



# Small hydropower plants lead to higher litter breakdown rates in by-passed sections than in impounded reaches

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## Abstract

Reservoirs and by-passed sections may alter downstream ecological processes of rivers, so understanding their effects is essential for watersheds impacted by small hydropower power plants (SHPs). We investigated the ecological impacts of river sections (upstream vs. reservoir vs. by-passed vs. downstream) of four run-of-river SHPs distributed in two Neotropical watersheds on leaf litter breakdown (*Eucalyptus grandis* and *Inga uruguensis* by  $k$  in  $d^{-1}$  and  $dd^{-1}$ ) and its associated invertebrate community. Hydropower schemes promoted breakdown rates, although mechanisms differed: increased shredder abundance in by-passed sections, and increased scrapper abundance in impounded sections, both for coarse mesh litterbags. Variation among river sections of SHPs was a more important driver of invertebrate colonization than was leaf litter species. Mass loss was higher for *E. grandis* (high-quality detritus) compared to *I. uruguensis*. The influence of litter quality was lower for invertebrates than for microorganisms, mainly due to fast litter breakdown. Clearly, changes in hydrology can cause severe damage and may impact river litter breakdown. The process of leaf litter breakdown proved to be a sensitive tool for assessing the impacts of SHPs.

**Keywords** Hydroelectricity · Flow regulation · Run-of-river · Water storage · Litter decomposition

## Introduction

The human population growth continues to increase the demand for electricity and water supply (Mbaka and Mwaniki 2016), which drives the construction of dams (Couto and Olden 2018). Considering the heterogeneous nature of dams (Mbaka and Mwaniki 2016; Couto et al. 2021), special

attention must also be given to the reservoir and by-passed stretch of hydropower power plants (Garrett et al. 2021). In this critical scenario, small hydropower power plants (hereafter SHPs) stand out in the Neotropical region as they are abundant in the landscape due to the ease of the environmental licensing process (Couto and Olden 2018; Garrett et al. 2021). Thus, the fast development of SHPs may require new approaches and updated environmental policies due to a lack of knowledge regarding the cumulative effects of SHPs on the landscape (Lange et al. 2018; Linares et al. 2019).

Understanding the effects of dams and by-passed stretches is necessary to improve environmental policies and regulations applied to SHPs (Couto et al. 2021; Garrett et al. 2021). The use of ecological processes such as leaf litter breakdown may provide new approaches for the evaluation of anthropogenic environmental changes in aquatic systems (Tank et al. 2010; Rezende et al. 2021a). On the other hand, little is known about how dams affect leaf litter breakdown in streams and rivers (Mbaka and Mwaniki 2016), and the effects of the by-passed stretch remain poorly known. Fewer relevant studies have been carried out in tropical and subtropical rivers (Salomão et al. 2019) compared to

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temperate rivers (Mbaka and Mwaniki 2016; Li et al. 2020). As a result, the known impacts that dams have on leaf litter breakdown are varied, complex and evaluated in a punctual manner across the landscape (Mbaka and Mwaniki 2016; Salomão et al. 2019; Li et al. 2020).

Reservoirs change the natural flow of rivers and alter the surrounding natural riparian vegetation via flooding events (Mbaka and Mwaniki 2016; Couto and Olden 2018). Changes in riparian vegetation caused by flooding events may alter ecosystem metabolism through changes in rates of leaf litter breakdown. Moreover, reservoirs decrease water flow (less turbulence), may also decrease the dissolved oxygen and, in association with increased temperature, may lead to losses in richness and biomass of decomposer fungi (Salomão et al. 2019). However, this depends on the size and renewal rate of the reservoir, as well as on the biological activity in there (Mbaka and Mwaniki 2016; Li et al. 2020). In general, reservoirs can negatively affect the community of decomposers, thereby impairing leaf litter breakdown (Mbaka and Mwaniki 2016; Li et al. 2020). This phenomenon is the result of decreased fungi biomass diminishing the quality of conditions for leaf litter breakdown, as well as the association with finer sediments decreasing habitat heterogeneity and, in turn, the richness of invertebrate detritivores (e.g., shredders) and litter consumption (Salomão et al. 2019). Additionally, the construction of a water storage reservoir and the formation of a by-passed stretch can change invertebrate movement and assemblage composition (Rezende et al. 2014a; Durães et al. 2016).

Relatively few studies have shown an increase (Short and Ward 1980), or no change at all, in leaf breakdown in response to water storage reservoirs at dams (Casas et al. 2000), compared to the high number of studies that have evidenced a decrease (Mbaka and Mwaniki 2016; Salomão et al. 2019; Li et al. 2020). Based on the premise that the insertion of a dam will (i) promote lentic system formation (Garrett et al. 2021) and homogenization of river characteristics (habitat and limnology), with slow physical abrasion of leaves that may negatively alter biological communities (e.g., invertebrate and microbial assemblages) (Mbaka and Mwaniki 2016; Farah-Pérez et al. 2020), and that (ii) by-passed section (if present) will receive direct impacts from the water storage reservoir (Couto and Olden 2018; Couto et al. 2021), we predict that reservoir and by-passed river sections will slowly litter mass loss and decrease invertebrate diversity. Therefore, we aimed to assess how leaf litter breakdown and decomposer assemblages respond to changes from water quality to geomorphology, as example the slow water flow, caused by SHPs in reservoir and by-passed river sections. Specifically, we investigated the ecological impacts of the river sections (upstream, reservoir, by-passed, and downstream) of four SHPs distributed along two Neotropical watersheds on leaf litter breakdown (exotic species of

*Eucalyptus grandis* and native species of *Inga uruguensis*) and its associated invertebrate community.

## Methods

### Study area

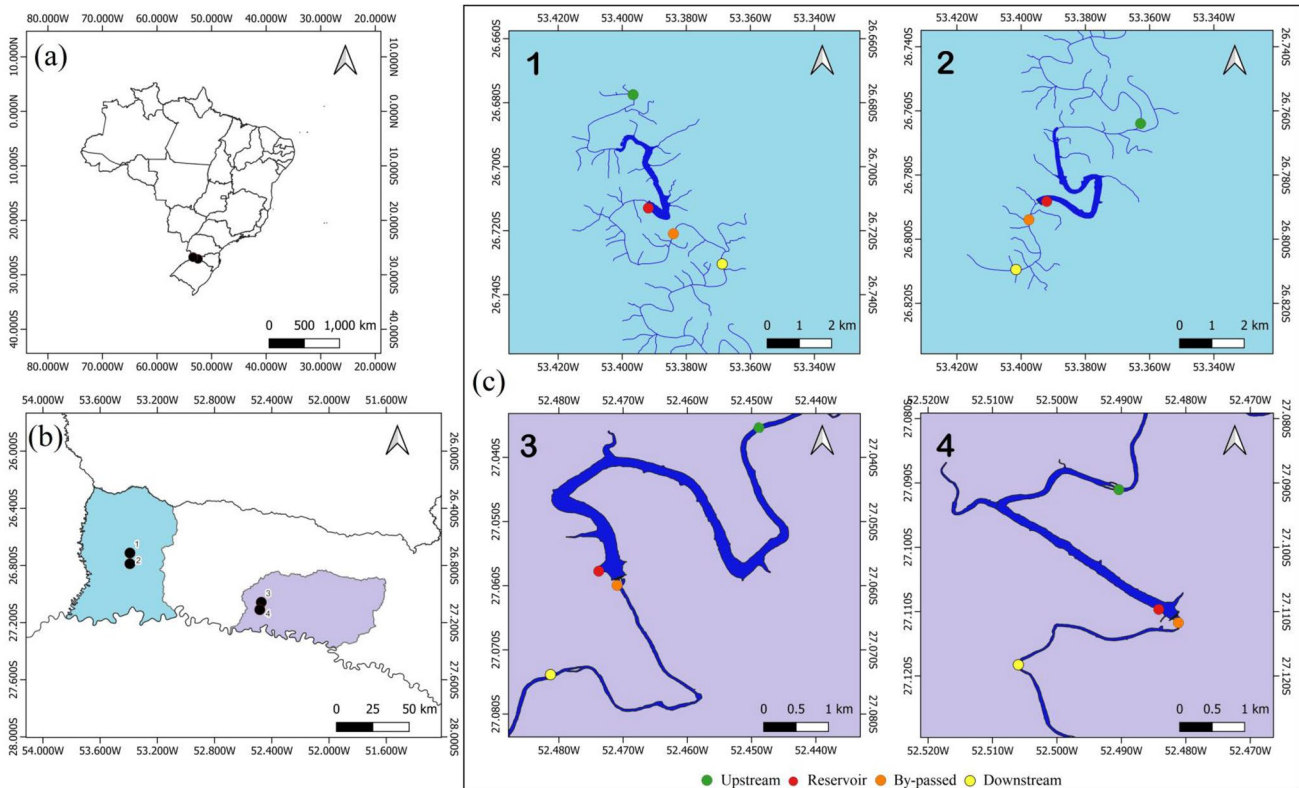
The study was carried out at two nested run-of-river SHPs in the Das Antas River Basin and two nested run-of-river SHPs in the Irani River Basin, both watersheds in the Uruguay River Basin, Brazil (Fig. 1A, B). In other words, one river per watershed with two nested SHP per river, one upstream from the other, with reservoirs built to rise the water level. In all SHPs, part of the flow is diverted through a canal to the powerhouse, thus leaving a by-passed reach. The vegetation of the study area is Mixed Ombrophilous Forest of the Atlantic Forest biome. The climate is Cfa (c.f. Köppen-Gieger, Humid subtropical), described as temperate subtropical (Peel et al. 2007).

Sampling points in the Das Antas River Basin were at around 425 m elevation, with a mean annual air temperature of 20 °C and a monthly range of 12 °C to 29 °C. Mean monthly precipitation throughout the year is 144 mm, ranging from 60 to 228 mm, with a mean annual total of 1723 mm. Sampling points in the Irani River Basin were at around 362 m elevation, with a mean annual air temperature of 20 °C and a monthly range of 12 °C to 28 °C. Mean monthly precipitation throughout the year is 134 mm, ranging from 36 to 288 mm, with a mean annual total of 1616 mm.

Land use in the study area is intense, primarily driven by agriculture activities and cattle ranching, with relatively highly degraded riparian zones. Sinuous and steep valleys form a series of rapids and waterfalls in both rivers, creating highly desirable conditions for hydropower development. The hydropower installations are of diverse schemes classified as SHPs (<30 MW). Most of the studied SHPs have moderate to low water storage, but some have considerably large reservoirs relative to the size of the rivers as their by-passed sections that can reach 8 km (Table SM1).

### Sampling design

Four river sections were selected for sampling at each of the four nested SHPs: one section with low impact and three sections under greater influence of the SHP (Fig. 1). The low-impact river section was the “upstream” section of the SHPs, characterized by flowing water habitats. The “reservoir” section is a lentic river section created by the impoundment of the SHPs and is located near the dam structure. The “by-passed” section is located downstream of the dam structure and upstream of the powerhouse outlet of each SHP.



**Fig. 1** Geographic location of sampling points in upstream, reservoir, by-passed, and downstream sections in relation to Brazil (A) and Santa Catarina State (B) with the Anta's River Basin indicated by green (C) and the Irani River Basin indicated by orange (D) (Color figure online).

The “downstream” section is characterized by flowing water habitat where water is returned to the river.

## Procedures

An experiment was conducted using leaves of *Eucalyptus grandis* W. Hill ex Maiden, an exotic species, and the most abundant silviculture species in the landscape of South Brazil, replacing the native riparian vegetation in many areas (including those with SHPs), and *Inga uruguensis* Hook. & Arn, a native species that is abundant in riparian vegetation. Previous studies in tropical streams have shown that litter of some species of *Eucalyptus* genus (e.g., *Eucalyptus cloeziana*, F. Muell. *E. grandis camaldulensis*) can be considered high quality (Rezende et al. 2010, 2014a, 2019a; Gonçalves et al. 2012a, b), whereas that of the genus *Inga* genus can be considered low quality (Rezende et al. 2014a, 2018, 2019a; Sena et al. 2020).

The experiment was conducted during two distinct sampling periods: (i) September through November 2021, the winter–spring transition for Das Antas River Basin, and (ii) March through April 2020, the summer–autumn transition for Irani River Basin. The mean temperature (18 °C) and mean rainfall (135 mm) of sampled periods are lower

compared to summer (20 °C and 163 mm), but higher compared to winter (13 °C and 135 mm) and autumn (15 °C and 142 mm). Three sampling points, spaced 10 m apart, were selected in each river section to incubate litter bags (coarse and fine meshes) containing leaf litter of each species; thus, 4 rivers × 4 sections × 3 points × 2 plant species × 2 periods × 2 litter bag mesh sizes, totaling 384 monospecific litter bags (sampling units).

## Physical and chemical parameters

During field expeditions for litterbags incubation and removal, water temperature (°C), electrical conductivity ( $\text{mS cm}^{-1}$ ), total dissolved solids ( $\text{g L}^{-1}$ ; TDS), nephelometric turbidity unity ( $\text{L}^{-1}$ , NTU), and dissolved oxygen (%) were in situ measured using a U-5000G Horiba Ltd multi-analyzer, whereas in situ pH was measured using a EcoSense pH100A YSI Inc.

The initial chemical composition of each plant species was assessed for nitrogen, phosphorus, toughness, and caloric content of the leaf litter. Total nitrogen content was determined by the Kjeldahl method (Cantarella and Trivelin 2001) and total phosphorus was determined by reaction with ascorbic acid following Flindt and Lillebø (2005). The

toughness of intact leaves was assessed by resistance to rupture (Graça and Zimmer 2005). The calorific value for each leaf litter was estimated by combustion using a calorimetric pump (C200 IKA model), previously calibrated with IKA certified (standard calibrations) benzoic acid using calibrated ignition wire and a decomposition vessel at 30 bar pressurized O<sub>2</sub> station.

### Leaf breakdown process, invertebrate community, and fungi biomass

Litter bags (0.5 mm for fine and 10 mm for coarse mesh size, 30×30 cm) were incubated during 15 or 45 days. Each litter bag contained 2 g ( $\pm 0.1$ ) of dry leaves and was incubated at a depth of 0.2 to 0.5 m in contact with the sediment. Litter bags were removed from the river after incubation and individually placed into insulated plastic bags and transported to the laboratory in thermal containers ( $\pm 4$  °C). In the laboratory, leaves were carefully removed from the litter bags and washed with distilled water over a 120  $\mu$ m mesh sieve, whereas invertebrates retained on the sieve were preserved in 70% alcohol for later identification (Cummins 1996; Cummins et al. 2005; Hamada et al. 2014).

The number of *taxa* (richness) and individuals (density as number of organisms per litter mass) of invertebrates were calculated for the aquatic invertebrate community. The invertebrates were classified into five feeding categories: gathering-collectors, filtering-collectors, shredders, scrapers, and predators (Pérez 1988; Cummins 1996; Cummins et al. 2005; Hamada and Ferreira-Keppler 2012). Of these categories, only the occurrence and frequencies of shredders and scrapers were used to determine the direct effects of river section on leaf litter.

Finally, remaining ash-free dry mass (AFDM) was determined by randomly selecting five leaves from each litter bag and cutting two disks (1.2 cm in diameter) from each, for a total of two sets with five discs. One disc set was dried, weighted, individually incinerated in a muffle furnace at 550 °C for 4 h, and then reweighted to allow the AFDM calculation. The other disc set was dried and weighed to estimate removal of additional disc sets for AFDM calculation. The remaining material was oven-dried at 60 °C for 72 h to determine its dry mass (Graça et al. 2005).

### Statistical analysis

The leaf litter breakdown rate ( $k \text{ d}^{-1}$ ) was calculated using the negative exponential model of percent mass lost over time ( $W_t = W_0 e^{-kt}$ ;  $W_t$  = remaining weight;  $W_0$  = initial weight;  $-k$  = decay rate;  $t$  = time in days). The rate  $k$  was also expressed in degree days ( $\text{dd}^{-1}$ ) by computing the thermal sums of each sampling date for each sampling river and section according to Gessner and Peeters (2020), based

on a reference temperature (sampling period mean for each point) of normalization of 1 in the degree-day model. River water temperature at each sampling point was used for litter correction.

A two-way factorial generalized linear mixed-effects analysis (glmer function of lme4 package) was performed to test the effect of leaf litter species (*Eucalyptus grandis* vs. *Inga uruguensis*), river section (upstream, reservoir, by-passed, and downstream), and their interaction (explanatory variable) on (i) mass loss with fine and coarse mesh, (ii) invertebrate richness, (iii) invertebrate density, (iv) shredder abundance, and (v) scraper abundance (response variables; Zuur et al. 2009). A random effect GLMMER analysis was performed considering seasonal period (winter–spring transition and summer–autumn transition), time (in days), and the nesting effect of river section (sampling site position; upstream  $\rightarrow$  reservoir  $\rightarrow$  by-passed  $\rightarrow$  downstream), this latter to account for the specific features of landscape variation.

The  $p$  values were obtained by likelihood ratio tests (Chi-squared distribution) of the full model against a partial model without the explanatory variables. The error distribution of each model was tested using the hnp function and package, and corrected for over or under dispersion. The Quasi-binomial family error distribution had the best fit for mass loss, shredder abundance, and scraper abundance; the Poisson family error distribution had the best fit for invertebrate richness; and the Gaussian family had the best fit for invertebrate density. The Gaussian family had the best fit for pH, conductivity, and turbidity, whereas the Poisson family had the best fit for total dissolved solids, dissolved oxygen, and temperature. A one-way GLMMER (considering the days and nesting effect) and orthogonal contrast analyses were also performed to test comparisons between river sections. A contrast analysis by orthogonal post hoc tests was then performed to interpret which of the factors differed from the others. The explanatory variables in the contrast analysis (orthogonal) were ordered by increasing input values, which were then tested pairwise with the treatments with the closest values. Stepwise model simplification was performed by sequentially adding treatment values that did not affect the model and testing against the following variable in the sequence (for more details, see chapter 9 in Crawley 2007).

Invertebrate community structure (by frequency and occurrence) among river sections, leaf litter species, and their interaction, was tested by PerMANOVA and pairwise-contrast analyses with Bonferroni correction. An indicator species analysis was also undertaken to determine which taxa were most important to community structure among river sections and leaf litter species in the process of leaf litter colonization by invertebrates. This method combines the abundance and frequency of each group (river sections and leaf litter species) of the study and the fidelity of the

occurrence of a *taxon* in a particular group to yield indicator values (IVs) for each *taxon* in each group (Dufrene and Legendre 1997). All analyses were performed using R software (R Core Team 2022).

## Results

### Physical and chemical parameters

Mean water temperature was 25.7 °C (standard error  $\pm 2.5$  °C), with highest values for the by-passed section (25.7  $\pm 2.5$  °C), followed by reservoir (25.5  $\pm 2.5$  °C), upstream (25.3 °C  $\pm 2.5$  °C), and downstream (25.0  $\pm 2.3$  °C). The water temperature from by-passed and reservoir stretches was significantly higher than from upstream and downstream stretches (GLMMER;  $\chi^2_{(6,21)} = 5.53$ ;  $p < 0.001$ ; contrast analysis;  $p < 0.05$ ). Mean water pH was 6.7 ( $\pm 0.25$ ) with higher values for the upstream section (6.8  $\pm 0.35$ ) than for reservoir, by-passed, and downstream (6.6  $\pm 0.25$  for all; GLMMER;  $\chi^2_{(6,21)} = 17.51$ ;  $p < 0.001$ ; Table SM2).

Dissolved oxygen (95  $\pm 21\%$ ) was highest for the upstream section (98  $\pm 9\%$ ), followed by by-passed (94  $\pm 8\%$ ), downstream (93  $\pm 8\%$ ), and reservoir (83  $\pm 7\%$ ; GLMMER;  $\chi^2_{(6,21)} = 6.98$ ;  $p < 0.001$ ). Total dissolved solids (0.049  $\pm 0.012$  g L<sup>-1</sup>) was higher for by-passed and downstream sections\*\*\* (0.052  $\pm 0.012$  g L<sup>-1</sup> and 0.049  $\pm 0.011$  g L<sup>-1</sup>, respectively) compared to upstream and reservoir (0.047  $\pm 0.011$  g L<sup>-1</sup> and 0.047  $\pm 0.012$  g L<sup>-1</sup>, respectively; GLMMER;  $\chi^2_{(6,21)} = 6.94$ ;  $p < 0.001$ ). On the other hand, there were no significant differences in electrical conductivity (mean 0.07  $\pm 0.01$  mS cm<sup>-1</sup> ranging from 0.07  $\pm 0.01$   $\mu$ S cm<sup>-1</sup> to 0.08  $\pm 0.02$   $\mu$ S cm<sup>-1</sup>; GLMMER;  $\chi^2_{(6,21)} = 2.07$ ;  $p = 0.5588$ ) and turbidity (mean 29  $\pm 42$  NTU ranging from 17  $\pm 19$  NTU to 39  $\pm 64$  NTU; GLMMER;  $\chi^2_{(6,21)} = 5.10$ ;  $p = 0.1649$ ) among sections (Table SM2).

Initial mean total nitrogen was 1.79 (standard error  $\pm 0.482$  mg.g<sup>-1</sup>) and 1.09 ( $\pm 0.061$  mg g<sup>-1</sup>) for leaf litter from *E. grandis* and *I. uruguensis*, respectively. Total phosphorus was 0.23 ( $\pm 0.012$  mg g<sup>-1</sup>) and 0.12 ( $\pm 0.01$  mg g<sup>-1</sup>) and initial leaf litter toughness was 0.77 ( $\pm 0.05$  cm g<sup>-1</sup>) and 0.36 ( $\pm 0.02$  cm g<sup>-1</sup>) for *E. grandis* and *I. uruguensis*, respectively. The calorific value of leaf litter was 7.03 ( $\pm 0.52$  kJ g<sup>-1</sup>) for *E. grandis* and 5.61 ( $\pm 0.41$  kJ g<sup>-1</sup>) for *I. uruguensis*.

### Leaf litter breakdown

Leaf breakdown rates ( $k$ ) for *E. grandis* in the upstream section were  $-0.0014$  d<sup>-1</sup> and  $-0.0125$  dd<sup>-1</sup> for coarse and  $-0.0077$  d<sup>-1</sup> and  $-0.0676$  dd<sup>-1</sup> for fine mesh. The downstream section had similar values, with  $-0.0014$  d<sup>-1</sup> and  $-0.0199$  dd<sup>-1</sup> for coarse and  $-0.0066$  d<sup>-1</sup> and

$-0.0520$  dd<sup>-1</sup> for fine mesh. The by-passed section had higher  $k$  values ( $-0.0154$  d<sup>-1</sup> and  $-0.1426$  dd<sup>-1</sup> for coarse mesh;  $-0.0116$  d<sup>-1</sup> and  $-0.1063$  dd<sup>-1</sup> for fine mesh) than did the reservoir section ( $-0.0123$  d<sup>-1</sup> and  $-0.0977$  dd<sup>-1</sup> for coarse mesh;  $-0.0105$  d<sup>-1</sup> and  $-0.0873$  dd<sup>-1</sup> for fine mesh).

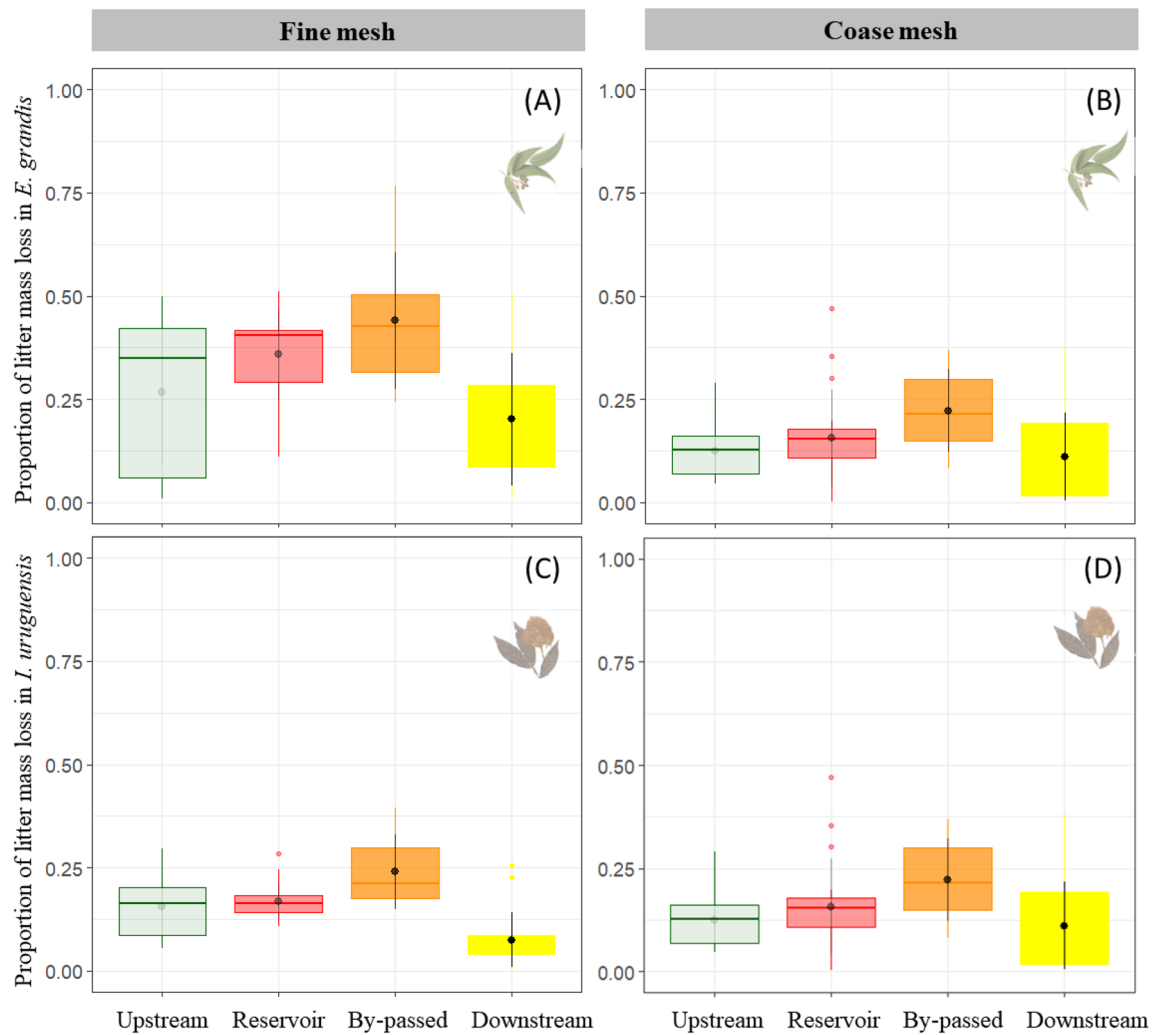
Leaf breakdown rates ( $k$ ) for *I. uruguensis* in the upstream section were  $-0.0038$  d<sup>-1</sup> and  $-0.0324$  dd<sup>-1</sup> for coarse mesh and  $-0.0056$  d<sup>-1</sup> and  $-0.0428$  dd<sup>-1</sup> for fine mesh, whereas, in the downstream section, they were  $-0.0021$  d<sup>-1</sup> and  $-0.0191$  dd<sup>-1</sup> for coarse mesh and 0.0024 d<sup>-1</sup> and  $-0.0186$  dd<sup>-1</sup> for fine mesh. The by-passed section had higher rates ( $-0.0057$  d<sup>-1</sup> and  $-0.0489$  dd<sup>-1</sup> for coarse mesh;  $-0.0057$  d<sup>-1</sup> and  $-0.0511$  dd<sup>-1</sup> for fine mesh) than did the reservoir section ( $-0.0023$  d<sup>-1</sup> and  $-0.0489$  dd<sup>-1</sup> for coarse mesh;  $-0.0038$  d<sup>-1</sup> and  $-0.0511$  dd<sup>-1</sup> for fine mesh).

Leaf litter mass loss for fine mesh (Fig. 2A and C) was highest in the by-passed section, followed by reservoir, and lowest in downstream and upstream sections (Table 1A). Leaf litter mass loss for coarse mesh (Fig. 2B and D) was higher for by-passed and reservoir sections than for downstream and upstream sections (Table 1B). There was higher mass loss for *E. grandis* (Fig. 2A and B) than *I. uruguensis* (Fig. 2C and D), for both fine (Table 1A; Table SM3) and coarse meshes (Table 1B; Table SM3).

### Invertebrate community

Invertebrate parameters (richness, density, scraper abundance, and shredders abundance) differed among river sections based on the interaction between river section and leaf litter species but did not differ between leaf litter species (Table 1; Fig. 3; Table SM3). Invertebrate richness was highest for the downstream section (Table 1C; Fig. 3A and B). Invertebrate density (Table 1D; Fig. 3C and D) and shredder abundance (Table 1E; Fig. 3E and F) were highest for the by-passed section. Scraper abundance was highest for the reservoir section but did not differ between leaf litter species and interaction between river section and leaf litter species (Table 1E; Fig. 3G and H).

Invertebrate community structure (Table SM4) only differed among river sections (PerMANOVA,  $F_{(3,173)} = 2.81$ ;  $p < 0.001$ ), and not between leaf litter species (PerMANOVA,  $F_{(1,175)} = 1.13$ ;  $p = 0.311$ ) and interaction between the two factors (PerMANOVA,  $F_{(3,173)} = 0.94$ ;  $p = 0.543$ ). Invertebrate community structure for the reservoir section differed from that for the other sections (pairwise comparisons, Bonferroni;  $p < 0.05$ ). Only Planorbidae (IV = 0.72;  $p = 0.024$ ) and Physidae (IV = 0.51;  $p = 0.032$ ) were found to be indicator *taxa* for the downstream section, with no indicator *taxon* being found for the other sections.



**Fig. 2** Litter mass loss in fine (A and C; proportion) and coarse (B and D; proportion) mesh for *Eucalyptus grandis* (A and B) and *Inga uruguensis* (C and D) among river sections (upstream, reservoir, by-

passed, and downstream). Boxes represent quartiles, bold line represents the median, black circle represents the mean, vertical lines represent the upper and lower limits, and circles represent outliers

## Discussion

### Impacts of by-passed and reservoir sections on the river ecosystem

By-passed increased the breakdown process, invertebrate density, and shredder abundance of the studied rivers. This finding was due to decreased water volume flow, as previously reported in the literature (Mbaka and Mwaniki 2016; Noel et al. 2016; Salomão et al. 2019). In general, the present result shows that small hydropower plants (SHPs) can affect ecosystem processes along different river sections, but mainly in the by-passed section, accelerating litter breakdown due to increased microbial activity due to high water temperature (Quintão et al. 2013; Heggenes et al. 2021) and fungi sporulation due to increased water turbulence (Alvim et al. 2015; Cid et al. 2019) resulting from the proximity to

the dam fall. By-passed sections can receive more nutrients-enriched water immediately after the dam by the increase in autochthone production expected due to the high invertebrate density found in the reservoir section. In this way, high invertebrate density and shredder abundance may increase leaf fragmentation (Sena et al. 2020; Rezende et al. 2021b), leading to higher leaf breakdown rates. By-passed sections may be more similar to streams than are other river sections (mainly the reservoir section) (Farah-Pérez et al. 2020), thereby favoring organisms that are adapted to small lotic systems, such as shredders (Rezende et al. 2014b; Salomão et al. 2019).

The reservoir section of SHPs also alters the ecosystem process of rivers through high litter breakdown and changes in the invertebrate community (Quintão et al. 2013), but by different mechanisms than those observed in the by-passed section (Mbaka and Mwaniki 2016; Li et al. 2020). The

**Table 1** Simplified two-way factorial generalized linear mixed-effects analysis (GLMMER) of the effects of leaf litter species (*Eucalyptus grandis* and *Inga uruguensis*) and river section (upstream, reservoir, by-passed, and downstream) on different response variables

Glmmer (sea-sonality: day: nesting)	Df	AIC	BIC	logLik	Deviance	ChisqChi	Df	Pr(> Chisq)	Contrast analysis
<b>A. Mass loss (FM)</b>									
Plant species	10	-208.1	-178.8	114.1	-228.1	60.3	163	<0.001	<i>I. uruguensis</i> < <i>E. grandis</i>
Habitat	10	-208.1	-178.8	114.1	-228.1	53.3	165	<0.001	Downstream = upstream < reservoir < by-passed
Interaction	10	-208.1	-178.8	114.1	-228.1	93.7	164	<0.001	
<b>B. Mass loss (CM)</b>									
Plant species	10	-109.7	-80.1	64.8	-129.7	53.6	163	<0.001	<i>I. uruguensis</i> < <i>E. grandis</i>
Habitat	10	-109.7	-80.1	64.8	-129.7	23.3	165	<0.001	Downstream = upstream < reservoir = by-passed
Interaction	10	-109.7	-80.1	64.8	-129.7	66.5	164	<0.001	
<b>C. Invertebrate richness</b>									
Plant species	10	305.6	324.4	-143.8	287.6	3.5	163	0.468	
Habitat	10	305.6	324.4	-143.8	287.6	11.9	165	<b>0.034</b>	By-passed = reservoir = upstream < downstream
Interaction	10	305.6	324.4	-143.8	287.6	13.0	164	<b>0.042</b>	
<b>D. Invertebrate density</b>									
Plant species	10	517.5	538.4	-248.7	497.5	6.6	163	0.154	
Habitat	10	517.5	538.4	-248.7	497.5	17.0	165	<b>0.009</b>	Reservoir = upstream = downstream < by-passed
Interaction	10	517.5	538.4	-248.7	497.5	18.0	164	<b>0.012</b>	
<b>E. Shredder abundance</b>									
Plant specie	10	275.8	296.7	-127.9	255.8	3.7	163	0.435	
Habitat	10	275.8	296.7	-127.9	255.8	13.0	165	<b>0.041</b>	Reservoir = downstream < upstream < by-passed
Interaction	10	275.8	296.7	-127.9	255.8	14.9	164	<b>0.036</b>	
<b>F. Scraper abundance</b>									
Plant species	10	449.7	470.7	-214.8	429.7	11.0	165	0.096	
Habitat	10	449.7	470.7	-214.8	429.7	19.9	163	<b>0.001</b>	Upstream = by-passed = downstream < reservoir
Interaction	10	449.7	470.7	-214.8	429.7	11.6	164	0.112	

Mass loss in fine mesh (A; proportion in FM), mass loss in coarse mesh (B; proportion in CM), invertebrate species richness (C; number of taxa), invertebrate density (D; individuals per leaf litter g), shredder abundance (E; %), and scraper abundance (F; %). The results of orthogonal contrast analysis are also given for significant results ( $p < 0.05$ )

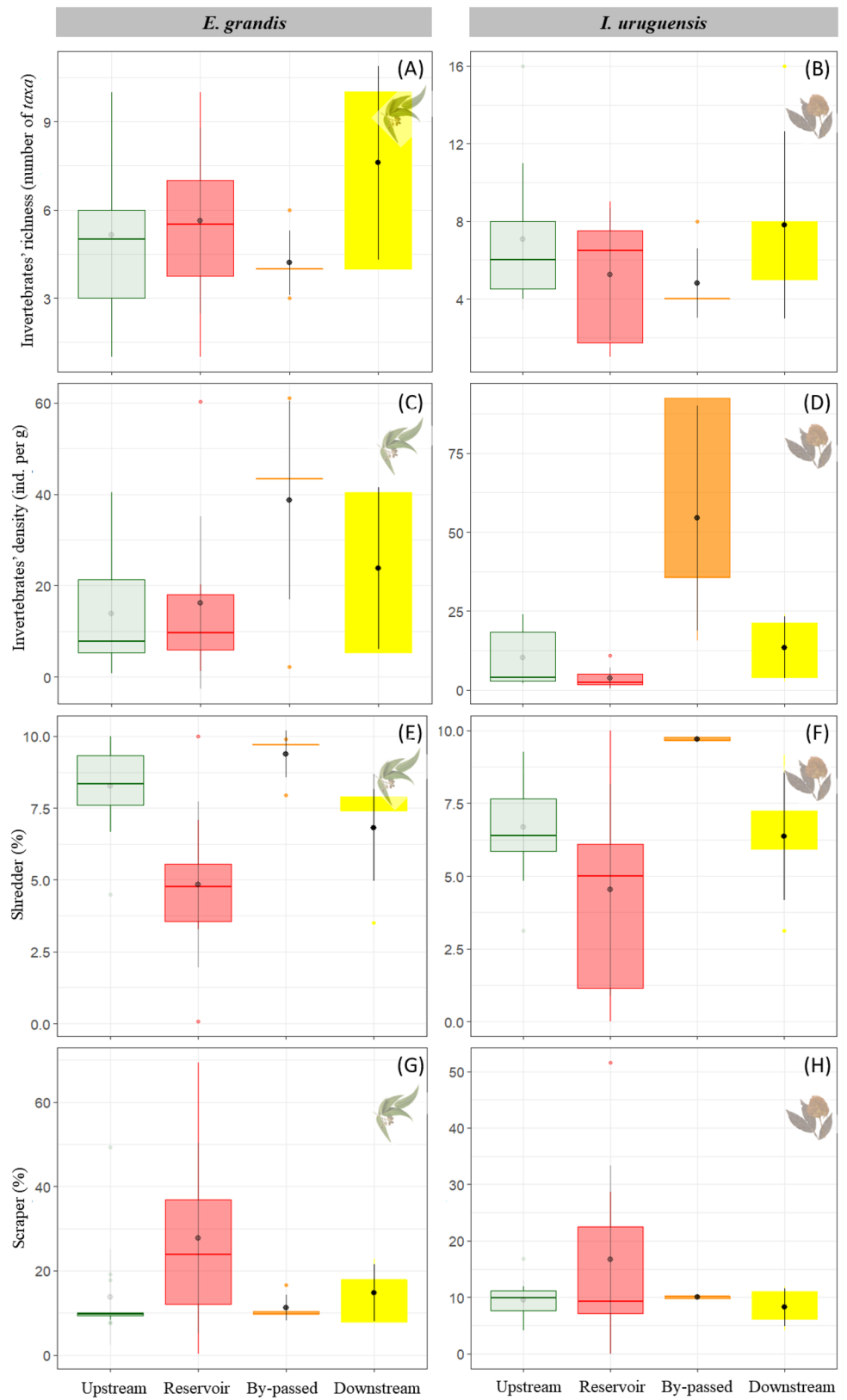
Bold values indicate significant differences

changes may be due to the formation of lentic systems as a result of reduced water flow, which would be expected to reduce the litter breakdown rate (Mbaka and Mwaniki 2016; Li et al. 2020). On the other hand, the reservoir section also accelerated leaf mass loss due to high temperature (Forster et al. 2012), which increases microbial decomposition activity (Martins et al. 2017; Heggenes et al. 2021). Also, less dissolved oxygen may drive the interaction among temperature and organisms size responses (Forster et al. 2012) facilitating the occurrence of (i) microorganisms; (ii) small invertebrates; and/or (iii) invertebrates with atmospheric respiration (e.g., gastropods scrapers) in reservoir section, as observed. A high abundance of scrapers were also found, which could favor litter fragmentation in coarse mesh. Scrapers may assume the ecological role of shredders and promote indirect litter fragmentation by scraping the substrate, such as gastropods that use their radulae to obtain

food (Quintão et al. 2013; Rezende et al. 2017a, 2019b), thus increasing litter breakdown.

River section was found to be a more important driver of invertebrate community colonization and structure than plant litter species, although a significant effect of this latter was also observed. A similar trend was observed in previous studies in the Neotropical region (Rezende et al. 2014a, 2021a; Salomão et al. 2019). On the other hand, changes in leaf quality may also drive litter processing (Sena et al. 2020; Boyero et al. 2021), although the present study indicated a lower effect than river section (Quintão et al. 2013; Rezende et al. 2014a). Furthermore, litter quality has less influence on the invertebrate community than do microorganisms (Rezende et al. 2014b, 2019a), despite the recognized importance of litter quality to colonization of invertebrates (Salomão et al. 2019; Nuven et al. 2022).

**Fig. 3** Invertebrate species richness (A and B; number of taxa), invertebrate density (C and D; individuals per leaf litter g), shredder abundance (E and F; %), and scraper abundance (G and H; %) for *Eucalyptus grandis* (A, C, E and G) and *Inga uruguensis* (B, D, F and H) among rivers sections (upstream, reservoir, by-passed, and downstream). Boxes represent quartiles, bold line represents the median, black circle represents the mean, vertical lines represent the upper and lower limits, and circles represent outliers



Therefore, this finding reinforces the importance of using field experiments with standardized litter for monitoring rivers using litter breakdown as a proxy, as litter type matters (Tiegs et al. 2013; Colas et al. 2019).

### Impacts of plant species on leaf litter breakdown rates

*Eucalyptus grandis* was found to have higher contents of nitrogen, phosphorus, and calorific value than *I. uruguensis*, which indicate a higher nutritional quality in the former and could explain its higher mass loss. The positive and direct effect of litter quality on breakdown rates is expected and well documented (Quintão et al. 2013; Rezende et al. 2014a; Salomão et al. 2019). No differences were found in invertebrate parameters (i.e., richness, density, scraper abundance, and shredder abundance) between plant species, which may evidence low leaf litter availability in river bed compared to autochthone resources (Rezende et al. 2014b), decreasing feeding preference of decomposing invertebrate community (Rezende et al. 2017b; Sena 2021). Therefore, the process of leaf litter leaching and/or microorganism colonization may drive differences in breakdown among plant species (Quintão et al. 2013; Alvim et al. 2015; Rezende et al. 2021a). This result does not rule out the importance of invertebrates; it just shows that microorganisms play a greater role, which is a common pattern found in the tropical literature (Gonçalves et al. 2014).

Overall, the estimated leaf litter breakdown rates ( $k$ ) found for the two species in almost all sections of both rivers are considered intermediate ( $0.010 > k > 0.005 \text{ d}^{-1}$ ), which is in accordance with the classification of temperate streams (Petersen and Cummins 1974). However, according to the classification proposed for tropical systems, the  $k$  values for the downstream section are low ( $k < 0.0041$ ) for both leaf litter species whereas those for the by-passed section are intermediate ( $0.0041 > k > 0.0173$ ) for both (Gonçalves et al. 2014). These classifications are mainly suitable for streams; thus, a smaller  $k$  is expected for rivers compared to streams due to the high autochthonous metabolism of rivers (Csiki and Rhoads 2010). Therefore, a new classification specific to rivers would be very important for directing the use of the leaf breakdown process as a tool for evaluating the impacts of SHPs.

### Invertebrate community

High invertebrate species richness in downstream sections may be explained by the cumulative effect of different upstream habitats, mainly the by-passed stretch, associated with larval drift movements (Rezende et al. 2014b; Durães et al. 2016). Aquatic invertebrate larvae preferentially show a gradual downstream movement according to Müller's "colonization

cycle" hypothesis (Müller 1982). Thus, downstream sections may receive larvae by drift movement from other upstream habitats (upstream, reservoir, and by-passed), which would explain the high richness found here. On the other hand, the high species richness in association with low density could indicate that these organisms are not fixing in the habitats of downstream environments. Whatever the case, this issue needs further investigation in future studies.

Reviews have shown that the reduced water flow caused by damming increases water temperature and total dissolved solids (Mbaka and Mwaniki 2015, 2016), as observed in the present study. Here, we found differences in invertebrate community structure among sections, mainly for the reservoir section. Changes in river morphology by damming can limit sediment transport and, consequently, increase sediment retention in these areas, increasing the deposition of fine particles (Salomão et al. 2019; Farah-Pérez et al. 2020). In this way, water retention and the subsequent reduction in flow by damming may change other abiotic variables, resulting in habitat homogenization for the invertebrate community (Mbaka and Mwaniki 2015; Salomão et al. 2019). Additionally, the other stretches (upstream, by-passed, and downstream), even with some level of impact, will preserve the characteristics of the lotic system (Farah-Pérez et al. 2020), and thus will have more similar invertebrate community structure (Mbaka and Mwaniki 2015; Salomão et al. 2019). This process may help explain the differences observed in invertebrate community structure between the reservoir and the other sections, highlighting the impacts of dams on this community.

Finally, Planorbidae and Physidae were found to be indicator taxa for the downstream section. Previous studies examining the downstream effects of SHPs also reported invasions by mollusks (Anderson et al. 2017; Linares et al. 2019). Therefore, it is evident that upstream impacts of reservoir and by-passed sections can affect the taxonomic dominance of the downstream invertebrate community (Salomão et al. 2019). Reservoirs of SHPs may impact the transport of dissolved nutrients and sediment of rivers downstream from the impoundment, resulting in an overall increase of biofilm and the deposition of fine sediments (Csiki and Rhoads 2010). Such changes in habitat characteristics have important implications for the invertebrates community, particularly for guilds of scrapers that rely on high biofilm colonization on substrates (Rezende et al. 2014b). A relevant aspect is that some mollusks are intermediate hosts of some diseases, such as snails of the family Planorbidae, the natural intermediate host of *Schistosoma mansoni* in Brazil. Therefore, the influence that SHPs have on the prevalence of diseases with intermediate hosts benefited by dams in riverine ecosystems with human communities needs further investigation.

## Conclusion

Small hydropower plants drastically affect river ecosystem process, but in the opposite direction of our prediction. The greater difference observed for the by-passed section was due to high water temperature, which increases decomposer metabolism, and high shredder abundance, which increases leaf fragmentation. Moreover, increased water temperature due to the formation of lentic systems in the reservoir section increases decomposition activity associated with high scraper abundance (indirectly litter fragmentation by scraping the substrate). Therefore, the prediction that reservoirs and by-passed stretches slow down litter mass loss and decrease the diversity of the invertebrate community was refuted by our data. Besides, we found that variation among river sections of SHPs is a more important driver of invertebrate colonization than is leaf litter species. Mass loss was higher for the high-quality litter of *E. grandis* compared to *I. uruguensis*, and the influence of litter quality was lower for the invertebrate community than for microorganisms, mainly for leaf litter with faster breakdown due to higher quality. Therefore, changes in hydrology and riparian vegetation have severe impacts on river process, and leaf litter breakdown proved to be a sensitive tool for assessing the impacts of SHPs.

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**Data availability** All data generated or analyzed during this study are included in this published article [and its supplementary information files] and/or are available from the corresponding author upon reasonable request.

## Declarations

**Conflict of interest** The authors declare that there is no conflict of financial or personal interests in this paper.

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