



Litter decomposition is driven by microbes and is more influenced by litter quality than environmental conditions in oil palm streams with different riparian types

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Abstract

Rapid and extensive conversion of tropical forests into oil palm (*Elaeis guineensis*) (OP) plantations pose serious threats to tropical stream processes. To mitigate land use change impacts on stream ecosystems, retention of riparian vegetation is typically proposed. We evaluated the effectiveness of a gradient of riparian qualities in oil palm streams: (1) natural forest; (2) OP-native forested buffer; (3) OP-native understory, no chemical input (OPOP) and (4) OP-no buffer, to mitigate impacts on in-stream litter processing. Leaf bag method entry using two leaf species of contrasting litter quality (*Macaranga tanarius* and OP) were deployed into streams. Across all riparian types, microbes were the main drivers of decomposition with negligible macroinvertebrate shredding activities. Leaf decomposition rates were more influenced by litter quality than changes in environmental conditions in the different riparian types. Across all sites, native *Macaranga* litter decomposed approximately 5× faster than OP litter possibly due to high structural compounds in OP leaves. *Macaranga* litter was also more susceptible to changes in environmental conditions as leaf decomposition positively correlated to phosphorus and potassium content. However, OP leaves were resilient to stream environmental changes and decomposed slower only at OPOP sites. These varying responses reveal complex interactions within tropical stream ecosystems. We suggest that riparian management strategies as well as plans to restore functioning in degraded tropical streams should ensure a wide diversity of native riparian tree species in order to effectively mitigate adverse OP plantation impacts on tropical stream functioning.

Keywords Microbial decomposition · Riparian buffer · Land use change · Litter quality · Stream functioning

Introduction

Forested headwater streams rely heavily on allochthonous inputs derived from surrounding riparian vegetation for aquatic productivity as most of the energy that fuels stream ecological processes come from detrital pathways regulated by microbial and aquatic invertebrate (shredders) decomposing activities (Fisher and Likens 1973; Graça and Canhoto 2006; Vannote et al. 1980). Several abiotic and biotic factors modulate decomposition rates such as climate, mainly temperature and rainfall (Ferreira and Chauvet 2011a), quality of litter (Loranger et al. 2002), environmental conditions such as nutrient availability in soil and water (Ferreira and

Chauvet 2011b; Kaspari et al. 2008) and the qualitative and quantitative compositions of decomposer communities (DeAngelis et al. 2013; Leroy and Marks 2006). With colossal scale conversions of forest into oil palm (OP) plantations (Food and Agriculture Organization of the United Nations 2014; Miettinen et al. 2011; Reynolds et al. 2011) particularly in Malaysia and Indonesia and rapid expansions expected in over 43 countries worldwide (Vijay et al. 2016), severe changes in land use would cause drastic modifications to riparian and environmental conditions subsequently affecting stream ecosystem productivity and functioning (Chellaiah and Yule 2018a).

When forests are converted into monoculture plantations, major changes in riparian vegetation severely alters the diversity, quantity and quality (e.g. nutrients, toughness and toxic secondary compounds) of leaf litter resources that enter streams (Casotti et al. 2015; Kominoski et al. 2011; Lacan et al. 2010; Leroy and Marks 2006; Silva-Junior et al. 2014). In addition, the absence of riparian vegetation

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previously shading and filtering plantation streams often leads to increased temperatures, sedimentation and nutrient runoff that influences microbial and aquatic invertebrate decomposition activity (Encalada et al. 2010). For example, warming (Brown et al. 2004; Davidson and Janssens 2006; Davidson et al. 2006) and moderate levels of nutrient enrichment (Woodward et al. 2012) accelerate chemical reactions and enhance biological activities while sedimentation increases turbidity of water, reducing light penetration and impairing photosynthesis, consequently reducing food supplies to certain aquatic organisms (Bilotta and Brazier 2008; Mercer et al. 2014). Previous studies assessing the impact of monoculture plantations (e.g. eucalyptus, pine, teak) on stream litter decomposition rates compared to pristine forested sites show results ranging from reduced litter decay (Casotti et al. 2015; Guevara et al. 2015; Yang et al. 2003) to increased litter decomposition rates at disturbed sites (Jinggut et al. 2012; Pandey et al. 2007), or to no difference between both sites (Bärlocher and Graça 2002; Foster et al. 2011). However, some studies also show inconsistent results between pristine and agriculturally impacted sites with litter processing rates mostly dependent on the quality of litter studied (Cizungu et al. 2014; Ferreira et al. 2006a). With oil palm plantations typically supporting fewer species compared to other tree crops (Almeida et al. 2016; Cunha et al. 2015; Gillespie et al. 2012; Lees et al. 2015; Luiza-Andrade et al. 2017; Sheldon et al. 2010; Turner and Foster 2009; Wang and Foster 2015), there could potentially be severe impacts on stream productivity with potential downstream implications.

Several studies recommend retaining or replanting vegetated riparian buffer zones to regulate inputs of organic matter and nutrients, decrease light incidence, change habitat and energy supply (e.g. volume and velocity of flow entering the system), stabilise channels and filter sediments and contaminant loads washed into streams (Casotti et al. 2015; Chellaiah and Yule 2018a; Quinn et al. 2004; Rios and Bailey 2006; Weigel et al. 2000). Casotti et al. (2015) found that along a gradient of riparian disturbance from pristine forests to clear-cut Eucalyptus plantations, leaf breakdown rates decreased and were highly influenced by the composition of decomposer communities affected by the availability of habitat and food resources. However, there is little information on aquatic ecosystems in general, with few studies focusing on the efficacy of riparian buffers in monoculture plantations to mitigate impacts on tropical stream litter decomposition.

In this study, we use a functional measure - leaf litter decomposition rates to measure the efficacy of different riparian buffer types (across a disturbance gradient) commonly used in OP plantations to mitigate impacts on stream ecological functioning (Kreutzweiser et al. 2008; Lecerf et al. 2011; Piggott et al. 2015; Woodward et al. 2012). We use the leaf litter bag method (Crossley and Hoglund

1962) with two litter species of contrasting litter traits, native (*Macaranga tanarius*) and exotic (OP) leaf species, that may have varying responses to stream environmental conditions. We hypothesise that (1) leaf decomposition rates would be higher in the more disturbed streams (OP plantation) compared to natural forest due to increased temperatures and nutrient levels which stimulate decomposer activities, (2) rates of leaf litter decomposition would differ between OP and *Macaranga* leaves due to differing litter qualities (C, N, P, K, phenols, tannin, lignin, cellulose, fibre, toughness), (3) rates of leaf litter decomposition would be similar in coarse bags and fine mesh bags as bacterial and fungal decomposition is expected to be dominant in tropical streams compared to macroinvertebrate shredder decomposition. Previously there have been two terrestrial study which examined effects of OP plantations on decomposition rates (Foster et al. 2011; Wong et al. 2016) but to our knowledge, none focusing on tropical stream functioning. Thus, this paper presents a pioneer study comparing commonly used riparian buffer types in OP plantations and their efficacy to mitigate negative impacts on stream litter decomposition in OP streams. Only by the understanding the key conditions governing organic matter processing can we begin to assess the resistance and resilience of stream ecosystems. Moderators could then be identified and useful mitigation measures for sustainable management of plantation stream ecosystems can be suggested.

Materials and methods

Study area and experimental sites

The experiment was conducted in streams within an industrial OP plantation area in Tawau, Sabah. Rainfall was heavy and regular all year round ranging from 2094 to 2184 mm/year with little seasonality (Chellaiah and Yule 2018a). Twelve study reaches (Fig. 1) were selected among first to third order streams across a disturbance gradient in one forest and three riparian buffer types bordering OP plantations (n = 3) (Table 1).

Study reaches were within separate catchments but were nested within larger catchments. Each stream was then assessed on the ground and selected as a replicate if it was similar in size, morphology and when applicable, age of plantation plot and extent of plantations. OP streams selected originated from forested fragments within the plantation and were at least 50 m away from major road networks (personal observation).

The physicochemical variables of the riparian and stream environment are described in Chellaiah and Yule 2018a. In brief, decreased foliage cover across the disturbance gradient increased the amount of light received at the stream, bank

Fig. 1 Map of Tawau, Sabah with the locations of sampling site (NF natural forest, OPF oil palm plantation with forested buffer, OPOP oil palm plantation with untreated buffer and native understorey, OPNB oil palm plantation with no buffer)

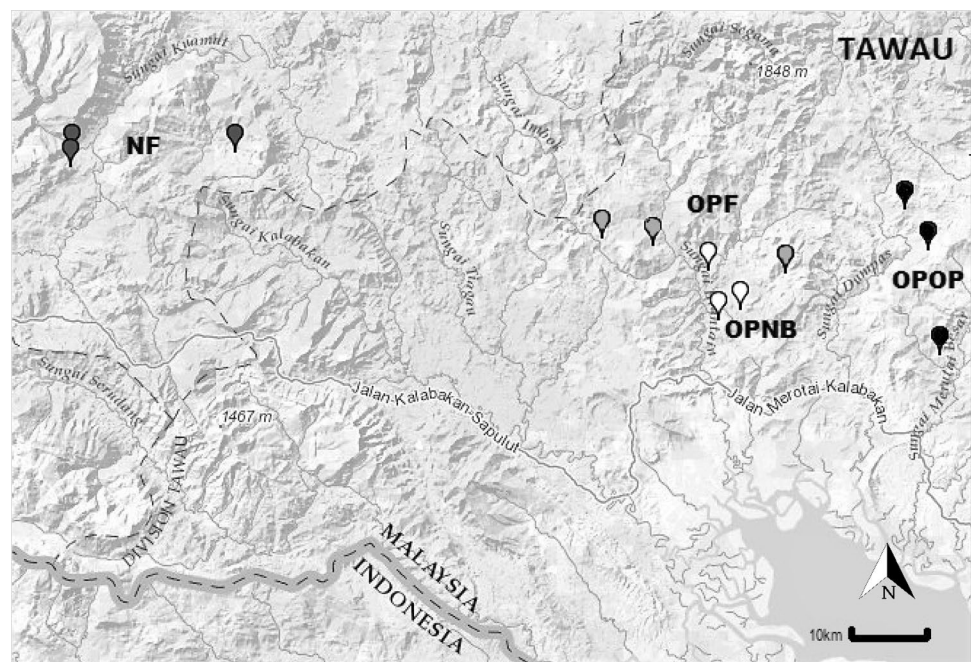


Table 1 Description of study streams within the different forest and riparian buffer types

Site code	Riparian type	Feature
NF	Native forest reference streams	Closest class I forest reserve to OP sites comprised of lowland dipterocarp forest
OPF	OP plantation streams with native riparian forest	Riparian buffer type most closely resembling natural forests with only minor selective logging 5–10 years ago with removal of tall and valuable trees
OPOP	OP plantation streams with untreated OP trees	Oil palm trees up to stream edge without chemical application (pesticide, herbicide and fertilizer) in buffer area with low quality understorey of shrubs/grasses
OPNB	Clear-cut OP plantation streams with treated OPs	Most disturbed riparian site with oil palm trees up to stream edge with chemical application

and within buffer zone levels. Stream temperatures gradually increased across the disturbance gradient with about 6 °C difference from the least disturbed (NF) to the most heavily disturbed sites (OPNB) (Chellaiah and Yule 2018a). OP sites also reported significantly higher phosphorus (P) and potassium (K) levels that can be attributed to the use of P and K rich fertilizers in the plantations that flow into streams (Chellaiah and Yule 2018a).

Leaf litter collection and initial nutrients analysis

We examined leaf litter from two tree species—indigenous *M. tanarius* (L.) Müll.Arg. (Family Euphorbiaceae) and exotic OP (*Elaeis guineensis* Jacq. family Areaceae). *Macaranga* was chosen as the reference species to be studied as it is a highly common early successional species and was found in all riparian types regardless of the rate of disturbance thus its leaves are likely to fall into rivers and it is an ecologically relevant species to investigate. Mature,

senescent leaves of *Macaranga* were collected just after abscission, from the perimeter of Ampang Forest Reserve (Selangor, Malaysia) while OP leaves collected were those cut by plantation workers to allow easy access to palm oil fruit. Consequently, these leaves were not necessarily senescent but they typified OP leaves that would be found in plantation streams. All litter was air-dried to a constant weight and measured based on Graça et al. (2005). Structural compounds (i.e., lignin, cellulose, fibre) were estimated with sequential neutral detergent/acid detergent digestion while litter toughness was measured using a penetrometer and expressed as ml/mm² (Graça et al. 2005). Total phenolic and total tannin content were determined following the Folin–Ciocalteu’s assay (Graça et al. 2005) with addition of polyvinylpyrrolidone (PVPP) to chelate tannins (Ong et al. 2015). To determine total carbon and nitrogen in leaf samples, samples were analysed using the combustion method using the CNS TruMac Analyzer® (LECO, Michigan, USA) while total phosphorus and

potassium was analysed using the dry ashing method following Jones (2001).

Rates of decomposition

A decomposition experiment was carried out between November 2015 and February 2016. $3 \text{ g} \pm 0.001 \text{ g}$ of each leaf species was placed in litter bags ($15 \text{ cm} \times 15 \text{ cm}$) of fine mesh ($< 0.5 \text{ mm}$) to assess microbial driven litter decomposition and coarse mesh (10 mm) to assess microbial and invertebrate driven litter decomposition (Graça et al. 2005) in three replicate streams in each riparian type. Bags ($n = 3$) were incubated in the streams and retrieved after 7, 14 and 30 days (total = 432 bags). Additional litter bags (day 0) were used to correct for handling mass loss during sample preparation and transportation. After collection, litter-bags were emptied and leaves thoroughly cleaned with fine brushes to remove extraneous material such as sediment and other debris. The residual wet weight of the cleaned litter was recorded. 1 g of wet weight was then separated and oven-dried for 24 h at $80 \text{ }^\circ\text{C}$ then ashed at $550 \text{ }^\circ\text{C}$ for 4 h in a muffle furnace (to account for mass loss due to humidity) to determine ash free dry mass (AFDM). Decomposition rates, k , were calculated by linear regression of \ln transformed data (negative exponential model), $M_t = M_0 \cdot e^{-kt}$ where, $M_t = \text{Mass at time } t$; $M_0 = \text{Mass at time } 0$; $k = \text{exponential decay coefficient (decomposition rate)}$; $t = \text{time in days}$ (Graça et al. 2005). To account for temperature differences between streams, decomposition rates were also expressed in terms of degree days by replacing time (t) by the sum of mean daily temperatures accumulated by the sampling day.

Data analysis

SPSS v16 (SPSS Inc, Chicago, USA) statistical analysis software was used to analyse data obtained. Prior to the analysis, data were tested for normality using Shapiro–Wilk test and Levene’s test of homogeneity of variance. Data sets that were not normally distributed were first transformed (i.e. \log_{10} , sqrt , arcsine) to meet normality, if not were analysed using a non-parametric test. T-tests were used to compare initial leaf physico-chemical properties of OP and

Macaranga leaves (Mann–Whitney U test for non-parametric data). To evaluate the decomposition process, a negative exponential model was used where the regression of the natural logarithm of the proportion of the remaining leaf dry mass and time elapsed (days) was calculated and the regression slope was used as the breakdown rate (k/day). Preliminary analysis showed no difference in rates of decomposition between each of the leaf type in each of the different riparian types between fine-mesh (kf) and coarse-mesh (kc) bag types (ANOVA, $p > 0.05$). Therefore, data from both types of mesh bag types were pooled for all subsequent analysis. The individual regressions (breakdown over time) was compared among riparian types for the whole dataset using two-way ANCOVA using \ln (AFDM remaining) as the dependent variable, riparian type and leaf species as the main factor and time (days) as covariate. When significant interaction between leaf species and riparian type was observed, we conducted separate one-way ANCOVA’s for each leaf species. To remove the potential effect of temperature on rates of litter decomposition among sites and over time, we calculated degree-day by substituting t with the average water temperature multiplied by the number of days the mesh bags were left in the stream to obtain breakdown rate ($k \text{ degree/day}$) (Riipinen et al. 2010) and repeated the analysis using days as covariate. Any significant observations at $\alpha = 0.05$ were tested using the Post Hoc Tukey’s pairwise comparisons test to identify where the differences lie.

Results

Characteristics of litter

Analysis revealed that all initial leaf litter variables measured were significantly different between OP and *Macaranga* leaves (Table 2). OP leaves had higher nutrient content [Carbon, C: $t(4) = 6.7$, $p = 0.003$; Nitrogen, N: $t(4) = 17.3$, $p < 0.001$; Phosphorus, P: $t(4) = 7.0$, $p = 0.002$; Potassium, K: $t(4) = 12.0$, $p < 0.001$] but were also significantly tougher ($U < 0.001$, $p < 0.001$) with higher fibre [$t(4) = 5.9$, $p = 0.004$] and lignin [$t(4) = -9.1$, $p = 0.001$] content compared to *Macaranga* leaves. Secondary defensive compounds, phenol:

Table 2 Physicochemical characteristics of oil palm and *Macaranga* leaf litter (means \pm SE)

	Oil palm	<i>Macaranga</i>		Oil palm	<i>Macaranga</i>
C (%)	42.2 ± 0.2^a	39.8 ± 0.3^b	Fibre (%)	46.8 ± 1.5^a	37.9 ± 0.6^b
N (%)	2.6 ± 0.07^a	1.3 ± 0.06^b	Cellulose (%)	17.7 ± 0.3^a	18.8 ± 0.4^b
P (%)	0.2 ± 0.01^a	0.1 ± 0.01^b	Lignin (%)	24.8 ± 1.5^a	10.9 ± 0.3^b
K (%)	0.9 ± 0.01^a	0.3 ± 0.04^b	Phenol (mg/g)	23.4 ± 2.8^a	73.7 ± 10.9^b
Toughness (ml/ mm^2)	471.3 ± 36.5^a	24.7 ± 1.2^b	Tannin (mg/g)	6.4 ± 3.6^a	59.1 ± 9.4^b

Treatments with the same letter are not significantly different ($p > 0.05$)

$t(4) = -4.5$, $p = 0.011$ and tannin [$t(4) = -5.2$, $p = 0.006$] as well as cellulose [$t(4) = 6.0$, $p = 0.004$] content were significantly higher in *Macaranga* leaves. The data indicates that OP leaves have higher nutrients with increased toughness, while *Macaranga* have higher secondary defensive chemical compounds.

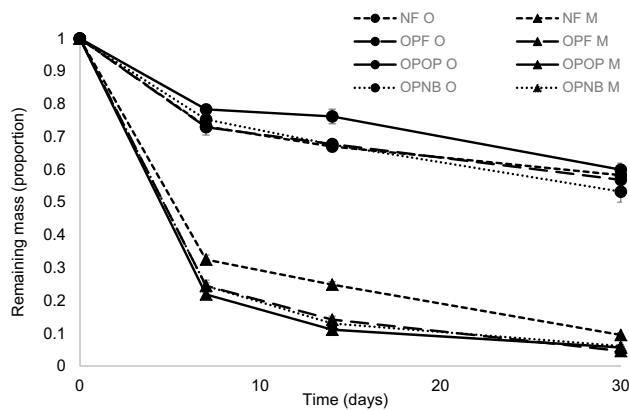


Fig. 2 Mean proportion of ash-free dry mass remaining of *Macaranga* and OP leaf litter incubated in the different forest and riparian buffer types over 30 days, pooled regardless of mesh size. Values are means \pm SE ($n = 18$)

Litter decomposition rates

Litter mass remaining over time for both OP and *Macaranga* decreased exponentially at all sites with the steepest decline in mass observed within the first week (Fig. 2). After 7 days of incubation, *Macaranga* lost 68–78% of mass but OP lost only 22–27% of its mass. Collectively by day 30, OP leaves had about 53–59% of mass remaining in all riparian types while *Macaranga* leaves had about 6–9% mass remaining in all riparian types (Fig. 2). Overall, *Macaranga* leaves had roughly 5 \times faster total decomposition rates ($k/\text{days} = 0.06\text{--}0.08$) than OP leaves ($k/\text{days} = 0.01\text{--}0.02$) in all riparian types (Table 3). The decay rates calculated (k/days) for the different riparian types according to leaf species type showed different trends (OP: OPNB > OPOP > OPF > NF; *Macaranga*: OPNB > OPF > NF > OPOP).

We found no significant effect of bag type (mesh size), either when considered individually or interacting with litter species or riparian types (ANOVA, $p > 0.05$). Thus, litter mass remaining from course and fine bags were pooled for all subsequent analyses. A two-way ANCOVA with leaf species and riparian types as treatment (pooled by bag type) showed that litter decomposition significantly differed among litter species ($F_{1,423} = 2612.0$, $p < 0.0001$) and riparian type ($F_{3,423} = 16.5$, $p < 0.0001$), with a significant

Table 3 Exponential decomposition rates (k) of *Macaranga* and oil palm leaf species (pooled for course and fine bags) incubated in the different forest and riparian buffer type, standard error (SE) and coefficient of determination of the regression (R^2) ($p < 0.0001$ in all cases)

Leaf species	Riparian type	k/day	SE	R^2	ANCOVA for whole dataset	ANCOVA separate for leaf species
Oil palm	NF	0.0097	0.0011	0.6040	A	a
	OPF	0.0108	0.0016	0.5055	B	a
	OPOP	0.0125	0.0017	0.5394	B	b
	OPNB	0.0161	0.0024	0.4861	B	a
<i>Macaranga</i>	NF	0.0564	0.0036	0.8255	A	a
	OPF	0.0734	0.0040	0.8597	B	b
	OPOP	0.0557	0.0046	0.7285	B	b
	OPNB	0.0886	0.0046	0.7577	B	b
Leaf species	Riparian type	k , degree/day	SE	R^2	ANCOVA for whole dataset	ANCOVA separate for leaf species
Oil palm	NF	4.15×10^{-4}	4.75×10^{-5}	0.6040	A	a
	OPF	4.28×10^{-4}	6.20×10^{-5}	0.5055	B	a
	OPOP	4.53×10^{-4}	6.11×10^{-5}	0.5394	BC	b
	OPNB	5.52×10^{-4}	8.29×10^{-5}	0.4861	C	a
<i>Macaranga</i>	NF	0.0024	1.55×10^{-4}	0.8255	A	a
	OPF	0.0029	1.60×10^{-4}	0.8597	B	b
	OPOP	0.0020	1.67×10^{-4}	0.7285	BC	b
	OPNB	0.0020	1.57×10^{-4}	0.7577	C	b

Treatments with the same letter are not significantly different ($p > 0.05$; capital letter for whole dataset, small letter separated by leaf species)

interaction between both factors ($F_{3,423} = 19.7$, $p < 0.0001$) (Table 3). Post hoc tests revealed that when the data were pooled regardless of leaf type, differences between the riparian types were attributed to slower rates of decomposition in forested sites (NF) compared to all the OP streams (Table 3). Additionally, since we found the different leaf types interacted differently in the different riparian types, we also conducted separate one-way analysis (using riparian type as treatment) for each leaf species to analyse how they decomposed differently within the different forest and riparian buffer types. We found that *Macaranga* ($F_{3,211} = 42.0$, $p < 0.0001$) leaves decomposed slower only in NF sites and were comparable among the different buffer types within OP plantations while OP ($F_{3,211} = 6.5$, $p < 0.0001$) leaves had significantly slower rates of decomposition only in the OPOP sites while all other riparian types were similar.

Since temperature was significantly different between the different riparian types (Chellaiah and Yule 2018a), we also conducted a two-way ANCOVA using degree-days as a covariate to compare decomposition rates. Using degree-days normalizes for the effect of temperature and assumes no biological activity at temperatures below freezing point. Significant effects of leaf species ($F_{1,423} = 2596.5$, $p < 0.0001$) and riparian type ($F_{3,423} = 8.6$, $p < 0.0001$) as well as the interaction between factors ($F_{3,423} = 19.6$, $p < 0.0001$) were detected. Post hoc analysis revealed that correcting for temperature revealed different trends between riparian types. When data were pooled for litter types, we found that decomposition rates were slowest in NF sites, OPF and OPNB had significantly different decay rates while OPOP were intermediate between these two buffer types (Table 3). However, when we conducted a separate ANCOVA for each leaf type (using degree-day as covariate), *Macaranga* ($F_{3,211} = 23.8$, $p < 0.0001$) and OP ($F_{3,211} = 8.5$, $p < 0.0001$) leaves behaved similarly with no significant impact of temperature.

Discussion

Microbial mediated decomposition is prevalent

Our results show that leaf litter decomposition and bacterial community structure in the different forest and riparian buffer present in OP streams is driven by microbes and is mostly dependent on the quality of litter and to a lesser extent, stream physicochemical conditions. When invertebrates were included in litter packs, we found negligible effects of shredding invertebrates on mass loss in all stream sites and leaf litter types, consistent with low shredder abundances found at these sites (Chellaiah and Yule, 2018b). This concurs with the widely accepted hypothesis that decomposition in tropical streams is dominated by

microbes due to higher water temperatures (Boyero et al. 2016, 2009; Dobson et al. 2002; Ferreira and Chauvet 2011a, b; Li et al. 2009) with minimal shredder involvement (Jinggut and Yule 2015; Mathuriau and Chauvet 2002; Rincón and Santelloco 2009). When stream water temperatures increases, biological activities of microbes is sped up with increased chemical reactions (Brown et al. 2004; Davidson and Janssens 2006) encouraging microbially mediated decomposition with increased fungal respiration and mycelial biomass growth (Batista et al. 2012; Dang et al. 2009; Ferreira et al. 2012; Geraldles et al. 2012; Martínez et al. 2014). However, the relative importance of shredders in tropical streams is very variable whereby certain studies reported abundant and diverse shredder assemblages in some streams (e.g. Cheshire et al. 2005; Yule et al. 2009) while others reported a general paucity of shredders in tropical streams (Jacobsen et al. 2008).

Litter quality

A major determinant that predicts microbial colonization and subsequently leaf decomposition rates is the quality of leaf litter (Bakker et al. 2011; Boyero et al. 2016; Chapin et al. 2011; Guendehou et al. 2014; Loranger et al. 2002). High quality litter with higher abundance of labile substances decomposes faster than low quality litter with high concentrations of recalcitrant compounds (Chapin et al. 2011; Fonte and Schowalter 2004). Senescent leaves of native *M. tanarius*, a pioneer tree genus widespread in southeast Asian forests that colonizes riparian areas (Ewers et al. 2011; Yule and Gomez 2009) were collected after abscission. Conversely green OP leaves were selected to emulate conditions in plantations as OP leaves are typically cut at the stem and thrown onto the ground and into streams for easier access to palm fruits by plantation workers. Trees resorb essential nutrients such as nitrogen, phosphorus and potassium from senescing leaves before abscission (Bruenig 2016; Hättenschwiler et al. 2008) thus senescent leaves contain less nutrients than green leaves (Ninemets and Tamm 2005). We found that OP leaves that were collected before natural senescence had higher nutrient contents (C, N, P, K) compared to *Macaranga* leaves. The range of values we found were consistent with findings by Behera et al. (2016) and Fairhurst and Mutert (1999) in terms of N,P and K. However, OP leaves had greater tensile strength and were tougher with higher levels of structural compounds such as lignin, cellulose and fibre that slow decomposition. *Macaranga* litter had higher secondary defensive chemical compounds but these are typically rapidly leached from leaves (Yule and Gomez 2009).

Leaf decomposition is mainly influenced by leaf-litter quality

Litter traits had a stronger effect on the rates of leaf litter breakdown with lesser effects due to changes in the surrounding environmental conditions (increased nutrients) in the different forest and OP buffered stream types. Our results show that the differences in the initial litter quality (e.g. C, N, P, K, phenol, tannin, cellulose, lignin, fibre, toughness) across the species correlated to the large variations observed in rates of *Macaranga* and OP leaf decomposition. Firstly, both leaf species showed fastest mass loss within the first week of immersion similar to results of other studies (Gomat-Chimbakala and Bernhard-Reversat 2006) and slowed down later on as the content of resources exploitable by microorganism decrease (Kögel-Knabner 2002). Contrary to the hypothesis that litter decomposition is positively dependent on litter nutrient content, particularly nitrogen (Jinggut and Yule 2015; Lowman et al. 2012), we found that mass loss in *Macaranga* leaves were substantially more than OP litter despite the latter species having higher initial nutrient content (e.g. C, N, P, K). Even after 30 days of immersion, *Macaranga* had 6.5% of mass remaining while OP had 56–59% of mass remaining. Similar to results from other studies, high amounts of heavier structural compounds such as lignin, cellulose, fibre coupled with high leaf tensile strength makes OP leaves harder to break down as this is a major deterrent to microbial colonization (Pérez-Harguindeguy et al. 2000; Quinn et al. 2000). Thus, the bulk of mass in OP leaves (56–59%) were retained longer subsequently slowing decay (Graça et al. 2005; Lowman et al. 2012; Newman et al. 2015). Whereas *Macaranga* leaves were more tender, making the litter more susceptible to microbial colonization and feeding as well as mechanical fragmentation [probably caused by stream flow and sedimentation (personal observation)]. Variances in different litter species responses to leaf mass loss was also reported in a study by Newman et al. (2015) that found that oak litter decomposed slower than maple leaf in a forested stream due to differences in litter properties with increased tannin, lignin and thicker cuticle in oak litter. In addition, increased nutrient availability on leaf surfaces due to fast decomposition of *Macaranga* leaves would further stimulate bacterial growth (Gulis and Suberkropp 2003a) and enhance mass loss.

Effect of riparian quality and environmental conditions on breakdown rates

When we examined the impact of riparian disturbances within the different forest and riparian buffer types on decomposition rates, we expected that streams with higher temperatures and nutrient content to have increased mass loss. However, both leaf species interacted differently to

environmental changes brought about by the different forest and riparian buffer types. *Macaranga* litter decomposed slower in the pristine sites and were similar in all OP streams regardless of the riparian buffer quality. The increased decay rate of *Macaranga* leaves in OP streams can be attributed to increased nutrient (P and K) content that enhances microbial decomposition (Biasi et al. 2017). *Macaranga* is a native species commonly found in tropical forests of Southeast Asia. Typically, tropical forests are P-limited due to high weathering (Chen et al. 2014; Yang et al. 2014). P-addition in tropical systems has been found to increase litter decomposition rates (Hobbie and Vitousek 2000; Kaspari et al. 2008; Qualls and Richardson 2000; Rejmánková 2001). In our selected streams, P and K concentrations were found to be significantly higher in OP streams compared to natural forested streams. We predict that microbial colonization on *Macaranga* litter that was previously nutrient limited, responded positively to increased nutrients from both the substrate and surface water with fertilizer runoff in the OP streams. Hence, breakdown rates in NF streams were lowest due to the constraints of microbial nutrient limitation by P concentrations. Previous studies found that moderate nutrient enrichment in streams accelerated breakdown rates by stimulating microbial conditioning with increased microbial biomass and respiration (Biasi et al. 2017; Gratton and Suberkropp 2001; Gulis et al. 2006; McKie and Malmqvist 2009; Rosemond et al. 2002; Tank and Webster 1998; Woodward et al. 2012). This is supported by many field and laboratory studies that found that P in the form of phosphate (PO_4^{3-}) is a potential limiting factor for microbial activity in streams (Gulis and Suberkropp 2003b; Schneider et al. 2012; Sridhar and Bärlocher 2000). When P is added, the reproductive activity of aquatic hyphomycetes, their colonization success and fungal-mediated leaf-litter decomposition is stimulated (Gulis and Suberkropp 2004; Sridhar and Bärlocher 2000) implying that P is important in driving differences in decay rates (Ardon et al. 2006; Rosemond et al. 2002). Increased potassium (K) concentration in the OP stream could also have contributed to increased decomposition rate of *Macaranga* leaves as supported by other studies (Makkonen et al. 2012; Santiago 2007). In contrast, we found different patterns for OP litter decay with slower decomposition only in OPOP although these streams had high stream temperature, as well as K and P content. Our results support previous observations from riparian zone studies (Casotti et al. 2015; Pozo et al. 1998) which suggested that other factors besides riparian vegetation and increased nutrient content in streams may impact the decay of some leaf species. Overall, the effect of moderate nutrient enrichment on decomposition is more uniform for *Macaranga* leaves with increased susceptibility to decomposition as P and K increases, but varied greatly for OP leaves among the riparian types. This is consistent

with previous studies that found low-nutrient litter responds more to nutrient enrichment compared to high-nutrient litter (Ferreira et al. 2006b; Gulis et al. 2006; Stelzer et al. 2003).

Besides nutrient enrichment, increases in stream temperature can also positively enhance microbial decomposition (Gonçalves et al. 2014; Martínez et al. 2014; Yule et al. 2015). Our results show a gradual increase in stream temperature across the disturbance gradient due to the elimination of forest canopy (Chellaiah and Yule 2018a) that could be expected to increase decomposer activity and enhance litter decay (Bärlocher and Graça 2002). However, we found that both leaf species did not decompose differently when the effects of temperature was excluded (k degree/days), contrary to results found by McKie and Malmqvist (2009). This is similar to findings by Encalada et al. (2010) that found no differences in microbial mediated decomposition between forest and pasture streams despite the higher temperature found in pasture sites. In addition, other environmental factors, like fragmentation caused by stream flow and sedimentation, could have contributed to decomposition rates, however were not accounted for in this study.

Implications: nutrient cycling and management

Land-use change in riparian areas influences the litter decomposition assay used in this study, depending on the litter species studied and management practices. Generally, we found that replacing native tropical forests with exotic monoculture oil palm plantation did impact stream litter decomposition rates. This agrees with earlier studies that also found differences in litter processing rates between exotic monoculture plantations (i.e. eucalyptus, pine, etc) and forested streams (see Abelho and Graça 1996; Barlow et al. 2007; Cizungu et al. 2014; Riipinen et al. 2010; Tateno et al. 2007). Contrary to this, other studies reported no differences in decomposition rates when forests are replaced with monoculture plantations (see Bärlocher and Graça 2002; Ferreira et al. 2006a; Foster et al. 2011; Kavvadias et al. 2001). However, our results also show that the extent of which exotic plantations can affect stream processing rates were predominantly dependent on the leaf litter quality, followed by the riparian buffer quality and varying stream environmental conditions. Similarly Tateno et al. (2007) found that the quality of leaf litter was a more important determinant of decomposition rates than differences in environmental conditions between an exotic black locust plantation and indigenous oak forest. Since plantations are typically dominated by a single species which drastically reduces diversity, quantity and quality of nutrients entering stream compared to natural tropical forests (Chellaiah and Yule 2018a; Singh et al. 2015). This could have potential implications for nutrient cycling within plantation stream ecosystems because changes in

riparian tree species composition alters organic matter input into streams, crucial for aquatic productivity (provision of energy and nutrients) (Fernandes et al. 2013). As aquatic pathways are often intimately linked to terrestrial networks, changes within stream and river catchments may also have downstream implications (Kordas et al. 2016; Malmqvist and Rundle 2002). For example, upstream changes in riparian vegetation affects organic matter degradation into particulate organic matter, which fuels downstream food webs altering river functioning (Power et al. 1996).

A decomposition experiment by Yang et al. (2003) in a monoculture plantation in subtropical China reveal that natural forests was best able to maintain site productivity due to high amount and quality of litter as well as faster rates of litter decomposition. On the contrary, our results demonstrate faster leaf decay in the nutrient enriched plantation streams that often leads to faster energy transfers between trophic levels, positively affecting local secondary production. However, oil palm plantations typically contribute less litter quantity and diversity with low quality exotic litter with high toughness that deters decomposition. Thus, the implications on wider ecosystem productivity is complicated especially since different litter quality responded differently to environmental changes. With susceptibility of aquatic environments to nutrient enrichment likely to intensify in the future, it is crucial to understand the implications of changes in biodiversity on ecosystem functioning. Especially since high levels of such input might counteract the stimulating effects of nutrients on litter decay rates and bacterial assemblages and can induce eutrophication which leads to anoxia, mobilization of heavy metals and physical smothering of benthic organisms (Woodward et al. 2012). Currently, assessment of management implications on the extent these changes affect ecosystem health and integrity is abstruse. Nevertheless, results from this study provides preliminary evidence that advances our understanding of how changing riparian biodiversity and quality can alter important ecosystem processes in streams when forests are converted into monoculture plantations. Our results indicate that riparian management strategies as well as plans to restore functioning in degraded streams should ensure a wide diversity of native riparian tree species in order to effectively mitigate adverse plantation impacts on stream ecosystem functioning.

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