual, chemical, and visual + chemical) compared to the control treatment

| GLM	Df	DF Residual	Dev. Residual%	Pr (> Chi)	Contrast analysis
A. Case-building					
NULL	58		65.53		
Forests	2	56	21.16	< 0.001	Atlantic > Amazon > Savanna
Treatment	3	53	6.42	0.016	Chemical = Visual = Both > Control
Forests: Treatment	6	47	6.88	0.085	
B. Case-building/biomass (g)					
NULL	58		30.13		
Forests	2	56	23.99	0.0032	Atlantic < Amazon = Savanna
Treatment	3	53	23.60	0.016	Chemical = Visual = Both = Control
Forests: Treatment	6	47	22.28	0.085	
C. Leaf consumption					
NULL	58		61.26		
Forests	2	56	26.54	< 0.001	Amazon > Atlantic = Savanna
Treatment	3	53	3.58	0.050	Chemical = Visual = Both > Control
Forests: Treatment	6	47	8.62	0.005	
D. Leaf consumption/biomass (g)					
NULL	58		39.27		
Forests	2	56	22.49	< 0.001	Amazon = Savanna > Atlantic
Treatment	3	53	19.91	0.099	Chemical = Visual = Both < Control
Forests: Treatment	6	47	18.32	0.668	
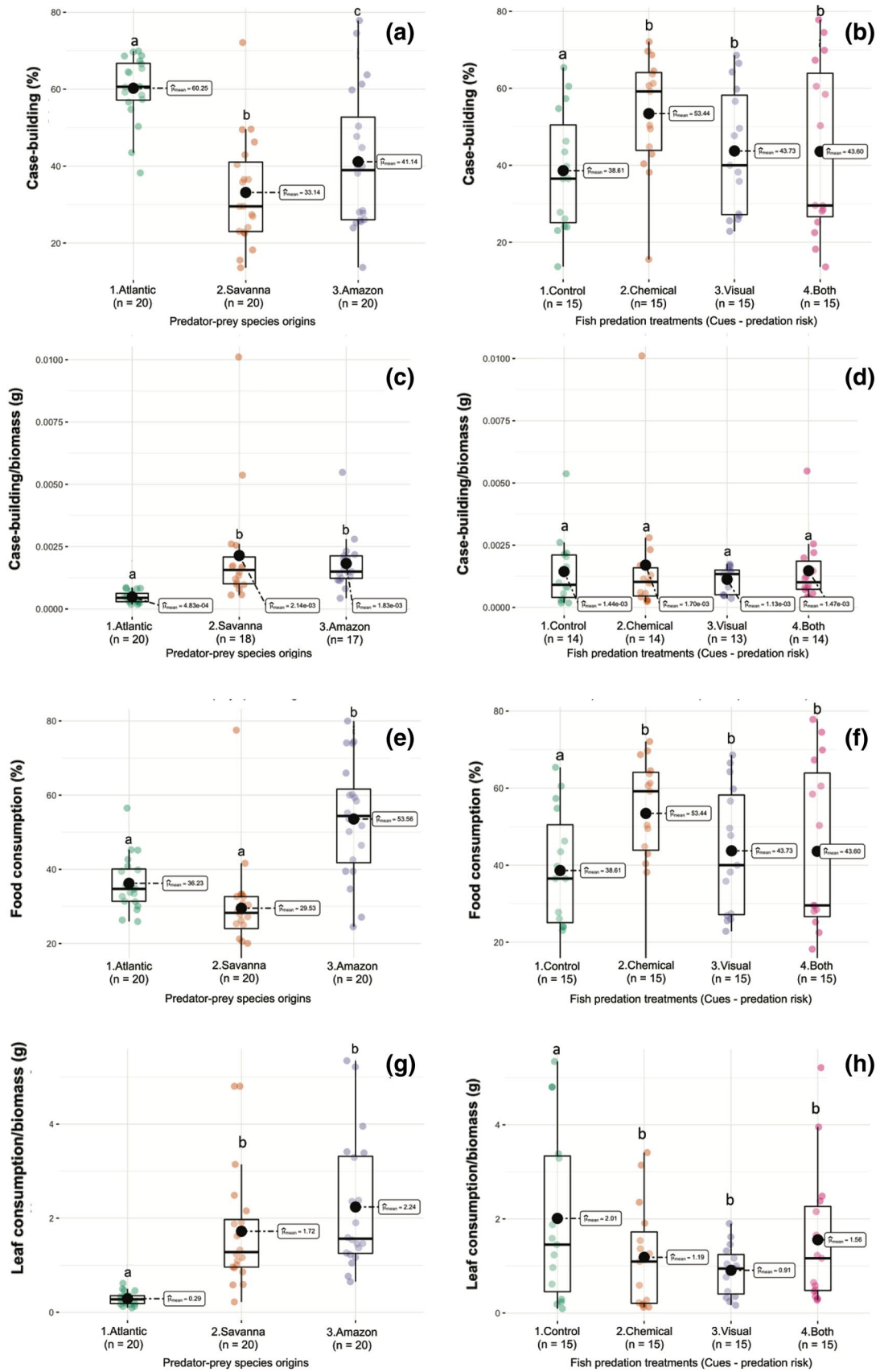
◄**Fig. 3** Mean values and boxplot of case-building (**a–d**) and the relationship with biomass of *Phylloicus* spp. among biomes (**a** and **c**) and treatments (**b** and **d**); leaf-litter consumption (**e–h**) and the relationship with *Phylloicus* biomass among biomes (**e** and **g**) and treatments (**f** and **h**). Boxes represent quartiles, black horizontal lines represent medians, and black dots represent means. Vertical lines represent the upper and lower limits. The letters above the boxes represent the results of the contrast analysis

Results

Differences were observed among the experiments performed over the three predation risk treatments, biome treatments, and their interactions (Table 1). In the Amazon Forest (*P. elektoros*), the larvae used significantly less leaf mass for case-building than consumption (44% vs. 50%, respectively, Fig. 3). They had to mean dry biomass of 2.3 mg/ind (standard error ± 0.39 mg/ind.). In the Atlantic Rainforest (*P. angustior*), this pattern reversed, where the larvae used significantly more leaf mass for case-building than consumption (60% vs. 36%, respectively, Fig. 3), and the larvae had mean dry biomass of 10.8 mg/ind. (± 1.01 mg/ind.). Like Atlantic Rainforest, *Phylloicus* sp. from the Savanna biome used significantly more leaf mass in case-building than consumption (32% vs. 26%, respectively, Fig. 3), but with lower values than in the other biomes (Fig. 3). The mean dry biomass in Savanna was 2.7 mg/ind (± 0.59 mg/ind.), a similar value found in organisms from Amazon Forest.

The use of leaves for case-building by larvae (%; uncorrected by biomass) differed in magnitude among the three biomes (Table 1a and Fig. 3a), and the magnitude of this use of leaves differed from the control when under the predation risk regardless of the type of cue (Table 1a and Fig. 3b). We found that case-building per unit of *Phylloicus* biomass was lower in Atlantic Rainforest than in the other biomes when corrected by larvae biomass (Table 1b and Fig. 3c), and the effect of predation risk cue type did not differ among the treatments with the fish present and control (Table 1b and Fig. 3d).

The total consumption of leaves by *Phylloicus* (corrected and uncorrected by biomass) in the Amazon Forest biome was higher than in the Savanna and Atlantic Rainforest biomes (Table 1c,d, and Fig. 3e,f). Consumption was higher in treatments than in control when not corrected for biomass (Table 1c and Fig. 3f). On the other hand, consumption was lower in treatments compared to control when corrected for biomass (Table 1d and Fig. 3h).

Discussion

Our results have shown evidence that predation risk, regardless of the type of stimulus, has an effect on the behavior of *Phylloicus,* probably due to a stress response to the presence of the predator. Predation risk increases case-building and leaf-litter consumption when the biomass of *Phylloicus* specimens from different biomes is not considered. Different responses were observed when comparing the consumption and case-building corrected for the biomass of the specimens of *Phylloicus*. Responses to predation risk may be associated with physiological alteration of neuroendocrine hormone levels intrinsic to each specie (not evaluated in this study) that stimulate protective behavior and consequently increases case-building activity and decrease consumption as reported in the literature (Charmandari et al. 2005; Beckerman et al. 2007; Hawlena and Schmitz 2010). In an experiment in the Brazilian Savanna, Navarro et al. (2013) observed that physiological stress in *Phylloicus* larvae caused by predation risk induced by the presence of predatory fish carcasses was responsible for decreased leaf-litter consumption rates as a survival strategy, resulting in lower rates of leaf decomposition. Therefore, interference in the feeding process of shredders, such as reduced consumption in response to stress from predation risk (Schmitz et al. 2010), can result in reduced biomass and, consequently, fewer energy resources for predators.

Our results indicated that *Phylloicus* larvae collected in three Brazilian biomes and under laboratory conditions, when offered as a resource, leaves of *M. guianensis*, had different ways of consumption and case-building in the presence of a fish predator. Larvae from the Savanna had lower mean consumption and case-building than the other two biomes based on uncorrected values for *Phylloicus* biomass. However, when corrected for biomass, the mean value for consumption was lower in Atlantic Forest than in the Savanna. Therefore, it could indicate that the size of specimens among biomes would be regulated by natural selection to avoid predation. We expected different litter use behaviors of organisms in different biomes under natural environmental conditions due to differences in habitat structure, the composition of the biota, the dynamics and availability of food resources, and other factors such as temperature and precipitation regimes (Wantzen et al. 2005; Alvim et al. 2015; Tonin et al. 2017). However, changes in resource use were more complex than the simple separation between forest and savanna ecosystems, as shown by using the same food resource and controlled temperature conditions.

In general, the difference in resource litter use among biomes was evident. The differences could be related to the different *Phylloicus* species used in the experiment, which may differ in other behavioral characteristics (including feeding and case-building). The differences in biome response could also be due partly to the different fish species, not just *Phylloicus* species. The most significant change in behavior due to perceived predatory risk was for the Atlantic Rainforest, which could suggest that *P. angustior* (the species from this biome) is more sensitive to predation risk because

they are larger prey with greater biomass and thus are more attractive to predators (Rodgers et al. 2015). On the other hand, *P. elektoros* in the Amazon Forest consumed more leaf-litter than *P. angustior* from Atlantic Rainforest and *Phylloicus* sp. from the Brazilian Savanna. Studies suggest that a higher risk of predation and water temperature may increase the metabolic rate, and change fragmentation activity, consequently increasing the energy requirements of these organisms (Navarro et al. 2013; Shah et al. 2020). However, we controlled the temperature and predator exposure conditions in our study. Therefore, our results indicated that the higher consumption by *P. elekitoros* in the Amazon rainforest may be due to their energy needs being higher than those of the other species.

We expected that protective behavior by *Phylloicus* sp. in the Savanna would include greater use of leaf-litter for case-building in the presence of predation risk. In a laboratory experiment in the Savanna, Navarro and Gonçalves (2017) evaluated the preference of *Phylloicus* for dry, green, and senescent leaves. They observed that the larvae seemed to be more dependent on the rigid physical structure of the leaves than on their chemical composition because the tough structure is essential for case-building and, thus, protection against predators. However, we did not observe this because *Phylloicus* sp. of Savanna larvae used less leaf-litter for case-building (not corrected for biomass) when they were at risk of predation, probably because the predator density used in the experiment in the Brazilian Savanna was not enough to produce a significant effect on case-building due to predation risk (Rezende et al. 2015).

In conclusion, the present study assessed the non-lethal effect of the predator on a leaf-litter shredder invertebrate. We observed through the treatments an increase in leaf consumption and case-building by *Phylloicus* with the predator's presence. It was observed mainly in the Atlantic Forest and Amazonian Forest biomes, showing an evident top-down mechanism in the food web of tropical streams. Therefore, our first hypothesis that predator risk would decrease feeding rate and increase sheltering activities was partially corroborated because when we had not corrected individuals' biomass, we found higher case-building in treatments with predation than in control. Besides, when corrected for biomass, the consumption was lower under predation (corroboration of the hypothesis), and case-building did not have a difference among treatments than the control treatment. We also refuted the isolated effect of visual or chemical stimuli on leaf-litter use by *Phylloicus* independent of the biome. The second hypothesis that leaf-litter consumption would be higher in Amazon Forest and Atlantic Rainforest than in the Savanna was also not corroborated due to mean values in the Savanna being close to those in the Atlantic Rainforest

if not corrected by biomass of *Phylloicus*. Besides, the mean values are comparable to those in the Amazon Forest when corrected by biomass.

Predation risk affected leaf-litter consumption and case-building by *Phylloicus* larvae in the Neotropical headwater streams from Amazon Forest, Atlantic Rainforest, and Brazilian Savanna biomes. The biomass of the different species of *Phylloicus* and the density of predators are essential factors to consider in this fragmentation leaf-litter, reinforcing the importance of these organisms for nutrient cycling in aquatic ecosystems. Our results will contribute to future studies, filling knowledge gaps on the role of shredders of leaf-litter and predator/prey relationships in aquatic ecosystems. Future replicating field experiments (Boyero et al. 2008) in each biome studied will help elucidate the intrinsic effects that were not considered in the present experiments.

Declarations

Conflict-of-interest The authors declare that they have no competing interests.

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