Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia

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ARTICLE INFO

ABSTRACT

Global biodiversity is being lost due to extensive anthropogenic land cover change. In Southeast Asia, biodiversity-rich forests are being extensively logged and converted to oil-palm monocultures. The impacts of this land-use change on freshwater ecosystems, and particularly on freshwater biodiversity, remain largely understudied and poorly understood. We assessed the differences between fish communities in headwater stream catchments across an established land-use gradient in Sabah, Malaysia (protected forest areas, twice-logged forest, salvage-logged forest, oil-palm plantations with riparian reserves, and oil-palm plantations without riparian reserves). Stream fishes were sampled using an electrofisher, a cast net and a tray net in 100 m long transects in 23 streams in 2017. Local species richness and functional richness were both significantly reduced with any land-use change from protected forest areas, but further increases in land-use intensity had no subsequent impacts on fish biomass, functional evenness, and functional divergence. Any form of logging or land-use change had a clear and negative impact on fish communities, but the magnitude of that effect was not influenced by logging severity or time since logging on any fish community metric, suggesting that just two rounds of selective impact (i.e., logging) appeared sufficient to cause negative effects on freshwater ecosystems. It is therefore essential to continue protecting primary forested areas to maintain freshwater diversity, as well as to explore strategies to protect freshwater ecosystems during logging, deforestation, and conversion to plantation monocultures that are expected to continue across Southeast Asia.

1. Introduction

Anthropogenic land cover change through agricultural expansion and intensification is currently a major driver of global biodiversity loss (MEA, 2005; Phalan et al., 2013). The destruction of tropical forests is of particular significance owing to the disproportionately high levels of biodiversity present in the tropics (Bradshaw et al., 2009; Laurance et al., 2012), marked declines in biodiversity when tropical forest is converted to other land-use types (Phalan et al., 2013), and the unabated levels of deforestation due to increasing human demands for food, timber and other products (Sodhi et al., 2004; Wilcove et al., 2013). Large areas of logged forest and agriculture will be key features of future tropical landscapes. Primary forests are critically important for conserving tropical biodiversity (Gibson et al., 2011) and once-logged forests in Southeast Asia have high conservation value for terrestrial taxa (Edwards et al., 2014), but focussing on these habitats alone is not sufficient. The impacts of this large scale land-use change and other

anthropogenic activities on freshwater ecosystems and biodiversity in tropical streams remains largely understudied and poorly understood (Ramirez et al., 2008). It is important to understand how these changing landscapes impact upon aquatic as well as terrestrial biodiversity, and to devise strategies that provide protection mechanisms.

The most widespread and destructive threat to aquatic ecosystems is habitat modification that results from converting natural areas to agricultural land (Allan and Flecker, 1993; Laurance et al., 2014). Extensive logging and deforestation across the tropics (Achard et al., 2002; Hansen et al., 2010) has caused large scale modifications to catchments, resulting in changes in water quantity, quality, de-regulation in stream hydraulics and increased sedimentation levels (Inoue and Nunokawa, 2005; Iwata et al., 2003). The effects of deforestation on the species richness of fish are variable. Species richness can be increased (Lorion and Kennedy, 2009), decreased (Brook et al., 2003; Toham and Teugels, 1999), or unaffected (Bojsen and Barriga, 2002) by tropical deforestation, with equally variable impacts on fish community

composition (Bojsen and Barriga, 2002; Giam et al., 2015).

In Borneo, freshwater fish community composition is thought to be structured more strongly by local, mesohabitat structures (pool, riffle, or run) than larger, catchment scale processes such as logging history, although time since logging activity was shown to positively affect the abundance of common cyprinids (Martin-Smith, 1998a, 1998b). In comparison, Iwata et al. (2003) showed different fish guilds or community metrics responded differently to deforestation. For example, the abundance of benthic fish and other taxa was lower in deforested catchments, which was attributed to increases in sedimentation, but nektonic (free-swimming) fish did not suffer reductions. It is suggested that deforestation or habitat alteration can affect fish communities by changing the taxonomic identities and functional diversity of communities, whereas mesohabitat differences affect the functional composition of communities (Casatti et al., 2012), causing reductions in functionally distinct species (Villéger et al., 2010).

Land-use change causes alterations in sediment load, nutrient runoff (e.g., from fertilisers), canopy cover and thus temperature, leaf litter and woody debris, to name but a few environmental variables (Luke et al., 2017). All of these impacts change the microhabitats that fish inhabit and can affect taxonomic or functional groups differently (e.g., Jones et al., 1999; Newcombe and Macdonald, 1991; Sazima et al., 2006). Moreover, more destructive logging practices can have a bigger impact. The practice of slash and burn agriculture led to long term degradation of streams because of its greater impact on vegetation and soil conditions than selective logging regimes (Iwata et al., 2003). The impacts of conversion of forest to oil-palm culture, however, can be mitigated by the retention of forest patches and riparian reserves. Aquatic diversity was maintained at pre-conversion species richness and functional diversity within oil-palm monocultures in the Indo-Malay region when riparian reserves were present (Giam et al., 2015). By contrast, stream sites within plantations lacking riparian reserves exhibited an average 42% reduction in aquatic species diversity (Giam et al., 2015). Despite this, there is considerable variation in the impacts of land-use change on freshwater ecosystems, leading to renewed calls to better understand the potential interactions of land-use change with other stressors specific to certain regions such as dams, drought or invasive species (Macedo et al., 2013; Taniwaki et al., 2017). Thus regional studies are needed to uncover local impacts of varying land-use on freshwater fish communities in order to determine and validate protection mechanisms to safeguard freshwater ecosystems in the long term.

The aim of this study was to determine how freshwater fish communities change in headwater stream catchments that vary over an established land-use gradient from protected forest areas, twice-logged forest, and oil-palm plantations with and without riparian buffers, in Sabah, Borneo. This is among the first studies in Southeast Asia comparing freshwater fish diversity across this suite of land-uses, and in such a close geographical space. We expected to see a decline in fish species richness (following the 42% decline previously reported by Giam et al., 2015), biomass, and all metrics of functional diversity, as forest is logged or converted to oil-palm plantations and in comparison to protected forest catchments (Giam et al., 2015; Iwata et al., 2003; Juen et al., 2016; Martin-Smith, 1998a, 1998b, 1998c; Mercer et al., 2014; Pye et al., 2017). Community composition is expected to change in disturbed habitats (Iwata et al., 2003; Kwik and Yeo, 2015), reducing to a subset of species present in protected forests. In addition, oil-palm streams with a forested riparian buffer (~30 m wide on both sides of the stream) were expected to have a higher richness, biomass and functional diversity than those without riparian buffers (Giam et al., 2015; Lorion and Kennedy, 2009). We predicted this would be due to changes in canopy cover over the streams impacting, for example, water temperature, litter fall and litter retention within the stream. With ongoing deforestation and conversion to oil-palm plantations in Southeast Asia, it is crucial to understand how these processes impact freshwater biodiversity in order to develop strategies to protect freshwater ecosystems

and maintain the ecosystem services they provide.

2. Methods

2.1. Study site

Study sites were located on small, headwater streams (3–10 m wide, ≤ 1.2 m maximum depth) in southeastern Sabah, Malaysian Borneo (117.5°N, 4.6°E). The landscape is a mosaic of protected forest (PF) areas consisting of primary lowland dipterocarp rainforest (Danum Valley Conservation Area and the Brantian Tatulit Virgin Jungle Reserve; catchment above ground biomass (AGB) average 350 T Ha^{-1}), twice-logged forest (LF2; AGB average 122 T Ha^{-1}) and salvage-logged forest (LF3; AGB average 95 T Ha^{-1}), and oil-palm plantations with (OPB) and without riparian reserves (OP; planted between 1998 and 2011; AGB average for all oil-palm streams is 38 T Ha^{-1}) (Pfeifer et al., 2016). The sites form part of the Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al., 2011). The landscape is drained by tributaries of the Brantian, Kalabakan and Segama rivers, all of which empty into the Celebes Sea.

We collected data from 23 headwater stream catchments, where possible matched to the SAFE project experimental streams (length ~ 2 km; catchment area ~ 260 ha; slope ~ 16°; (Ewers et al., 2011)). Five catchments were in protected areas (four at Danum Valley Conservation Area, and one in the Brantian Tatulit Virgin Jungle Reserve; Fig. 1). Three catchments were in continuous twice-logged forest (selectively logged in the 1970s and again in the 1990s–2000s) and six in recently salvage-logged forest in the SAFE project experimental area (selectively logged in the 1970's and 1990s–2000s, and salvage-logged between 2013 and 2015). Another five catchments were in oil-palm plantations with riparian reserves of approximately 30 m width, and four oil-palm catchments without riparian reserves. Oil-palm catchments had palms that varied in time since planting from 4 to 11 years. Each catchment was an independent tributary, ensuring spatial independence of data. Within each catchment, a 100 m transect was established.

2.2. Fish sampling

Field work was conducted between February–July 2017. We sampled fishes on clear-weather days using three capture methods, performed in the following order at each transect: (1) three pass electro-fishing (model EFGI 650; Bretschneider Spezialelektronic), (2) cast netting (2.75 m diameter net with 1 cm mesh), and (3) tray (push) netting (dimensions 60 × 45 cm, 2 mm mesh). Tray (push) netting involves capturing fish by placing a rectangular steel-framed net downstream of possible habitat (undercut banks, leaf litter and rocky areas) while disturbing the habitat, e.g., by kicking. In each transect, before sampling began, we placed stop nets (2 mm mesh) at upstream and downstream boundaries to prevent immigration and emigration of fish during our sampling period. We employed these methods to target all major fish microhabitats so as to obtain comprehensive and unbiased descriptions of fish communities (Giam et al., 2015; Kennard et al., 2006).

Captured fishes were identified to species (Inger and Chin, 2002; Kottelat, 2011), measured, uncommon species (< 30 individuals previously weighed; 9% of individuals) were weighed using a portable balance, and most (85%) were returned to the stream at the point of capture. Prior to this study, 5136 fish had been weighed and measured at these stream transects for other studies (CW, unpub. data), so for common species we recorded their length only and used length-mass regressions to estimate weight (Appendix 2–1). A subset of fish (up to three individuals of each species from each stream) were preserved as vouchers for proof of identification. These fish specimens were euthanized with MS-222, fixed in 10% formalin, and transferred to 75% ethanol for storage in the Lee Kong Chian Natural History Museum, National University of Singapore. Fish capture, handling and
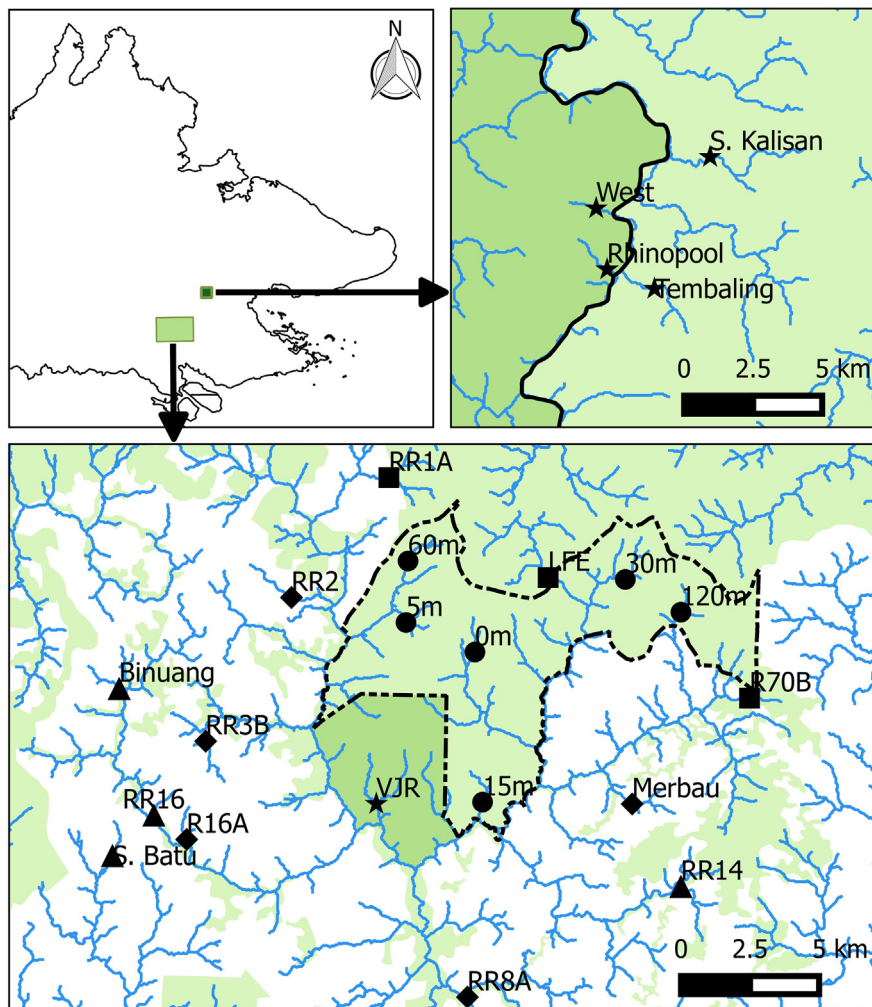
Fig. 1. Schematic and map showing the study areas in Sabah, Malaysian Borneo, and the location of the twenty three stream sites that were used in this study. Protected forest is darker green (within Danum Valley Conservation Area to the left of the black line in the top right map), logged forest in paler green and oil-palm plantations in white. Stream sampling locations vary in symbol by land-use: protected areas (star), twice-logged forest (square), salvage-logged forest (circle), oil-palm plantation with riparian reserve (diamond), and without riparian reserve (triangle).

euthanisation protocols were approved by the Animal Welfare and Ethical Review Body at Imperial College London.

2.3. Environmental variables

Twelve stream scale and four riparian vegetation scale variables were measured at every transect. Instream variables were: temperature (°C), dissolved oxygen (mg/L), conductivity (μS/cm), pH, and turbidity (NTU) measured with a YSI Professional Plus, wetted width (m), depth (cm), mean surface current speed (m/s; measured by timing a tennis ball travelling 2 m, repeated three times), substrate (%; sand, gravel, pebbles, large rocks, bedrock), littoral leaf cover (%; measured in a 50 cm transect across the stream and recorded to the nearest 10%), sedimentation (presence or absence), and canopy cover (densiometer readings oriented upstream, downstream, and to the left and right banks). Each was measured every 10 m along the 100 m transects. Riparian vegetation measurements of canopy cover (densiometer readings upstream, downstream, towards stream and away from stream), density of trees (relascope), percentage vine cover (assessed visually and recorded to the nearest 10%) and a general forest quality score (0–5, 0 = oil-palm; 1 = no trees, open canopy with ginger/vines or low scrub; 2 = open with occasional small trees over ginger/vine layer; 3 = small trees fairly abundant/canopy at least partially closed; 4 = lots of trees, some large, canopy closed; 5 = closed canopy with

large trees, no evidence of logging) (Ewers et al., 2011) were measured visually every 50 m, starting at the 0 m point on the transect, 10 m away from the stream edge and on both sides of the stream for 500 m.

2.4. Fish community metrics

Fish catch data was collated per stream, combining the three sampling methods. In addition to local species richness per stream, we calculated functional diversity and fish biomass. Functional diversity is defined as the variation in species traits that influence ecosystem function (Petchey and Gaston, 2006). We focussed on one aspect: energy flow (Giam et al., 2015; Violle et al., 2007). Functional traits known to affect energy flow in stream ecosystems through their impact on a species' life history, feeding strategy, habitat use, and locomotion were compiled from the literature (e.g., Roberts, 1989), FishBase (www.fishbase.org), and field observations of behaviour, form and function of freshwater fishes within SAFE, in other parts of Borneo as well as Southeast Asia by the authors over the past seven years (unpublished data). The traits were average body size, body shape, trophic position, mouth position, presence of jaw teeth, gregariousness, presence of barbels, vertical position in water column, and air-breathing capability (Appendix 1.2, 1.3). Fish biomass and biomass per functional trait were calculated using regression equations (Appendix 2.1). These were calculated where enough individuals ($N > 30$) of each species

had been caught and weighed. This was extrapolated to calculate the mass of all individual fish of that species. General regression equations that varied according to body morphology were calculated for species with low catch rates to determine body mass.

2.5. Data analyses

We quantified functional diversity with three complementary metrics: functional richness (F_{ric}), functional divergence (F_{div}), and functional evenness (F_{eve}) (Villéger et al., 2008). These metrics were chosen as they can be used to indicate whether species within a given habitat are performing similar (i.e. redundant) or different (i.e. complementary) roles for a given function or service. Functional richness is the volume of trait space occupied by a community (Laliberté and Legendre, 2010). Functional divergence is the divergence in distribution of species in trait space. Functional evenness quantifies community evenness in trait space. Functional redundancy, the number of taxonomically distinct species that exhibit similar ecological functions, was also explored to determine the strength and shape of the relationship between taxonomic and functional richness (Lawton and Brown, 1994; Naeem, 1998). We used the FD package (Laliberté et al., 2014) in R 3.4.1 (R Core Development Team, 2017) to calculate these metrics using presence-absence data of the fish in each stream. We used a null model to distinguish whether the observed change in functional richness was higher or lower than expected given the species richness observed (Petchey, 2004). We used simulations to create a random (null) distribution of functional richness values for each given species richness per transect. Holding species richness constant for each land-use type, we randomly selected species from the species pool (the total number of species in the study) to calculate a null functional richness for each richness level. We used 1000 iterations to produce a null distribution of values and tested whether the actual, observed functional richness for each community was significantly higher or lower than the mean of the null functional richness distribution.

We fitted and analysed generalised linear models (GLMs) of local species richness, the three metrics of functional diversity, total biomass, and biomass per functional trait across the land-use gradient. All data were compiled per transect, resulting in 23 data points per model. Biomass per functional trait was calculated for all traits, excluding mean length by assigning the biomass of each species to the functional trait of that species, at each transect. Functional redundancy at each stream was analysed using a generalised linear model, testing if the interaction between local species richness and land-use had a significant impact on functional richness.

We then investigated the mechanisms that may be controlling local species richness by comparing univariate GLMs to identify the strongest instream environmental correlates of local species richness (Appendix 3). Multiple tests were applied to the same dataset of species richness, so a Bonferroni correction (0.05/n; $n = 21$; corrected $\alpha = 0.002$) was applied to all P-values. For all the species richness models a Poisson or Quasipoisson error distribution was applied (dependent upon the results of a test for over dispersion using the AER package (Kleiber et al., 2017)). For all other models a Gaussian error distribution was applied (Zuur et al., 2009). Log-likelihood ratio tests were used to assess model significance.

To determine whether each land-use supported different communities, and what environmental variables may be associated with these differences in fish communities, we used the vegan package (Oksanen et al., 2013) in R 3.4.1 to perform redundancy analysis (RDA). We chose to use RDA because Detrended Correspondence Analysis on the community composition data showed the gradient lengths to be < 2, indicating linear responses (Lepš and Šmilauer, 2003). Euclidean distances of abundance data were maintained using the 'Hellinger transformation'. Adonis permutational multivariate analysis of variance (perMANOVA) models from the package 'vegan' (Oksanen et al., 2013) was performed to quantify differences between land-uses. We used P-

values (generated by 999 permutations) to assess significance and R^2 values to assess effect size of land-use in explaining community composition. Forward selection was used to rank all (instream and riparian) environmental variables in order of importance in terms of their association with differences in species composition (significant conditional effects set at $P < 0.05$).

3. Results

We identified 34 species from 2902 fish captures (see Appendix 4.1 for species list). The most common species in terms of abundance and presence across all land-uses were *Barbodes sealei* ($N = 603$, 21% of the total), *Nematobramis everetti* ($N = 851$, 29%), *Rasbora* cf. *sumatrana* ($N = 528$, 18%) and *Tor tambra* ($N = 183$, 6%). Sixteen species were only detected in a single land-use type, most of which were also rare (< 10 individuals; *): *Crossocheilus elegans*, *Garra borneensis*, *Lobocheilos erinaceus**, *Lobocheilos unicornis**, *Luciosoma pelligrinii**, *Betta ocellata**, *Mastacembelus unicolor**, *Homalopteroides stephensoni*, *Macrognathus keithi** (only in protected rainforest); *Rasbora elegans* (only in twice-logged forest); *Protomyzon borneensis** (only in salvage-logged forest); *Barbonymus balleroides*, *Clarias anfractus**, *Cyclocheilichthys repasson**, and *Channa striata** (only in oil-palm streams with a riparian reserve); and *Oreochromis mossambicus* (only in oil-palm streams without a riparian reserve). Nine of these 16 species were found only in protected rainforest (see Appendix 4.1, 4.2 for species list and presence) in the Segama catchment. A further 10 species were found only in the Brantian catchment (Appendix 4.2), showing variability between catchments. Several of the species that we detected in just one or the other catchment have previously been observed in the other catchment (we captured *Barbonymus balleroides* and *Cyclocheilichthys repasson* only in the Brantian, and *Betta unimaculata* and *Mastacembelas unicolor* only in the Segama; but all four species are known to be present in both catchments; personal observation). We detected one known introduced species, *Oreochromis mossambicus* (Mozambique tilapia), and one possibly introduced, *Channa striata*, in the oil-palm sites.

We found a significant impact of land-use on local species richness (Fig. 2a; $\chi^2_{(4)} = 21.45$, $P < 0.001$), with richness highest in protected rainforest and lower in all other land-uses. There was no significant difference between oil-palm and logged forest, or between streams with different logging histories. Functional richness of protected forest streams was significantly higher than that of all disturbed sites (Fig. 2b; $\chi^2_{(4)} = 30.72$, $P < 0.001$), but this decline at disturbed sites was not significantly different from that expected according to a random loss of species as determined by the null model. Sites within each land-use showed different patterns in relation to the null model, but no significant differences between land-use types ($\chi^2_{(1)} = 1.18$, $P = 0.28$; Fig. 2c). There was no significant interaction between local species richness and land-use in explaining functional richness ($\chi^2_{(4)} = 2.06$, $P = 0.724$), suggesting the same level of functional redundancy in all land-uses.

There was no significant impact of land-use on functional evenness ($\chi^2_{(4)} = 3.18$, $P = 0.528$), functional divergence ($\chi^2_{(4)} = 6.53$, $P = 0.163$), or total biomass ($\chi^2_{(4)} = 0.84$, $P = 0.933$). Biomass per functional trait highlighted a significant difference across the land-uses in benthopelagic fish ($\chi^2_{(4)} = 10.49$, $P = 0.032$) and fish with superior mouths ($\chi^2_{(4)} = 13.698$, $P = 0.008$). Biomass was higher in forested streams than in oil-palm streams for benthopelagic fish that are predominantly grazers, but lower in forested streams than oil-palm streams for fish with superior mouths that are surface feeding invertivores.

Univariate generalised linear models (Appendix 3) showed that species richness increased with littoral leaf litter cover ($\chi^2_{(4)} = 14.57$, $P = 0.003$) and was positively correlated with percentage gravel ($\chi^2_{(4)} = 11.97$, $P = 0.011$) (Fig. 4), but was not correlated with other instream environmental variables (Appendix 3.1). Neither of the two variables that were correlated with species richness varied significantly among land-uses (leaf litter ($\chi^2_{(4)} = 4.83$, $P = 1.000$), percentage gravel
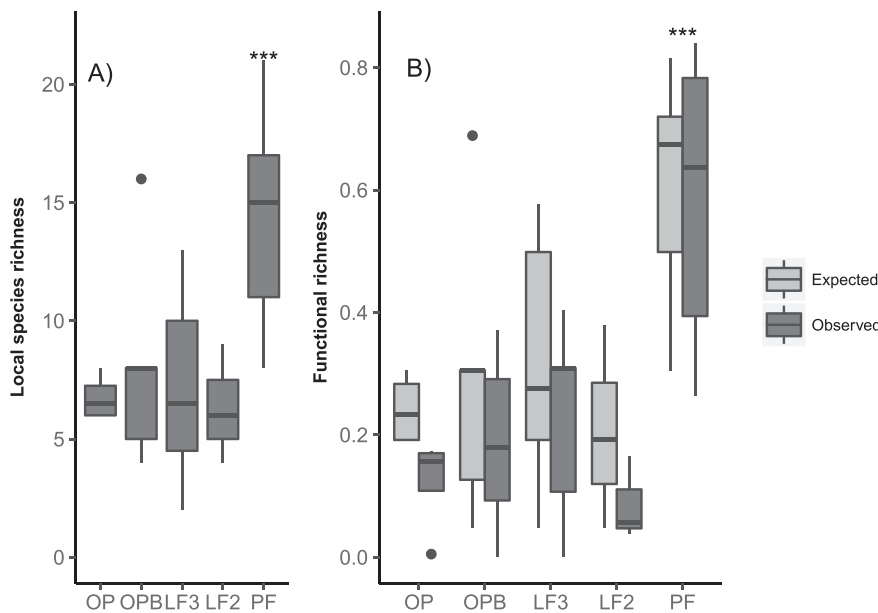
Fig. 2. Box and whisker plots of local species richness (A), and the observed and expected functional richness across a land-use gradient (B). Box and whisker plots indicate the median (dark band), interquartile range (within each rectangle), and the highest and lowest values of the data, excluding outliers, in the whiskers, with outlying points as black dots. OP = oil-palm plantation without riparian buffer, OPB = oil-palm plantation with riparian buffer, LF3 = salvage-logged forest after the third round of logging, LF2 = twice-logged forest, and PF = protected forest catchments. '*' indicate the significance of each model and which land-use is significantly different from the others (*** = $P < 0.001$).

($\chi^2_{(4)} = 4.20$, $P = 1.000$)), whereas some other variables did: temperature ($\chi^2_{(4)} = 33.22$, $P < 0.001$), stream canopy cover ($\chi^2_{(4)} = 21.338$, $P < 0.001$), sedimentation ($\chi^2_{(4)} = 50.87$, $P < 0.001$), riparian canopy cover ($\chi^2_{(4)} = 20.49$, $P < 0.001$), riparian vine cover ($\chi^2_{(4)} = 27.78$, $P < 0.001$), riparian tree density ($\chi^2_{(4)} = 35.78$, $P < 0.001$) and riparian forest quality ($\chi^2_{(4)} = 181.07$, $P < 0.001$).

Freshwater fish community composition was similar between all land-uses (perMANOVA $R^2 = 0.20$, $P = 0.282$), but had the strongest associations with substrate (percentage of sand, gravel and bedrock), average depth and littoral leaf litter cover (Table 1; Fig. 3). All disturbed sites with anthropogenic land-uses have a restricted number of species within each stream transect, but have high variability in species presence across the landscape, indicated by the large confidence interval ellipses in comparison to protected forest streams (Fig. 3). The average depth and percentage of sand were strongly correlated with Axis 1 ($r = -0.587$ and 0.419, respectively), which represented a gradient from forest cover (negative values) through to oil-palm plantations with no riparian reserve (positive values). Pelagic or bentho-pelagic, invertivorous and omnivorous fish occurrence were correlated with this gradient, with greater occurrence in forested streams. Littoral leaf litter cover and percentage bedrock were correlated with axis 2 ($r = -0.375$ and 0.725 respectively), which comprised a gradient of occurrence of benthic, algal feeding fish. Negative values indicated a greater percentage of littoral leaf cover, lower percentage bedrock and

Table 1

Results of redundancy analysis (RDA) forward selection to test the effects of environmental variables on fish communities across land uses, listing all significant ($P < 0.05$) environmental variables (λ_2 variance explained and P value), and the resultant intraset correlation coefficients of significant environmental variables for the first two axes of the RDA for freshwater fish community composition.

Environmental variable	λ_2	P	Axis 1	Axis 2
% bedrock	0.07	0.001	−0.177	0.821
Average depth	0.05	0.004	−0.675	−0.080
% gravel	0.04	0.025	−0.109	0.054
% sand	0.04	0.013	0.482	0.015
Littoral leaf litter cover	0.03	0.030	0.293	−0.424

λ_2 shows the variation explained, and associated significance, for each variable as it was included into the model by forward selection. Significance of each environmental variable was calculated using Monte Carlo permutation tests with 999 random permutations.
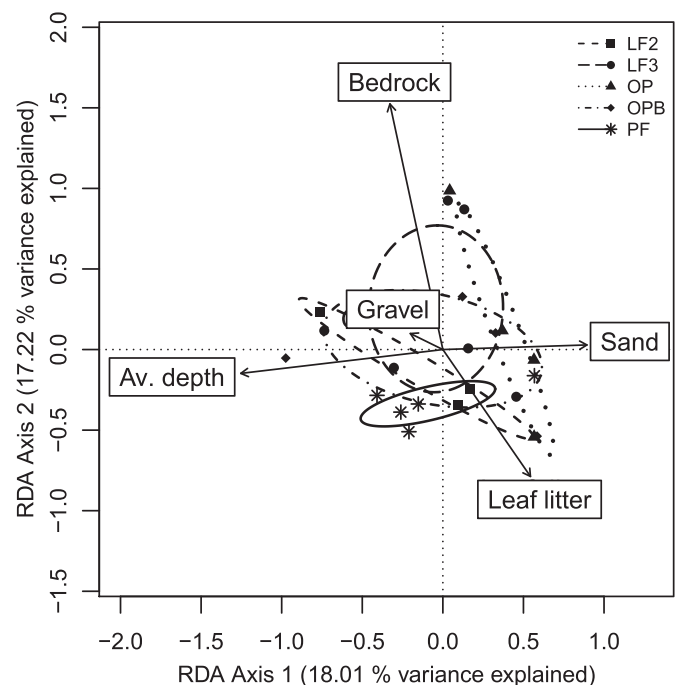

Fig. 3. Ordination bi-plot showing redundancy analysis (RDA) of fish community composition and significant ($P < 0.05$) environmental variables across all land-uses. Points represent each stream community composition and ellipses show 95% confidence interval of each land-use.

higher numbers of benthic algal feeders in protected forests, and positive values represented disturbed catchments: logged or oil-palm plantations with and without riparian reserves.

4. Discussion

Catchment land-use has a significant impact on the species richness of freshwater fish communities, but not on community level biomass or composition. Any disturbance (logging or conversion) from protected forest catchments sees a significant loss of functionally distinct species and reduced functional richness of the communities, but there was no change in functional redundancy among land-uses. Several endemic,
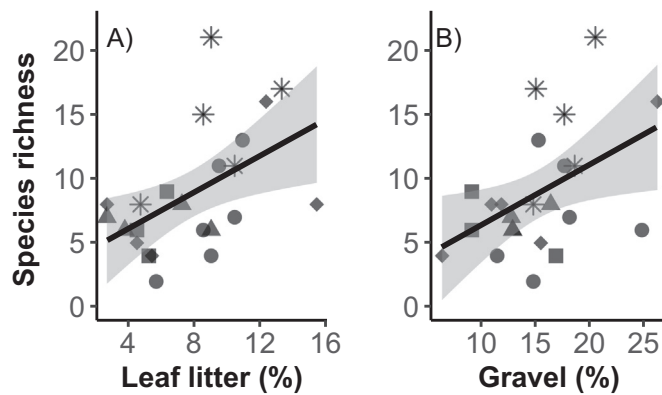
Fig. 4. Relationship between local species richness and (A) littoral leaf litter cover, and (B) percentage gravel. Each point represents the local species richness and leaf litter cover/percentage gravel in a particular site. The land-use of the site are represented by the following symbols – star: protected forest; square: twice-logged forest; circle: salvage-logged forest; diamond: oil-palm with riparian buffer; and triangle: oil-palm with riparian reserve. Black line and shaded area are the Poissons generalised linear model and 95% confidence intervals.

fast flowing, hill stream specialist species were only found in low numbers inside protected forest catchments, suggesting these range-restricted species are likely to be threatened by land-use change (Giam et al., 2011).

Quantitative studies in Borneo show that with sustainable land-use conversion, the impact of land-use on freshwater communities is minimal. However each study has only compared different logging regimes (Beamish et al., 2003; Iwata et al., 2003; Martin-Smith, 1998a, 1998b, 1998c) or oil-palm plantations with or without riparian reserves (Giam et al., 2015) to continuous or primary rainforest. The impact of land conversion for oil-palm or other agricultural plantations can be mitigated by the retention of forest fragments and riparian reserves (Giam et al., 2015), and the impact of selective logging is suggested to be more benign to freshwater fish (Iwata et al., 2003; Martin-Smith, 1998a, 1998c) than clear cutting and agricultural conversion (Beamish et al., 2003; Giam et al., 2015). This study suggests, however, that streams in all disturbed land-uses (selective logging, salvage-logging and conversion to oil-palm plantation) suffer losses in species and functional richness relative to protected rainforest.

We had expected to see a greater difference in species richness or community composition between protected or primary forest streams and oil-palm streams, than between logged forest and oil-palm streams. In addition, we had expected species richness to be lower in the recently, salvage-logged forest streams (logged from April 2013 to July 2016), than the twice-logged forest streams (last logged > 10 years ago) due to the severity and time since logging activities. This logging timeframe is within the life span (2–5 years) of small, tropical freshwater fish (Ng and Tan, 1997). Yet logging history was not included as a stand-alone factor in our statistical models. We had only a limited sample size to test for this effect, but visual inspection of Fig. 2 suggested there was no difference among twice, selectively-logged forests, and three times-logged (with the third round being salvage-logging) forests for any fish community metric. This suggests that time since logging, type of logging and number of times the forest is logged have no additional impact on fish communities.

Interestingly, there was also no significant difference in species richness or functional diversity between logged forest and oil-palm catchments (Fig. 2), contrary to what we had expected. This indicates that all forms of disturbances have strong negative influences on fish communities. In contrast to Giam et al. (2015), however, local species richness in oil-palm streams with and without riparian reserves was very similar, and our data are not consistent with the expectation that

oil-palm streams with riparian reserves can maintain 'forest-like' conditions within a stream. The differing results between this study and Giam et al. (2015) may be due to fewer microhabitats covered and/or a smaller metacommunity of fishes in the hill streams we sampled as opposed to the lowland streams sampled by Giam et al. (2015).

Together, our results indicate that any land-use change has lasting, negative impacts on the freshwater ecosystem, and that undisturbed, protected forest areas are essential in protecting freshwater diversity. But how does disturbance, through logging or deforestation, and land-use change to oil-palm plantation, disrupt fish communities? Our data indicate that littoral leaf litter cover is the instream variable with the biggest influence on fish communities. The highest proportion of littoral leaf litter cover was seen in protected forests and cover decreased in logged and oil-palm streams. The diversity and composition of riparian derived leaf litter has previously been shown to exert strong influences on the community structure and functioning of stream ecosystems (Kominoski et al., 2011; Kominoski and Pringle, 2009; LeRoy and Marks, 2006). This likely occurs because leaf litter supports fish communities by providing cool and dark microhabitats, shelter from predators (Sazima et al., 2006), and increasing and spatially concentrating food resources such as macroinvertebrates, biofilm and algae (Pringle et al., 1988; Wallace et al., 1997).

Sedimentation also had a substantial impact on species richness, with richness decreasing as sedimentation increased. Besides providing leaf litter inputs, less disturbed forests and forested riparian reserves can minimise soil erosion and substrate deposition from upstream within the catchment (Jones et al., 1999; McIntosh and Laffan, 2005). Other results from our study site have indicated that as forest gets removed from the whole catchment, or riparian reserves get converted to oil-palm, streams become shallower, wider and have a greater proportion of sand and sediment influx due to reduced bank stability (Luke et al., 2017). Higher levels of siltation and sedimentation can damage gill tissue, reduce fish spawning grounds and benthic food resources (Jones et al., 1999; Newcombe and Macdonald, 1991), and thus reduce fish species richness. Our field data corroborate this, with a greater number of benthic or benthopelagic species occurring in protected forest streams that are dominated by gravel and larger substrates as opposed to those with greater proportions of sediment or sand substrate. Our results here are consistent with those of Giam et al. (2015), implicating the same environmental variables as local drivers of fish community richness despite working in quite different stream systems (e.g. hill streams vs. lowland and slightly alkaline vs. acidic streams, in this study vs. Giam et al. (2015), respectively). As Luke et al. (2017) showed, there are clear differences in these variables across the land use gradient we examined.

We did not record water chemistry, in particular concentrations of nitrates and phosphates, in our study despite their potential impact on fish species richness (Covich et al., 1999; Yule et al., 2009). At our study site, nitrate levels are known to be as much as $12\times$ lower, and phosphorus levels up to $3\times$ higher, in less disturbed forested streams than in oil-palm catchments (Luke et al., 2017). All values of nitrate and phosphorus concentrations recorded at our study site were, however, lower than at a comparable study site in Sarawak (Mercer et al., 2014), and are within recommended limits for sensitive aquatic species on the basis of Malaysian National Water Quality Standards (Ministry of Natural Resources and Environment Malaysia, 2014). We therefore discount the possibility that the differences in species richness we observed among land-uses are due to the small differences in nitrates and phosphates within this area.

One potential confounding factor in our study is that the majority of protected rainforest catchments were located in a different catchment (Segama) to the majority of the modified land-use catchments (Brantian). However, seven out of the nine species only caught in the Segama catchment in this study are nevertheless known to occur within the Brantian catchment (CW, personal observation) or have been recorded in other catchments across Eastern Sabah (Inger and Chin,

2002). This observation provides support that the drop in species richness from protected rainforest to logged rainforest is a real effect of land-use rather than a correlative pattern arising from a study design encompassing multiple catchments.

Despite reductions in species richness with habitat disturbance, community composition was not significantly different across the land-uses. This result indicates that disturbed stream catchments are more variable in fish composition, but that many species are retained in more than one land-use type, suggesting the community-level differences among land-use types are negligible. The relatively small gradients in community composition that we did observe in the RDA were driven by environmental variables that are consistent with our prior observations about the determinants of species richness, with leaf litter, substrate and stream depth all exerting an influence. Loach and catfish species that specialise in benthic microhabitats were absent or at a lower abundance in disturbed catchments. However, pelagic or benthopelagic species dominated in all landscapes with *Barbodes sealei*, *Nematabramis everetti*, *Rasbora* cf. *sumatrana*, and *Tor tambra* — the four most common species — all being pelagic invertivores or omnivores that do not appear to specialise in benthic habitats.

Worryingly, two introduced species were captured in oil-palm streams without riparian reserves. Mozambique tilapia (*Oreochromis mossambicus*) and common or striped snakehead (*Channa striata*) are both common food fish that are routinely introduced to tropical streams (Diana, 2009; Gozlan et al., 2010). The source of the introduced species at our study sites is unknown but they are likely to have been from aquaculture. Both species were present in low numbers and each was confined to a single stream, so we suggest these detections represent the early stages of a relatively new invasion event. It is becoming increasingly important to track how invasive or introduced species interact with native species in disturbed habitats, especially due to the ongoing expansion of agricultural frontiers in the tropics (Taniwaki et al., 2017), so our early detection of an invasion event may provide an important research opportunity.

This study found that freshwater fish in small headwater streams appear to suffer significant losses in richness with any disturbance (logging or conversion to oil-palm) from protected forests. However, there was no significant difference between streams of different logging history despite twice-logged and salvage-logged forests varying in the number of times they had been logged, the cumulative severity of logging and in the time since logging. We had expected to see a further decease in richness with a third, more recent round of logging, but did not detect any impact on top of the effects of the two prior rounds of selective logging. However, in contrast to Giam et al. (2015), streams in oil-palm plantations with riparian reserves maintain the same levels of species richness than streams without riparian reserves. It is therefore essential to continue protecting primary, forested areas to maintain freshwater diversity, and explore strategies to protect freshwater ecosystems during logging, deforestation and conversion to plantation monocultures that are expected to continue across Southeast Asia.

Competing interests

The authors have no competing interests.

Role of the funding source

Acknowledgements

Appendix A. Supplementary data

Dendrogram of function groups (1.1), description of functional traits (1.2) and functional traits for each species (1.3; Appendix 1). Biomass regression equations (Appendix 2). Univariate GLMs of species richness, land-use and all environmental variables (Appendix 3). Species list and presence in each catchment (Appendix 4). Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.04.004.

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