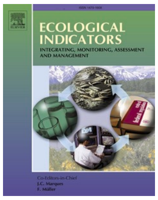
Ecological Indicators 154 (2023) 110819

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Agricultural impacts on lowland tropical streams detected through leaf litter decomposition

Javier Pérez [a,b,1], Luz Boyero [a,b,c], Ana Raquel Tuñón [d], Brenda Checa [e], Francisco Correa-Araneda [f], Alisson Guerra [a], Anyi Tuñón [a], Dania Castillo [a], Edgar Pérez [a], Gabriela García [a], Randhy Rodríguez [a], Aydeé Cornejo [a,b,g,1,*]

[a] *Ecology and Aquatic Ecotoxicology Laboratory. Research Center for Emerging and Zoonotic Diseases, Gorgas Memorial Institute of Health Studies, 0816-02593, Divisa, Veraguas Province, Panama*
[b] *Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), Leioa, Spain*
[c] *IKERBASQUE, Bilbao, Spain*
[d] *Environmental Quality Laboratory of the Ministry of Environment, Panama City, Panama*
[e] *Pesticide Residue Laboratory, Agricultural Development Ministry (MIDA), Panama City, Panama*
[f] *Unidad de Cambio Climático y Medio Ambiente (UCCMA), Instituto Iberoamericano de Desarrollo Sostenible (IIDS), Universidad Autónoma de Chile, Temuco, Chile*
[g] *National Research System of Panama, Panama*

ARTICLE INFO

Keywords:
Anthropogenic impacts
Eutrophication
Leaf litter breakdown
Functional indicators
Panama
Pesticide toxicity
Tropical latitudes

ABSTRACT

Stream ecosystems are highly vulnerable to changes in land use and vegetation in their catchments for two reasons: firstly, they receive inputs of nutrients, contaminants and sediments through runoff; and secondly, terrestrial leaf litter is the major basal resource supporting their food webs. Leaf litter decomposition by microorganisms and detritivores is thus a key stream ecosystem process, and a valuable functional indicator of impacts associated to agriculture and other alterations of human origin. Here, we investigated the joint effects of land use changes associated to agriculture (low, medium and high intervention areas: LI, MI and HI, respectively) in a tropical lowland catchment in Panama, through a decomposition experiment using three leaf litter types differing in nativeness (*Ficus insipida*, native to the study area; *Alnus acuminata*, native to Panama but not present in the study area; and *Musa balbisiana*, exotic to Panama). Lowland tropical areas are often poor in litter-consuming detritivores, and we accordingly observed a high contribution of microorganisms to total decomposition (>60% on average). However, only in the presence of detritivores, decomposition of *Alnus* discriminated among different degrees of agricultural intervention, being higher at the LI area. Leaf litter of the native *Ficus* showed higher microbial decomposition than the other types, possibly in relation to a home-field advantage effect. Despite the scarcity of detritivores in tropical lowland streams compared to tropical highland or temperate streams, our study indicates that their activity reflects impacts of land use change on these streams and they should therefore be included in assessments of anthropogenic impacts.

1. Introduction

Agriculture is a major cause of land transformation globally, ever since human population growth and food production dramatically increased as a result of the Industrial Revolution (Taylor and Rising, 2021). Such changes in land use have produced significant alterations in ecosystems and biodiversity (Raven and Wagner, 2021), so much that they are considered a primary cause of the sixth mass extinction (Lewis, 2006). Agricultural land nowadays occupies ca. 40% of the Earth's land surface (Graeber et al., 2015), and tropical biomes are among the most impacted because of their very high rates of land conversion (Gibbs et al., 2010), with tropical deforestation contributing enormously to global warming (Roe et al., 2019). While tropical forests cover ca. 10% of the Earth's land surface, they are of prime global importance because they store and process large amounts of carbon and host up to two-thirds of the world's biodiversity (Lewis, 2006).

The conversion of forests into agricultural land often occurs associated to the introduction of exotic plant species (Boscutti et al., 2018).

---

[*] Corresponding author.
E-mail address: acornejo@gorgas.gob.pa (A. Cornejo).
[1] J.P. (0000-0001-6305-4151) and A.C. (0000-0001-6789-5847) equally contributed to this work.

https://doi.org/10.1016/j.ecolind.2023.110819
Received 26 May 2023; Received in revised form 11 August 2023; Accepted 14 August 2023

These can be either crop species (Maracahipes-Santos et al., 2020), or invaders that occupy the niche of removed native plants (Waddell et al., 2020). Impacts of exotic plants on ecosystems can thus add up to those of land use changes, with possible interactive effects of both factors, which may be additive but could also be synergistic or antagonistic (Jackson et al., 2016). Stream ecosystems are particularly affected by the above factors because they often rely on terrestrial plant litter inputs to support their food webs (Wallace et al., 1997) and also because they receive inputs of nutrients, contaminants and sediments associated to agriculture (Cornejo et al., 2019b). As a result of land conversion to agriculture, tropical stream communities can be impacted (Cornejo et al., 2019b) and ecosystem functioning altered (Cornejo et al., 2020b). Similarly, exotic plants can affect stream communities and key ecosystem processes (Ferreira et al., 2018), but the simultaneous effects of both factors on stream ecosystems is unknown in the tropics and elsewhere, to our knowledge.

Here, we investigated the combined effects of land use change associated to agriculture and the presence of exotic plant species on stream ecosystem functioning in a tropical catchment, by means of the key process of leaf litter decomposition (von Schiller et al., 2017), which represents a functional indicator of ecosystem integrity (Mollá et al., 2017; Pérez et al., 2021b), being sensitive to nutrient enrichment (Ferreira et al., 2015; Gulis and Suberkropp, 2003), pesticides (Cornejo et al., 2020a; Rasmussen et al., 2012), and other stressors associated to agricultural intervention (Bruder et al., 2016; Cornejo et al., 2020b). We measured not only total decomposition, but also microbial and detritivore-mediated litter decomposition, given that the relative contribution of these two processes is often a good indicator of how the stream ecosystem is impacted by environmental change (Gessner and Chauvet, 2002).. We measured decomposition experimentally in streams affected by several degrees of agricultural intervention within the study catchment (low, medium and high; LI, MI and HI, respectively) using litter from three riparian plant species: one native species widespread in the study catchment; one species native to Panama but not present in the study catchment; and one exotic species. Additionally, we examined the assemblages of microbial decomposers and litter-consuming detritivorous invertebrates, in order to detect biological changes associated to functional changes, as well as whole invertebrate assemblages, which can provide additional information about the impact of the studied stressors (Cornejo et al., 2019b).

We hypothesized that (1) microbial decomposition would increase with agricultural intervention degree (PI < MI < HI), in direct relation to nutrient enrichment associated with this gradient (Ferreira et al., 2015; Smith and Schindler, 2009). We also predicted that (2) decomposition mediated by detritivores would decrease with agricultural activity (PI > MI > HI), in direct relation to a decrease in detritivore abundance and diversity provoked by the higher concentration of pesticides and increased sedimentation in more impacted streams (Cornejo et al., 2020b; Cornejo et al., 2019b). Given that litter decomposition in tropical streams is often predominantly microbial (Boyero et al., 2011b), we expected (3) greater effects on microbial than on detritivore-mediated decomposition, and thus that changes in total decomposition would reflect changes in microbial decomposition. Finally, we predicted that (4) plant species would differ in their capacity to reflect impacts of land use change depending on their degree of nativeness (being greatest in the species widespread in the study catchment and lowest in the exotic species), due to a home-field advantage effect, although this effect could be obscured by differences in litter traits among species (Fugère et al., 2020; Luai et al., 2019).

2. Material and methods

2.1. Study area and site selection

Our study area was the Panama Canal catchment, which is located between the latitudes 8° 38′ and 9° 31′ N and the longitudes 79° 15′ and 80° 06′ W (ANAM, 2013), in the Central Water Region of Panama (Fig. 1), being all study sites located within a 25-km radius. The catchment area is 3,338 km^2 and it flows into the Caribbean Sea. It includes three climatic types (very humid tropical, humid tropical and tropical savannah) and has an average annual precipitation of 2,700 mm, with a rainy season from March to November and a dry season from January to March (ACP, 2007). Agriculture is practiced in different parts of the catchment, including crops of corn, rice, vegetables, tubers, citrus, plantain, banana, other fruits, and coffee (ACP, 2008; Cornejo et al., 2017).

We conducted our study in February – March 2022 on the western part of the catchment, which contains areas with three clearly differentiated degrees of intervention (Table 1): a protected area with low intervention (LI), an area with moderate intervention (MI) and an area with high intervention (HI). Within each of these areas, we selected three representative stream sites (all 1st or 2nd order independent streams), which did not differ in altitude (LI, 34 – 54 m asl; MI, 46 – 145 m asl; HI, 43 – 96 m asl) but showed differences in riparian canopy vegetation cover (LI, > 70%; MI, 40 – 69%; HI, < 39%) and plant riparian species richness (LI, > 40 species; MI, 21 – 40 species; HI, < 10 species). At each site, we selected a 100-m representative stream reach where we characterized the habitat and water physicochemistry, collected samples, and conducted a leaf litter decomposition experiment as described in the sections below.

2.2. Site characterization

At each site, we visually estimated riparian vegetation cover (%) and plant species richness. We measured *in situ* the pH, temperature (°C), conductivity (μS cm^{-1}), turbidity (mg L^{-1}) and dissolved oxygen (mg L^{-1} and % saturation) using a multiparametric probe (YSI 556), and collected two different sets of water samples that were transported to the laboratory on ice. The first set was analysed for concentrations (mg L^{-1}) of total solids (method SM 2540B), biochemical oxygen demand (SM 5210B), total and fecal coliforms (SM 9222B, 9222 D), and nitrate and soluble reactive phosphate (SM 4500-NO$_3$ B and SM 4500-P B5 and E) (Rice et al., 2012).The second set was kept at 4 °C and analysed within 24 h for pesticides (see Supplementary Methods for more information). Based on the habitat variables we calculated the Panamanian water quality index, ICA (Dinius, 1972; Ortega-Samaniego et al., 2022) and the Habitat quality index (Cornejo et al., 2019a) for each site.

We sampled benthic invertebrates at each site using a 30-cm wide, 0.5 mm mesh D-net, on day 28 of the experiment described below. We used a multihabitat sampling approach, which proportionally covered the main habitats present at the site, with a total of twenty 0.5-m sampling units (or 3 m^2) per site (Barbour et al., 1999; Cornejo et al., 2019b). Net contents were filtered through a 0.5-mm sieve and placed in a white tray first, where coarse substrate was discarded, and then in a 500-mL bottle with 96% ethanol. Invertebrates were identified to the lowest possible taxonomic level using available literature (Beketov et al., 2009; Gutiérrez-Fonseca, 2010; Hawkes, 1998; Menjivar Rosa, 2010; Ramírez and Gutiérrez-Fonseca, 2014; Tomanova et al., 2006; Pacheco-Chaves, 2010; Springer et al., 2010), and separated into litter-consuming detritivores and other invertebrates under a stereoscopic microscope in the laboratory. Based on these data, we calculated the BMWP/PAN index for each site (Cornejo et al., 2019b).

2.3. Litter decomposition experiment

We conducted the experiment using three riparian tree species widespread in Panama, including one native and widespread in the study catchment [*Ficus insipida* Willd., (Moraceae)], one native to Panama but not present in the study catchment [(*Alnus acuminata* Kunth. (Betulaceae)], and one exotic [(*Musa balbisiana* L. (Musaceae)]; hereafter *Ficus*, *Alnus* and *Musa*. Litter quality was assessed through specific leaf area [SLA; the ratio of leaf area (mm^2) to leaf dry mass (DM; mg)],

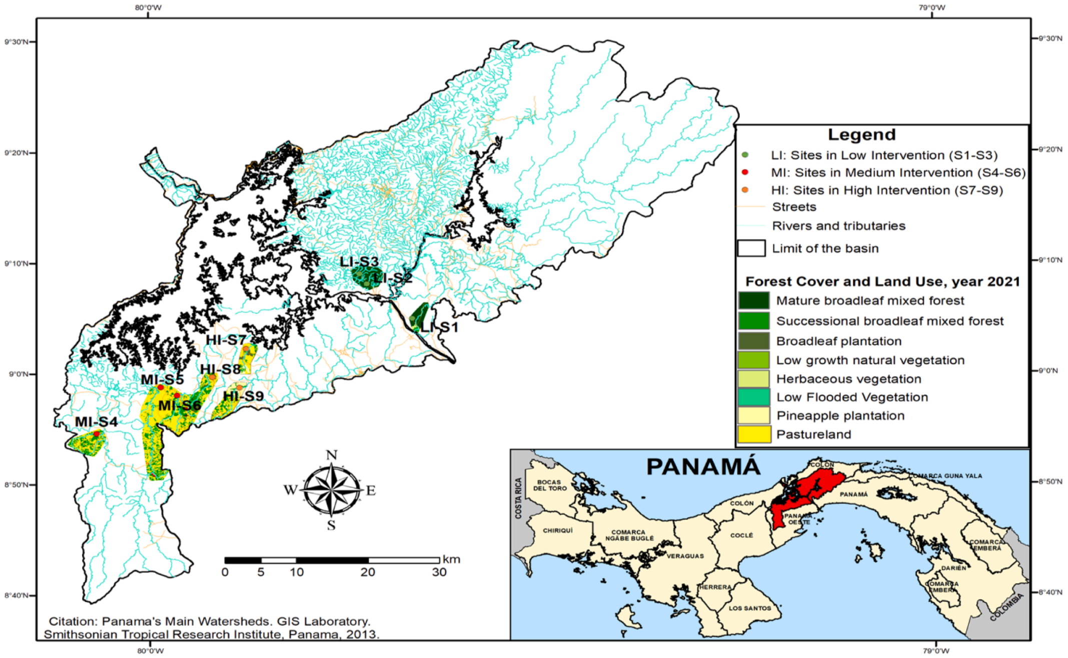


Fig. 1. Location of the nine study sites (S1-S9) located in three areas with different degree of agricultural intervention (low intervention, LI; medium intervention, MI; and high intervention, HI) within the Panama Canal catchment, located in the central part of Panama.

which was quantified by cutting 20 discs from different air-dried leaves of each species using a 17-mm diameter cork borer, avoiding main leaf nerves, and weighing them to the nearest 0.01 mg; and nitrogen (N) concentration (%), obtained from unpublished data (L. Boyero, unpubl.) and the literature (López-Rojo et al., 2021; Ramu et al., 2017). Litter of *Alnus* had the highest quality (SLA = 10.8 ± 1.9 mm^2 mg^{-1}; N = 2.40 ± 0.08%), followed by *Musa* (SLA = 13.3 ± 0.5 mm^2 mg^{-1}; N 1.17 ± 0.58%) and *Ficus* (SLA = 10.7 ± 1.1 mm^2 mg^{-1}; N = 1.09 ± 0.09%).

We collected recently senesced litter from the riparian forest floor at the study catchment (*Ficus*) or the Parque Internacional La Amistad (8.9°N, −82.6°W; *Alnus*), or dry leaves from plants at the study catchment (*Musa*). Once in the laboratory, litter was air dried and cut in ca. 5 × 5 cm fragments, excluding the basal petiole insertion. We used extra leaf litter to estimate litter mass loss (LML) due to leaching of soluble compounds, by introducing this leaf litter in glass jars with 400 mL of filtered (100 μm) stream water from the experimental site for 48 h, with water replacement at 24 h (1 g per species and replicate; n = 3). Leaf litter from each replicate was oven-dried (70 °C, 72 h) and weighed to estimate the relationship between initial air DM and post-leaching oven DM (López-Rojo et al., 2021).

We prepared 540 sets of leaf fragments (20 per species and site), weighed them individually (1.00 ± 0.05 g), hooked them on safety pins in groups of 20 (same species), and introduced each group within a fine-mesh (0.5 mm) or coarse-mesh (10 mm) bag (20 × 15 cm). Fine-mesh bags preclude the entrance of invertebrates and thus allow the quantification of microbial decomposition, and coarse-mesh bags serve to quantify total decomposition, with detritivore-mediated decomposition being estimated later (see below). On February 1, 2022, we deployed the litterbags at the nine studied sites, attached in pairs (fine- and coarse-mesh) with nylon rope to stakes that were hammered into the stream substrate. We collected one third of the bags on day 0 to estimate litter mass handling losses (which were observed to be negligible); and the other two thirds on days 14 and 28, respectively. Litterbags were collected by placing a net immediately downstream and introducing them into ziplock bags, which were transported to the laboratory on ice. In the laboratory, litter was carefully rinsed using filtered (100 μm) stream water on a 500-μm sieve to remove sediments and invertebrates. Then it was oven dried (70 °C, 72 h), weighed to estimate final DM, incinerated (500 °C, 4 h) and re-weighed to estimate final ash-free dry mass (AFDM). Decomposition was quantified through proportion of LML, which was calculated as the difference between initial and final AFDM (g) divided by initial AFDM (g), with initial AFDM being corrected by the proportion of LML due to leaching. Microbial and total decomposition were quantified through LML in fine- and coarse-mesh litterbags, respectively, and detritivore-mediated decomposition was calculated as the difference in LML between paired coarse- and fine-mesh bags. Leaf litter ash content (%) was used as a proxy for sediment deposition.

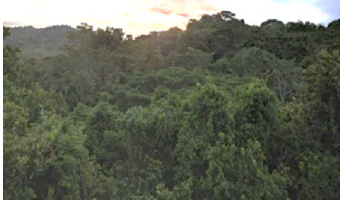
2.4. Processing of invertebrate and aquatic hyphomycete samples

Invertebrates collected from coarse-mesh bags were preserved in 70% ethanol, and identified and separated as above, recording the abundance and taxonomic richness for detritivores and total invertebrates per bag. Five leaf discs of *Ficus* and *Musa* were incubated in 200 mL glass flasks, which were previously filled with 40 mL of filtered water from the corresponding stream with constant aeration (*Alnus* was excluded from this analysis for logistical reasons). After 48 h, the resulting conidial suspensions were transferred to 45 mL centrifuge tubes, fixed with 2 mL of 37% formalin, and two drops of trypan blue were added. A 10 mL aliquot of the suspension was filtered (Millipore SMWP 5 mm pore size) for conidial identification and counting. Filters were stained with trypan blue and conidia identified (Descals et al., 1977; Ingold, 1975), counting 100 fields under × 200 magnification in an OLYMPUS DP72 microscope. Sporulation rates were expressed as number of conidia per g of leaf DM per day of incubation time.

2.5. Data analyses

Statistical analyses were performed in R software, v. 4.2.1 (R Core Team, 2022). We first explored bivariate scatterplots and Pearson correlations to select the most relevant and uncorrelated environmental variables ($r \geq 0.70$) to be used in further analyses (Fig. S1; Zuur et al., 2009); these variables were suspended solids, TU_{max}, NO_3 concentration, total phosphorus and riparian vegetation cover (%), with other variables discarded. We used Principal Component Analysis (PCA; rda

Table 1
Location and physicochemical characterization of the nine study sites (S1-S9) located in three areas with different degree of agricultural influence: low intervention, LI; medium intervention, MI; and high intervention, HI); BDL = Below detection level.

									
Land use category	**LI** Low intervention			**MI** Medium intervention			**HI** High intervention		
ID	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**
Site location									
Latitude (°N)	9.08233	9.13467	9.14961	8.90992	8.97947	8.96720	9.03729	8.99470	8.97898
Longitude (°W)	−79.66442	−79.72239	−79.73170	−80.06747	−79.98559	−79.96469	−79.87689	−79.91990	−79.88531
Altitude (m a.s.l.)	54	35	34	145	90	46	96	93	43
Habitat characterization									
Stream width (m)	6.5	8.5	7.8	7.3	6.2	9.9	9.7	8.4	6.4
Water depth (cm)	130.0	128.0	120.0	157.0	149.0	185.0	170.0	161.0	137.0
Current velocity (m/s)	0.1	0.2	0.4	0.5	0.4	0.7	0.3	0.2	0.2
Sediment deposition (%)	20.0	30.0	10.0	40.0	50.0	30.0	90.0	70.0	80.0
Riparian vegetation cover (%)	90.0	80.0	80.0	60.0	40.0	60.0	10.0	30.0	10.0
HQI (Habitat quality index)	166.0	180.0	190.0	87.0	81.0	90.0	44.0	45.0	41.0
Physicochemical variables									
Temperature (°C)	23.8	23.9	24.1	24.6	28.2	27.7	25.7	25.6	26.2
pH	7.1	7.1	7.4	7.2	7.1	7.3	7.2	7.4	7.1
Turbidity (NTU)	1	2.8	1.9	5.3	5.2	3.2	5.0	5.00	9.8
Dissolved O_2 (mgL^{-1})	7.6	6.8	7.7	5.7	6.8	7.6	5.9	7.5	3.3
Dissolved O_2 (% sat.)	89.9	80.9	91.2	68.1	87.1	96.3	72.1	91.9	40.7
N-Nitrate ((μgL^{-1})	BDL	BDL	BDL	BDL	BDL	BDL	1355	1355	1581
Total P (μgL^{-1})	80	BDL	BDL	BDL	BDL	120	BDL	130	BDL
ICA (Panamanian water quality index)	83	80	87	82	84	83	76	77	60
Biological variables									
Total coliforms	8.3	54	8.4	35	20	25	5.2	7.9	8.3
Fecal coliforms	2	2	0.4	4	1	3	0.9	0.6	6.4
BMWP/PAN index	88	73	74	42	47	43	27	39	2
Pesticides									
Ametryn (μgL^{-1})	BDL	BDL	BDL	BDL	BDL	BDL	0.11	0.11	0.13
Atrazine (μgL^{-1})	BDL	BDL	BDL	BDL	BDL	BDL	BDL	0.11	BDL
Bifenthrin (μgL^{-1})	BDL	BDL	BDL	BDL	BDL	BDL	BDL	BDL	0.14
TU_{max}							−5.45	−5.89	0.10

function of *vegan* package) to explore variation among sites, in terms of habitat and physicochemical variables that could indicate stream impairment because of agriculture (Fig. S2). We explored the correlation between the ICA index and the habitat quality index, riparian vegetation cover and BMWP/PAN index, in order to corroborate the established agricultural intervention gradient.

To examine how leaf litter decomposition of the different plant species responded to the agricultural influence gradient, we used linear mixed-effects models [lme function and restricted maximum likelihood (REML) estimation on the *nlme* package (Pinheiro et al., 2020)], with microbial (hypothesis 1), detritivore-mediated (hypothesis 2) and total decomposition (hypothesis 3) as response variables, and intervention degree (LI, MI and HI) and litter type (*Ficus*, *Alnus* and *Musa*) as categorical predictors. We included the interaction between agricultural influence and litter type in the models to test whether litter type mediated the agricultural influence on decomposition (hypothesis 4). We included stream sites as random component, due to the nested sampling design, and examined the improvement of model fit after including this component with the Akaike Information Criterion corrected for sample size (AICc). We inspected residuals from each model to ensure there were no visual patterns or violation of linear model assumptions.

Finally, we investigated the variation in the abundance and taxon richness of detritivore and total invertebrates in coarse-mesh bags (14 and 28 d) and benthic samples, using linear mixed-effects models and confidence intervals, with site as random factor; agricultural influence (LI, MI and HI) was a fixed factor in both cases, and litter type (*Ficus, Alnus* and *Musa*) was also a fixed factor for coarse-mesh bags.

3. Results

3.1. Site characteristics

Study sites located in the three intervention areas showed a gradient in sediment deposition and turbidity (LI < MI < HI), and in dissolved oxygen, riparian vegetation cover and the habitat quality index (LI > MI > HI), variables that were correlated with the ICA (Fig. S1). There were no clear differences in other variables such as width, depth, current velocity, temperature, pH or coliforms (Table 1). Nitrates were below detection level at LI and MI sites, and total P at two sites in each area. Three pesticides were detected, including two herbicides (ametryn and atrazine) and one insecticide (bifenthrin), all at HI sites (Table 1). The first axis of the PCA separated LI and MI sites from HI sites, based on riparian vegetation cover, suspended solids and nitrates; and the second axis separated sites with higher pesticide toxicity (mostly site S9 at HI) and higher P concentration (sites S1 at LI, S6 at MI, and S8 at HI; Table 1, Fig. S2). The habitat quality index and riparian vegetation cover correlated with the ICA, which supported the studied agricultural intervention gradient (Fig. 2), with particularly clear differences between HI sites and the less impacted sites at MI and PI.

In benthic samples, we collected a total of 1,140 invertebrates, which belonged to 38 families, 12 orders and 5 classes (Table S1, Fig. S3). The

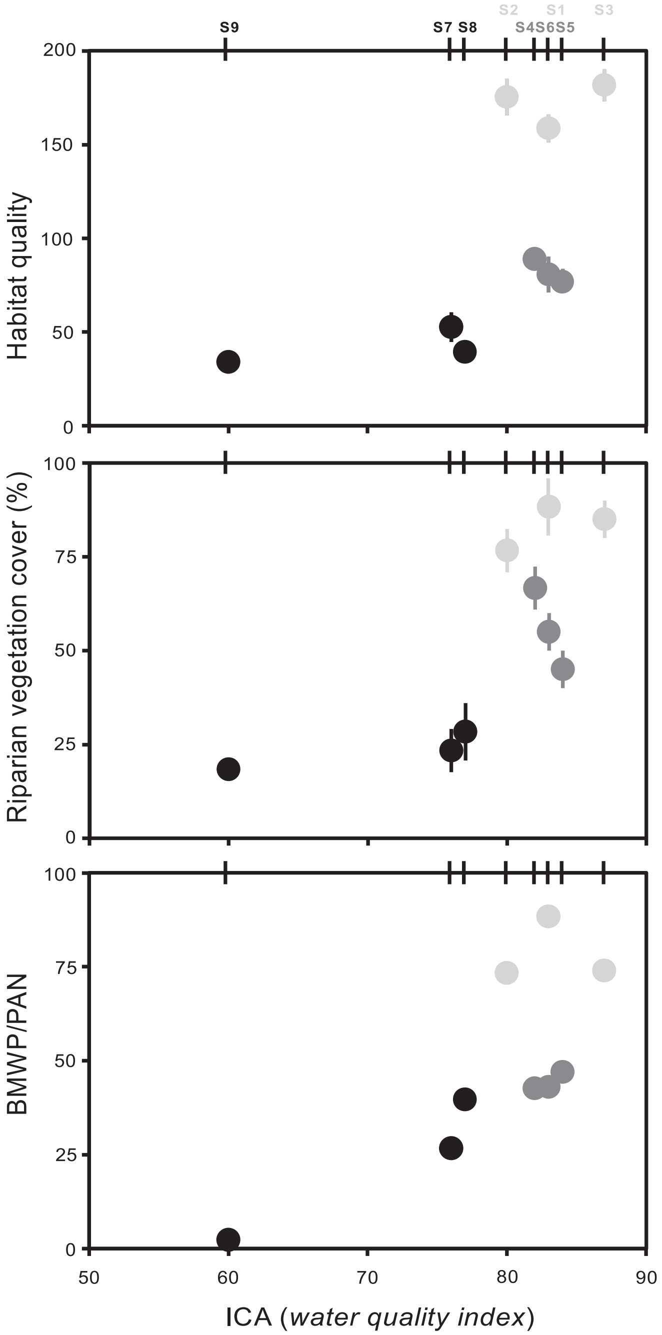


Fig. 2. Correlation between the Panamanian water quality index (ICA) and the habitat quality index, riparian vegetation cover and BMWP/PAN index, in streams located in three areas with different degrees of agricultural intervention [sites S1-S3: low intervention, LI; S4-S6: medium intervention, MI; and S7-S9: high intervention, HI).

most common families, which accounted for > 60% of invertebrates in benthic samples, were Ephemeroptera: Leptophlebiidae (19%), Trichoptera: Philopotamidae (16%), Diptera: Chironomidae (14%), Trichoptera: Hydropsychidae (10%) and Coleoptera: Elmidae (5%). The BMWP/PAN scores reflected the agricultural intervention gradient and also correlated with the ICA (Fig. 2).

3.2. Litter decomposition

After 14 d of instream incubation, the proportion of LML ranged from 0.16 to 0.52 in fine-mesh bags (microbial decomposition) and from 0.13 to 0.66 in coarse-mesh bags (total decomposition), considering all litter types (Fig. S4); after 28 d, it ranged from 0.22 to 0.79 in fine-mesh bags and from 0.22 to 0.91 in coarse-mesh bags (Fig. 3). Microbial decomposition represented 92% and 86% of total decomposition at 14 d and 28 d, respectively (on average for all sites and litter types), being detritivore-mediated decomposition a relevant fraction only at LI sites for *Alnus* (33–37% of total decomposition).

Microbial decomposition differed among litter types, and the effect was evident already at 14 d of exposure (Table 2), being decomposition higher in *Ficus* than in the other two species (Fig. 3). At day 28, there was a significant interaction between intervention area and litter type (Table 2), but post-hoc tests did not show any clear differences among areas for any of the litter types (Fig. 3). Detritivore-mediated decomposition did not differ among areas or litter types at day 14, but at day 28 there was a significant intervention area by litter type interaction, with differences between areas (LI > MI = HI), being evident only for *Alnus* litter (Fig. 3). For total decomposition, differences among litter types were evident from day 14, and there was again a significant interaction between both factors (Table 2), with higher decomposition at LI and MI than for HI for *Alnus* only (Fig. 3).

In coarse mesh bags, we collected 3,772 invertebrates belonging to 23 families, 8 orders and 2 classes (Tables S2). The most common families (>85%) were Chironomidae (49%), Leptophlebiidae (24%), Caenidae (7%), Hydropsychidae (4%) and Leptohyphidae (4%). Litter-feeding detritivores were present at the LI sites (Trichoptera: Calamoceratidae, Coleoptera: Ptilodactylidae and Diptera: Tipulidae), but absent at MI and HI sites, which had more generalist detritivores that are typically classified as collector-gatherers (Chironomidae; and Haplotaxida: Tubificidae at HI sites) and filter-feeders (Philopotamidae). Invertebrate and detritivore abundances were higher in coarse-mesh bags with *Alnus* than in those with the other species. In contrast, there were no differences among intervention areas, or among benthic samples of different areas or litter types (Fig. S5, Fig. 4, Table 3, Table S5).

Aquatic hyphomycete taxon richness and sporulation rates were low in general, with only 15 sporulating taxa identified (Table S2-S4), and no significant differences in any of these variables among intervention areas or litter types (Table 4; Tables S3-S4; Table S6; Fig. S6). Sporulation rates tended to be higher at MI sites, and taxon richness tended to be lower in *Ficus* and *Musa* litter (which shared the same sporulating species), but differences were not significant.

4. Discussion

In many tropical streams, leaf litter decomposition is mainly mediated by microorganisms, which can be explained by the scarcity of most litter-consuming detritivores at high temperatures (Boyero et al., 2011a). This was reflected in our study, where microorganisms accounted for >60% of total leaf litter mass loss on average. Litter-consuming detritivores were poorly represented in general, but especially in streams of the medium and high intervention areas, where typical litter consumers (i.e., several families of Trichoptera, Plecoptera and Amphipoda) were virtually absent, and only chironomids were observed to feed on leaf litter. This situation contrasts with highland areas of Panama, where several families of the above orders are common (e.g., Lepidostomatidae, Ptilodactylidae or Hyalellidae; Cornejo et al., 2020b). Thus, in a study conducted at the Chiriquí Viejo catchment, located in western Panama and also affected by agriculture, but located at > 1600 m asl (compared to < 150 m asl in this study), detritivores in the low intervention area contributed on average 81% and 60% to total decomposition of *Alnus* and *Ficus*, respectively.

Contrary to our expectations (hypothesis 1), microbial decomposition was not influenced by agricultural intervention in our study area. When assessed in microcosm experiments, nutrient enrichment consistently enhances microbial activity, although the magnitude of effects can vary with other environmental factors (e.g., it increases with temperature; Ferreira and Chauvet, 2011). In contrast, results of field

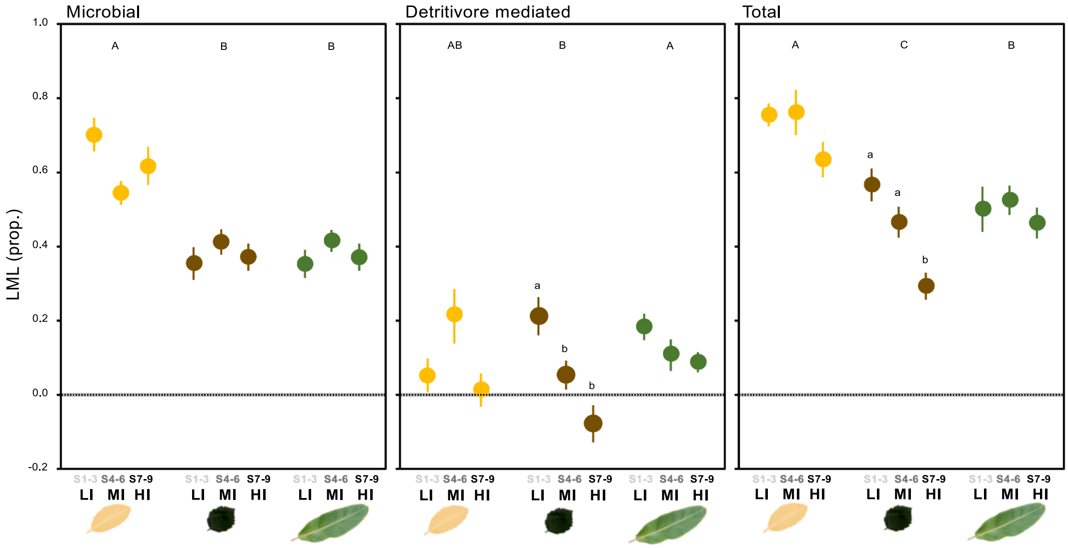


Fig. 3. Microbial, detritivore-mediated and total decomposition (mean ± SE proportion of litter mass loss; LML) of three litter types after 28 d of incubation in streams located at three study areas with different degree of agricultural influence (low intervention, LI; medium intervention, MI; and high intervention, HI). Different letters indicate significant differences between areas ($p < 0.05$). ● = *Ficus insipida*; ● = *Alnus acuminata*; ● = *Musa balbisiana*.

Table 2
Results of linear models examining variation in microbial, detritivore-mediated and total decomposition (quantified as the proportion of litter mass loss) among degrees of agricultural intervention (LI, MI and HI), litter types (*Alnus*, *Ficus* and *Musa*) and their interaction; df = degrees of freedom, *F* = F statistic; *p* = p-value.

		14 d			28 d		
Response variable	**Factor/interaction**	**df**	***F***	***p***	**df**	***F***	***p***
Microbial decomposition	Agricultural intervention degree (AID)	6	0.84	0.477	6	0.03	0.972
	Litter type (LT)	120	52.23	**<0.001***	120	43.27	**<0.001***
	AID × LT	120	0.69	0.599	120	2.99	**0.021***
Detritivore-mediated decomposition	AID	6	2.50	0.142	6	1.98	0.218
	LT	120	1.86	0.159	120	0.91	0.405
	AID × LT	120	0.69	0.598	120	4.07	**0.004***
Total decomposition	AID	6	3.56	0.096	6	1.07	0.399
	LT	120	57.02	**<0.001***	120	65.50	**<0.001***
	AID × LT	120	2.82	**0.028***	120	2.95	**0.023***

studies are more variable, with some studies showing higher decomposition at higher nutrient levels, and others reporting no influence (Ferreira et al., 2015; Gulis and Suberkropp, 2003). Dissolved nutrients are more accessible to aquatic hyphomycetes than leaf litter nutrients, and thus eutrophic conditions that do not reach toxic levels can promote respiration and sporulation rates and hence leaf litter mass loss (Duarte et al., 2009; Suberkropp and Chauvet, 1995). The absence of consistent effects in the field, however, has been attributed to nutrients not being limiting at any study site (Royer and Minshall, 2003), or to either N or P remaining limiting even when the other nutrient increases (Tank and Webster, 1998). This second explanation could apply to our study because, while nitrate was high in streams of the high intervention area, total P was below detection levels at many sites, which may have limited microbial activity in the most impacted sites. It is also possible that factors other than nutrients associated with the agricultural intervention level (e.g., pesticide concentration or sedimentation) may have counteracted the effect of nutrients, rendering an overall lack of effect (Pérez et al., 2013).

Detritivore-mediated decomposition varied across intervention areas in the predicted gradient (hypothesis 2), which was also reflected in total decomposition (hypothesis 3): LI differed significantly from the other two areas for detritivore-mediated decomposition (LI > MI = HI), and HI differed from the other two areas for total decomposition (LI = MI > HI). Other studies have also shown a detriment in detritivore abundance and species richness, and hence a decrease in detritivore-mediated decomposition rates, as a result of agricultural intervention (Cornejo et al., 2020b) or other sources of alteration (Fenoy et al., 2020; Lecerf et al., 2006). Here, we did not find significant differences among areas in the abundance or species richness of litter-consuming detritivores in coarse-mesh bags or benthic samples, which contrasts with the above-mentioned study conducted in a highland Panamanian agricultural catchment, where detritivore abundance and richness were higher in the low intervention area than in the medium and high intervention areas (Cornejo et al., 2020b). These differences could be attributed to the identities of litter-consuming detritivores found in both studies: here, these were mostly chironomids, which are much more tolerant to pollutants than those found in the other study, which included typical litter-consuming detritivores such as caddisflies (genera *Lepidostoma* and *Phylloicus*), amphipods (*Hyallela*), beetles (*Anchytarsus*) and craneflies (*Tipula*). Thus, the detriment in water quality across the agricultural gradient studied here might have not driven drastic reductions in litter-consuming detritivore numbers as observed in other cases, although they reduced their feeding activity as explained above.

Litter decomposition rates varied across plant species, as predicted (hypothesis 4), although these differences were significant only for microbial decomposition. The pattern followed by total decomposition was similar to that of microbial decomposition (hypothesis 3), but differences among species were not significant. In particular, *Ficus* decomposed (microbially) approximately 1.5 times faster than the other two species, which decomposed at similar rates. This contrasts with the observed gradient in litter quality (*Alnus* > *Musa* > *Ficus*), and could be related to a home-field advantage effect, which consists of litter

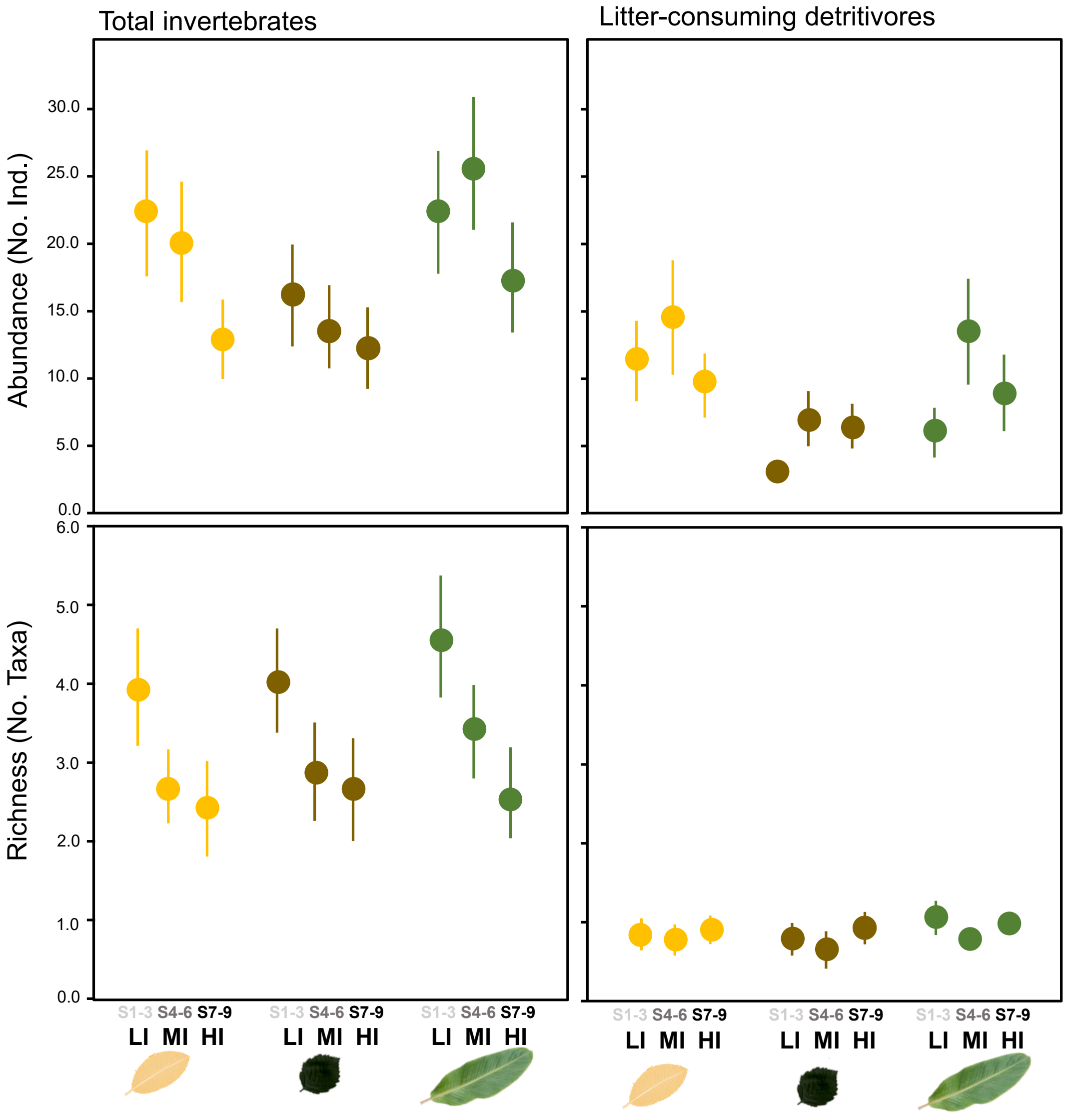


Fig. 4. Abundance (number of individuals) and taxon richness (number of taxa) of total invertebrates and litter-consuming detritivores collected from coarse-mesh litterbags after 28 d of incubation, in streams located in three areas with different degree of agricultural influence (low intervention, LI; medium intervention, MI; and high intervention, HI). ● = *Ficus insipida*; ● = *Alnus acuminata*; ● = *Musa balbisiana*.

decomposing faster near its origin than at distant sites due to specialization of local decomposer assemblages to characteristics of this litter (Bachega et al., 2016). Although this hypothesis was initially proposed for terrestrial decomposition, assuming that plants created specific conditions that favored the decomposition of their own litter in the soil (Gholz et al., 2000), studies have shown a possible home-field advantage effect also for instream decomposition, although this effect seems to be weaker for broadleaf than for conifer species (Yeung et al., 2019) and weaker than effects of litter traits (Fenoy et al., 2016).

Litter quality usually correlates with decomposition rates, but this occurs mainly in the presence of detritivores (Tonin et al., 2017), when litter traits are major decomposition drivers, at least in temperate regions (Martínez et al., 2015). However, the role of litter quality for microbial decomposition is not as straightforward, with litter traits other than nutrient contents being potentially more important for microbial decomposers (Fenoy et al., 2022; López-Rojo et al., 2021), which can obtain nutrients also from the water column (Krauss et al., 2011; Pérez et al., 2018). It is possible that litter traits not measured here could have influenced the faster decomposition of *Ficus* compared to the other species, although a home-field advantage effect cannot be discarded (Fenoy et al., 2016). It is also noteworthy that aquatic hyphomycete sporulation rates associated with *Ficus* and *Musa* litter were very low, which possibly reflected suboptimum conditions (Pérez et al., 2014). While optimum temperatures for these microorganisms often are 10 – 15 °C (Bärlocher et al., 2013), water temperature in our study sites was 24 – 28 °C, which may also have precluded finding differences in microbial decomposition among agricultural intervention areas (Pérez et al., 2018; Rajashekhar and Kaveriappa, 2000), in contrast with the observed variation in colder, highlands areas of Panama (Cornejo et al., 2020b). Under these warmer conditions, other microbial decomposers such as heterotrophic bacteria may have functionally replaced aquatic hyphomycetes (Marks, 2019; Pascoal et al., 2005).

In conclusion, drivers of leaf litter decomposition in lowland tropical streams seem to differ from those of tropical highland streams (Cornejo et al., 2020b), the latter having characteristics more similar to temperate streams in terms of the important role of litter-consuming detritivores in the process (Boyero et al., 2011b). However, even if microbially-mediated decomposition is predominant in lowland tropical streams, detritivore-mediated decomposition still seems to be a better tool to detect impacts of agriculture (and possibly other types of human

Table 3

Results of linear models examining variation in the abundance and taxonomic richness of litter-consuming detritivores (detr.) and total invertebrates (inv.) found in coarse-mesh litterbags among degrees of agricultural intervention (LI, MI and HI), litter types (*Alnus*, *Ficus* and *Musa*) and their interaction; and those found in benthic samples among degrees of agricultural intervention; df = degrees of freedom, *F* = F statistic; *p* = p-value.

		14 d			28 d		
Response variable	**Factor/interaction**	**df**	***F***	***p***	**df**	***F***	***p***
Litterbags							
Detr. abundance	Agricultural intervention degree (AID)	6	0.23	0.800	6	0.37	0.707
	Litter type (LT)	120	6.19	**0.003***	120	5.86	**0.004***
	AID × LT	120	0.23	0.920	120	0.98	0.424
Detr. richness	AID	6	0.84	0.476	6	1.24	0.355
	LT	120	0.51	0.602	120	0.88	0.418
	AID × LT	120	0.44	0.783	120	0.27	0.897
Inv. abundance	AID	6	0.23	0.801	6	0.54	0.607
	LT	120	3.54	**0.032***	120	3.35	**0.038***
	AID × LT	120	0.75	0.562	120	0.44	0.778
Inv. richness	AID	6	0.81	0.489	6	2.44	0.168
	LT	120	0.17	0.847	120	0.56	0.562
	AID × LT	120	0.72	0.578	120	0.08	0.988
Benthic samples							
Detr abundance	AID				6	2.56	0.157
Detr richness	AID				6	2.35	0.069
Inv. abundance	AID				6	1.42	0.313
Inv. richness	AID				6	1.19	0.231

Table 4

Results of linear models examining variation in aquatic hyphomycete (AH) taxon richness and sporulation rate found in fine-mesh litterbags among degrees of agricultural intervention (LI, MI and HI), litter types (*Ficus* and *Musa*) and their interaction; df = degrees of freedom, *F* = F statistic; *p* = p-value.

		14 d			28 d		
Response variable	**Factor/interaction**	**df**	***F***	***p***	**df**	***F***	***p***
AH taxon richness	Agricultural intervention degree (AID)	6	3.23	0.1115	6	0.53	0.6125
	Litter type (LT)	66	0.53	0.4679	52	0.75	0.3909
	AID × LT	66	0.54	0.5841	52	0.67	0.5161
AH sporulation rate	AID	6	2.73	0.1438	6	1.14	0.3796
	LT	66	3.95	0.0509	52	0.13	0.7197
	AID × LT	66	0.73	0.4869	52	1.44	0.2466

intervention) in lowland tropical streams, being therefore, a complementary functional indicator of ecosystem integrity. We thus recommend that standard substrates such as cotton strips or tongue depressors, often used as bioassessment tools (Cavallet et al., 2022; Ferreira et al., 2021), are used only in combination with natural litter in order to detect impacts. In particular, litter of *Alnus* spp. (alone or in combination with more nutrient-poor litter; Pérez et al., 2021a) seems to be an appropriate substrate for this purpose, even in cases where the species are not native to the study area.

Funding

Funding was obtained from the Ministry of Economy and Finance (MEF) through Investment Project 019910.001, administered by AC at ICGES; Investment Project 102720201.704, administered by ART at the Ministry of Environment; and Investment Project 101030118, administered by BCh at the Ministry of Agricultural Development (MIDA). AC was supported by the National Research System of Panama (SNI; National Researcher Category II; Contract No. 88–2022); AG, by a fellowship from the University of Panama (Contract No. CUFI-2021-EG-CNET-001); and GC, by a fellowship from IFARHU-SENACYT (Contract No. 270–2018-1011). JP and LB are supported by Basque Government funds (IT1471-22). FCA is supported by ANID funds (Anillo ATE220060 and FONDECYT 1231551).

CRediT authorship contribution statement

Javier Pérez: Conceptualization, Methodology, Investigation, Supervision, Data curation, Writing – original draft, Writing – review & editing. **Luz Boyero:** Conceptualization, Methodology, Investigation, Supervision, Writing – original draft, Writing – review & editing. **Ana Raquel Tuñón:** Funding acquisition, Investigation, Methodology, Data curation, Writing – review & editing. **Brenda Checa:** Funding acquisition, Investigation, Methodology, Data curation, Writing – review & editing. **Francisco Correa-Araneda:** Methodology, Investigation, Writing – review & editing. **Alisson Guerra:** Methodology, Investigation, Data curation, Writing – review & editing. **Anyi Tuñón:** Methodology, Investigation, Data curation, Writing – review & editing. **Dania Castillo:** Methodology, Investigation, Data curation, Writing – review & editing. **Edgar Pérez:** Methodology, Investigation, Data curation, Writing – review & editing. **Gabriela García:** Methodology, Investigation, Data curation, Writing – review & editing. **Randhy Rodríguez:** Methodology. **Aydeé Cornejo:** Conceptualization, Methodology, Formal analysis, Investigation, Supervision, Project administration, Funding acquisition, Data curation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank José Villarreal, from the Institute of Agricultural Research of Panama (IDIAP), for his support with plant nutrient analyses; Blas Armién and Rosa E. Carrillo de Vargas, from the Center for Research in Emerging and Zoonotic Diseases of the Gorgas Memorial Institute (CIEEZ-ICGES), for facilitating the logistics and space for conducting the experiment; Anakena Castillo and Carlos Nieto, for their support with literature revision; Alberto Cumbrera, from the Analyst SIG Unit of the ICGES, for making the map; Nathalie Ríos for her support with the graphical abstract; and Naiara Lopez-Rojo, for her support with data analyses. Water physicochemical analyses were conducted at the Environmental Quality Laboratory of the Panamanian Ministry of Environment; pesticide analyses, at the Pesticide Residues Laboratory from the Panamanian Agricultural Development Ministry (MIDA); and all other analyses, at the Ecology and Aquatic Ecotoxicology Freshwater Laboratory at the CIEEZ-ICGES.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110819.

References

ACP, 2007. Estudio de impacto ambiental categoría III proyecto de ampliación del Canal de Panamá- Tercer Juego de Esclusas. Autoridad del Canal de Panamá, Panamá, República de Panamá.

ACP, 2008. Informe de calidad de Agua de la Cuenca del Canal. República de Panamá.

Bachega, L.R., Bouillet, J.-P., de Cássia Piccolo, M., Saint-André, L., Bouvet, J.-M., Nouvellon, Y., de Moraes Gonçalves, J.L., Robin, A., Laclau, J.-P., 2016. Decomposition of Eucalyptus grandis and Acacia mangium leaves and fine roots in tropical conditions did not meet the Home Field Advantage hypothesis. For. Ecol. Manage. 359, 33–43.

Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency. Office of Water, Washington, D.C. USA.

Bärlocher, F., Kebede, Y.K., Gonçalves, A.L., Canhoto, C., 2013. Incubation temperature and substrate quality modulate sporulation by aquatic hyphomycetes. Microb. Ecol. 66 (1), 30–39.

Beketov, M.A., Foit, K., Schäfer, R.B., Schriever, C.A., Sacchi, A., Capri, E., Biggs, J., Wells, C., Liess, M., 2009. SPEAR indicates pesticide effects in streams–comparative use of species- and family-level biomonitoring data. Environ. Pollut. 157 (6), 1841–1848.

Boscutti, F., Sigura, M., De Simone, S., Marini, L., Ohlemuller, R., 2018. Exotic plant invasion in agricultural landscapes: a matter of dispersal mode and disturbance intensity. Appl. Veg. Sci. 21 (2), 250–257.

Boyero, L., Pearson, R.G., Dudgeon, D., Graça, M.A.S., Gessner, M.O., Albariño, R.J., Ferreira, V., Yule, C.M., Boulton, A.J., Arunachalam, M., Callisto, M., Chauvet, E., Ramírez, A., Chará, J., Moretti, M.S., Gonçalves, J.F., Helson, J.E., Chará-Serna, A.M., Encalada, A.C., Davies, J.N., Lamothe, S., Cornejo, A., Li, A.O.Y., Buria, L.M., Villanueva, V.D., Zúñiga, M.C., Pringle, C.M., 2011a. Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. Ecology 92 (9), 1839–1848.

Boyero, L., Pearson, R.G., Gessner, M.O., Barmuta, L.A., Ferreira, V., Graça, M.A.S., Dudgeon, D., Boulton, A.J., Callisto, M., Chauvet, E., Helson, J.E., Bruder, A., Albariño, R.J., Yule, C.M., Arunachalam, M., Davies, J.N., Figueroa, R., Flecker, A.S., Ramírez, A., Death, R.G., Iwata, T., Mathooko, J.M., Mathuriau, C., Gonçalves, J.F., Moretti, M., Jinggut, T., Lamothe, S., M'erimba, C., Ratnarajah, L., Schindler, M.H., Castela, J., Buria, L.M., Cornejo, A., Villanueva, V.D., West, D.C., 2011b. A global experiment suggests climate warming will not accelerate litter decomposition in streams but may reduce carbon sequestration. Ecol. Lett. 14, 289–294.

Bruder, A., Salis, R.K., McHugh, N.J., Matthaei, C.D., Treseder, K., 2016. Multiple-stressor effects on leaf litter decomposition and fungal decomposers in agricultural streams contrast between litter species. Funct. Ecol. 30 (7), 1257–1266.

Cavallet, B.V., Silva, E.R., Baretta, C.R.D.M., Rezende, R.d.S.,, 2022. Effect of agriculture land use on standard cellulosic substrates breakdown and invertebrates' community. Community Ecol. 23, 277–288.

Cornejo, A., López-López, E., Sedeño-Díaz, J.E., Ruiz-Picos, R.A., Macchi, P., Kohlmann, B., Correa-Araneda, F., Boyero, L., Bernal-Vega, J., Ríos, T., Avila Quintero, I.M., Tuñón, A.R., 2019a. Protocolo de biomonitoreo para la vigilancia de la calidad del agua en afluentes superficiales de Panamá. Instituto Conmemorativo Gorgas de Estudios de la Salud.

Cornejo, A., López-López, E., Ruiz-Picos, R.A., Sedeño-Díaz, J.E., Armitage, B., Arefina, T., Nieto, C., Tuñón, A., Molinar, M., Ábrego, T., Pérez, E., Tuñón, A.R., Magué, J., Rodríguez, A., Pineda, J., Cubilla, J., Avila Quintero, I.M., 2017. Diagnóstico de la condición ambiental de los afluentes superficiales de Panamá. Ministerio de Ambiente, Gobierno de la República de Panamá, Panama.

Cornejo, A., Tonin, A.M., Checa, B., Tuñon, A.R., Pérez, D., Coronado, E., González, S., Ríos, T., Macchi, P., Correa-Araneda, F., Boyero, L., Cañedo-Argüelles Iglesias, M., 2019b. Effects of multiple stressors associated with agriculture on stream macroinvertebrate communities in a tropical catchment. PLoS One 14 (8), e0220528.

Cornejo, A., Pérez, J., Alonso, A., López-Rojo, N., Monroy, S., Boyero, L., 2020a. A common fungicide impairs stream ecosystem functioning through effects on aquatic hyphomycetes and detritivorous caddisflies. J. Environ. Manage. 263, 110425.

Cornejo, A., Pérez, J., López-Rojo, N., Tonin, A.M., Rovira, D., Checa, B., Jaramillo, N., Correa, K., Villarreal, A., Villarreal, V., García, G., Pérez, E., Ríos González, T.A., Aguirre, Y., Correa-Araneda, F., Boyero, L., 2020b. Agriculture impairs stream ecosystem functioning in a tropical catchment. Sci. Total Environ. 745, 140950.

Descals, E., Sanders, P.F., Ugalde, U., 1977. Hifomicetos ingoldianos del País Vasco. Sociedad de Ciencias Aranzadi 3, 237–260.

Dinius, S.H., 1972. Social accounting system for evaluating water resources. Wat Resour Res 8 (5), 1159–1177.

Duarte, S., Pascoal, C., Garabétian, F., Cássio, F., Charcosset, J.-Y., 2009. Microbial decomposer communities are mainly structured by trophic status in circumneutral and alkaline streams. Appl. Environ. Microbiol. 75 (19), 6211–6221.

Fenoy, E., Casas, J.J., Díaz-López, M., Rubio, J., Guil-Guerrero, J.L., Moyano-López, F.J., Nakatsu, C., 2016. Temperature and substrate chemistry as major drivers of interregional variability of leaf microbial decomposition and cellulolytic activity in headwater streams. FEMS Microbiol. Ecol. 92 (11), fiw169.

Fenoy, E., Moyano, F.J., Casas, J.J., 2020. Warming and nutrient-depleted food: two difficult challenges faced simultaneously by an aquatic shredder. Freshwater Science 39 (3), 393–404.

Fenoy, E., Pradhan, A., Pascoal, C., Rubio-Ríos, J., Batista, D., Moyano-López, F.J., Cássio, F., Casas, J.J., 2022. Elevated temperature may reduce functional but not taxonomic diversity of fungal assemblages on decomposing leaf litter in streams. Glob. Chang. Biol. 28 (1), 115–127.

Ferreira, V., Chauvet, E., 2011. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. Glob. Chang. Biol. 17, 551–564.

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A.S., 2015. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol. Rev. Camb. Philos. Soc. 90 (3), 669–688.

Ferreira, V., Boyero, L., Calvo, C., Correa, F., Figueroa, R., Gonçalves, J.F., Goyenola, G., Graça, M.A.S., Hepp, L.U., Kariuki, S., López-Rodríguez, A., Mazzeo, N., M'Erimba, C., Monroy, S., Peil, A., Pozo, J., Rezende, R., Teixeira-de-Mello, F., 2019. A global assessment of the effects of eucalyptus plantations on stream ecosystem functioning. Ecosystems 22 (3), 629–642.

Ferreira, V., Silva, J., Cornut, J., Sobral, O., Bachelet, Q., Bouquerel, J., Danger, M., 2021. Organic-matter decomposition as a bioassessment tool of stream functioning: a comparison of eight decomposition-based indicators exposed to different environmental changes. Environ. Pollut. 290, 118111.

Fugère, V., Lostchuck, E., Chapman, L.J., 2020. Litter decomposition in Afrotropical streams: effects of land use, home-field advantage, and terrestrial herbivory. Freshwater Science 39 (3), 497–507.

Gessner, M.O., Chauvet, E., 2002. A case for using litter breakdown to assess functional stream integrity. Ecol. Appl. 12 (2), 498–510.

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob. Chang. Biol. 6, 751–765.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. PNAS 107 (38), 16732–16737.

Graeber, D., Boechat, I.G., Encina-Montoya, F., Esse, C., Gelbrecht, J., Goyenola, G., Gucker, B., Heinz, M., Kronvang, B., Meerhoff, M., Nimptsch, J., Pusch, M.T., Silva, R.C., von Schiller, D., Zwirnmann, E., 2015. Global effects of agriculture on fluvial dissolved organic matter. Scientic Reports 5, 16328.

Gulis, V., Suberkropp, K., 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshw. Biol. 48, 123–124.

Gutiérrez-Fonseca, P.E., 2010. Capítulo 6: Plecoptera. Rev. Biol. Trop. 58, 139–148.

Hawkes, H.A., 1998. Origin and development of the biological monitoring working party score system. Water Res. 32 (3), 964–968.

Ingold, C.T., 1975. An illustrated guide to aquatic and water-borne hyphomycetes (fungi imperfecti) with notes on their biology. Freshwater Biological Association 30, 1–95.

Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Glob. Chang. Biol. 22 (1), 180–189.

Krauss, G.-J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., Bärlocher, F., 2011. Fungi in freshwaters: ecology, physiology and biochemical potential. FEMS Microbiol. Rev. 35 (4), 620–651.

Lecerf, A., Usseglio-Polatera, P., Charcosset, J.-Y., Bracht, B., Chauvet, E., 2006. Assessment of functional integrity of eutrophic streams using litter breakdown and benthic macroinvertebrates. Arch. Hydrobiol. 165 (1), 105–126.

Lewis, S.L., 2006. Tropical forests and the changing earth system. Philos. Trans. R. Soc. Lond. B Biol. Sci. 361 (1465), 195–210.

López-Rojo, N., Pérez, J., Pozo, J., Basaguren, A., Apodaka-Etxebarria, U., Correa-Araneda, F., Boyero, L., 2021. Shifts in key leaf litter traits can predict effects of plant diversity loss on decomposition in streams. Ecosystems 24 (1), 185–196.

Luai, V.B., Ding, S., Wang, D., 2019. The effects of litter quality and living plants on the home-field advantage of aquatic macrophyte decomposition in a eutrophic urban lake, China. Sci. Total Environ. 650, 1529–1536.

Maracahipes-Santos, L., Silvério, D.V., Macedo, M.N., Maracahipes, L., Jankowski, K.J., Paolucci, L.N., Neill, C., Brando, P.M., 2020. Agricultural land-use change alters the structure and diversity of Amazon riparian forests. Biol. Conserv. 252, 108862.

Marks, J.C., 2019. Revisiting the fates of dead leaves that fall into streams. Annu. Rev. Ecol. Evol. Syst. 50 (1), 547–568.

Martínez, A., Monroy, S., Pérez, J., Larrañaga, A., Basaguren, A., Molinero, J., Pozo, J., 2016. In-stream litter decomposition along an altitudinal gradient: does substrate quality matter? Hydrobiologia 766 (1), 17–28.

Menjivar Rosa, R.A., 2010. Guía ilustrada para el estudio ecológico y taxonómico de los insectos acuáticos del Orden Diptera. In: Springer, M., Sermeño Chicas, J.M. (Eds.), FormuLación De Una Guía Metodológica Estandarizada Para Determinar La Calidad Ambiental De Las Aguas De Los Ríos De El Salvador, Utilizando Insectos Acuáticos. Editorial Universitaria UES, San Salvador, El Salvador.

Mollá, S., Casas, J.J., Menéndez, M., Basaguren, A., Casado, C., Descals, E., González, J. M., Larrañaga, A., Lusi, M., Martínez, A., Mendoza-Lera, C., Moya, O., Pérez, J., Riera, T., Roblas, N., Pozo, J., 2017. Leaf-litter breakdown as an indicator of the impacts by flow regulation in headwater streams: Responses across climatic regions. Ecol. Ind. 73, 11–22.

Ortega-Samaniego, Q.M., Fraiz, A., Dominici, A., Osorio, H., Ramos-Merchante, A., Arauz, E., Paches, M., Romero, I., 2022. Evaluation of the ecological state using the water quality index and fluvial habitat index. of the urban basins of Panama. WIT Trans. Ecol. Environ. 259, 87–98.

Pacheco-Chaves, B., 2010. Guía ilustrada para el estudio ecológico y taxonómico de los insectos acuáticos del Orden Hemiptera en El Salvador., in: Springer, M., Sermeño Chicas, J.M. (Eds.), Formulación de una guía metodológica estandarizada para determinar la calidad ambiental de las aguas de los ríos de El Salvador, utilizando insectos acuáticos. Editorial Universitaria UES, San Salvador, El Salvador.

Pascoal, C., Cássio, F., Marcotegui, A., Sanz, B., Gomes, P., 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. J. N. Am. Benthol. Soc. 24 (4), 784–797.

Pérez, J., Basaguren, A., Descals, E., Larrañaga, A., Pozo, J., 2013. Leaf-litter processing in headwater streams of northern Iberian Peninsula: moderate levels of eutrophication do not explain breakdown rates. Hydrobiologia 718 (1), 41–57.

Pérez, J., Galán, J., Descals, E., Pozo, J., 2014. Effects of fungal inocula and habitat conditions on alder and eucalyptus leaf litter decomposition in streams of northern Spain. Microb. Ecol. 67 (2), 245–255.

Pérez, J., Martínez, A., Descals, E., Pozo, J., 2018. Responses of aquatic hyphomycetes to temperature and nutrient availability: a cross-transplantation experiment. Microb. Ecol. 76 (2), 328–339.

Pérez, J., Basaguren, A., López-Rojo, N., Tonin, A.M., Correa-Araneda, F., Boyero, L., 2021a. The role of key plant species on litter decomposition in streams: alder litter as experimental model. In: Swan, C.M., Boyero, L., Canhoto, C. (Eds.), The Ecology of Plant Litter Decomposition in Stream Ecosystems. Springer.

Pérez, J., Correa-Araneda, F., López-Rojo, N., Basaguren, A., Boyero, L., 2021b. Extreme temperature events alter stream ecosystem functioning. Ecol. Ind. 121, 106984.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., Team, R.C., 2020. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-151. URL: CRAN.R-project. org/package=nlme.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria.

Rajashekhar, M., Kaveriappa, K.M., 2000. Effects of temperature and light on growth and sporulation of aquatic hyphomycetes. Hydrobiologia 441, 149–153.

Ramírez, A., Gutiérrez-Fonseca, P.E., 2014. Functional feeding groups of aquatic insect families in Latin America: a critical analysis and review of existing literature. Revista de Biología Tropical (International Journal of Tropical Biology) 62, 155–167.

Ramu, R., Shirahatti, PrithviS, Anilakumar, K.R., Nayakavadi, S., Zameer, F., Dhananjaya, B.L., Nagendra Prasad, M.N., 2017. Assessment of nutritional quality and global antioxidant response of banana (Musa sp. CV. Nanjangud Rasa Bale) pseudostem and flower. Pharmacognosy Research 9 (5), 74.

Rasmussen, J.J., Wiberg-Larsen, P., Baattrup-Pedersen, A., Monberg, R.J., Kronvang, B., 2012. Impacts of pesticides and natural stressors on leaf litter decomposition in agricultural streams. Sci. Total Environ. 416, 148–155.

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. PNAS 118 (2).

Rice, E.W., Baird, R.B., Eaton, A.D., Clesceri, L.S., 2012. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, American Water Works Association, Water Environment Federation.

Roe, S., Streck, C., Obersteiner, M., Frank, S., Griscom, B., Drouet, L., Fricko, O., Gusti, M., Harris, N., Hasegawa, T., Hausfather, Z., Havlík, P., House, J.o., Nabuurs, G.-J., Popp, A., Sánchez, M.J.S., Sanderman, J., Smith, P., Stehfest, E., Lawrence, D., 2019. Contribution of the land sector to a 1.5 °C world. Nat. Clim. Chang. 9 (11), 817–828.

Royer, T.V., Minshall, G.W., 2003. Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives. J. N. Am. Benthol. Soc. 22 (3), 352–358.

Smith, V.H., Schindler, D.W., 2009. Eutrophication science: where do we go from here? Trends in Ecology and Evolution 24, 201-207.

Springer, M., Ramírez, A., Hanson, P., 2010. Macroinvertebrados de agua dulce de Costa Rica I. Revista de Biología Tropical 58 (Supl 4).

Suberkropp, K., Chauvet, E., 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. Ecology 76, 1433–1445.

Tank, J.L., Webster, J.R., 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. Ecology 79 (6), 2168–2179.

Taylor, C.A., Rising, J., 2021. Tipping point dynamics in global land use. Environ. Res. Lett. 16 (12), 125012.

Tomanova, S., Goitia, E., Helešic, J., 2006. Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams. Hydrobiologia 556 (1), 251–264.

Tonin, A.M., Boyero, L., Monroy, S., Basaguren, A., Pérez, J., Pearson, R.G., Cardinale, B. J., Gonçalves, J.F., Pozo, J., Briones, M., 2017. Stream nitrogen concentration, but not plant N-fixing capacity, modulates litter diversity effects on decomposition. Funct. Ecol. 31 (7), 1471–1481.

von Schiller, D., Acuna, V., Aristi, I., Arroita, M., Basaguren, A., Bellin, A., Boyero, L., Butturini, A., Ginebreda, A., Kalogianni, E., Larranaga, A., Majone, B., Martinez, A., Monroy, S., Munoz, I., Paunovic, M., Pereda, O., Petrovic, M., Pozo, J., Rodriguez-Mozaz, S., Rivas, D., Sabater, S., Sabater, F., Skoulikidis, N., Solagaistua, L., Vardakas, L., Elosegi, A., 2017. River ecosystem processes: a synthesis of approaches, criteria of use and sensitivity to environmental stressors. Sci. Total Environ. 596–597, 465–480.

Waddell, E.H., Banin, L.F., Fleiss, S., Hill, J.K., Hughes, M., Jelling, A., Yeong, K.L., Ola, B.B., Sailim, A.B., Tangah, J., Chapman, D.S., 2020. Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. Landsc. Ecol. 35 (9), 1891–1906.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277 (5322), 102–104.

Yeung, A.C.Y., Kreutzweiser, D.P., Richardson, J.S., 2019. Stronger effects of litter origin on the processing of conifer than broadleaf leaves: a test of home-field advantage of stream litter breakdown. Freshw. Biol. 64 (10), 1755–1768.