



Effects of *Phylloicus* case removal on consumption of leaf litter from two Neotropical biomes (Amazon rainforest and Cerrado savanna)

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Abstract

Phylloicus (Trichoptera, Calamoceratidae) is a stream invertebrate widely distributed across Neotropical biomes, which larvae use allochthonous leaf litter as food resource and to build a case that offers protection against predation. Seasonal changes in leaf litter accumulation on the streambed may affect *Phylloicus* larvae due to variations in availability of food and case-building material; however, it is unclear how these two processes influence each other. We assessed how case removal affected leaf litter consumption by *Phylloicus* larvae from two Neotropical biomes (Amazon rainforest and Cerrado savanna), which were experimentally offered leaf litter of *Goupia glabra* and *Maprounea guianensis* (common riparian species from the rainforest and savanna biomes, respectively). Our treatments included (i) direct effect of case removal, where larvae had their case removed during the experiment; (ii) time-lag effect, where the case was removed and larvae were allowed to rebuild the case before starting the experiment; and (iii) control, where cases were not removed. Leaf litter consumption by *Phylloicus* was 9.16 ± 7.47 mg/mg on average, being higher in the savanna than in the rainforest experiment (possibly in relation to a higher difference between the rainforest stream temperature and the experimental temperature, which may have inhibited larval activity), and higher on *M. guianensis* than on *G. glabra* (most likely due to the higher leaf litter quality of the former species). Consumption was higher in the time-lag effect treatment than in the direct effect and control treatments, which could be explained by an increase in the larval energetic demand for case building.

Keywords Aquatic insects · Microcosm experiments · Leaf litter decomposition · Leaf quality · Life history

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Introduction

The genus *Phylloicus* Müller, 1880 (Trichoptera, Calamoceratidae) is a common macroinvertebrate in many Neotropical streams. *Phylloicus* larvae use allochthonous leaf litter available on the stream substrate as food item and to build a case that serves as protection against predation (Graça 2001; Prather 2003). Therefore, changes in leaf availability in streams have the potential to affect these leaf-shredding larvae, and may help to explain their relatively low density in some tropical streams (Boyero et al. 2011, 2012). *Phylloicus* has a multivoltine life cycle with asynchronous larval development, and early instars can be affected by rainfall seasonality through its influence in water flow (Reyes-Torres and Ramírez 2018). Increased flow can entail (i) higher physical abrasion and, hence, the impairment or loss of larval cases, which can increase the risk of predation by fish and Odonata (Williamson 1993; Murray et al. 2018), and (ii) lower food

availability, as leaf litter can be rapidly transported downstream (Padial and Thomaz 2006; Leite et al. 2016).

Rainfall seasonality varies across Neotropical biomes, such as the Amazon rainforest and the Cerrado savanna, with higher seasonality in the latter (Tonin et al. 2017). Moreover, leaf quality differs between these two biomes: while many trees in the Cerrado savanna have low-quality leaves, with high concentrations of lignin, cellulose, tannins, and polyphenols, leaves of many rainforest trees have high amounts of nitrogen (N), phosphorus (P), and other nutrients (De Sousa-Neto et al. 2017; Rezende et al. 2018). Given that deforestation of the Amazon rainforest has expanded the range of some Cerrado savanna trees towards some Amazonian areas, in a process known as savannization, comparing ecosystem processes between both biomes (hereafter rainforest and savanna biomes) is highly relevant, as it can help understanding the ecological consequences of savannization (Silverio et al. 2013; Gonçalves et al. 2017).

Our objective was to assess the effects of case removal on leaf litter consumption by *Phylloicus* from the rainforest and savanna biomes. We experimentally mimicked the loss of larval cases (which would happen during high-flow events) and assessed changes in larval feeding activity of *Phylloicus* that may alter leaf litter decomposition, a key ecosystem process in headwater streams (Wallace and Webster 1996). We tested the following hypotheses: (i) case removal increases leaf litter consumption by *Phylloicus* larvae, due to the higher energetic requirements entailed by building a new case; and (ii) the increase would be greater when available leaf litter is from the savanna, due to its low quality and, hence, the greater amount of food required to meet the energetic demands of case building.

Materials and methods

Study sites and leaf litter collection

Phylloicus larvae were collected from the Barro Branco stream (02° 55' 03" 01' S, 59° 53' 59" 59' W; Ducke Reserve, Manaus county, Amazon State of Brazil; Amazon rainforest biome) and the Capetingá stream (15° 57' 40.75" S, 47° 56' 38.04" W; Gama-Cabeça de Veado watershed, Federal District of Brazil; Cerrado savanna biome); in both cases, this genus is a dominant leaf-shredding invertebrate in terms of biomass. At time of collection, stream channel was 1.5 m (rainforest stream) and 2 m (savanna stream); water depth, 0.15 and 0.20 m; water velocity, 0.41 ± 0.09 and 0.37 ± 0.08 m s; dissolved oxygen, 6.62 ± 0.06 and 6.97 ± 0.59 mg L; electrical conductivity, 10.71 ± 0.41 and 16.73 ± 0.46 μ S cm; water temperature, 24.52 ± 0.52 and 19.54 ± 1.01 °C; and pH, 4.63 ± 0.08 and 6.09 ± 0.11 . Water velocity was measured with a Sigma Sports flowmeter (model FP101, Global Water), and

dissolved oxygen, conductivity, temperature, and pH with a Horiba (U-50) multiparameter.

We selected one plant species that was representative, in terms of quantity and quality, of the riparian vegetation of each biome (Tonin et al. 2017): *Goupia glabra* Aubl. (Goupiaceae, 1775) was chosen to represent the rainforest vegetation, and *Maprounea guianensis* Aubl. (Euphorbiaceae, 1775) for the savanna vegetation. Senescent leaves were collected in the riparian zone of each stream using a 0.5-mm mesh net suspended 2 m above the ground and below the target trees.

Invertebrate sampling and identification

Phylloicus larvae were collected by active searching and using a kick net, with 4 h of sampling effort at each site. Larval cases were measured in situ and only individuals with case length of approx. 1.5 cm were kept. Larvae were transported to the laboratory in coolers and placed in containers (15.5 × 15.5 × 12 cm) with bottled water and gravel substrate previously sterilized in an oven for 4 h at 550 °C (Martins et al. 2017). *Phylloicus* species were identified by rearing larvae in containers filled with stream water, with constant aeration, and the opening covered by a 0.5-mm mesh. Newly hatched adults were collected daily, preserved in ethanol, and sent to the National Institute for Amazonian Research for identification. Larvae collected in the rainforest biome belonged to *Phylloicus elektoros* (Prather 2003), and larvae collected in the savanna biome belonged to an undescribed species, referred hereafter as *Phylloicus* sp. Even if these are different species, they were considered as functionally equivalent because of their similar body and case size and morphology.

Leaf litter characterization

We assessed the concentrations (%) of N, P, lignin, cellulose, and polyphenols of *G. glabra* and *M. guianensis* leaf litter. Conditioned leaves were cut into 1.98-cm-diameter discs and freeze-dried (Terroni, LT-AISI 304 model), and sets of five discs were weighed in a Shimadzu balance (AUW220D model) with a precision of 0.01 mg. N was assessed using a CHN basic analyzer (Carlo Erba 1500 for WI; Thermo Electron Corp. Milan, Italy); P, using the ascorbic acid method after acid digestion; lignin and cellulose, according to Gessner (2005); and polyphenols, according to Bärlocher and Graça (2005).

Experimental procedure

We conducted two microcosm experiments, one at the Laboratório de Citotaxonomia e Insetos Aquáticos (National Institute for Amazonian Research) and the other at the

Limnology/AquaRiparia Laboratory (University of Brasília). Larvae were acclimated individually in containers placed in an experimental room for 3 days, with continuous aeration, temperature set at 20 °C, a light:dark natural regime of 12:12 h, and fed ad libitum with leaf litter of *Calophyllum brasiliensis*, a species that occurs naturally in the riparian zones of both biomes (Salomão et al. 2019). Water dissolved oxygen (measured with a Jenway 970 m) was 6.6 ± 0.2 and 6.9 ± 0.3 mg L and (rainforest and savanna experiments, respectively); electrical conductivity (Jenway 430 m), 72.8 ± 5.4 and 20.1 ± 1.5 μ S cm; and pH (Jenway 430 m), 4.7 ± 0.1 and 6.5 ± 0.1 ; these variables were measured daily in all containers. Larvae were individually transferred to new containers with the same characteristics, but without leaf litter, for a second (24-h) acclimatization phase, and, finally, transferred to experimental microcosms.

In each experiment, we used 24 experimental microcosms, each with a single *Phylloicus* larva (Fig. S1) to avoid aggressive and competitive interactions between individuals that could interfere with consumption (Rezende et al. 2015). Each microcosm was provided with five leaf litter discs (1.98 mm diameter; 0.05 ± 0.01 g) of either *G. glabra* or *M. guianensis*, and randomly assigned to one of three treatments ($n = 4$ per treatment/plant species combination): (i) direct effect of case removal: cases were carefully removed from larvae using tweezers just before starting the experiment (Fig. S1 A); (ii) time-lag effect of case removal: cases were removed, and then, 3 g of *C. brasiliensis* leaf litter were provided to each larva for case building during the first 3 days of acclimatization; and (iii) control: cases were not removed before the experiment (Fig. S1 B). Additionally, we had ten microcosms in each experiment that contained leaf litter but no larvae (5 with *G. glabra* and 5 with *M. guianensis*) and were used to estimate microbial leaf litter decomposition. The experiment lasted for 7 days, after which leaf litter discs were collected, dried at 60 °C for 48 h, and weighed to quantify their final dry mass (DM). Larvae were also collected, uncased, dried at 60 °C for 48 h, and weighed to quantify their final DM. Larval cases were also dried and weighed separately.

Statistical analysis

We quantified consumption by *Phylloicus* as the percentage of leaf litter mass loss (LML) in the microcosm, that is, the difference between initial and final leaf litter DM (mg) divided by initial DM (mg) $\times 100$. These values were corrected by (i) microbial decomposition (mean LML in microcosms without larvae); (ii) final larval biomass (mg), to avoid potential effects due to differences in larval size; and (iii) larval case (only in the direct effect treatment, where larvae built a case during the experiment).

Data were checked for normality with the Kolmogorov–Smirnov test (Crawley 2007). We examined differences in consumption, final larval DM, and final larval case DM (dependent variables) among treatments (direct effect, time-lag effect, and control), plant species (*M. guianensis* and *G. glabra*), biomes (rainforest and savanna), and their interactions, with three-way ANOVA (Gaussian distribution in package “vegan” and function “glm”) followed by Tukey post hoc tests (function “lsmeans”). Differences in microbial decomposition and leaf litter traits between plant species and biomes were also examined with two-way ANOVA. All models were tested for under or overdispersion (package and function “hnp”). All analyses were carried out in R (The R Core Team, version 3.3.0).

Results

Leaf litter characterization

For *M. guianensis*, N concentration was $0.076 \pm 0.065\%$ (mean \pm standard deviation); P concentration, $0.001 \pm 0.002\%$; lignin concentration, $23.21 \pm 1.94\%$; cellulose concentration, $15.34 \pm 1.22\%$; and polyphenol concentration, $36.02 \pm 18.42\%$. For *G. glabra*, N concentration was $1.20 \pm 0.13\%$; P concentration, $0.033 \pm 0.003\%$; lignin concentration, $28.17 \pm 0.81\%$; cellulose concentration, $18.22 \pm 0.32\%$; and polyphenol concentration, $6.01 \pm 0.91\%$.

Leaf consumption and case biomass

Leaf litter consumption (corrected by larval biomass) was 9.16 ± 7.47 mg/mg overall. Consumption was higher in the savanna (12.81 ± 11.86 mg/mg) than the rainforest biome (5.51 ± 3.89 mg/mg), and in *M. guianensis* (13.92 ± 12.56 mg/mg) compared to *G. glabra* (4.39 ± 4.37 mg/mg; Tables 1 and S1; Figs. 1 and S2). Moreover, the interaction between both factors was significant, with greater differences between species in the savanna biome (19.96 ± 14.44 mg/mg for *M. guianensis* and 5.65 ± 4.37 mg/mg for *G. glabra*) than in the rainforest biome (7.88 ± 3.48 mg/mg and 3.13 ± 1.77 mg/mg, respectively; Tables 1 and 2; Figs. 1 and 2). Consumption was twofold higher in the time-lag effect (12.56 ± 14.91 mg/mg) treatment than in the direct effect (9.78 ± 8.62 mg/mg) treatment and control (5.13 ± 4.10 mg/mg) treatment (Fig. 1). The three-way interaction was significant (Tables 1 and 2; Figs. 1 and 2), indicating differences between the amazon and savanna biomes for the time-lag and direct treatments in *M. guianensis*; between *M. guianensis* and *G. glabra* in the time-lag and direct treatments from the savanna biome; and between all combinations of treatments for *M. guianensis* from the savanna biome (Table 2; Fig. 2).

Table 1 Results of three-way ANOVA testing effects of biome (savanna and rainforest), treatment (control, direct effect and time-lag effect), plant species (*G. glabra* and *M. guianensis*), and their interactions on leaf consumption by *Phylloicus* larvae (a); and two-way ANOVA testing effects of biome, plant species, and their interaction on microbial decomposition (b)

	Df	Deviance resid	Df res	Dev	F values	P value	Analysis of contrast
(a) Consumption by <i>Phylloicus</i>							
Null			47	5159.1			
Biome	1	639.2	46	4519.9	17.2	< 0.001	
Plant species	1	1090.6	45	3429.4	29.3	< 0.001	
Treatment	2	451.5	43	2977.9	6.1	0.005	
Biome: species	1	274.8	42	2703.1	7.4	0.010	Table 2
Biome: treatment	2	766.0	40	1937.1	10.3	< 0.001	Table 2
Species: treatment	2	321.3	38	1615.8	4.3	0.021	Table 2
Biome: species: treatment	2	276.7	36	1339.1	3.7	0.034	Table 2
(b) Microbial decomposition							
Null			19	2171.3			
Biome	1	1755.2	18	416.1	251.8	< 0.001	
Plant species	1	0.7	17	415.4	0.1	0.756	
Biome: species	1	303.9	16	111.5	43.6	< 0.001	Table 2

Case DM at the end of the experiment was 34 ± 21 mg and 29 ± 18 mg for larvae fed *G. glabra* and *M. guianensis*, respectively, in the amazon biome; and 28 ± 13 mg and 23 ± 11 mg for *G. glabra* and *M. guianensis* in the savanna biome; however, differences between species, biomes, and their interaction were not significant. The effect of treatment was also not significant, but there was a significant interaction between biome and treatment and between plant species and treatment (Table S1 and Fig. S2).

Larval DM at the end of the experiment was twofold higher in the savanna (5.5 ± 4.1 mg) than in the rainforest biome (2.7 ± 1.5 ; Table S1; Fig. S2). In both biomes, DM was higher when larvae were fed *G. glabra* (7.4 ± 4.8 mg and 3.4 ± 2.4 mg for savanna and rainforest biomes, respectively) than when fed *M. guianensis* (3.7 ± 2.5 mg and 2.1 ± 1.3 mg for savanna and rainforest, respectively; Table S1; Fig. S2). The effect of treatment was not significant, but there was a significant interaction between biome and treatment.

Leaf decomposition by microorganisms

Microbial decomposition was $19.52 \pm 9.69\%$ on average, with higher values for the savanna ($28.76 \pm 0.02\%$) compared to the rainforest biome ($10.28 \pm 4.64\%$; Table 1; Fig. 3). The interaction between biome and species was significant, with higher decomposition of *G. glabra* ($32.21 \pm 4.83\%$) than *M. guianensis* ($25.31 \pm 2.05\%$) in the savanna biome, and higher decomposition of *M. guianensis* ($14.39 \pm 1.74\%$) than *G. glabra* ($6.17 \pm 0.54\%$) in the rainforest biome (Tables 1 and 2; Fig. 3).

Discussion

Caddisfly larvae often give priority to case building compared to feeding because of the urgent need for protection from predators (Moretti et al. 2009). Accordingly, our results showed that larvae that were deprived of their cases, but had the opportunity to rebuild their cases consumed more leaf litter than those in the other treatments. Such increase in leaf litter consumption may be a response to a higher energetic demand of *Phylloicus* larvae for case building (Hutchinson and King 1980; Grutters et al. 2015). Increased consumption could also be related to the higher energy cost of breathing in uncased larvae (Williams et al. 1987), because the undulating movement of the larval body creates a flow of water over the gills that improves gas exchange and aids in breathing (Williams et al. 1987).

Moreover, larvae increased their feeding activity not just after the loss of their case, but rather a few days after the case was rebuilt. This was observed by the higher consumption in the time-lag effect treatment compared to the others (especially for consumption of *M. guianensis* in the savanna biome), and could be explained by an urgent response to increased predation risk (Richardson and Brown 1992; Williamson 1993; Rezende et al. 2015). Thus, only after the larva feels again protected by a new case, its feeding activity intensifies (Richardson and Brown 1992; Rezende et al. 2015). Still, the process of leaf litter shredding for case rebuilding contributes to litter breakdown, which may compensate for their lower feeding activity (Rezende et al. 2014, 2018; Graça et al. 2015).

Consumption of *M. guianensis* was higher than that of *G. glabra*. Another study conducted in the savanna

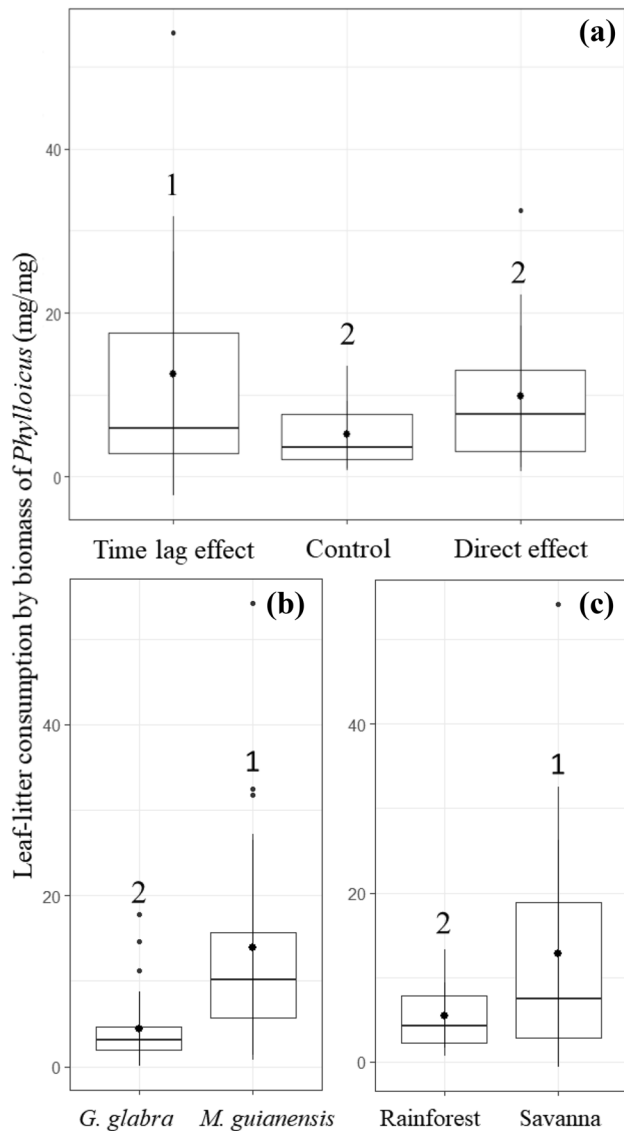


Fig. 1 Leaf litter consumption by *Phylloicus* larvae (corrected by larval biomass; mg/mg) subjected to different case-building treatments (time-lag effect, control, and direct effect; **a**), plant species (*Goupiia glabra* and *Mafrunea guianensis*; **b**) and biomes (rainforest and savanna; **c**). Boxes represent quartiles, the bold line is the median, large circles are means, vertical dashed lines are the upper and lower limits, and small circles are outliers. Different numbers (1 and 2) indicate significant differences by Tukey post hoc tests

biome showed that *Phylloicus* larvae preferred leaf litter of *M. guianensis* compared to *Inga laurina* and *Richeria grandis* (Rezende et al. 2018). *M. guianensis* leaves have lower lignin and cellulose and higher polyphenol concentrations compared to *G. glabra* leaves. The lower concentrations of structural compounds such as lignin and cellulose are related to increased leaf litter palatability and faster consumption by shredders (Poorter and De Jong 1999; Rezende et al. 2014, 2018). Other tropical studies examining leaf litter with a wide range of leaf

litter quality have shown that it can be a key determinant of shredder consumption, mainly by leaf hardness and nitrogen and phosphorus concentration (Moretti et al. 2009; Oliveira et al. 2014; Leite et al. 2016; Reis et al. 2018; Rezende et al. 2018). Given that *M. guianensis* was more consumed than *G. glabra* and that larvae that consumed *G. glabra* had higher biomass, it is possible that the greater consumption of *M. guianensis* compensated for its lower nutrient concentration (*M. guianensis*: $N = 0.76 \text{ mg g}^{-1}$, $P = 0.01 \text{ mg g}^{-1}$; *G. glabra*: $N = 12 \text{ mg g}^{-1}$; $P = 0.33 \text{ mg g}^{-1}$). Other studies have also indicated a positive relationship between nutrient concentrations and biomass of *Phylloicus* (Navarro et al. 2013; Tonello et al. 2016) as in this study.

Consumption by *Phylloicus* was greater in the savanna than the rainforest biome. This could be due to the fact that the experimental temperature (20 °C) was closer to that of the savanna stream (a difference of 0.5 °C), which may favour the activity of *Phylloicus* sp. from the savanna biome. In contrast, *P. elektoros* could have reduced its activity due to the much lower temperature in the experiment compared to the stream (a difference of 4.5 °C) (Gonçalves et al. 2017; Martins et al. 2017). It is also possible that there are interspecific differences between both *Phylloicus* species in terms of consumption rates, but we think that this is unlikely as explained above.

We found a higher influence of the leaf litter type (i.e., plant species) than of the biome effect for the litter consumption by *Phylloicus*. This reinforces the importance of leaf litter quality for *Phylloicus*, most likely not only for feeding but also for case building (Martínez 2006; Moretti et al. 2009; Reis et al. 2018). A global study of plant litter breakdown in streams showed that leaf litter quality and phylogenetic diversity effects had a higher influence on breakdown compared to abiotic variables, including temperature, although different mechanisms seemed to operate at different latitudes (Boyero et al. 2016). Other global studies have also demonstrated the main role of leaf litter quality on breakdown in streams (Zhang et al. 2019) and terrestrial systems (Cornwell et al. 2008). These results as a whole suggest that changes in riparian vegetation composition may be more important than environmental changes for leaf litter consumers.

On the other hand, we found that biome had a higher influence than plant species on microbial decomposition (by Deviance values in Table 1). This could be explained by differences in the composition of microbial communities between the savanna and rainforest streams, although we cannot confirm this hypothesis, because we did not examine

Table 2 Results of contrast analysis by pairwise Tukey post hoc tests between biomes (savanna and rainforest), treatments (control, direct effect and time-lag effect; categorical variables), plant species (*G. glabra* and *M. guianensis*), and their interactions on leaf consumption by *Phylloicus* (a) and microbial decomposition (b)

Biome	Specie	Treatment	Contrast	Estimate	SE	Df	t ratio	P value
(a) Consumption by <i>Phylloicus</i>								
	<i>G. glabra</i>	Time lag	Amazon: Savanna	- 5.60	4.31	36	- 1.298	0.202
	<i>M. guianensis</i>	Time lag	Amazon: Savanna	- 28.68	4.31	36	- 6.649	< 0.001
	<i>G. glabra</i>	Control	Amazon: Savanna	3.23	4.31	36	0.749	0.458
	<i>M. guianensis</i>	Control	Amazon: Savanna	1.64	4.31	36	0.38	0.706
	<i>G. glabra</i>	Direct	Amazon: Savanna	- 5.17	4.31	36	- 1.199	0.238
	<i>M. guianensis</i>	Direct	Amazon: Savanna	- 9.21	4.31	36	- 2.136	0.039
Amazon		Time lag	<i>G. glabra</i> : <i>M. guianensis</i>	- 4.33	4.31	36	- 1.004	0.322
Savanna		Time lag	<i>G. glabra</i> : <i>M. guianensis</i>	- 27.41	4.31	36	- 6.356	< 0.001
Amazon		Control	<i>G. glabra</i> : <i>M. guianensis</i>	- 2.40	4.31	36	- 0.556	0.581
Savanna		Control	<i>G. glabra</i> : <i>M. guianensis</i>	- 3.99	4.31	36	- 0.926	0.360
Amazon		Direct	<i>G. glabra</i> : <i>M. guianensis</i>	- 7.51	4.31	36	- 1.742	0.090
Savanna		Direct	<i>G. glabra</i> : <i>M. guianensis</i>	- 11.55	4.31	36	- 2.679	0.011
Amazon	<i>G. glabra</i>		Time lag: Control	- 3.31	4.31	36	- 0.769	0.724
Amazon	<i>G. glabra</i>		Time lag: Direct	- 0.59	4.31	36	- 0.138	0.989
Amazon	<i>G. glabra</i>		Control: Direct	2.72	4.31	36	0.631	0.804
Savanna	<i>G. glabra</i>		Time lag: Control	5.51	4.31	36	1.278	0.416
Savanna	<i>G. glabra</i>		Time lag: Direct	- 0.16	4.31	36	- 0.039	0.999
Savanna	<i>G. glabra</i>		Control: Direct	- 5.67	4.31	36	- 1.317	0.395
Amazon	<i>M. guianensis</i>		Time lag: Control	- 1.38	4.31	36	- 0.321	0.944
Amazon	<i>M. guianensis</i>		Time lag: Direct	- 3.77	4.31	36	- 0.876	0.658
Amazon	<i>M. guianensis</i>		Control: Direct	- 2.39	4.31	36	- 0.555	0.844
Savanna	<i>M. guianensis</i>		Time lag: Control	28.92	4.31	36	6.708	< 0.001
Savanna	<i>M. guianensis</i>		Time lag: Direct	15.68	4.31	36	3.637	0.002
Savanna	<i>M. guianensis</i>		Control: Direct	- 13.24	4.31	36	- 3.071	0.011
(b) Microbial decomposition								
Amazon			<i>G. glabra</i> : <i>M. guianensis</i>	8.22	2.26	16	3.633	0.021
Savanna			<i>G. glabra</i> : <i>M. guianensis</i>	- 6.91	2.26	16	- 3.053	0.049
	<i>G. glabra</i>		Amazon: Savanna	26.05	2.26	16	11.511	< 0.001
	<i>M. guianensis</i>		Amazon: Savanna	10.92	2.26	16	4.825	0.004

microbial communities in this study. Microbial decomposition rates usually increase with rising temperature, because this accelerates microbial metabolism (Martins et al. 2016, 2017; Djukic et al. 2018; Pérez 2018), but we kept temperature constant at 20 °C. Moreover, we used bottled water in our microcosms, but potential differences in microbial communities could arise, because *Phylloicus* larvae had been previously acclimated in stream water from each biome and some microorganisms could have been transferred to the microcosms. Again, this hypothesis would need further testing.

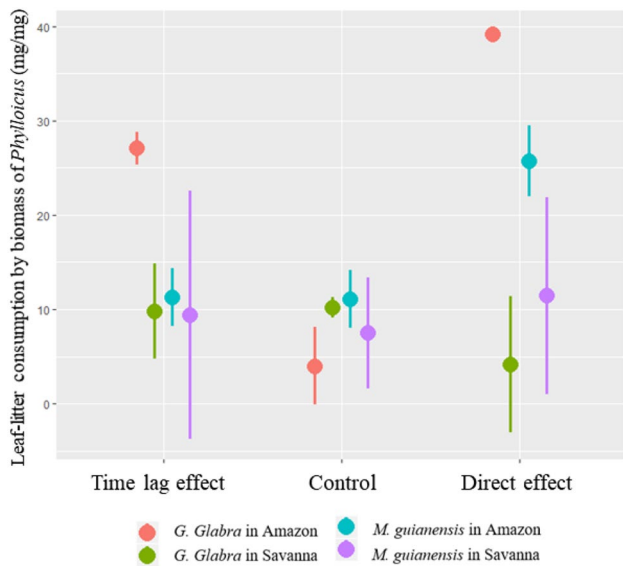


Fig. 2 Mean and standard deviation of leaf litter consumption by *Phylloicus* larvae (corrected by larval biomass; mg/mg) of different case-building treatments (time-lag effect, control, and direct effect) between plant species (*Goupia glabra* and *Maprunea guianensis*) and biomes (rainforest and savanna)

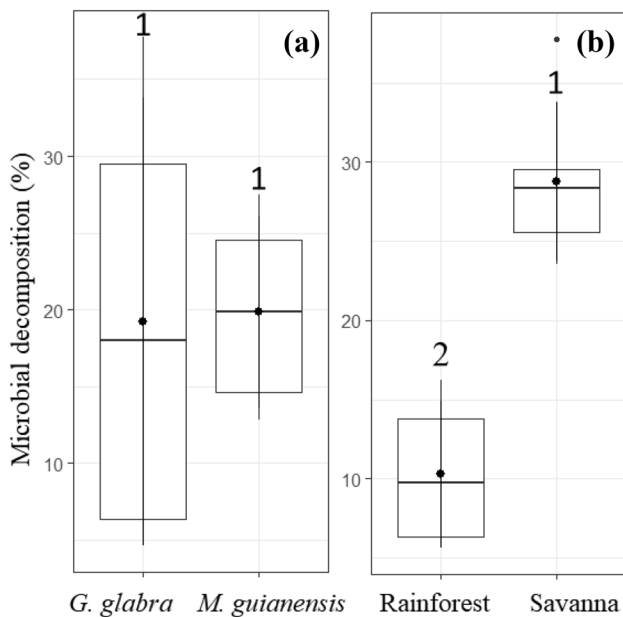


Fig. 3 Microbial decomposition (%) of two plant species (*Goupia glabra* and *Maprunea guianensis*; **a**) in two biomes (rainforest and savanna; **b**). Boxes represent quartiles, the bold line is the median, large circles are means, vertical dashed lines are the upper and lower limits, and small circles are outliers. Different numbers (1 and 2) indicate significant differences by Tukey post hoc tests

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