



Processing of decomposing fruits by macroinvertebrates in a Central Amazonian stream food web

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Received: 10 June 2025 / Accepted: 6 January 2026 / Published online: 5 February 2026
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Abstract

Food webs in small, forested streams rely heavily on litterfall for energy, but the role of fruitfall remains understudied. We conducted a field experiment comparing the decomposition of two fruits with hard pericarps (*Astrocaryum vulgare* and *Bactris gasipaes*) and five with soft pericarps (*Genipa americana*, *Mangifera indica* [non-native], *Mauritia flexuosa*, *Syzygium cumini* [non-native], and *Talisia esculenta*). Whole and cut fruits were incubated in fine- and coarse-mesh litter bags for 62 days to simulate undamaged and vertebrate-damaged fruitfall. We expected that fruits with thin pericarps or cut fruits would decompose faster than hard-pericarp fruits, because both macroinvertebrates and microbes could access the soft tissue. This expectation was partially confirmed; cut fruits generally decomposed faster and supported higher invertebrate richness, while hard-pericarp fruits resisted decomposition regardless of treatment. In the whole fruit experiment, 785 invertebrates were recorded, dominated by *Endotribelos* (Diptera: Chironomidae; 96%). Abundance was highest in *S. cumini* and lowest in *A. vulgare*, with higher values in coarse-mesh bags. *A. vulgare* had 17× more remaining mass than other fruits, with no mesh-size effects, indicating strong resistance to decomposition. In the cut-fruit experiment, 2715 invertebrates from 14 families were recorded, with *A. vulgare* again showing the highest remaining mass (34× more than other species). The remaining mass did not differ between mesh types, emphasizing microbial activity. Richness was highest in *G. americana* and *A. vulgare* and lowest in *M. indica*. Intact pericarps limited invertebrate access, as richness increased in cut fruits. Both whole and cut fruits can complement leaf litter as an energy source in Amazonian stream food webs.

Keywords Aquatic insects · *Endotribelos* (Chironomidae) · Fruitfall · Organic matter processing

Introduction

Densely shaded forest stream food webs use riparian-produced organic matter as an energy source because there is often little instream primary production (Sánchez-Hernández 2023). Most studies have focused on the importance of decomposing leaf litter, because this input is large and a

relatively continuous energy source for detritivores in head-water streams (Boyero et al. 2021; Cereghetti et al. 2025). Consequently, the consumption of microbially processed leaf litter by macroinvertebrates is well documented in both temperate and tropical streams (Boyero et al. 2016; Marks 2019; Rabelo et al. 2024). Comparative research shows that leaf litter decomposition rates vary widely among riparian species (Sena et al. 2024). These variations in processing rates occur in response to several variables, including leaf traits, water temperature, nutrient concentrations, and the effects of bacteria, fungi, and invertebrates on leaf processing (Graça et al. 2015; Boyero et al. 2016). In addition, leaf decomposition may increase seasonally as nutrient-rich fruits and flowers from riparian sources increase (Rezende et al. 2017).

However, decomposition rates of fruitfall in tropical streams are not well understood. Leaf-litter traits such as thickness, secondary chemical compounds, lignin, and phenol content, and degree of fragmentation alter the rate at

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which fungi and bacteria decompose leaf litter (Graça et al. 2015; Boyero et al. 2016; Gonçalves et al. 2017; Marks 2019). We expected that several of the same traits that influence leaf decomposition (García-Palacios et al. 2016; Ramos et al. 2021) would also likely influence the rate of decomposition of instream fruits. For example, the durability of the fruit pericarp (i.e., outer cover) was expected to initially limit fruit decomposition by limiting microbial and macroinvertebrate access to the soft, fleshy fruit tissue, similar to the way that greater leaf thickness and hardness slow leaf decomposition. In temperate streams, several riparian fruits and seed pods seasonally increase litter inputs and can affect leaf decomposition rates (Madureira and Ferreira 2022; Arcusa et al. 2024; Pereira et al. 2024). In tropical streams such as the Amazon, riparian leaf litter represents 58% to 82% of allochthonous organic matter, while reproductive parts (flowers, fruits, and seeds) account for up to 8% (Tonin et al. 2017).

Although the input of riparian fruit is often relatively low in some streams, many fish species consume fruit seasonally (Kubitzki and Ziburski 1994; Correa et al. 2018; Araujo et al. 2020; Ferreira et al. 2024). In contrast to the detailed studies of fishes feeding on tropical fruits, there are few studies of macroinvertebrates associated with fruit processing (Covich and McDowell 1996; Larned et al. 2001; Covich et al. 2024) or fruit use as food (Coat et al. 2009) and microhabitats (Roque et al. 2005). Relative to leaf fall, asynchronous tropical fruit production among different riparian species can provide complementary food supplements for detritivores, frugivores, and omnivores because the nutrient and caloric content of these fruits is typically higher than that of leaf litter (e.g., Coat et al. 2009). The direct consumption of ripe, fleshy fruits and the microbes associated with them are potentially important dietary supplements at different times of the year (Genini et al. 2009; Morelato et al. 2013). Differences in toughness, sugar content, mineral nutrients (nitrogen and phosphorus), and secondary compounds can slow or accelerate fruit decomposition. Deposition and access to damaged fallen fruit increase when monkeys and birds drop partially eaten fruits from overhanging riparian trees (Sabino and Sazima 1999). Feeding by these vertebrates on overhanging riparian fruit alters fruit availability to the benthos when fish aggregate in response to increased local fruit availability (Sabino and Sazima 1999; Nogueira et al. 2023).

Most previous food-web studies on fruitfall in tropical streams have focused on consumption by fishes and their roles in seed dispersal (e.g., Kubitzki and Ziburski 1994; Araujo et al. 2020; Nogueira et al. 2023). Recent results indicate several fishes prefer fleshy fruits (Correa et al. 2018; Araujo et al. 2020), perhaps because there is a greater diversity of fleshy-fruit species for vertebrate species to select from in tropical ecosystems with high rainfall and stable

warm temperatures (Chen et al. 2017; Nascimento et al. 2020; Ramírez et al. 2021). Coat et al. (2009) reported that fruitfall in the Grande-Anse River, Guadeloupe, included breadfruit, guavas, and mangos that had a higher nutritional value (C:N = 16.3) than the other forms of detritus (C:N = 28.1) in this Caribbean food web. Direct field observations (Resh and Szalay 1995; Fraiola 2006; Covich et al. 2024) have also documented the importance of fruitfall among several species of tropical freshwater macroinvertebrates in different contexts. In addition to the use of decomposing fruit for food, the dominant genus of chironomids (*Endotribelos* Grodhaus, 1987) we observed was previously found to use palm fruit (*Syagrus romanzoffiana* (Chamisso) Glassman) as its habitat (Roque et al. 2005, 2009). These chironomid larvae likely occur widely in other decomposing fruitfall because they are well adapted to low dissolved oxygen concentrations (Roque and Trivinho-Strixino 2008).

Globally, land-use changes have modified natural forests, especially in the tropics (Leal et al. 2020; Firmino et al. 2021; Martins et al. 2021; De Matos et al. 2022). In riparian forests, centuries of human occupation and horticultural practices have left a strong legacy: people selectively removed native vegetation while retaining fruit-producing trees and introducing non-native species that often persisted after abandonment (Clement 2006). As a result, present-day riparian forests throughout the Amazon and other tropical regions frequently contain a mixture of native and exotic fruit trees (Vila-Ruiz et al. 2014; Jung et al. 2018; Levis et al. 2018; Nascimento et al. 2022). Mango (*Mangifera indica* L.), for instance, introduced in the sixteenth century, is now one of the most common riparian species in both urban and rural watersheds (Celentano et al. 2014; dos Santos 2020). In some altered landscapes, non-native fruit trees such as *M. indica* and *Syzygium cumini* (L.) Skeels. represent up to 15% of riparian woody species (Santos et al. 2016).

This combination of native and non-native species creates “legacy riparian forests” with complex spatial and temporal patterns of fruit input to streams. While native fruits may be adapted to local consumers and decomposition pathways, exotic fruits may differ in nutritional content, chemical defenses, or pericarp toughness, potentially altering microbial colonization, decomposition rates, and shredder survival (De Matos et al. 2022). Consequently, the balance between native and exotic inputs can be crucial for sustaining freshwater food webs, because fruitfall contributes to organic matter processing, nutrient cycling, and the maintenance of water quality (Ferreira et al. 2023; Golgher et al. 2023). However, the loss of native riparian forests through deforestation and replacement by plantations threatens this balance (Dala-Corte et al. 2020; Rojas-Castillo et al. 2024). Understanding how native versus non-native fruits are processed in streams is therefore essential to predict the consequences of vegetation change and climate stressors on tropical stream functioning

(Mendoza et al. 2017; Zingel et al. 2024; Hughes et al. 2023). Our objective was to determine how rates of decomposition of riparian fruits vary among riparian species and the differences in macroinvertebrate colonization. Specifically, we hypothesized that (1) fruits with softer pericarps would decompose more rapidly than those with harder, more lignified tissues, (2) cut fruits would decompose faster than whole fruits because fragmentation increases microbial access and invertebrate entry, and (3) species identity would shape macroinvertebrate colonization, with higher richness and abundance expected in fruits with soft tissues and higher nutritional quality. To test this, we selected seven common fruit species from Central Amazonian riparian forests, including five natives (*A. vulgare*, *B. gasipaes*, *M. flexuosa*, *G. americana*, and *T. esculenta*) and two widely introduced species (*M. indica* and *S. cumini*). These species differ markedly in pericarp traits (hard versus soft), providing an ecologically realistic basis for testing our hypothesis.

Material and methods

Study area

The Barro Branco stream is a first-order blackwater tributary of the Cuieiras River, located in the Ducke Reserve (10,000 ha), Central Amazon near Manaus (02°55' S, 59°53' W). The region lies between two contrasting large rivers: the Rio Negro, an acidic, nutrient-poor blackwater river with very low conductivity and inorganic nutrients, and the Rio Amazonas, a nutrient-rich whitewater river carrying high sediment loads from the Andes (Sioli, 1984; Furch, 1984). Small blackwater streams such as Barro Branco are characterized by low nutrient concentrations, acidic waters, and high dissolved organic carbon, reflecting their dependence on riparian litter inputs (Martins et al. 2014). The climate is humid equatorial, with mean annual precipitation of 2286 mm and temperature of 27 °C (Mendonça et al. 2005; Ferreira et al. 2023). The Barro Branco stream is characterized by acidic pH (4.6 ± 0.1), high dissolved oxygen levels (6.6 ± 0.1 mg/L), low electric conductivity (10.7 ± 0.4 µS/cm), and an average water temperature of 24.5 ± 0.5 °C (Martins et al. 2014).

Fruit species

The seven fruit species selected represent common riparian inputs in Central Amazonian streams and include both native and non-native taxa. Among the natives, the palms *Astrocaryum vulgare* (*tucumã*) and *Bactris gasipaes* (*pupunha*) are culturally and economically important, providing fruits for local consumption and regional markets (Pinedo-Vasquez et al. 1990; Clement et al. 2010). *Mauritia flexuosa* (*buriti*) is another widely distributed palm, whose fruits are locally consumed and

traded, while its multiple uses support the livelihoods of riverine communities (Santos and Coelho-Ferreira 2012). *Genipa americana* (*jenipapo*) produces edible fruits used in beverages and jellies and is also valued for medicinal purposes and as a source of natural dyes (Nascimento et al. 2024; Saliba et al. 2024). *Talisia esculenta* (*pitomba*) is consumed throughout Brazil, with fruits rich in phenolic compounds of nutritional and economic relevance (Saliba et al. 2024). The non-native species include *Mangifera indica* (*manga*), one of the world's most cultivated tropical fruits, widely traded in Amazonian markets and with potential ecological impacts through its litter inputs (CABI 2018a; Galán Saúco 2015), and *Syzygium cumini* (*jamelão*), a naturalized tree whose fruits are consumed and used in traditional medicine, but which is also considered invasive in many tropical regions (Ayyanar and Subash-Babu 2012; Qamar et al. 2022; CABI 2018b).

Procedures

We conducted two experiments between November 2022 and January 2023 in the Barro Branco stream using whole fruits and cut fruits (simulating monkey and bird effects). In the whole fruit experiment, we used whole fruits of *A. vulgare*, *B. gasipaes*, *M. indica*, *M. flexuosa*, *S. cumini*, and *T. esculenta*. In the cut-fruit experiment, we used cut fruits of *A. vulgare*, *B. gasipaes*, *G. americana*, *M. indica*, *M. flexuosa*, and *T. esculenta*. *S. cumini* was only included in the whole fruit experiment because its relatively soft pericarp and small fruit size caused it to disintegrate when cut, making it unsuitable for retention in the coarse mesh litter bags. In contrast, *G. americana* has large fruits, and using whole fruits in the experiment may result in higher organic matter content compared with other species. The whole and cut fruits were dried at room temperature and then weighed on precision balances (accuracy=0.01 mg). To determine the initial mass, ten pieces of each fruit species were used to calculate a correction factor (CF). The CF was calculated using the formula $CF = \text{mean ODMi} / \text{mean ADMi}$; where ODMi is the oven-dried (60 °C for 72 h) mass and ADMi is the air-dried mass. We oven-dried fruits after removal from the streams to determine the final mass.

In the whole-fruit experiment, we used 72 litter bags (3 bags per species $\times$ 2 removal dates $\times$ 2 mesh sizes $\times$ 6 species), with 3 bags per species removed at 15 and 62 days. In the cut-fruit experiment, we used 144 litter bags (3 bags per species $\times$ 4 removal dates $\times$ 2 mesh sizes $\times$ 6 species), each containing fruit from a single species. Three bags per species were collected at 4, 15, 30, and 62 days. Litter bags were removed, individually placed in plastic bags, and transported in insulated containers to the laboratory, where they were placed in a refrigerator (4 °C) until the time of processing. Microbial decomposition was inferred indirectly from fine-mesh litterbags, which excluded macroinvertebrates and thus isolated microbial activity (Boyero et al., 2011; Pérez et al., 2025).

In the Laboratório de Citotaxonomia e Insetos Aquáticos—LACIA at the Instituto Nacional de Pesquisas da Amazônia—INPA, located in Manaus about 26 km (~40 min by car) from the study stream, fruits were washed over a 120- μ m mesh sieve, and all retained invertebrates were preserved in 70% ethanol for identification at low taxonomic level using Amazonian taxonomic keys (Hamada and Ferreira-Keppler 2012; Hamada et al. 2019). Taxon richness was defined as the number of distinct taxa (genus or family when genus-level identification was not possible) recorded per litterbag, while abundance corresponded to the total number of individuals of all taxa combined. Both metrics were calculated separately for each litter bag.

Data analyses

We calculated the fruit decay coefficient (k) using the negative exponential model: $k = -(\ln [\text{final mass}/\text{initial mass}]/\text{time})$. Mass was expressed in grams and time in days (Petersen and Cummins 1974). Remaining mass (%) was calculated using the formula: $\text{RM} (\%) = (\text{FM}/\text{IM}) \times 100$, where IM is the initial dry mass of the fruit and FM is the final dry mass after removal from the litter bags. For both the cut-fruit and whole-fruit experiments, to evaluate the effects of fruit species and litter bag mesh size on remaining mass, invertebrate richness, and abundance, we fitted generalized linear models (GLMs). Remaining mass (proportional data) was analyzed using a GLM with a quasibinomial distribution and logit link. Richness and abundance (count data) were analyzed with GLMs assuming a quasi-Poisson distribution and log link to account for overdispersion relative to the Poisson assumption.

Model significance was assessed with type III likelihood-ratio tests using the car package (Fox and Weisberg 2019). When significant main effects or interactions were detected, post hoc pairwise comparisons were performed with estimated marginal means (EMMs) and Tukey's adjustment, using the emmeans package (Lenth 2024). Model assumptions were verified by inspection of residuals, dispersion parameters, and goodness-of-fit diagnostics. All analyses were conducted in R version 4.4.1 (R Core Team 2024).

Results

Whole-fruit experiment

Remaining mass

In the whole fruit experiment, the fruit decomposition rate (k) ranged from -0.063 (*M. flexuosa*) to -0.007 d^{-1} (*A. vulgare*) in coarse mesh bags (see Table S1) and from -0.050 (*B. gasipaes*) to -0.007 d^{-1} (*A. vulgare*) in fine mesh bags. At the end of the experiment, the remaining mass of *A. vulgare* ($65.8 \pm 8.3\%$) was up to 17 times higher

than that of the other fruit species (Fig. 1 and Table 1). Overall, the remaining mass was slightly higher in fine mesh bags ($19.5\% \pm 21.5\%$) compared with coarse mesh bags ($15.4\% \pm 24.0\%$). A significant interaction effect was observed between fruit species and litter bag mesh size on the remaining mass (Table 1). For *A. vulgare*, the remaining mass was similar for both mesh sizes, whereas for other fruit species, the remaining mass was up to three times higher in the fine mesh bags (Fig. 1).

Invertebrate abundance

We recorded a total of 785 invertebrates from eight families in the orders Coleoptera, Diptera, Plecoptera, Trichoptera, and Decapoda (Supplementary Table S2). *Endotribelos* (Diptera: Chironomidae) comprised 96% of the collected invertebrates and was the dominant taxon across all fruit species. After 62 days, the mean abundance of invertebrates was higher in *S. cumini* (18.0 ± 37.8 individuals; Fig. 2 and Table 1) and lower in *A. vulgare* (11.2 ± 21.1 individuals). Invertebrate abundance was similar in coarse (7.9 ± 22.3 individuals) and fine mesh bags (5.2 ± 6.6 individuals). A significant interaction effect was found between fruit species and litter bag mesh size on invertebrate abundance (Table 1). *A. vulgare* showed higher abundance in fine mesh bags. For *M. indica*, *M. flexuosa*, *B. gasipaes*, and *T. esculenta*, abundances were similar between mesh types. In contrast, *G. americana* had higher abundance in coarse mesh (Fig. 2).

Invertebrate richness

At the end of the experiment (62 days), invertebrate richness was higher in *M. indica* but similar across litter bag mesh sizes (Fig. 3 and Table 1). However, a significant interaction effect between fruit species and litter bag mesh size on invertebrate richness was observed (Table 1). Specifically, mean richness was higher in coarse mesh bags for *M. flexuosa* and *S. cumini*. Conversely, mean richness was higher in fine mesh bags for *A. vulgare*, *M. indica*, *B. gasipaes*, and *T. esculenta*. For *M. indica*, richness was similar between mesh types (Fig. 3).

Cut-fruit experiment

Remaining mass

In the cut-fruit experiment, the fruit decomposition rate (k) ranged from -0.109 (*M. indica*) to -0.011 d^{-1} (*A. vulgare*) in the coarse mesh bags (see Table S1) and from -0.076 (*M. indica*) to -0.012 d^{-1} (*A. vulgare*) in the fine mesh

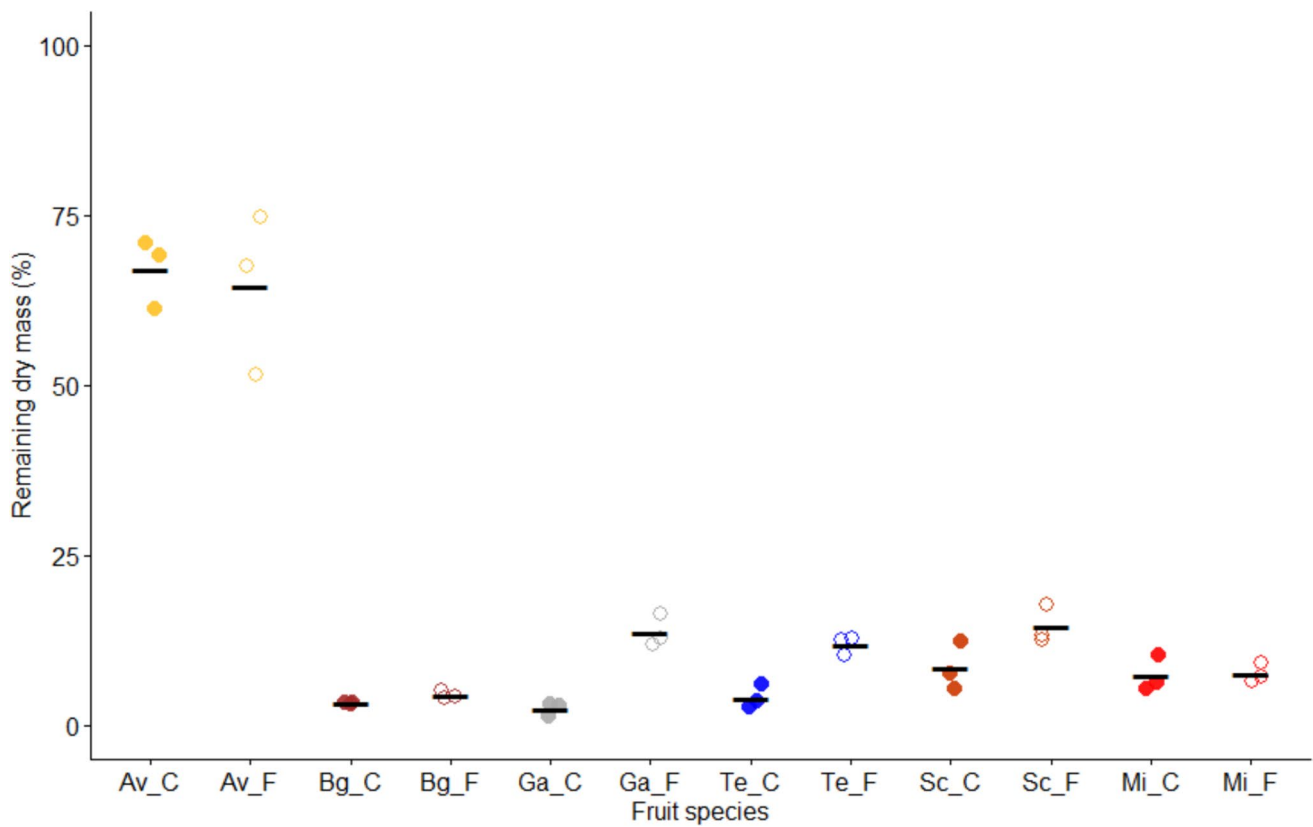


Fig. 1 Remaining dry mass (%) of whole-fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

Table 1 Summary of statistical results (generalized linear models and Tukey tests) for remaining mass, invertebrate abundance, and richness in the whole-fruit experiments

	DF	χ^2	P	Tukey
Remaining mass (%)				
Spp	5.24	909.67	< 0.001	AV > SC = MF = TE = MI = BG
Mesh	1.24	22.39	< 0.001	Fine > coarse
Spp:Mesh	5.24	30.62	< 0.001	
Abundance				
Spp	5.24	8.09	0.151	SC = MI = TE = AV = BG = MF
Mesh	1.24	0.20	0.991	Coarse = fine
Spp:Mesh	5.24	19.73	0.001	
Richness				
Spp	5.24	13.80	0.017	MI > AV = BG = MF = SC = TE
Mesh	1.24	0.99	0.840	Coarse = fine
Spp:Mesh	5.24	13.34	0.020	

The bold values indicate statistically significant effects ($P < 0.05$)

Spp, fruit species; Mesh, litter bag mesh size; AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

bags. Significant differences were observed in the remaining mass between fruit species at the end of the 62-day experiment (Table 2). The remaining mass of *A. vulgare* (mean $\pm$ SD: $23.1 \pm 5.2\%$) was up to 34 $\times$ higher than that

of other fruit species (Fig. 4 and Table 2). The remaining fruit mass did not differ significantly between coarse ($6.8 \pm 10.8\%$) and fine mesh bags ($5.7 \pm 8.2\%$). However, a significant interaction effect was found between fruit

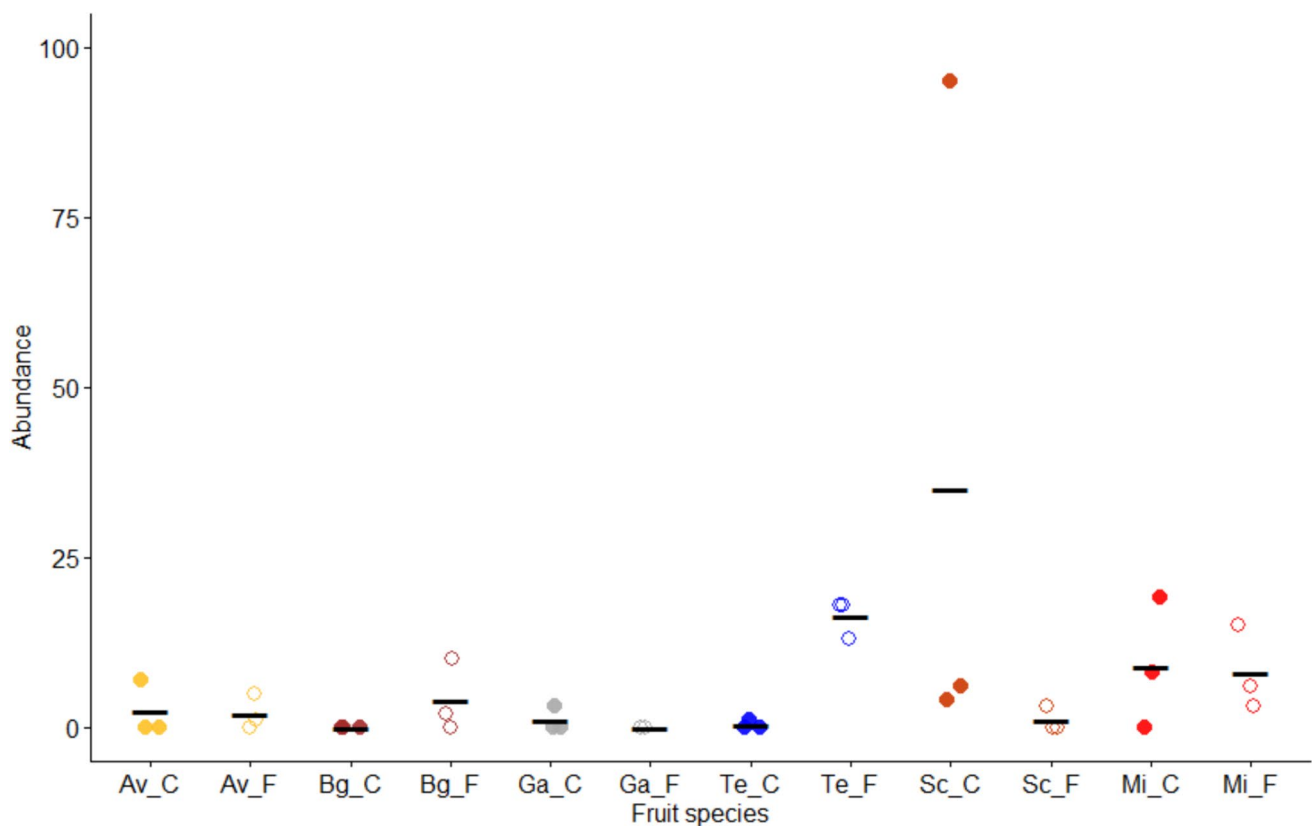


Fig. 2 Invertebrate abundance on whole fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

species and litter bag mesh size on the remaining mass (Table 2). For *A. vulgare* and *S. cumini*, the remaining mass was up to 1.3× higher in coarse mesh bags, whereas for *T. esculenta* and *M. indica* it was up to 2× higher in fine mesh bags. In addition, for *B. gasipaes* and *G. americana*, the remaining mass was 10 and 16 times higher in fine mesh bags, respectively (Fig. 4).

Invertebrate abundance

We recorded a total of 2715 invertebrates from 14 families across the orders Coleoptera, Diptera, Ephemeroptera, Trichoptera, and Decapoda (Supplementary Table S2). *Endotribelos* (Diptera: Chironomidae) constituted 98% of the collected invertebrates and was the predominant taxon across all fruit species. At the end of the 62-day experiment, the mean abundance of invertebrates differed significantly among fruit species (Fig. 5 and Table 2). The higher mean abundances were observed for *G. americana* (14.2 ± 28.0 individuals) and *A. vulgare* (11.2 ± 21.1 individuals). Invertebrate abundance was significantly higher

in fine mesh bags (5.9 ± 16.3 individuals) compared with coarse mesh bags (0.8 ± 2.4 individuals). A significant interaction effect was not observed between fruit species and litter bag mesh size on invertebrate abundance (Table 2). Invertebrates were more abundant in *A. vulgare* in fine mesh bags, while *G. americana* had higher values in coarse mesh bags; the difference exceeded 17 individuals in both cases. In contrast, other species exhibited similar abundances across mesh types. (Fig. 5).

Invertebrate richness

At the end of the experiment (62 days), invertebrate richness varied significantly among fruit species (Fig. 6 and Table 2). Higher mean richness was observed in *G. americana* (1.0 ± 0.6 species) and *A. vulgare* (0.8 ± 0.6 species), while *M. indica* had the lower mean richness (0.1 ± 0.3 species). Richness was similar between coarse mesh bags (0.4 ± 0.7 species) and fine mesh bags (0.6 ± 0.7 species). In addition, the interaction effect between fruit species and litter bag mesh size on invertebrate richness was not significant (Table 2).

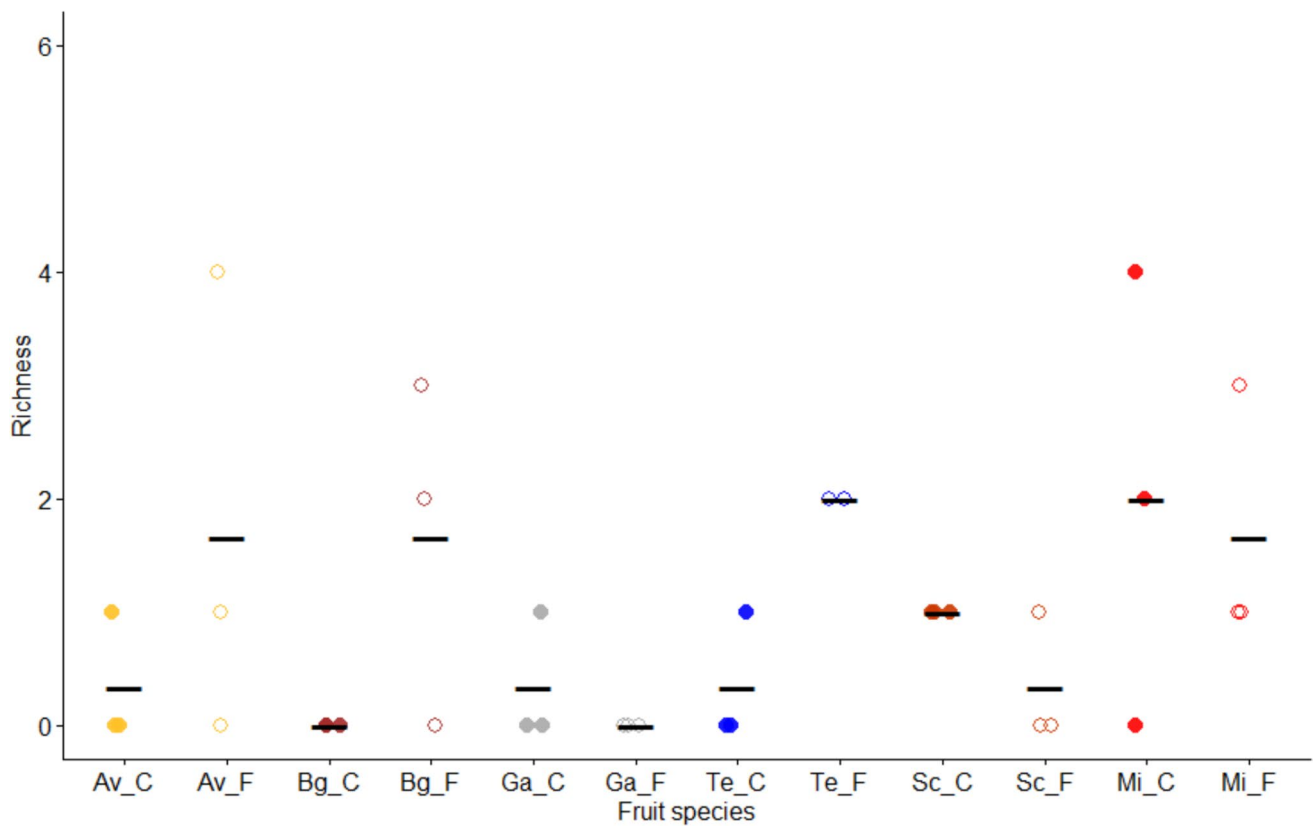


Fig. 3 Invertebrate richness on whole-fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

Table 2 Summary of statistical results (generalized linear models and Tukey tests) for remaining mass, invertebrate abundance, and richness in the cut-fruit experiment

	DF	χ^2	P	Tukey
Remaining mass (%)				
Spp	5.76	1422.42	< 0.001	AV > BG = GA = MI = SC = TE
Mesh	1.76	14.90	0.060	Coarse = fine
Spp:Mesh	5.76	25.43	< 0.001	
Abundance				
Spp	5.76	13.69	0.018	GA = AV > SC = BG = TE = MI
Mesh	1.76	3.71	0.491	Fine > coarse
Spp:Mesh	5.76	1.09	0.855	
Richness				
Spp	5.76	14.56	0.012	GA = AV > SC = BG = TE > MI
Mesh	1.76	5.63	0.218	Coarse = fine
Spp:Mesh	5.76	8.16	0.148	

The bold values indicate statistically significant effects ($P < 0.05$)

Spp, fruit species; Mesh, litter bag mesh size; AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

Comparison of the cut-fruits × whole-fruits experiments

At the end of the experiment, significant differences were observed between whole and cut fruits in terms of remaining

mass, invertebrate abundance and richness. The mean remaining mass of whole fruits ($19.3 \pm 24.2\%$) was three times higher than that of cut fruits ($6.4 \pm 9.6\%$; $F_{1,111} = 16.66$; $p < 0.001$). Similarly, the mean abundance of invertebrates was significantly higher on whole fruits (7.8 ± 17.6 individuals) compared

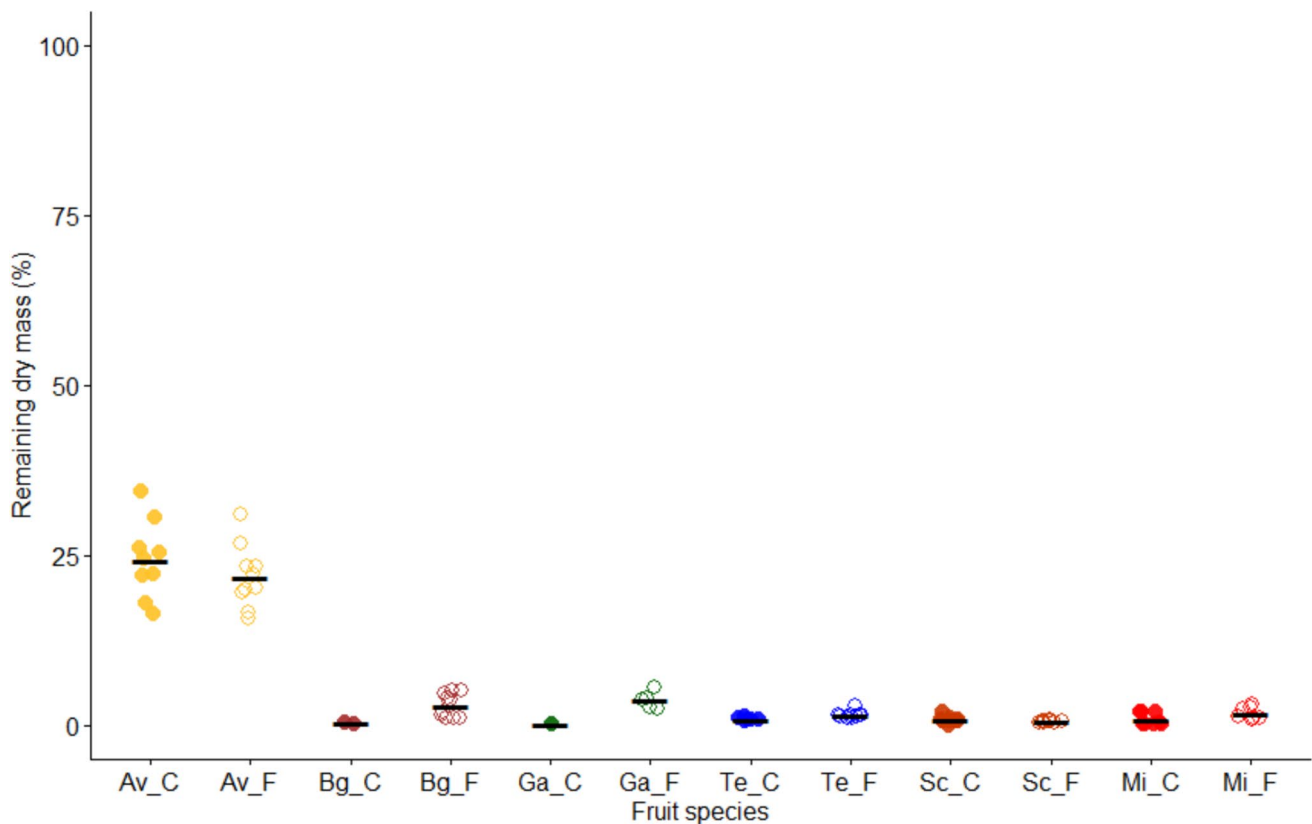


Fig. 4 Remaining dry mass (%) of cut-fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

with cut fruits (3.2 ± 11.1 individuals; $F_{1,111} = 2.95$; $p = 0.048$). In addition, the mean richness of invertebrates associated with whole fruits (1.1 ± 1.2 species) was higher than in cut fruits (0.5 ± 0.7 species; $F_{1,111} = 30.80$; $p < 0.001$).

Discussion

Our results indicate that fruit decomposition in Amazonian streams is strongly influenced by species-specific traits, supporting our initial expectation that fleshy fruits with thin pericarps decompose more rapidly than those with harder tissues. *Astrocaryum vulgare* showed markedly higher remaining mass compared with other species, reflecting its rigid pericarp and high content of phenolic compounds (Kahn and Millán 1992; CABI 2022; Machado et al. 2021), which likely reduce microbial colonization and restrict macroinvertebrate access. In contrast, *Syzygium cumini* and *Genipa americana* showed rapid mass loss and greater invertebrate colonization. Their soft mesocarps, high moisture and sugar content, and low fiber rigidity favor microbial activity and invertebrate entry (Bakewell-Stone 2022; Kumar et al. 2023). These traits, combined with lower concentrations of

secondary compounds, can enhance palatability and result in faster decomposition (Graça 2001; Martins et al. 2025).

The structural integrity of the fruit significantly influenced both the decomposition rate and the composition of the invertebrate community. Whole fruits decomposed more slowly over 62 days and supported greater invertebrate abundance and richness than cut fruits. The intact pericarp likely acts as a physical barrier that delays microbial and shredder activity, thereby extending resource availability. In contrast, cut fruits decomposed faster owing to the exposed mesocarp, which facilitates decomposer access. While cut fruits decomposed rapidly, whole fruits created more persistent and heterogeneous microhabitats, promoting higher species richness. Additionally, the slower decomposition observed in whole fruits may partly be due to the persistence of undecomposed seeds, which could have slightly underestimated fruit mass loss. These findings underscore the role of natural mechanical disturbances in shaping the pace and pathways of organic matter decomposition in tropical streams.

Our field experiment is the first to quantify processing rates of tropical fruits and to document the differences among species of macroinvertebrates associated with fruit-fall. All seven types of fruits in our study decomposed faster than most leaves of the 53 riparian species previously

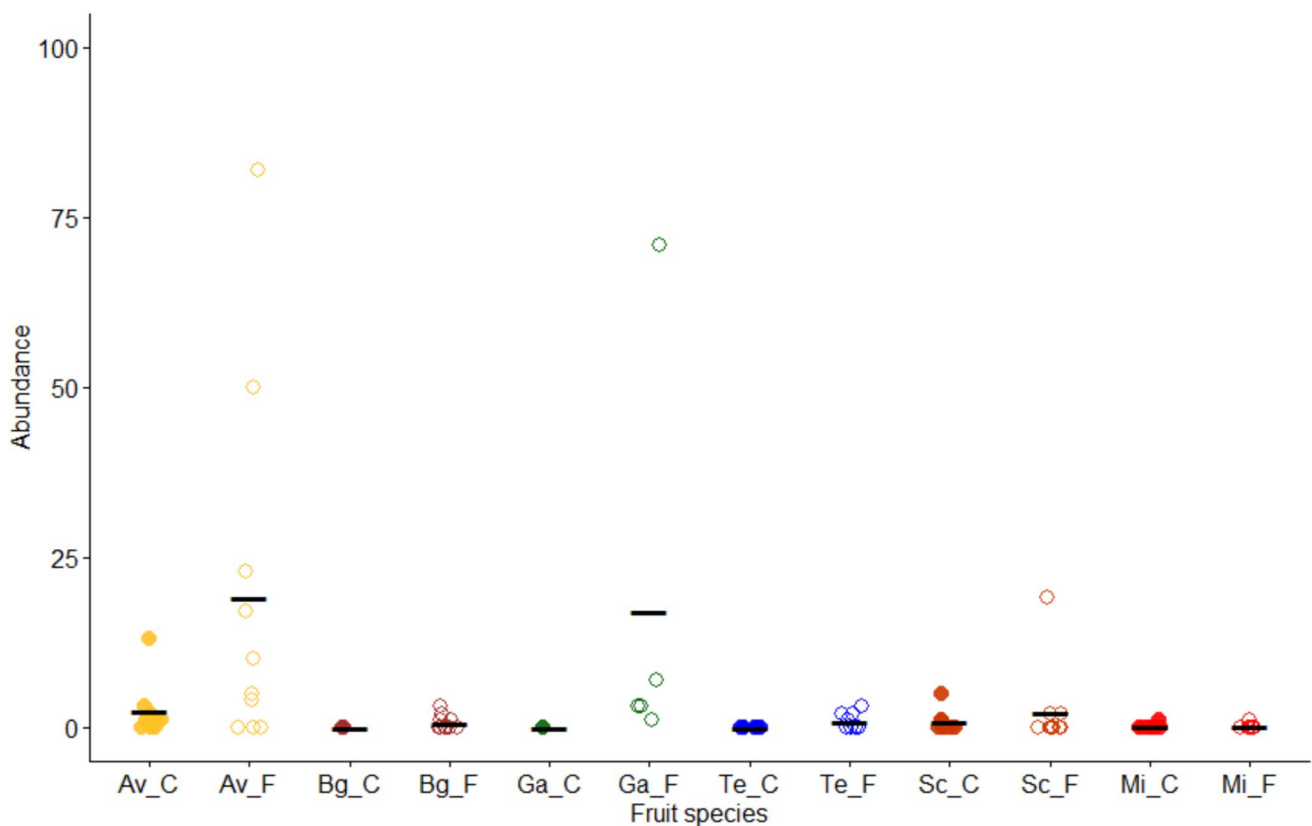


Fig. 5 Invertebrate abundance on cut-fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bactris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

studied from Manaus in similar Amazonian streams (Martins et al. 2020). Our study also provides the first observations on the role of biotic colonization of intact and cut fruits in a tropical stream. As expected, both whole- and cut-fruits decomposed rapidly. Differences in decomposition among fruit species may also be linked to fruit chemistry, since many tropical fruits contain compounds such as flavonoids and anthocyanins that can inhibit microbial activity (Sudheeran et al. 2020; Yadav et al. 2022). Although we did not measure chemical composition or microbial groups directly, such traits could help explain the persistence of certain species and highlight the importance of future studies integrating decomposition experiments with chemical and microbial analyses.”

As expected, the mesh size of the bags affected the remaining mass, which varied among fruit species. *Talisia esculenta*, *Mangifera indica*, *Bactris gasipaes*, and *Genipa americana* had a significantly higher remaining mass in fine-mesh bags. This pattern could result because: (1) macroinvertebrates play a key role in processing these fruits owing to their general ability to break down larger materials or (2) fine mesh bags retain particles more effectively, which could lead to an underestimation of mass loss in this treatment. No significant differences were observed between mesh types

in *Astrocaryum vulgare*, supporting the hypothesis that its hard pericarp physically limits shredder access, resulting in predominantly microbial-driven decomposition. Invertebrate abundance was affected by the interaction of litterbag mesh size and fruit species. *A. vulgare* showed higher abundance in fine-mesh bags, suggesting that predator exclusion and microhabitat stabilization may favor colonization by small-bodied detritivores (Lecerf 2017). Conversely, the higher invertebrate abundance in *G. americana* in coarse-mesh bags may reflect the greater water circulation, oxygenation, and biofilm development typically associated with larger mesh size, which can enhance microbial activity and invertebrate colonization (Boulton and Boon, 1991), such as *Endotribelos*. In contrast, invertebrate richness was more influenced by the fruit species. In the whole-fruit experiment, *M. flexuosa* and *S. cumini* had higher richness in coarse mesh bags, while *A. vulgare*, *M. indica*, *B. gasipaes*, and *T. esculenta* had higher richness in fine mesh bags.

The dominance of *Endotribelos* in all species during fruit decomposition experiments corroborates previous studies. Roque et al. (2005) demonstrated that *Endotribelos* larvae are primary colonizers of fallen fruits in Atlantic Forest streams. These larvae are likely favored by the nutrient-rich, sheltered conditions within fruit tissue. These

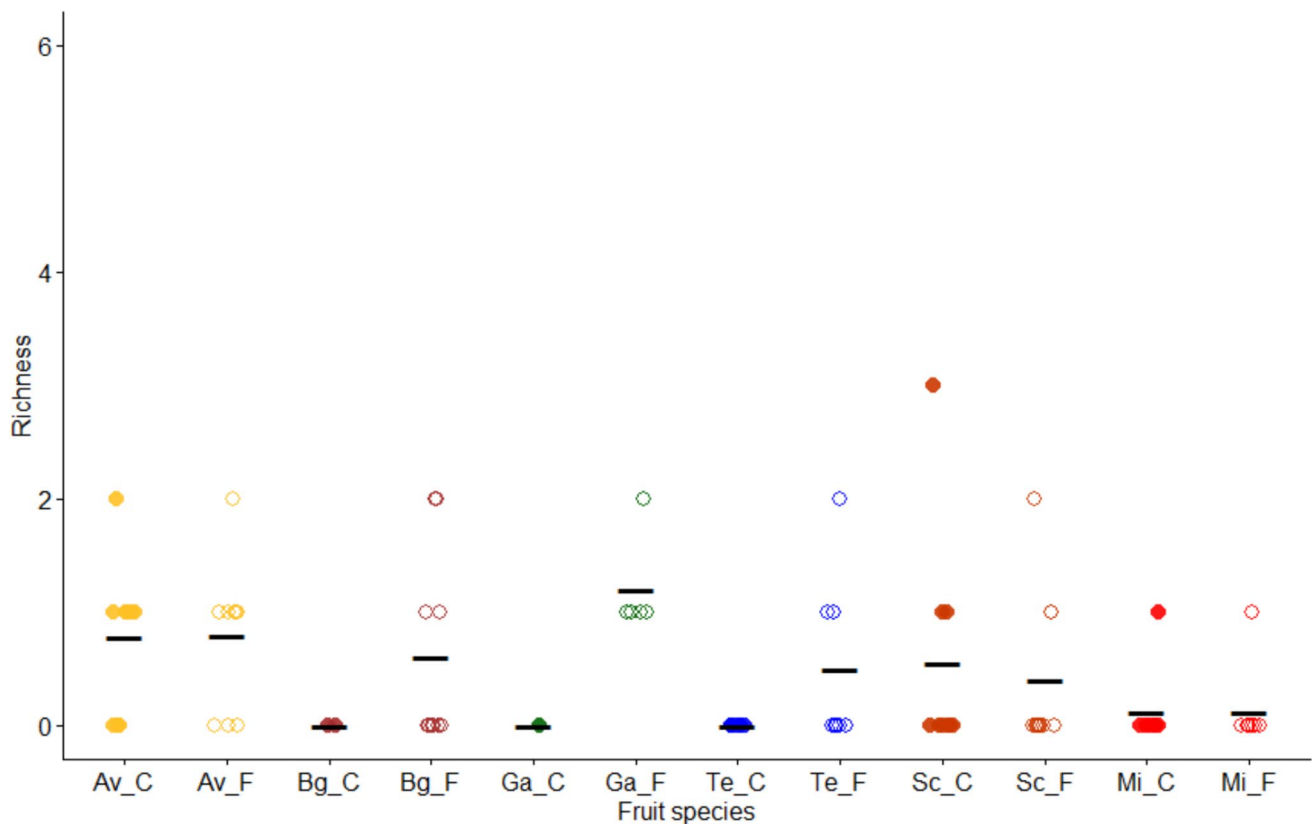


Fig. 6 Invertebrate richness on cut-fruits in coarse (c) and fine (f) mesh litterbags in an Amazonian stream. AV, *Astrocaryum vulgare*; BG, *Bac-tris gasipaes*; MI, *Mangifera indica*; MF, *Mauritia flexuosa*; SC, *Syzygium cumini*; TE, *Talisia esculenta*

larvae can inhabit various substrates, including macrophytes and detritus, but especially submerged fallen fruits in low-order streams in the Atlantic Forest and the Amazon region (Roque and Trivinho-Strixino 2008). Roque et al. (2009) found that densities of this frugivorous chironomid decline in riparian areas with degraded forest cover, highlighting their reliance on intact forest cover. -->

Our findings demonstrate that riparian fruits can serve as an important energy source, but often neglected, component of detrital energy flow in tropical streams. Although leaf litter is a more continuous input, fruitfall contributes nutrient-rich, labile carbon that supports microbial growth and drives secondary production. The contrasting decomposition patterns observed among fruit species reinforce the idea of functional complementarity in food webs (Poisot et al. 2013). Fruits that decompose slowly, such as *A. vulgare* palm, remain in the stream for a long time; these fruits may provide sustained habitat and food for specialist detritivores. Conversely, species such as *S. cumini* decompose rapidly, releasing nutrients in short pulses. Together, these complementary resource dynamics enhance the temporal and trophic heterogeneity of stream ecosystems. This functional complementarity increases the temporal and trophic

heterogeneity of detrital pathways, with implications for carbon retention, nutrient turnover, and higher-level consumers.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-026-01267-6>.

Acknowledgements APC thanks the Instituto Nacional de Pesquisas da Amazônia for their logistical support and hospitality. We are grateful to the Brazilian National Council for Scientific and Technological Development (CNPq) for granting a research productivity fellowship to NH (307134/2025-3). RTM received a Postdoctoral Fellowship (PDS) from CNPq (process no. 101112/2024-6). We additionally acknowledge support from the POSGRAD Program of FAPEAM and the INCT ADAPTA III funded by CNPq—Brazilian National Research Council (409202/2024-0) and CAPES—Coordination for the Improvement of Higher Education Personnel. This research was further supported by grants from CNPq, including the Universal Research Project (process no. 403758/2021-1) and the Scientific Expeditions—Amazon+10 Initiative (process no. 400700/2024-7). Support for APC from the Fulbright Commission in Brazil is gratefully acknowledged.

Author contributions RTM, RBPG, ISR, and APC were responsible for the study's conceptual design and data collection. RTM, RBPG, and APC prepared the initial draft of the manuscript. RTM, RBPG, ISR, NH and APC contributed to the revision process and approved the final version for submission.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento

de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). Conselho Nacional de Desenvolvimento Científico e Tecnológico, 101112/2024-6, 307134/2025-3, Fulbright Association

Data availability Data are provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

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