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Litter quality influences bacterial communities more strongly than changes in riparian buffer quality in oil palm streams

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ABSTRACT: The conversion of tropical forests into oil palm *Elaeis guineensis* (OP) monoculture alters stream physicochemical conditions, potentially threatening freshwater ecosystems. Understanding the responses of bacterial assemblages to environmental changes and riparian management efforts are vital for our understanding of stream ecosystem functioning. We used 16S rRNA gene sequencing techniques to investigate bacterial community dynamics on decomposing litter of 2 contrasting qualities, *Macaranga tanarius* and OP, in streams across a gradient of riparian disturbance in OP plantations. Bacterial community composition was more heavily influenced by litter quality, such as increased structural compounds (i.e. toughness, lignin, fibre) and nutrients in OP litter and increased secondary compounds in *Macaranga* litter, rather than changes in stream conditions due to different riparian buffer qualities. Bacterial colonization on *Macaranga* was susceptible to the increased stream temperatures and nutrients in OP streams, whereas significant alterations in bacterial community composition on OP litter were observed that were possibly due to long-term agricultural disturbances. Both litter species were dominated by *Proteobacteria* and *Bacteroidetes* with *Chitinophaga* and *Caulobacteraceae* contributing most to the differences observed. Compared to pristine streams, bacterial diversity and richness were significantly higher in OP streams with no buffer, whereas OP streams with forested riparian buffer and untreated buffer (i.e. no chemical inputs) had intermediate values. In conclusion, bacterial assemblages were regulated by the quality of litter. We therefore propose the retention of riparian vegetation with high tree diversity to mitigate impacts on the formation of litter bacterial assemblages and the ecosystem processes they mediate in oil palm plantation streams.

KEY WORDS: Bacterial decomposers · 16S rRNA genes · Oil palm plantations · Litter quality · Riparian buffer

1. INTRODUCTION

Bacteria, fungi and macroinvertebrates play crucial roles in regulating energy flow in stream ecosystems through decomposition of organic matter, a process that contributes to the majority of energy input in stream ecosystems (Baldy et al. 1995, Hieber & Gessner 2002, Gulis & Suberkropp 2003a, Buesing & Gessner 2006). As leaves enter streams, microbial assemblages will colonize, macerate and metabolize leaf tissues, enhancing decomposition and increasing litter palatability for macroinvertebrate consumption (Gessner et al. 2007). Tropical stream studies commonly find that bacterial- and fungal-mediated decomposition plays a more significant role than macroinvertebrate shredding activities, particularly in disturbed streams (Yule et al. 2009, Boyero et al. 2012, Jinggut & Yule 2015). Among microbial groups, the contribution of fungi to decomposition is commonly reported to be higher than bacterial decomposing activities,

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which is attributable to the high fungal biomass found on decaying leaves (Gulis & Suberkropp 2003b, Pascoal et al. 2005, Xu et al. 2013). However, the contribution of bacterial communities to decomposition may be underestimated (Pascoal & Cássio 2004), as several studies have reported the substantial role bacterial decomposers play in leaf litter decomposition (López-Mondéjar et al. 2015, 2016) especially during earlier phases of decomposition (Rousk et al. 2010, DeAngelis et al. 2013, Ewers et al. 2015). Despite this, bacterial communities contributing to leaf litter decomposition in tropical stream ecosystems have been poorly studied (Wantzen et al. 2008, Keiblinger et al. 2012, Kim et al. 2014, Tláskal et al. 2016).

Bacterial communities are influenced by stream environmental conditions (e.g. temperature, water chemistry, pH, alkalinity, nutrient concentration) as well as leaf litter quality (e.g. nutrient concentration, structural compounds) (Rousk et al. 2010, Lee-Cruz et al. 2013, Kim et al. 2014, Cho et al. 2016, Tin et al. 2018). In Southeast Asia, particularly Indonesia and Malaysia, rapid conversion of tropical forests into monoculture oil palm *Elaeis guineensis* plantations changes stream environmental conditions and reduces the diversity and quantity of litter input (Chellaiah & Yule 2018a), potentially modifying bacterial community distribution and the stream processes they mediate (Bergfur & Friberg 2012, Yang et al. 2014, López-Mondéjar et al. 2015, Cho et al. 2016). With the extent of oil palm plantations expected to increase in over 43 oil palm-producing countries worldwide (Vijay et al. 2016), there is a pressing need to understand the impacts on stream bacterial communities and function. For example, bacterial biomass and diversity reportedly increase when exposed to nutrient-enriched streams, stimulating bacterial activity and often leading to faster leaf decomposition (Gulis & Suberkropp 2003a,b, Pascoal et al. 2005, Mesquita et al. 2007). In addition, changes in the quantity and diversity of litter available for uptake by bacterial decomposers also impacts the distribution of decomposer communities and rates of litter decomposition (Aneja et al. 2006, Kim et al. 2014, Tláskal et al. 2016).

To reduce plantation impacts on stream abiotic factors and biotic communities, retention of riparian buffer areas have been widely proposed (Langer et al. 2008, Zainudin et al. 2013); however, there is little ecological information available on the efficacy of riparian buffers in regulating bacterial structure–function linkages in tropical streams. Furthermore, there are limited studies addressing the impacts of changes in the dynamics of bacterial communities colonizing leaf litter on litter decomposition activities in monoculture plantations (Das et al. 2007, Newman et al. 2015, Zeng et al. 2017). Thus, we aim to address this knowledge gap by characterizing the composition of bacterial communities that colonize decomposing litter in tropical streams and evaluate how bacterial communities respond to the quality of litter and changes in riparian and stream conditions when tropical forests are converted into oil palm plantations.

To measure the efficacy of riparian buffer types in mitigating plantation impacts on stream bacterial communities, we assessed bacterial diversity, richness and community composition as monitoring tools (Lecerf et al. 2011, Woodward et al. 2012, Piggott et al. 2015). Illumina 16S rRNA gene sequencing was used to identify and quantify (i.e. no. of reads) bacterial taxa on the decomposing leaf litter. Traditional methods that measure biomass, total numbers and production rates (Baldy et al. 2002, Hieber & Gessner 2002) provide measurements of the activity of the bacteria or amount of decomposition but offer little detail on microbial community composition. However, with 16S rRNA gene sequencing, although we cannot measure production rates, we can provide information on the taxa present on decomposing leaves at a fine taxonomic level — data that are currently extremely scarce in the tropics. Oil palm plantations have been reported to alter soil bacterial composition (Lee-Cruz et al. 2013) compared to that found in primary tropical forests, although Tin et al. (2018) found similar bacterial diversity in both oil palm plantation and forest soils. However, these were both terrestrial studies. To our knowledge, no previous studies have focused on tropical stream bacterial communities, particularly across a gradient of riparian disturbance.

We focused on different riparian buffer types commonly used in oil palm plantations in Borneo that are subjected to differing degrees of disturbance (i.e. forested buffer, native understorey without chemical application, no buffer with chemical application up to stream edge). Two leaf species (i.e. exotic oil palm and native *Macaranga tanarius*) with contrasting qualities (i.e. nutrients, structural and secondary compounds; for detailed description, see Chellaiah & Yule 2018b) were used to quantify decomposer bacterial colonization. This also provided an opportunity to study changes in bacterial decomposers present in streams that are subjected to varying riparian buffer qualities in relation to distinct leaf litter traits to determine whether leaf quality or riparian changes have the greater effect on bacterial communities. We hypothesized as follows: (1) Leaf species will have distinct bacterial communities as bacterial coloniza-

tion is dependent on leaf physicochemical traits (Kim et al. 2014). (2) Conversion of pristine forests into oil palm plantations will significantly alter the bacterial communities. Particularly, we predicted higher bacterial diversity and richness in oil palm streams due to the effect of nutrient enrichment and reduced riparian density and canopy cover that promotes stream warming, which in turn increases bacterial colonization and decomposition activities (Pietikäinen et al. 2005). (3) The extent to which riparian changes impact bacterial community structure will be dependent on the quality of riparian buffer, with the higher quality forested buffer being most similar to native forested streams compared to heavily disturbed oil palm streams.

2. MATERIALS AND METHODS

2.1. Study sites

The study was conducted in 2 agricultural concessions, (Sabah Softwoods Berhad and Benta Wawasan Sdn Bhd) and a Class I forest reserve (Maliau Basin Conservation Area) in the Tawau region of Sabah, Borneo (Fig. 1; described in detail in Chellaiah & Yule 2018a). This region experiences high rainfall throughout the year with little seasonality (Chellaiah & Yule 2018a). We selected three 1st to 3rd order headwater streams in 4 riparian buffer types across a gradient of riparian disturbance. The pristine forest (NF), Maliau Basin Conservation Area, is an old growth forest dominated by Dipterocarpaceae with riparian areas of high density (no. of trees per 100 m^2), tree diversity and structural complexity of vegetation. Oil palm streams with a forested buffer (OPF) are plantation streams with riparian buffer types most closely reflecting forested streams. The native riparian forest was left intact in the riparian area with only the taller and more valuable trees being extracted when the surrounding area was logged for oil palm planting nearly 15 yr ago. The next site type is oil palm streams with oil palm trees right up to the stream edge; however, with a native understorey due to the absence of chemical inputs (herbicide, pesticide, fertilizer) in the designated buffer area (OPOP). Lastly, the most disturbed sites are oil palm streams with no buffer, with chemical inputs and oil palm trees planted right up to the stream edge (OPNB).

As described in Chellaiah & Yule (2018a), stream temperatures increased significantly by nearly 6°C across the disturbance gradient, being lowest in the undisturbed NF (23.3°C) and highest in the most disturbed OPNB (29.2°C) streams. Temperatures in OPF and OPOP streams were intermediate, at 25.2°C and 27.6°C, respectively. Daytime dissolved oxygen levels were significantly different between stream sites with NF and OPNB (84.0 and 90.2%) having lower levels than OPF (94.2%) and OPOP (95.9%), which had the highest. pH values were significantly lowest in NF and OPF sites (7.3), intermediate in OPNB (7.4) and highest in OPOP (7.6) sites. In terms of stream nutrient content, we found that NF sites had the significantly lowest levels of total phosphorus, P (0.3 µg ml^{-1}) and total potassium, K (2.2 µg ml^{-1}) compared to oil palm streams. P was intermediate in OPOP (0.5 µg ml^{-1}) and highest in OPF (0.7 µg ml^{-1}) and OPNB (0.8 µg ml^{-1}) sites. K was intermediate in the higher (OPF; 4.5 µg ml^{-1}) and lower (OPOP; 6.5 µg ml^{-1}) quality riparian buffer and significantly higher in OPNB sites (8.6 µg ml^{-1}).

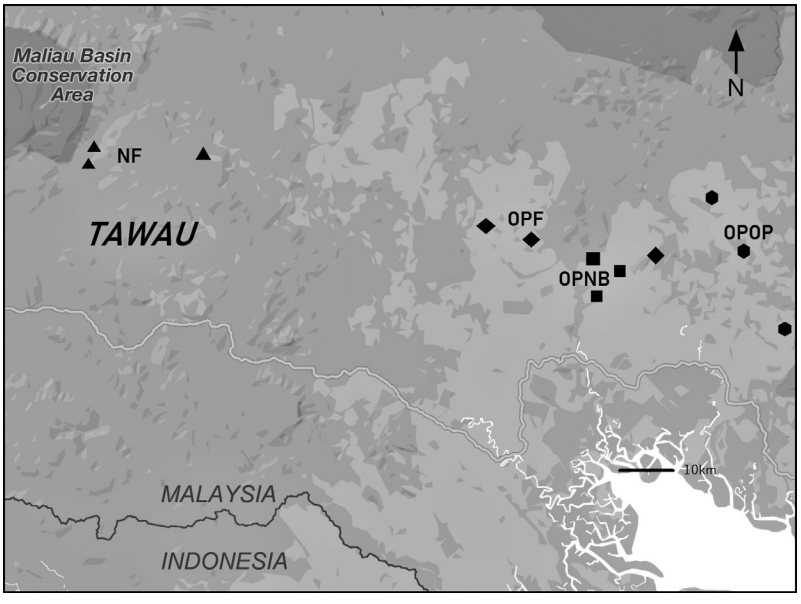

Fig. 1. Location of study sites in the Tawau region of Sabah, Borneo. NF: native forest; OPF: oil palm streams with a forested buffer; OPOP: oil palm streams with oil palm trees up to the stream edge but with a native understory; OPNB: oil palm streams with no buffer. Different shades indicate different land uses. The light grey line across the image (left to right) is the main road

2.2. Field sampling

The study was conducted from November 2015 to February 2016, at the

same time as a litter bag experiment measuring rates of litter decomposition at the different stream sites (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/a083p167_supp.pdf; discussed in detail in Chellaiah & Yule 2018b). At each stream site, to avoid cross-contamination for molecular work, independent litter bags with a mesh size of 0.01 mm were filled separately with 3 ± 0.001 g of native *Macaranga tanarius* (collected from Ampang Forest Reserve, West Malaysia and air-dried to a constant weight) and exotic oil palm (collected from Sabah Softwoods Berhad and air-dried to a constant weight). These leaf species have contrasting litter quality (Table S1; described in detail in Chellaiah & Yule 2018b), with *Macaranga* litter containing higher concentrations of secondary compounds such as phenolic and tannic acid and having softer leaves while oil palm leaves are characterized by higher levels of structural compounds (i.e. lignin, fibre) and tougher leaves with higher nutrient concentrations (i.e. carbon, nitrogen, phosphorus, potassium). The prepared litter bags were attached to nylon strings 0.5 m apart, then submerged in study streams (Fig. 1) with moderate flow at a relatively homogeneous depth (~0.15 m) and retrieved after 1 wk of immersion for subsequent analysis.

2.3. DNA extraction, PCR amplification and sequencing

Litter bags were collected (n = 3 for each riparian type) and frozen at −20°C until further examination. In the laboratory, genomic DNA was extracted from litter using the MoBIO PowerSoil DNA Isolation Kit (MoBio Laboratories) following the manufacturer's instructions. Genomic DNA was quantified using the TECAN Infinite M200 PRO NanoQuant (Tecan Group) and was then stored at −20°C for further analysis. The V3/V4 hypervariable region of the 16S rRNA gene was amplified from genomic DNA using forward (5′-CCT ACG GGA GGC AGC AG-3′) and reverse primers (5′-ATT ACC GCG GCT GCT GG-3′) with a unique 6 bp barcode sequence attached to the reverse primer for multiplexing (Shaufi et al. 2015). PCR amplifications were carried out in 25 µl reaction mixtures which contained 12.5 µl of NEB Next High-Fidelity 2× PCR Master Mix (New England Biolabs), 1 µl of 10 µM forward and reverse primers and 1 µl DNA template topped up with PCR-grade water. The PCR reaction included an initial denaturation step at 98°C for 30 s, followed by 25 cycles of 98°C for 10 s, 60°C for 30 s and 65°C for 30 s, and a final extension step at 72°C for 5 min in a SureCycler 8800 Thermal Cycler (Agilent). A negative PCR control without template DNA (replaced with sterile H_2O) was used to determine possible amplification of contaminants. The PCR products were assessed for bands using 1% agarose gel electrophoresis to confirm the presence of DNA amplicons. 16S rRNA gene amplicons were quantified by qPCR using the KAPA Library Quantification Kit (KAPA Biosystems) and Eco Real-Time PCR System (Illumina). The amplicons were normalized, pooled and sequenced on an Illumina Miseq desktop sequencer (2 × 250 bp paired end run) at the Genomics Facility at Monash University Malaysia.

2.4. Bioinformatics analysis

Overall quality of Illumina reads was first assessed using FastQC v0.11.2 (www.bioinformatics.babraham.ac.uk/projects/fastqc/). Raw reads were then processed with the CLC Genomics Workbench 5.1 (www.qiagenbioinformatics.com) where quality filtering (phred score >Q20, sequence length >200 bp, no ambiguous bases) was performed. Chimera were removed using UCHIME 4.2.40 (Edgar et al. 2011) algorithms as implemented in USEARCH v.7.0.1090 (Edgar 2010). Clusters of operational taxonomic units (OTUs) were dynamically built at a threshold of 97% pairwise similarity and taxonomically classified against the default Greengenes reference database in QIIME (Caporaso et al. 2010). Chloroplasts, mitochondria and rare OTUs (singletons), which could potentially have originated from sequencing errors, were removed from the dataset (Kunin et al. 2010). Sequence data was deposited to the Sequence Read Archive (SRA) at the NCBI under BioProject accession number PRJNA419069.

2.5. Data analysis

Rarefaction curves and diversity indices were generated using QIIME, with the bacterial OTUs defined at a 97% threshold of 16S rRNA gene sequence similarity. We compared the Shannon-Wiener diversity index as well as total richness (observed OTUs) and estimated richness (Chao1) using a 2-way ANOVA in SPSS v16 with leaf species and riparian type as factors (n = 3). We then calculated and compared the relative abundance of individual phyla (>1%), also using a 2-way ANOVA across leaf species and riparian type. Any significant observations at $\alpha = 0.05$ were tested using the post hoc Tukey's pairwise com-

parisons test to identify where the differences lay. Pearson's correlation was performed to determine correlations between diversity measurements as well as relative abundance of each phyla (>1%) and stream environmental conditions. Ordination of bacterial taxa across the different riparian and leaf types was analysed by non-metric multidimensional scaling (NMDS) plot, generated using PRIMER v6 (Primer-E) (Clarke & Gorley 2006). A 2-way permutational multivariate analysis of variance (PERMANOVA) test was then performed with 999 permutations and pairwise comparisons were tested with Monte Carlo sampling (Anderson et al. 2008) using leaf species and riparian type as factors to account for differences in bacterial community composition. When differences were detected, SIMPER analysis was performed using the OTU table to see which bacterial taxa contributed to the dissimilarity between factors (Clarke 1993), and this was reported to the lowest possible taxonomic resolution. To explore the relationship between environmental variables that correlated best with the similarities in the bacterial community compositions, the BIO-ENV (BEST, Clarke & Ainsworth (1993)) procedure was conducted using Spearman's rank correlation coefficient and a maximum number of stream variables per solution of ≤10. Prior to analysis, environmental variables were normalized and variables that were highly correlated (|r| > 0.8) were evaluated and removed.

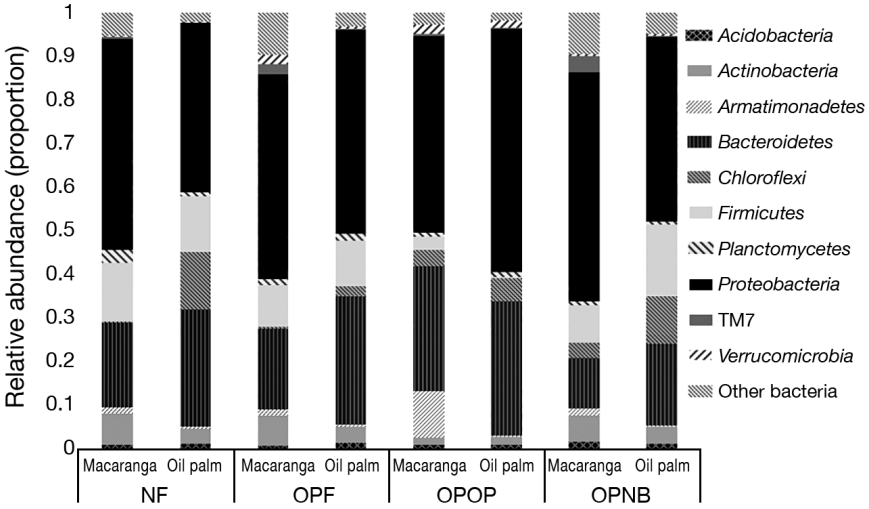

Fig. 2. Phylogenetic assignment of bacterial sequences (level phylum) from *Macaranga* and oil palm litter in the different forest and riparian buffer types. The relative abundance of each phylum within the different leaf and riparian types was averaged (n = 3). Groups are only presented if their relative abundance was at least 1% in the whole sample. Any phyla accounting for less than 1% abundance are shown as 'other bacteria'. See Fig. 1 for definitions of study sites

3. RESULTS

3.1. Bacterial communities

A total of 1 247 584 sequences that passed quality control reads were assigned to the domain bacteria (97.1%). The sequences were further clustered into 654 OTUs assigned to 43 different phyla using a 97% similarity cut off. From Fig. 2, it can be seen that there was a distinct pattern in bacterial phyla distribution between leaf litter and riparian types with leaves dominated by *Proteobacteria* (38.4–55.3%, mean = 45.8%), *Bacteroidetes* (11.2–30.3%, mean = 22.5%), *Firmicutes* (0.3–16.1%, mean = 9.0%), *Chloroflexi* (0.03–13.0%, mean = 4.8%), *Actinobacteria* (1.7–6.8%, mean = 4.2%), *Armatimonadetes* (0.3–10.4%, mean = 2.0%), *Planctomycetes* (0.8–3.0%, mean = 1.3%) and *Acidobacteria* (0.7–1.5%, mean = 1.1%). The generated rarefaction curves (Fig. S2) suggest that some of the samples did not reach sequencing saturation, while for most samples, the sequencing work was comprehensive enough to cover bacterial diversity as the rarefaction curves tended to reach a saturation plateau. This indicates that at a 3% genetic distance, the sequencing effort was large enough to capture the complete diversity in our samples.

Bacterial richness differed between *Macaranga* and oil palm leaves, whereas both bacterial diversity and richness differed between the different forest and riparian buffer types, (Table 1). Across the disturbance gradient, bacterial diversity and richness increased, with lowest values recorded in NF while OPNB showed the highest number of observed OTUs and species richness (Chao1) (Table 1). A 2-way ANOVA showed that species richness (Chao1) was significantly different between *Macaranga* and oil palm leaf types ($F_{3,16}$ = 1.722, p = 0.001) with oil palm always showing higher richness than *Macaranga* litter. When the different riparian buffer types were compared, significant differences were only detected ($F_{3,16}$ = 0.580, p = 0.047) between the OPNB and NF sites. We also found significant differences in the number of OTUs observed among riparian type ($F_{3,16}$ = 1.994, p = 0.022) and leaf species ($F_{3,16}$ = 1.994,

Table 1. Observed and estimated OTU richness and diversity index for 16S rRNA gene libraries of each plot (means ± SE; n = 3). Capital letters indicate significant differences between *Macaranga* and oil palm leaf types (regardless of riparian type) and lower case letters indicate significant differences between riparian types (regardless of leaf species). Data were calculated at 3% genetic distance level with QIIME. See Fig. 1 for definitions of study sites

		Shannon	Chao1	Observed OTUs
NF	*Macaranga*	5.89 ± 0.15^{a}	316.86 ± 93.68^{Aa}	205.33 ± 29.45^{Aa}
	Oil palm	6.22 ± 0.45^{a}	1763.11 ± 49.22^{Ba}	1056.33 ± 45.83^{Ba}
OPF	*Macaranga*	7.55 ± 0.91^{ab}	783.91 ± 343.24^{Aab}	654.67 ± 293.70^{Aab}
	Oil palm	6.96 ± 0.63^{ab}	1761.02 ± 105.10^{Bab}	1135.67 ± 105.52^{Bab}
OPOP	*Macaranga*	6.47 ± 0.74^{ab}	1286.46 ± 460.08^{Aab}	940.00 ± 271.37^{Aab}
	Oil palm	5.92 ± 0.35^{ab}	1624.66 ± 274.68^{Bab}	1076.33 ± 85.55^{Bab}
OPNB	*Macaranga*	8.13 ± 0.14^{b}	1613.39 ± 386.67^{Ab}	1196.33 ± 245.52^{Ab}
	Oil palm	7.09 ± 0.38^{b}	2111.44 ± 77.41^{Bb}	1295.33 ± 75.08^{Bb}

p = 0.006). Oil palm leaves had higher numbers of OTUs compared to *Macaranga* leaves at all riparian buffer types. Post hoc tests revealed significant effects between OPNB sites and NF sites with the former having nearly 2 times more observed OTUs regardless of leaf type (Table 1). Shannon diversity between riparian types was significantly different between NF and OPNB sites ($F_{3,16} = 0.580$, p = 0.023). There was no significant interaction between leaf and riparian type on the bacterial diversity and richness measurements mentioned (p > 0.05). When these diversity measurements were compared to stream and leaf litter physicochemical properties (Tables S2 & Table S3, respectively), we found that Chao1 and OTU numbers were significantly correlated with leaf litter qualities corroborating our results indicating that the diversity and OTU richness are affected by litter traits. We also found that the number of OTUs on our leaves were positively affected by stream temperatures (Table S2).

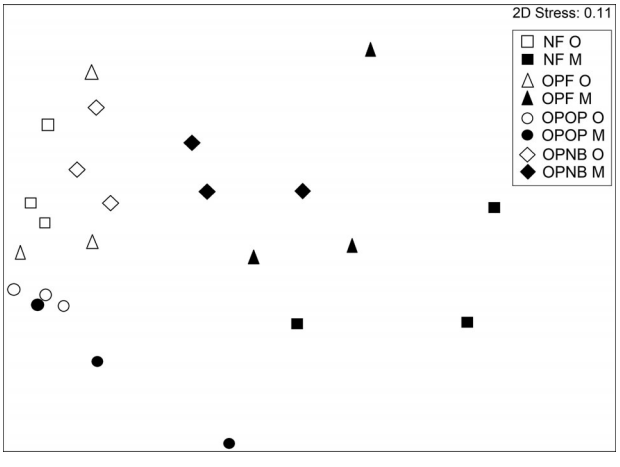

Fig. 3. NMDS plot of bacterial taxonomic variation between leaf species (M: *Macaranga*; O: oil palm) and the different forest and riparian buffer types based on Bray-Curtis similarity matrix of relative abundances (stress = 0.11). See Fig. 1 for definitions of study sites

3.2. Distinct bacterial communities on decomposing litter across the different riparian types

We performed an ordination analysis to compare the bacterial community composition between the different leaf species and riparian buffer types (Fig. 3). The NMDS result revealed that the composition of the bacterial communities in leaf litter samples clearly differed between the 2 leaf species (*Macaranga* and oil palm). This was corroborated by a 2-way PERMANOVA analysis (using riparian and litter type as factors) where we found that litter species significantly affected bacterial composition (p < 0.001; Table 2) indicating a high degree of dissimilarity between *Macaranga* and oil palm leaves. We also found significant effects of riparian buffer type on bacterial community composition (p < 0.002). As can be seen in Fig. 3, only OPOP clustered differently to all other stream sites and this was corroborated with the pairwise PERMANOVA that also showed that bacterial communities in OPOP differed significantly from the other sites. The PERMANOVA did not reveal a significant interaction between leaf type and riparian types (Table 2). The BIO-ENV analysis showed that the associations between bacterial communities and environmental variables were not strong (combined correlation coefficient of <0.15) (Table 3). In addition, BEST analysis confirmed that the correlation between the environmental variables and the bacterial distribution was non-significant at p = 0.474.

Table 2. Results of 2-way PERMANOVA test for the effects of riparian type and leaf species on the taxonomic composition of bacterial communities in the different forest and riparian buffer types. Results in bold are significant at p < 0.05

Source	df	SS	MS	pseudo-*F*	p
Riparian type	3	11 850	3950.1	2.3208	**0.002**
Leaf species	1	10 035	10035	5.8957	**0.001**
Riparian type × Leaf species	3	6456.7	2152.2	1.2645	0.093
Residual	16	27 233	1702.1		
Total	23	55 575			

Table 3. BIO-ENV results of single and multiple environmental parameters affecting the bacterial taxa distribution pattern

Environmental parameters	Spearman's correlation coefficient
pH, Na	0.143
Na	0.134
pH, temperature, Na	0.131
pH, conductivity, Na	0.125
pH, P, Na	0.120
pH, temperature, conductivity, Na	0.114
pH, conductivity, P, Na	0.113
pH, temperature, P, Na	0.111
pH, temperature, conductivity, P, Na	0.111
pH, conductivity, K, Na	0.090

3.3. Bacterial taxa on decomposing litter

Given that the bacterial communities clustered separately across the different leaf species and riparian types, we analysed the bacterial taxa responsible for the observed differences in greater detail. We observed some differences in the cumulative abundances of bacterial phyla on each leaf species in the different riparian buffer types (Table S4). *Proteobacteria*, followed by *Bacteroidetes*, were the most dominant phyla across all samples, followed interchangeably by *Firmicutes*, *Chloroflexi*, *Actinobacteria*, *Armatinomadetes*, *Planctomycetes*, *Acidobacteria*, TM7 and *Verrucomicrobia*, which cumulatively represented >1% of relative abundance (Table S4). We also recorded the phyla *Chlamydiae*, *Chlorobi*, OD1, SR1, *Spirochaetes* and TM6, which were cumulatively less than 1%. Five phyla differed significantly between the leaf species: *Chloroflexi*, *Actinobacteria*, *Armatimonadetes*, TM7 and *Verrucomicrobia* (Table S4); and 4 phyla differed significantly among the different riparian types: *Firmicutes*, *Actinobacteria*, TM7 and *Verrucomicrobia* (Table S4).

The 2 most abundant bacterial phyla, *Proteobacteria* followed by *Bacteroidetes*, were found to be dominant in both *Macaranga* and oil palm litter (*Proteobacteria*: $F_{1,16}$ = 0.403, p = 0.535; *Bacteroidetes*: $F_{1,16}$ = 2.375, p = 0.143) and were found in high relative abundance in the forest and all oil palm plantation sites (*Proteobacteria*: $F_{3,16}$ = 0.603, p = 0.622; *Bacteroides*: $F_{3,16}$ = 1.759, p = 0.195). A 2-way ANOVA revealed no significant differences between leaf species and riparian types in terms of *Proteobacteria* and *Bacteroidetes* (Table S4). However, SIMPER analysis (Table S5) showed that the biggest contributors to differences (% dissimilarity) between oil palm and *Macaranga* leaves were *Caulobacteraceae* (6.53%), *Enterobacteriaceae* (3.89%), *Uliginosibacterium* (2.57%) and *Novosphingobium* (1.98%) from the phylum *Proteobacteria* and *Chitinophaga* (10.45%), *Flavobacterium* (2.73%) and *Prevotella copri* (2.31%) from the phylum *Bacteroidetes* (for relative abundance values, see Table S6). Comparing the different riparian buffer sites, we found that OPOP was dissimilar (%) to NF (68.87%), OPF (65.78%) and OPNB (67.51%). The biggest % differences were attributed to *Caulobacteraceae*, which was found at significantly higher levels in OPOP sites compared to all other riparian types (Table S7; for relative abundance values, see Table S8). We also found significant correlations with water quality, with *Proteobacteria* positively correlated with pH (Table S9) and *Actinobacteria* negatively correlated with pH, temperature and conductivity (Table S9).

4. DISCUSSION

The crucial role of bacteria in litter decomposition has been commonly reported (Xu et al. 2013, López-Mondéjar et al. 2016, Tláskal et al. 2016). In this study, we discuss changes in bacterial community structure in relation to litter quality as well as changes in stream physicochemical conditions brought about by differences between riparian buffer management in oil palm streams and native forested streams. We also discuss how varying bacterial responses to these factors affect leaf decomposition rates with reference to our previously published results (Chellaiah & Yule 2018b). These results indicated that microbially mediated decomposition is the dominant contributor to mass loss of both litter types across all of the sites (Chellaiah & Yule 2018b). Although microbial decomposition is mediated by both bacterial and fungal activities, we only focus on bacterial decomposers in this study. In a terrestrial study in Borneo, Ewers et al. (2015) found that bacteria played a greater role than fungi in the early phases of decomposition of *Macaranga* sp. They also found higher resilience of bacteria to disturbance (logging) compared to fungi.

4.1. Impact of litter quality on bacterial communities

Our results show that bacterial community and alpha-diversity measures were more strongly predicted by differences in leaf litter quality than by the differing environmental conditions across the disturbance gradient. Both *Macaranga* and oil palm litter had dis-

tinct bacterial communities with significantly different alpha-diversity measures across the different riparian types and this is attributed to the contrasting litter traits observed for both species. Previous studies have documented that leaf litter quality has an important effect on bacterial community structure and colonization patterns (Xu et al. 2013, Newman et al. 2015, Purahong et al. 2016). For example, Kembel et al. (2014) and Purahong et al. (2016) found that nutrients such as C, N, K and P in leaf litter are correlated with bacterial community structure on leaves. Artigas et al. (2011) found that the presence of tough, lignin-rich litter affects bacterial biomass accumulation. Our results agree with those of these studies, as we found significant differences between the 2 leaf species studied in terms of bacterial richness (Chao1) and observed OTU abundance (Table 1). This can be attributed to the significant differences in the litter traits measured, such as nutrients (C, N, P, K), structural compounds (leaf toughness, cellulose, fibre, lignin) and secondary compounds (phenolic and tannin acid), between oil palm and *Macaranga* leaves. Thereby, we provide evidence supporting the hypothesis that distinct leaf litter traits support different bacterial assemblages and decompose differently. Specifically, oil palm litter had greater lignin and fibre concentrations, C, N, P, K, and toughness with lower tannin and phenolic acid concentrations compared to *Macaranga* litter, which decayed 3 times faster than oil palm leaves after 1 wk of immersion in the different riparian types (see Chellaiah & Yule 2018b). However, some studies have found contradictory results, with leaf quality having little to no effect on microbial assemblages (Das et al. 2007, Kominoski et al. 2011, Wurzbacher et al. 2016). Das et al. (2007) found that although oak leaves have a higher lignin concentration and greater toughness than sugar maple leaves and much slower decomposition rates, both species had similar microbial communities. It is important to note that our results have limitations and caution should be practiced when extrapolating our results as only 2 species were compared.

Interestingly, oil palm litter with higher concentrations of recalcitrant structural compounds and a slower decay rate had a higher bacterial richness than the softer *Macaranga* leaves. In contrast, Newman et al. (2015) found that bacterial colonization decreased in litter with higher levels of refractory materials such as lignin. We predict that this higher bacterial richness can be attributed to the higher initial nutrient concentration (C, N, P and K) in oil palm leaves which stimulates bacterial colonization (Kembel et al. 2014), whereas bacterial colonization on *Macaranga* litter may be limited by lower concentrations of nutrients such as N (Alfredsson et al. 2016). However, as C, N, P and K are actively leached and used by bacteria, high abundances of recalcitrant structural compounds (e.g. lignin, fibre) are left behind. Since bacteria are unable to easily mineralize these complex polymers (Boulton & Boon 1991), greater microbial action is required to break them down (Das et al. 2007), thus impeding bacterial decomposition activity on oil palm leaves. The softer *Macaranga* litter with its wider surface area decomposed faster despite the lower richness observed. Additionally, other factors, such as physical fragmentation and fungal activity, could cause the differences in decomposition rates recorded for both species; however, this was not measured in this study.

4.2. Varying litter bacterial responses to riparian vegetation quality

Macaranga and oil palm litter showed dissimilar kinetics as the bacterial colonization and alpha diversity on each litter type responded differently to the changes in stream physicochemical characteristics brought about by differences in riparian quality (Table 1). Generally, bacterial colonization on *Macaranga* leaves was more susceptible to alterations in stream environmental conditions while oil palm leaves had comparable colonization patterns regardless of riparian type. These different responses of the bacterial assemblage on each leaf species corresponded to our observed litter decomposition rates (Chellaiah & Yule 2018b). A significantly higher P content was recorded in oil palm streams compared to forested streams (Chellaiah & Yule 2018a), which correlated positively with the bacterial diversity on *Macaranga* litter. The increased bacterial OTU abundance, diversity and richness across the disturbance gradient may have aided *Macaranga* litter processing (Gulis & Suberkropp 2003a, Drury et al. 2013, Zeglin 2015) as we observed significantly reduced *Macaranga* decomposition only in the pristine forested streams (Chellaiah & Yule 2018b). Our findings concur with many studies that show that bacterial production on leaves responds positively to stream nutrient enrichment (Pascoal et al. 2005, Das et al. 2007, Bergfur & Friberg 2012). This suggests that nutrient concentrations in stream waters can be a limiting factor to bacterial colonization on *Macaranga* litter and, in turn, rate of mass loss. In addition, the increased susceptibility of bacterial colonization on the nutrient-poorer *Macaranga* litter relative to oil palm litter in

the nutrient-enriched streams suggests that *Macaranga* litter is more nutrient limited. This indicates that not only nutrient concentrations in stream waters limit bacterial colonization, but also that the initial nutrient concentration in litter can be a limiting factor (Gulis & Suberkropp 2003a). Additionally, variations in stream temperatures could also alter the bacterial assemblages as we found a positive correlation between bacterial OTU abundance and stream temperature. Increased stream temperatures have been reported to positively affect bacterial colonization (Pascoal & Cássio 2004, Pietikäinen et al. 2005, Bergfur & Friberg 2012). However, the effect of temperature on bacterial decomposers is unclear, with some reporting an insignificant effect (Weyers & Suberkropp 1996) while others have found a negative relationship between stream temperatures and bacterial colonization (Das et al. 2007).

In contrast to *Macaranga* leaves, we did not observe a trend in bacterial colonization on oil palm leaves related to increases in nutrients and stream temperatures. We suggest that since oil palm leaves are a swamp species, they are particularly resilient to harsh environmental conditions and thus were not influenced by changes in the surrounding environmental parameters in our study sites as much as the native *Macaranga* species. However, we did find significantly slower oil palm leaf decay in OPOP sites (see Chellaiah & Yule 2018b) that can be attributed to the differences in bacterial community composition, with significantly lower diversity, OTU abundance and richness recorded on oil palm leaves from OPOP than on those from all other sites. A possible explanation is that, in the OPOP plantation site, bacterial composition responded to long-term changes in environmental conditions with changes in taxonomic structure and sets of functional interactions between organisms (Karthikeyan et al. 2001, Laplante & Derome 2011) since OPOP sites were logged in the 1970s and replanted with cocoa and acacia species before being replanted with oil palm trees 15 yr ago. The forests surrounding the OPF and OPOP streams were only logged and converted into oil palm plantations less than 15 yr ago; thus bacterial communities may have recovered as they are highly resilient and can recover after logging (Lee-Cruz et al. 2013). Similarly, Slabbert et al. (2014) also reported that long-term disturbances in riparian zones can influence bacterial community structure. Our results clearly show that bacterial assemblages inhabiting chemically similar environments can differ remarkably as a consequence of leaf litter quality, which has impacts on decomposition rates.

4.3. Impact of riparian type on bacterial assemblages

Riparian ecosystems have been reported to influence bacterial community structure (Krause et al. 2013, Slabbert et al. 2014). Where native tropical forests had been converted into oil palm plantations, we found clear differences in bacterial assemblages with our most disturbed oil palm streams with no buffer (OPNB) having the highest bacterial species diversity, richness and OTU abundances, while forested (NF) streams had the lowest values (Table 1). The increase in bacterial colonization on litter in plantation streams can be attributed to the increased stream temperatures and nutrient content resulting from reduced canopy cover and riparian vegetation density and the usage of fertilizers in plantation (Gulis & Suberkropp 2003b, Bergfur & Friberg 2012, Chellaiah & Yule 2018a). Similarly, a study by Tripathi et al. (2012) across a gradient of land use change in Malaysia reported that agricultural sites had significantly higher bacterial richness and diversity compared to tropical forests. In addition, the conversion of forests into oil palm plantations has also been reported to affect bacterial community structure. A terrestrial study by Tin et al. (2018) in Sabah, Borneo found that oil palm plantations had higher bacterial species diversity and OTU abundance compared to naturally forested soil sites. Although Lee-Cruz et al. (2013) also found that bacterial community composition was significantly altered by conversion of forests into oil palm plantations, they recorded comparable alpha-diversity measures in both oil palm and forested sites. However, these studies did not consider riparian vegetated buffer strips and were terrestrial studies. When riparian buffers were retained in the oil palm plantations — that is, the sites with native forested buffer (OPF) and untreated oil palm with an understory (OPOP) — we found intermediate effects on bacterial diversity and richness. Of these 2 riparian buffer types, we found that the bacterial richness in forested buffers more closely resembled natural conditions. This implies that the retention of riparian vegetation in agricultural land is able to mediate impacts on bacterial decomposer assemblages on litter with consequent effects on bacterial-mediated decomposition rates. In contrast, Kominoski et al. (2011) found no differences in bacterial community structure in streams with differing riparian forest composition; however, stream litter decomposition rates still differed across sites.

4.4. Community structure of bacterial litter decomposers in the initial phase of litter decomposition

The phyla *Proteobacteria*, followed by *Bacteroidetes*, dominated on both *Macaranga* and oil palm litter across the different riparian buffer types (Fig. 2). High relative abundances of *Proteobacteria* and *Bacteroidetes* on decomposing substrates are commonly reported, and contribute to the degradation of organic matter, carbon cycling and potentially the uptake and mineralization of dissolved inorganic matter in aquatic environments (Baldrian et al. 2012, Schneider et al. 2012, Kim et al. 2014, Purahong et al. 2016). We also detected the presence of the phyla *Firmicutes*, *Chloroflexi*, *Actinobacteria*, *Armatinomadetes*, *Planctomycetes*, *Acidobacteria*, TM7 and *Verrucomicrobia* at decreasing relative abundance at our sites. All of these are also common in aquatic environments and are known to be involved in the decomposition of organic materials (Ivanova & Dedysh 2012, Tláskal et al. 2016, Zhang et al. 2016, Wu et al. 2017, Zhao et al. 2017). However, despite the overall similarity, with many bacterial taxa common on both leaf types, we observed a clear shift in bacterial community composition between *Macaranga* and oil palm litter, supporting our hypothesis that litter quality affects bacterial distribution (Table 2). These dissimilarities are mostly attributed to differences in abundance at the family, genus and species taxonomic levels. The taxon accountable for the highest amount of dissimilarity with higher relative abundance on oil palm leaves was *Chitinophaga*, a bacterial genus belonging to the phylum *Bacteroidetes* which decomposes chitin, a polysaccharide polymer like cellulose commonly found in the cell wall of fungal mycelia (Kaku et al. 2006). Fungal colonization enhances mycelia production on decomposing litter causing increases in chitin-degrading bacteria like *Chitinophaga* (Eckardt 2008, Brabcová et al. 2016). The large differences in *Chitinophaga* on oil palm and *Macaranga* leaves could be because initial nutrient concentrations (C, N, P, K) were higher in oil palm leaves, enhancing fungal succession and biomass (Gulis et al. 2006). A recent study by Larsbrink et al. (2017) found that *Chitinophaga* can also degrade plant cell wall hemicellulose. The second highest dissimilarity between oil palm and *Macaranga* leaves is attributed to *Caulobacteraceae*, belonging to the phylum *Proteobacteria*, which is able to degrade structural compounds like hemicellulose, cellulose and lignin substrates (Wilhelm 2016). Consistently, we found a higher relative abundance of *Caulobacteraceae* on the tougher oil palm leaves with increased lignin concentration compared to *Macaranga*.

Contrary to our hypothesis, bacterial composition differed only in oil palm plantation streams without fertilizer and herbicide application in buffer areas (OPOP) and was similar in all other riparian types. This distinction could be due to the significant differences found in overall *Firmicutes*, *Actinobacteria*, TM7 and *Verrucomicrobia* relative abundances in OPOP streams compared to all other riparian types. Tin et al. (2018) found that oil palm plantation soil had significantly more *Actinobacteria* than forest soils, but our results show significantly lower numbers of this phyla in OPOP sites. When looked at on a finer taxonomic scale, the largest differences between sites were due to extremely high relative abundances of *Caulobacteraceae* from the phylum *Proteobacteria* in OPOP (20%) compared to all other sites (2 to 3%). Studies have shown that high pH levels can positively influence bacterial assemblages, including *Proteobacteria* (Rousk et al. 2009, Tripathi et al. 2012, Cho et al. 2016). Similarly, we found significant positive correlations between pH levels and *Proteobacteria* relative abundance. Since the OPOP sites had significantly higher pH compared to all other sites, this could contribute to the higher relative abundances of *Caulobacteraceae* on the leaves. We also found higher relative abundance of *Chitinophaga* at OPOP sites. Although high presence of *Chitinophaga* typically indicates a higher decomposition rate (Brabcová et al. 2016), we found that oil palm leaf decomposition was significantly slower in OPOP sites (Chellaiah & Yule 2018b). However, we predict these differences to be due to long-term agricultural impacts combined with the overall lower diversity and richness of bacteria on oil palm leaves at the OPOP sites compared to all other riparian types. This could cause several key species essential for litter decomposition to be lost, thus slowing down decay rates.

5. CONCLUSION

The present study reveals interesting insights into bacterial community dynamics and their relationship with leaf litter quality as well as stream riparian management and identifies litter decomposition traits related to bacterial community colonization. Colonization by bacterial decomposers was most affected by leaf litter quality, with lesser impacts from changes in stream conditions. Distinct assemblages of bacterial taxa were found on both leaf types, while among riparian types, only OPOP showed a significantly

different composition — probably due to the impacts of long-term agricultural disturbances. Additionally, both leaf types responded differently to changes in riparian conditions. The bacterial community structure and assemblages on *Macaranga* litter were shaped by the physical and chemical parameters of the streams, whereas oil palm leaves were more impacted by long-term agricultural disturbances. These results are important as the massive changes in the quality, quantity and diversity of litter input when highly diverse tropical forests are converted into monoculture oil palm plantations severely impact the distribution of bacterial decomposers with potential effects on stream ecosystem functioning. Despite these differences, the phyla *Proteobacteria* and *Bacteroidetes*, both commonly reported to be involved in decomposition, were most abundant in all litter and riparian types.

In terms of riparian types, retaining forested and untreated (i.e. no chemical application) buffers in oil palm plantations did moderate the bacterial assemblages present on leaf litter. However, the presence of the higher quality riparian buffer with forested vegetation best mitigated effects on bacterial community composition, diversity and richness, being most similar to pristine streams, while impacts on the leaf decay rate were unclear. The inconsistencies in the responses of these ecosystem functions to varying environmental conditions highlight the need for further longer-term assessments for effective monitoring and management of the effects from anthropogenic disturbances when the area surrounding tropical streams are converted into monoculture plantations (Bernhardt et al. 2006, McKie & Malmqvist 2009). Nevertheless, the combined approach was useful as we found general consistencies in our interpretation of the effects of litter quality and stream environmental condition on decomposition and bacterial community assemblages in the different riparian types. In conclusion, our findings emphasize the importance of retaining high tree diversity in the riparian buffer zones to mitigate impacts of monoculture plantations on litter inputs and stream characteristics that influence the formation of litter bacterial community structure and assemblage.

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