ORIGINAL ARTICLE

Freshwater Biology WILEY

The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia

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Abstract

1. Land-use change and agricultural expansion have caused marked biodiversity loss in Southeast Asia, but impacts on freshwater communities have been very little studied. Semi-aquatic bugs are abundant in streams, provide prey for many other animals, and are sensitive to environmental change, making them a relevant group for studying land-use change.

2. We investigated the effects of logging and conversion of forest to oil palm plantations on semi-aquatic bugs in Sabah, Malaysia, and the potential value of retaining riparian buffer strips in plantations, by sampling across 12 rivers along an existing land-use gradient. We recorded catchment, riparian, and stream-scale environmental variables and surveyed semi-aquatic bugs within streams in old-growth forest, logged forest, and oil palm plantation with (OPB) and without buffer strips (OP). We recorded the abundance, richness, total biomass, and proportion of juveniles and winged adult individuals of all species, together with the sex ratio of a common morphospecies (*Ptilomera* sp.), as possible indicators of disturbance effects.

3. Average abundance and average richness, but not total biomass, of all semi-aquatic bugs were lower in areas with higher habitat disturbance. In particular, average abundance in old-growth forest was more than two, four, and six times higher than that in logged forest, OPB, and OP, respectively. Average richness in old-growth forest was higher than in logged forest by two species, but more than two and three times higher than in OPB and OP, respectively.

4. The presence of riparian buffer strips in oil palm had little effect on the abundance and richness of semi-aquatic bugs. We found no significant differences in the proportion of juveniles, winged adult individuals, or the sex ratio of *Ptilomera* sp. along the disturbance gradient.

5. In conclusion, oil palm plantations were associated with lower average abundance and richness of semi-aquatic bugs than forest sites, but community composition

did not differ markedly between logged and old-growth forests. We also found that the forested buffer strips maintained within our oil palm plantation study sites did not protect forest species of semi-aquatic bugs. Maintaining forest may therefore provide the best option for the conservation of semi-aquatic bugs, but further studies of the effects of land-use change and management options are needed across Southeast Asia.

1 | INTRODUCTION

Since the 1960s, streams have become among the most threatened habitats on earth because of human impacts (Dudgeon et al., 2006; Reid et al., 2019). Land-use and climate change, introduced species, overfishing, construction of dams and channelisation, and pollution by contaminants and microplastics, are all major threats to stream ecosystems (Allan, 2004; Hester & Gooseff, 2010; Reid et al., 2019). At the catchment scale, conversion of forest for logging and agriculture causes erosion, sedimentation, and altered nutrient cycles within streams, through inputs of pollutants by surface, subsurface, and groundwater runoff (Hancock, 2002; Sidle et al., 2006; Syers, 1979). This in turn reduces the diversity or abundance of many stream-dwelling taxa, due to loss of habitat and supplies of food (e.g., leaf litter), as well as increased water temperature, and concentrations of nutrients and other pollutants (Chopra et al., 2011; Lima et al., 2022; Luke, Dow, et al., 2017; Md Rawi et al., 2013; Weijters et al., 2009).

More local-scale effects of change within riparian habitats and streams themselves also influence stream communities and conditions directly. For example, planting of crops to the edge of streams can reduce bank stability and riparian habitat complexity, and applications of pesticides and fertilisers can increase chemical inputs to streams (Corbacho et al., 2003; Tanaka et al., 2021; Wantzen & Mol, 2013). Loss of tree cover around streams can also reduce shading and result in warming of water, which can alter the growth, survival, and reproduction of aquatic species (Sweeney, 1993). In contrast, practices such as maintaining forested margins along streams can buffer microclimatic conditions within streams, stabilise banks, and filter nutrients from the surrounding agricultural landscapes (Luke et al., 2019). Forested margins also provide resources for aquatic species through allochthonous inputs, such as dead leaves, wood, and terrestrial fauna, which fall onto the water (Chellaiah & Yule, 2018; Tank et al., 2010). The loss of forested riparian strips in agricultural catchments has been associated with decreases in species richness and changes in the structure of macro-invertebrate communities (Arnaiz et al., 2011).

In Southeast Asia, logging and forest conversion for agriculture (e.g., oil palm plantations) have expanded significantly since the 1980s (Gibbs et al., 2010; Pendrill et al., 2022). Forest conversion to oil palm has caused declines in richness and abundance of numerous taxa (Meijaard et al., 2020) as well as declines in biomass (e.g., Turner & Foster, 2009) and altered species composition (Savilaakso et al., 2014). Despite known impacts on the terrestrial environment, and likely consequences for waterways, there have been relatively few studies assessing the effects of land-use change on freshwater ecosystems in Southeast Asia (Dudgeon et al., 2006; van Klink et al., 2021). However, the few studies conducted indicate that many forest species that are associated with freshwater systems are lost when habitat is converted (Kano et al., 2019; Konopik et al., 2015; Luke, Dow, et al., 2017; Mercer et al., 2014). Considering the high levels of biodiversity in Southeast Asia (Myers et al., 2000) and the high number of freshwater species that are vulnerable to environmental change (Strayer & Dudgeon, 2010), more evidence on the impacts of human-driven land modifications is urgently needed in this region.

Semi-aquatic bugs (Gerromorpha, Hemiptera) are a group of insects that are intimately associated with both freshwater and riparian habitats and are abundant in streams (Andersen, 1982). Generally, they exploit the water surface throughout their life-cycle (Andersen, 1982), where they feed on and are eaten by various aquatic and terrestrial species (Foster & Treherne, 1981; Spence & Andersen, 1994; Zimmermann & Spence, 1989). Such adaptations make this group vulnerable to environmental changes in both the water and in the surrounding catchment and riparian environment. For example, changes in surface tension caused by water pollution could affect the movement of semi-aquatic bugs on the water surface, reducing their ability to catch prey and avoid predators (Hall et al., 1985). Deforestation may also reduce the litter supply used as a substrate for egg laying by some species in this group (Bush & Hu, 2005; Sweeney, 1993), and the number of prey items for the bugs (Ceneviva-Bastos & Casatti, 2014). Studies from other areas have found that semi-aquatic bugs are sensitive to habitat change. For instance, research in the Brazilian Amazon found a lower richness of semi-aquatic bugs in agricultural areas following forest conversion (Cunha et al., 2015; Cunha & Juen, 2017) and changes in their community structure in Brazilian savanna streams with deforested margins (Dias-Silva, Brasil, Veloso, et al., 2020).

Habitat change can also affect the physiology and breeding success of semi-aquatic bugs. For example, one study in Brazil found a higher abundance of winged individuals in forest streams than in oil palm plantations, perhaps owing to reduced resources in oil

palm (Cunha et al., 2020). Furthermore, since female insects can be more vulnerable to food stress than their male counterparts (Teder & Kaasik, 2023), change in habitat could affect sex ratios in populations. The proportion of adults to juvenile bugs could also be affected, for example through reduced reproductive success (especially if the number of adult females in a population is reduced due to environmental change), although we are not aware that this has yet been investigated, particularly in semi-aquatic bugs.

Ptilomera, a widespread genus in the Gerridae, is distributed from India to Southeast Asia (Polhemus & Polhemus, 2001). They can be recognised easily by their relatively large body size (up to *c.* 2 cm), in comparison to many species of semi-aquatic bugs (Polhemus & Polhemus, 2001). *Ptilomera* are often common in streams (Polhemus & Polhemus, 2001) and can be sexed easily by examining structures at the abdominal apex, which differ between males and females. Males have a curved paramere with setae, but females have dorsolateral lobes present on the last abdominal segment (Jehamalar et al., 2018). Owing to their commonness and clear sexual dimorphism, *Ptilomera* therefore represent a potentially useful group for measuring the impacts of habitat change on sex ratios.

To date, no studies have assessed the effects of land-use change on semi-aquatic bugs in Southeast Asia. Currently, there is no information about the conservation status of any species in this group in Southeast Asia (IUCN, 2022), despite the high level of threat posed by land-use change in this region (Hughes, 2017). We investigated the impact of catchment and riparian forest quality and stream environmental conditions on: (1) the abundance, total biomass, richness, and community composition of semi-aquatic bugs, and (2) the proportion of juvenile versus adult, winged versus wingless, and female versus male *Ptilomera* sp.

2 | MATERIALS AND METHODS

2.1 | Study sites

During 2011–2014 we surveyed streams in the Danum Valley Conservation Area (117°48.750 E and 5°010 N), Maliau Basin Conservation Area (116°540 E, 4°490 N), and the SAFE Project landscape (Stability of Altered Forest Ecosystems, area in the Kalabakan Forest Reserve, 116°570 E to 117°420 E, 4°380 N to 4°460 N, Ewers et al., 2011) in Sabah, Malaysian Borneo (Figure 1). The climate category in the region is tropical, and the average annual air temperature is 27°C (Daisuke et al., 2013). Generally, there is little seasonality (Luke, Barclay, et al., 2017). The sites are characterised by high average annual rainfall (i.e., 2,882.9 mm

Streams

1. OG - Maliau
2. OG - Rhinopool
3. OG - VJR

4. LF - 1
5. LF - 2
6. LF - 3
7. LF - 4

8. OPB - Gaharu
9. OPB - Keruing
10. OPB - Merbau

11. OP - Selangan Batu
12. OP - Binuang

Legend

- Old growth forest catchment
- Logged forest catchment
- Oil palm with buffer catchment
- Oil palm catchment
- Conservation area
- SAFE experimental area

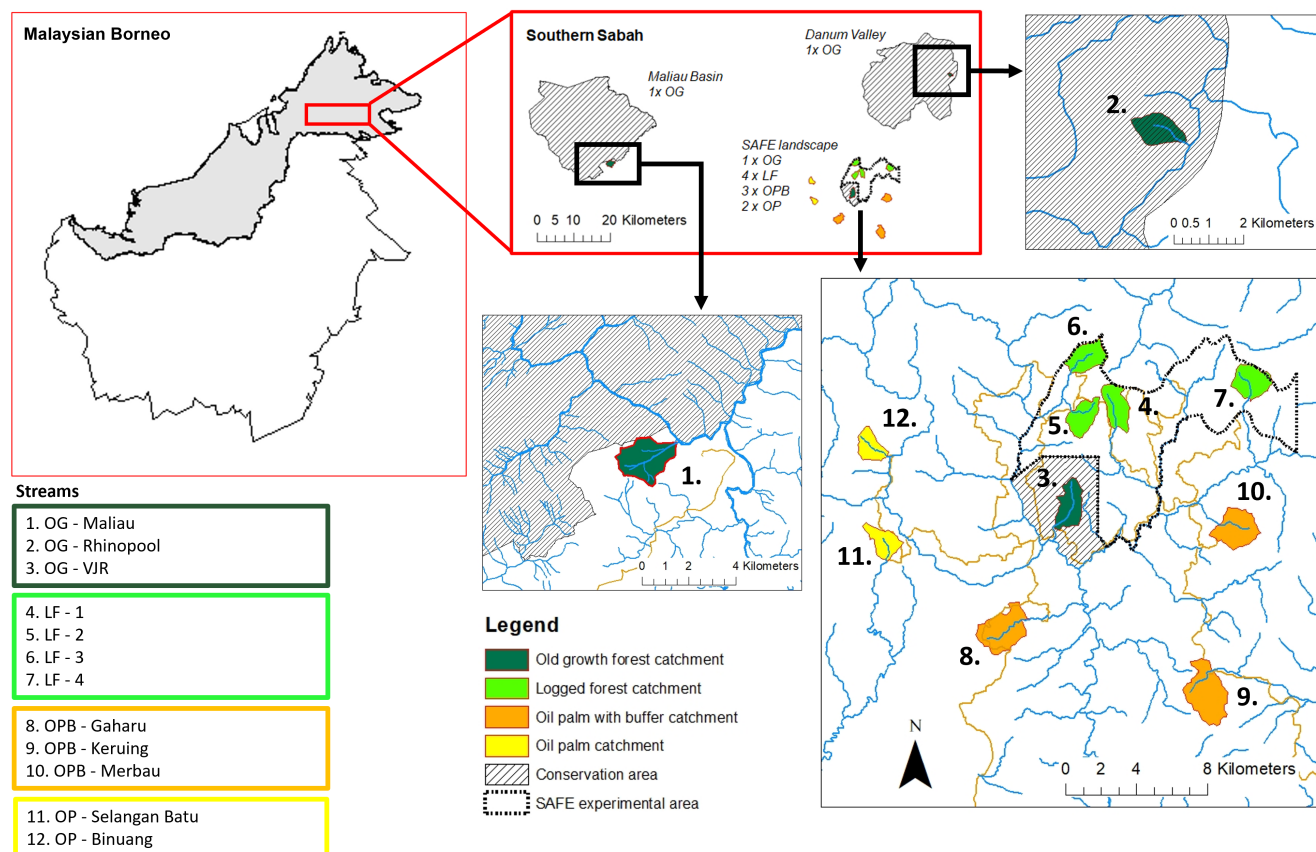**FIGURE 1** Map of stream sites in this study. Sites were in Sabah, Malaysian Borneo and comprised stream sites surrounded by old-growth forest (OG), selectively logged forest (LF), oil palm with riparian buffer strip (OPB), and oil palm without riparian buffer strip (OP) catchments. See Luke, Dow, et al., 2017; Luke, Barclay, et al., 2017 for further details. Map is obtained from Harianja, Luke, et al., 2023.

in Danum Valley, and 2,455 mm in the SAFE Project sites, Luke, Barclay, et al., 2017).

We selected 12 streams to survey that represented a gradient of land use change, choosing from an existing network of streams, established as part of the larger SAFE Project. Habitats comprised old-growth forest (OG), logged forest (LF), as well as oil palm plantations with and without riparian buffer strips. We surveyed three stream sites surrounded by OG: Danum Valley (Rhinopool), Maliau Basin (Maliau), and the Virgin Jungle Reserve (VJR) at the SAFE Project. There has never been any logging in the Rhinopool site, whilst the Maliau and VJR sites have been logged at non-commercial levels. Logging in Maliau occurred around 2009, to provide timber for the field centre. Although the VJR has not been legally logged, it shows evidence of illegal logging, which is likely to have occurred when the surrounding area was logged around 1978, and again in three rounds of logging in the late 1990s to the early 2000s (Struebig et al., 2013).

Selectively LF sites were located within the SAFE Project experimental area, whilst oil palm plantation sites with and without riparian buffer strips (OPB, OP, respectively) were located close to the project area (Figure 1). LF consisted of four stream sites (LF-1, 2, 3, and 4). The catchments of these sites were all commercially logged during the 1970s, removing a total of about 113 m³ of timber per hectare, and then had a further 66 m³ of timber per hectare removed during further rounds of logging in the 1990s and 2000s (Luke, Barclay, et al., 2017). During the study, there was no active management in the LF sites.

Oil palm sites with riparian buffers strips were in Gaharu, Keruing, and Merbau oil palm estates, while OP were in Binuang and Selangan Batu estates, and all were under similar management by Benta Wawasan, an oil palm plantation company. OPB catchments mainly consisted of mature oil palm (planted between 1999 and 2009), but each had varying amounts of riparian vegetation and forest cover remaining along stream margins (Luke, Barclay, et al., 2017), while in OP, oil palm was of a similar age and planted up to the stream margin. The average width of forested buffer strips in Gaharu, Keruing, and Merbau were 331, 68, and 26 m respectively, and were continuous in all cases, with some plantation roads crossing the catchments (Luke, Dow, et al., 2017). Oil palms in all estates were planted approximately 9 m apart, together with a cover crop established at the time of planting to reduce erosion (Luke, Barclay, et al., 2017).

Within each stream, data were collected approximately 2 km downstream from the stream source, to ensure comparability in catchment area and relative position in the catchment across streams. At this point (termed as the 0-m point), the sites' mean altitude and slopes were 236 m asl ± SE 26 m and 18.2° ± SE 0.8° respectively, and the size of the upstream catchments were 3.2 km² ± SE 0.3 km² (Luke, Dow, et al., 2017). The average channel and wetted widths recorded across streams in the study ranged from 6.0 to 15.9 m and 3.3 to 7.9 m, respectively, the average maximum depths ranged from 13.5 to 52.1 cm, and average flow speeds ranged from 0.1 to 1 m/s (see Table S1 for data on individual stream).

2.2 | Environmental data collection

2.2.1 | Catchment quality

Catchment scale forest quality data were obtained from forest stand structure maps, produced by Pfeifer et al. (2016). The maps were created using RapidEyeTM satellite images taken in 2012 and 2013 as well as ground measurements of forest quality from 193 plots in the SAFE Project sites in 2010 and 2011. These gave information about average above ground living biomass (t/ha), percentage forest cover, and leaf area index across the study landscape (Luke, Dow, et al., 2017; Pfeifer et al., 2016). We clipped forest stand structure maps to the scale of each stream catchment, which was approximately 2 km upstream from the 0-m point (Figure S1), using an ASTER Digital Elevation Model (a product of METI and NASA) and ArcMap Hydrology toolbox (Environmental Systems Research Institute (ESRI, 2014), and then computed the average forest quality values for each catchment (Luke, Dow, et al., 2017). For more details about the measurement of catchment forest quality, see Luke, Dow, et al. (2017) and Pfeifer et al. (2016).

2.2.2 | Riparian quality

We assessed riparian forest quality at each stream site during June–December 2011–2013. We resurveyed all stream sites (except Rhinopool) in May–August 2014. Measurements at each site were taken at points at 50-m intervals along a 500-m transect going upstream from the 0-m starting point (Figure S1). At each point, measurements were taken approximately 10 m up the left and right side of the banks, or at the nearest area of level ground beyond that. Data were collected along a 500-m transect going upstream to quantify conditions upstream of the transect, as well as within the transect itself. This was because upstream effects were most likely to affect downstream communities. The 500-m scale was chosen as a compromise to achieve this, while also being feasible on foot in the field.

We recorded canopy openness using a spherical densiometer (Lemmon, 1956), percentage vine cover by eye, forest quality using the SAFE Project scale which provides a rapid assessment of local vegetation composition and structure (Ewers et al., 2011), and density of trees using a relascope (Bitterlich, 1984). Canopy openness was measured by holding the densiometer at chest height facing upstream, away from stream, downstream, and towards stream. We then calculated the mean of the canopy openness for each point. Both percentage vine cover and forest quality were assessed visually within 10 m of each measurement point. The SAFE Project forest quality scale ranged from 0 to 5, with 0 = oil palm; 1 = very poor—no trees, open canopy with ginger/vines or low scrub; 2 = poor—open with occasional small trees over ginger/ vine layer; 3 = okay – small trees fairly abundant/ canopy at least partially closed; 4 = good—a lot of trees, some large, canopy closed; 5 = very good – closed canopy with large trees, no evidence of logging. The measurement of tree density with a relascope was done by turning 180° from upstream,

away from stream, and downstream and counting the number of trees seen above the division size. We used a half-circle turn to avoid gaps created by the stream. The 180° calculation was then doubled to give an estimate for 360°, after which it was doubled again to get an estimate of tree basal area (m^2/ha). Finally, we calculated the averages of all variables to represent each stream.

2.2.3 | Stream quality

Within-stream environmental data measurements in each site were taken singly in non-flood conditions in either April–August 2012, November–December 2012, or April–June 2013, along a 200-m transect from the 0-m point and going upstream (Figure S1). Data collected provided information about the structure, habitat complexity, as well as the physicochemical and biological characteristics of the streams. Several stream physical characteristics were measured at points at 10-m intervals along the transect, including: flow speed by recording the time needed for a tennis ball to travel along a 2-m string (measured at the point of the fastest flow [rapids or riffles], repeated three times and averaged), canopy openness measured using a spherical densiometer in the middle of each stream at four directions (upstream, left, and right sides of the stream, and downstream, average taken), and wetted width of the stream using a tape measure.

Characteristics of the whole river channel were also assessed by recording the percentage cover of rocks, pebbles, sand, dead wood, rapids, riffles, connected pools, and isolated pools between pairs of successive 10-m points, as well as slope using a clinometer. Pools, riffles, and rapids were characterised according to water speed, with pools being still water without ripples, riffles being flowing water with a rippled surface, and rapids being fast-flowing white water. Finally, we collected data on the stream chemical characteristics, which were recorded at points at 50-m intervals and included: water temperature, pH, and conductivity, measured using electronic probes (Hanna Combo pH and EC Meter, Hanna Instruments, Woonsocket, RI, U.S.A.). These chemical characteristics were collected once at each stream (except Rhinopool) between April and December 2012, and once in June 2013 only at Rhinopool. We then calculated the averages of each variable for each stream for use in later analyses.

2.3 | Semi-aquatic bug collection and processing

Within each stream site, semi-aquatic bugs were collected once in July–September 2011, June–August 2012, or May–June 2013 using hand-held nets with mesh size of 1 mm or less (a method that has been used before successfully in similar surveys [e.g., Ditrich et al., 2008]), from five sub-transects along the 200-m transects used for environmental measures (so starting at the 0-m point as well). Each sub-transect was 10 m long, and was randomly placed within the 200 m, but in a way that ensured upper (130–200 m),

middle (70–130 m), and lower (0–70 m) parts of the 200-m transect were all represented (hereafter, the sub-transect is termed as 10-m transect, Figures S1 and S2). We chose this method of sampling to ensure that combined samples were representative of each stream catchment (rather than of a specific sample area, the characteristics of which varied across the 200-m transect), and this could be compared to environmental characteristics at the scale of the whole catchment. All the bugs found along each 10-m transect were collected and then stored in 70% ethanol. Adult bugs were identified to family and morphospecies level using identification books and relevant papers (Andersen, 1982; Chen & Nieser, 1992, 1993a, 1993b; Chen & Zettel, 1998; Nieser & Chen, 1992; Polhemus & Polhemus, 1988; Polhemus & Zettel, 1997), with advice from taxonomic experts (see Section Acknowledgements for details).

The biomass of semi-aquatic bugs was calculated using body length measurements (measured to the nearest 1 mm for each individual using graph paper) with power regression body length–biomass equations developed in another study by Harianja, Luke, et al. (2023). Calculations were done by considering families and body forms of the bugs collected in this study: $y = 0.040x^{2.271}$ for Cylindrostethinae, Gerrinae, and Ptilomerinae; $y = 0.072x^{2.218}$ for Halobatinae; and $y = 0.041x^{2.320}$ for Veliidae, with y being the biomass and x being the body length of individual bugs. Total biomass (sum of biomass) of semi-aquatic bugs from each stream was then used for subsequent analyses.

To consider whether there were changes in the demographic structure of the bug community, we separated adult and juvenile individuals based on the number of tarsal segments and wing presence (i.e., if the tarsi had only one segment and/or no wings, the individual was a juvenile, if there were at least two segments and/or wings, it was an adult; Andersen, 1982). Finally, *Ptilomera* sp., were separated into males and females.

2.4 | Data analysis

All analyses and visualisations were carried out in R version 4.0.4 (R Core Team, 2021) with R Studio version 2022.07.1 + 554 (R Studio Team, 2020). Analyses were done with basic R syntax and package *dplyr* (Wickham et al., 2021), *car* (Fox & Weisberg, 2019) to check the equality of variance using Levene's test, and *plotrix* (Lemon, 2006) to calculate standard errors. For visualisations, packages used were *tidyverse* (Wickham et al., 2019), *cowplot* (Wilke, 2020), and *gridExtra* (Auguie, 2017). For specific analyses and visualisations, we used differing packages with details given below.

2.4.1 | Catchment, riparian, and stream quality

We ran three separate principal component analyses (PCAs) on untransformed data to reduce dimensionality and summarise the variables representing environmental conditions across our sites (separate PCA for catchment, riparian, and stream scales), and to generate

uncorrelated key axes of environmental variation (Tables S3–S5, Figures S2–S4; Jolliffe, 1986). Before running the PCA, we did not make any transformation to our data. For each PCA, we used a correlation matrix in which we normalised the environmental data due to differing units (Jolliffe, 1986), using the scaling = TRUE function in R. For the stream quality PCA, we excluded one of the percentage cover categories (sand) from analyses, because its value was already implied by inclusion of all other percentage cover categories. As predictors for the subsequent analyses, we used principal component (PC) axes that explained the majority of variation among environmental variables (choosing axes which explained >60% of the variation for each scale, which we used as our stopping criteria [see Jolliffe, 1986]) for each of catchment, riparian, and stream scales. We used base R syntax to run PCAs, and *factoextra* (Kassambara & Mundt, 2020) to produce PCA biplots.

To assess the extent of variation in environmental conditions at the catchment and riparian scales, and therefore whether variables could be used as separate independent predictors in later analyses, we ran a correlation test between the catchment and riparian first PC scores. We found that there was a moderate but not significant correlation between the catchment and the riparian scales ($r = 0.562$, $t = 2.151$, df = 10, $p = 0.056$), so we decided to do further analyses separately, as the scales included non-overlapping information.

2.4.2 | Impacts of land-use change on semi-aquatic bug abundance, total biomass, richness, and community composition

Repeat sampling of bug communities across multiple years at Maliau and Selangan Batu showed no significant interannual differences in abundance, total biomass, or richness data (Appendix S1). Hence, collection period was not included in analyses. In streams with repeat sampling, data from just 1 year (2012) were used for subsequent analyses. We used generalised linear models (GLMs) to assess the effects of environmental conditions (separate models for catchment, riparian, and stream-scale PC scores, considering that environmental variables were measured at different scales) on the summed values per river of semi-aquatic bug abundance, total biomass, and richness. Juveniles were excluded in the richness analysis, as it was not possible to assign them reliably to morphospecies, but they were included in the abundance and total biomass analyses. Site PC scores and semi-aquatic bug variables (abundance, total biomass, and richness) were used as predictor and response variables respectively.

Models took the following structure: Abundance/ Total Biomass/ Richness ~ CatchmentPC1/ RiparianPC1/ StreamPC1 + StreamPC2. For these models, we multiplied the scores of StreamPC2 by −1, so we could produce visualisations with scores that follow the gradient of land-use, from the most to least disturbed. For abundance, a negative binomial model with log link was chosen because of overdispersion. For total biomass, we used a Gaussian distribution with identity link. For richness, a Poisson model with log link was used. In all models, we checked the residuals for normality and

homogeneity of variance using diagnostic plots created on fitted and residual values. Because there was an outlier in the abundance data (a replicate from Rhinopool that had very high abundance), we ran analyses both with and without the outlier to check the influence of this point on our conclusions. We used *lme4* (Bates et al., 2015) to run GLMs, and *MASS* (Venables & Ripley, 2002) to run negative binomial models. To check overdispersion for GLMs, we used *performance* (Lüdecke et al., 2021), while *see* (Lüdecke et al. 2021) and *Rcpp* (Eddelbuettel, 2013; Eddelbuettel & Balamuta, 2018; Eddelbuettel & Francois, 2011) were used to check model assumptions.

We ran a canonical correspondence analysis with 999 random permutation tests to assess the effects of environmental conditions at each scale (CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2) on the community composition of semi-aquatic bugs (using adult individuals only). We used *vegan* (Oksanen et al., 2020) to run constrained canonical analyses and produce the canonical correspondence analysis triplot.

2.4.3 | Impacts of land-use change on the proportion of juveniles/adults, winged/wingless individuals for all species, and female/male *Ptilomera* sp.

We assessed the effects of environmental conditions across land-use types on the proportion of juveniles and winged adults for all species and female *Ptilomera* sp. We used GLMs with CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2 scores as predictors and the proportion data as response variables. Binomial families with logit link were chosen in all cases. In all models, we checked the residuals for normality and homogeneity of variance using diagnostic plots.

3 | RESULTS

3.1 | Catchment, riparian, and stream quality

Principal component analyses showed that the PC1 at both catchment and riparian scales explained most of the variation in the environmental variables (92% and 77.7%, respectively). At the catchment scale, PC1 scores were positively correlated with high values of forest cover (PC1 loading 0.594), leaf area index (PC1 loading 0.583), and aboveground biomass (PCA loading 0.552; Table S3, Figure S2). At the riparian scale, PC1 scores were positively correlated with high values of forest quality (PCA loading 0.554), basal area (PCA loading 0.503), and vine cover (PCA loading 0.392), as well as low canopy openness (PCA loading −0.534; Table S4, Figure S3). At the stream scale, PCA scores were more evenly spread between axes 1 and 2, with PC1 and PC2 scores explaining 45.7% and 19.1% of the variation, respectively (therefore summarising 64.8% of the variation in environmental variables). PC1 scores were positively correlated with high percentage cover of rocks (PC1 loading 0.380), steep

slopes (PC1 loading 0.357), and high percentage cover of isolated pools (PC1 loading 0.291), and low water temperature (PC1 loading −0.350), low canopy openness (PC1 loading −0.293), and fewer connected pools (PC1 loading −0.302; Table S5, Figure S4). In addition, PC2 scores were correlated with high percentage cover of riffles (PC2 loading 0.461) and rapids (PC2 loading 0.217), high canopy openness (PC2 loading 0.307), and rapid flow speed (PC2 loading −0.453, the negative sign represented less time needed for a tennis ball to travel along a 2-m string), as well as low percentage cover of deadwood (PC2 loading −0.411), and low percentage cover of connected pools (PC2 loading −0.337; Table S5, Figure S4).

3.2 | Impacts of land-use change on semi-aquatic bug abundance, total biomass, richness, and community composition

In total, 10,420 individual bugs comprising 5,082 adults and 5,338 juveniles were found across all streams in this study (Table S8). The collected bugs were from two families (Gerridae and Veliidae),

12 genera, and 38 morphospecies (identifications for adults only; Table S9). *Ptilomera* sp. and *Rhagovelia* sp.1 were the most common species, found in all and almost all streams across the disturbance gradient, respectively (Table S9). Two morphospecies in the Veliidae, *Microvelia* sp.1 and 2, were completely absent from OPB and OP but were found in relatively high numbers (compared with the other morphospecies in this study) in LF and OG streams (Table S9). In general, the average abundance of the bugs in OG (mean = 1958, $SE \pm 1031$) was more than two, four, and six times that in logged-forest (mean = 661, $SE \pm 170$), OPB (mean = 431, $SE \pm 59$), and OP (mean = 306, $SE \pm 243$), respectively. Average richness was higher in OG (mean = 13.6, $SE \pm 2.9$) than in logged-forest (mean = 11.0, $SE \pm 2.3$), although only by two species, and more than two and three times that in OPB (mean = 6.0, $SE \pm 2.1$) and OP (mean = 4.0, $SE \pm 1.0$), respectively.

There was lower abundance of semi-aquatic bugs in streams associated with lower CatchmentPC1, RiparianPC1, and StreamPC2 scores (Table 1, Figure 2). Overall, a similar pattern was seen for the richness of semi-aquatic bugs, that is lower richness, with lower CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2 scores

TABLE 1 Estimated regression parameters, standard error, and z/t and p-values of models used to assess the effects of environmental conditions on abundance, total biomass, and richness of adult semi-aquatic bugs at catchment, riparian, and stream scales.[a]

Model	Factors	Estimate	SE	z/t value[b]	p-value[c]
Abundance ~ CatchmentPC1	Intercept	6.500	0.171	37.919	**<0.001***
	CatchmentPC1	0.398	0.107	3.697	**<0.001***
Abundance ~ RiparianPC1	Intercept	6.558	0.195	33.568	**<0.001***
	RiparianPC1	0.384	0.116	3.308	**<0.001***
Abundance ~ StreamPC1 + StreamPC2	Intercept	6.531	0.184	35.403	**<0.001***
	StreamPC1	0.112	0.076	1.479	0.139
	StreamPC2	0.331	0.117	2.810	**0.004**
Total Biomass ~ CatchmentPC1	Intercept	1512.57	244.31	6.191	**<0.001***
	CatchmentPC1	77.47	153.60	0.504	0.624
Total Biomass ~ RiparianPC1	Intercept	1512.6	231.0	6.547	**<0.001***
	RiparianPC1	165.7	136.9	1.211	0.254
Total Biomass ~ StreamPC1 + StreamPC2	Intercept	1512.57	244.90	6.176	**<0.001***
	StreamPC1	94.59	101.10	0.936	0.373
	StreamPC2	−89.87	156.52	−0.574	0.579
Richness ~ CatchmentPC1	Intercept	2.138	0.102	20.806	**<0.001***
	CatchmentPC1	0.256	0.057	4.442	**<0.001***
Richness ~ RiparianPC1	Intercept	2.129	0.106	20.020	**<0.001***
	RiparianPC1	0.290	0.082	3.526	**<0.001***
Richness ~ StreamPC1 + StreamPC2	Intercept	2.096	0.106	19.605	**<0.001***
	StreamPC1	0.114	0.039	2.874	**0.004**
	StreamPC2	0.267	0.056	4.710	**<0.001***

[a]Environmental conditions at each scale are represented by scores obtained from the principal component (PC) analyses, i.e., CatchmentPC1, RiparianPC1, StreamPC1, and StreamPC2, which represent environmental conditions at catchment, riparian, and stream scales, respectively. The first PC scores (PC1) at catchment and riparian scales explained most variation among environmental variables. For the stream scale, two PC scores (PC1 and PC2) were needed to explain most (>60%) of the variation, so both were included in the analyses. The p-values in bold fonts are <0.05 and indicate significant effects of environmental conditions at the corresponding scale on the abundance, total biomass, or richness of semi-aquatic bugs.

[b]z value if the model used either Poisson or negative binomial distribution, t value if the model used Gaussian distribution.

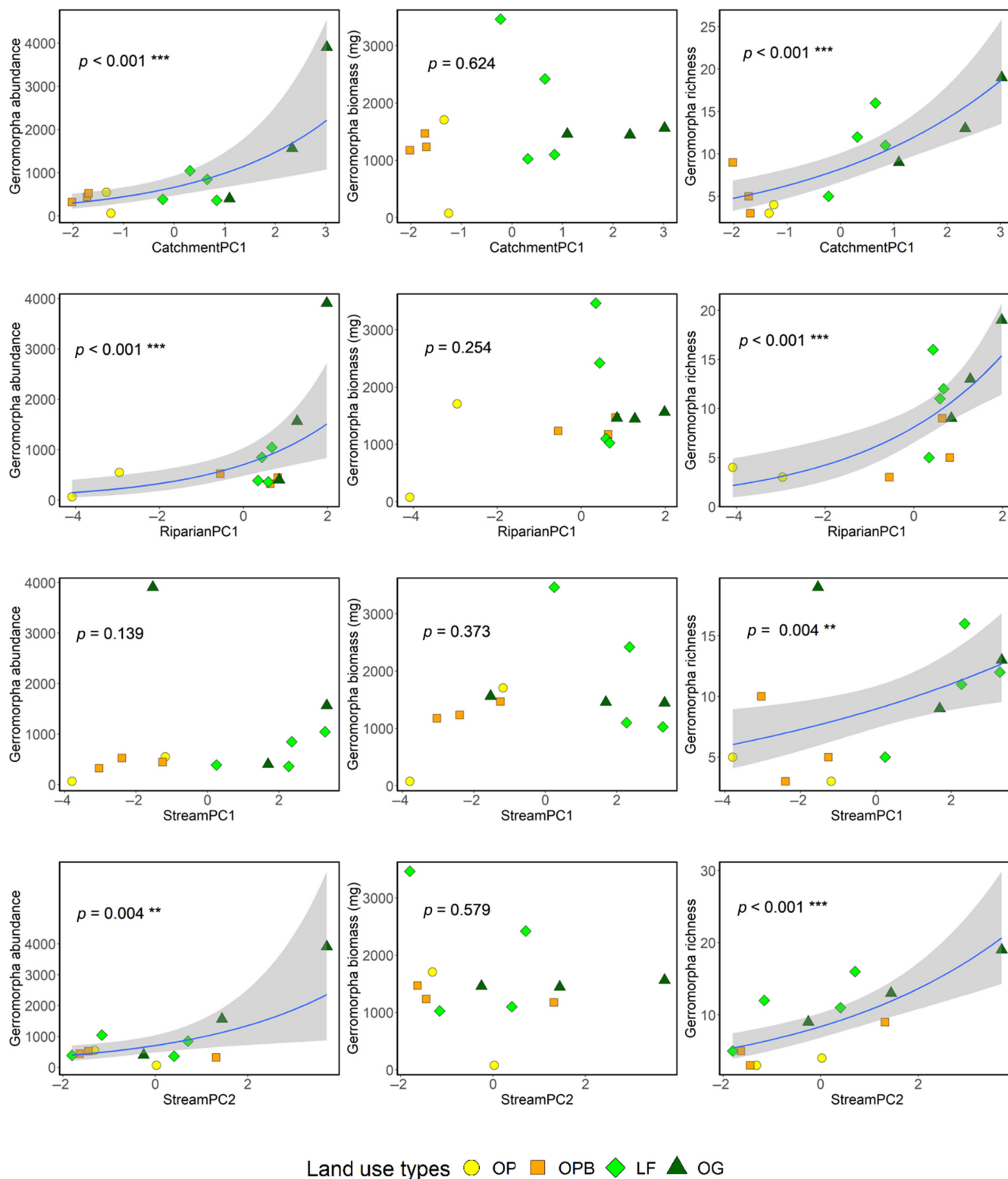[c]**, $0.001 < p\text{-value} < 0.01$; ***, $p\text{-value} < 0.001$.

FIGURE 2 Correlations between environmental conditions across three scales (CatchmentPC1, RipariranPC1, and StreamPC1 and StreamPC2 representing catchment, riparian, and stream scales, respectively) on the abundance, total biomass, and species richness of semi-aquatic bug communities (Gerromorpha). Abundance and total biomass included both juvenile and adult individuals. Richness included adults only. Smoothed regression lines for significant relationships are shown. Shaded areas represent confidence intervals. OP, oil palm no buffer; OPB, oil palm with buffer strips; LF, logged forest; OG, old growth forest. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses. **, $0.001 < p$-value < 0.01; ***, p-value < 0.001.

(Table 1, Figure 2). Despite the rapid decline in abundance and richness with higher levels of degradation, there was no significant effect of catchment, riparian, or stream environmental conditions on total biomass (Table 1, Figure 2). This reflected the significant contribution of several species of smaller-bodied Veliidae bugs towards the total abundance in the less degraded habitats, but not to total biomass (Figure S5). This was because the larger-bodied bugs (either Veliidae or Gerridae) persisted in the more degraded

TABLE 2 Output of canonical correspondence analysis assessing the effects of environmental conditions at catchment, riparian, and stream scales (CatchmentPC1, RiparianPC1, StreamPC1 and StreamPC2, respectively) on the community composition of semi-aquatic bugs across stream sites in this study, with p-values obtained from 999 random permutation tests under reduced model.[a]

Predictor	Chi-square	F	p-value[b]
CatchmentPC1	0.374	4.309	**0.005****
RiparianPC1	0.124	1.432	0.159
StreamPC1	0.109	1.255	0.195
StreamPC2	0.184	2.123	**0.029***

[a]Community composition used adult bug data only. The p-values <0.05 are shown in bold and indicate a significant effect of a particular predictor on the community composition of semi-aquatic bugs.
[b]*, $0.01 < p\text{-value} < 0.05$; **, $0.001 < p\text{-value} < 0.01$.

habitats, resulting in the lack of significant difference in the total biomass across the disturbance gradient (Figure S5). At all scales, there was no clear difference between OPB and OP in terms of the abundance, total biomass, or richness of bugs, with these sites tending to cluster together in plots (Figure 2). Removal of Rhinopool resulted in the same trends for abundance, total biomass, and richness of bugs at both catchment and riparian scales. However, there were a few changes at the stream scale, with StreamPC1 becoming a significant predictor of abundance, but with Stream PC2 becoming non-significant (Table S10, Figure S6).

At the community level, there was clustering of sites related to the similarity in the composition of bugs, with CatchmentPC1 and StreamPC2 being significant drivers of the composition (Table 2, Figure 3). Community composition differences among stream sites were largely driven by singletons or doubletons (Table S9).

3.3 | Impacts of land-use change on the proportion of juveniles/adults, winged/wingless individuals, and female/male *Ptilomera* sp.

We found no significant relationship between the quality of catchment, riparian, and stream conditions on the proportion of juveniles to adults or winged to wingless individuals of semi-aquatic bugs, or in the proportion of female to male *Ptilomera* sp. (Table 3, Figure 4).
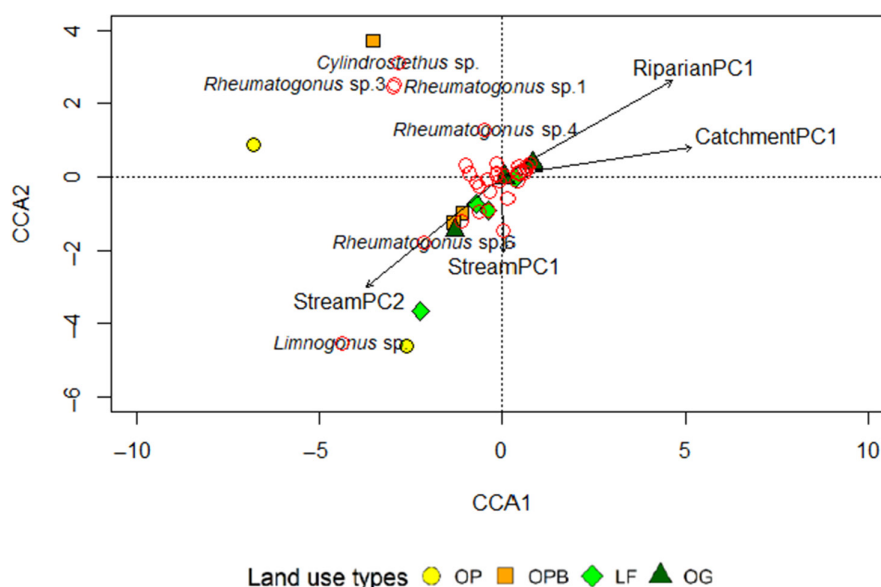

FIGURE 3 A canonical correspondence analysis tri-plot showing the correlation between environmental conditions at catchment, riparian and stream scales (CatchmentPC1, RiparianPC1, StreamPC1 and StreamPC2, respectively) and the community composition of semi-aquatic bugs across stream sites in this study. On the plot, environmental conditions are shown as arrows. Community composition is represented by morphospecies of adult bugs, shown as circles with no colour but red borders. Stream sites are shown as coloured shapes with black borders, representing land-use types (yellow circle=oil palm no buffer strips-OP, orange square=oil palm with buffer strips-OPB, green diamond=logged forest-LF, dark green triangle=old growth forest-OG). Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses. The closer a morphospecies is to a stream site, the higher the probability of finding that species in that stream. Morphospecies that were outliers are labelled. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses.

TABLE 3 Estimated regression parameters, standard error, and z and p-values of generalised linear models used to assess the effects of environmental conditions at catchment, riparian, and stream scales on the proportion of juveniles to adults, winged to wingless semi-aquatic bugs, and female to male *Ptilomera* sp.[a]

Model	Factors	Estimate	SE	z value	p-value[b]
Proportion of juveniles ~ CatchmentPC1	Intercept	0.427	0.597	0.715	0.475
	CatchmentPC1	−0.193	0.375	−0.516	0.606
Proportion of juveniles ~ RiparianPC1	Intercept	0.517	0.657	0.788	0.431
	RiparianPC1	−0.478	0.512	−0.934	0.350
Proportion of juveniles ~ StreamPC1 + StreamPC2	Intercept	0.440	0.609	0.723	0.470
	StreamPC1	−0.103	0.248	−0.414	0.679
	StreamPC2	0.269	0.388	0.695	0.487
Proportion of winged individuals ~ CatchmentPC1	Intercept	−2.556	1.125	−2.271	**0.023***
	CatchmentPC1	0.122	0.681	0.180	0.856
Proportion of winged individuals ~ RiparianPC1	Intercept	−2.543	1.112	−2.286	**0.022***
	RiparianPC1	−0.053	0.624	−0.085	0.932
Proportion of winged individuals ~ StreamPC1 + StreamPC2	Intercept	−2.620	1.195	−2.193	**0.028***
	StreamPC1	0.179	0.489	0.368	0.713
	StreamPC2	0.034	0.783	0.044	0.964
Proportion of female *Ptilomera* sp. ~ CatchmentPC1	Intercept	0.579	0.604	0.959	0.337
	CatchmentPC1	0.116	0.385	0.302	0.763
Proportion of female *Ptilomera* sp. ~ RiparianPC1	Intercept	0.579	0.604	0.959	0.338
	RiparianPC1	−0.101	0.373	−0.271	0.786
Proportion of female *Ptilomera* sp. ~ StreamPC1 + StreamPC2	Intercept	0.677	0.665	1.017	0.309
	StreamPC1	−0.197	0.277	−0.713	0.476
	StreamPC2	0.403	0.496	0.812	0.417

[a]In all cases, generalised linear models with binomial distribution were used. The p-values <0.05 are in bold and indicate significant effects.

[b]*, $0.01 < p$-value < 0.05.

4 | DISCUSSION

Semi-aquatic bug abundance and richness were lower in sites with lower catchment and riparian forest quality, and within streams with certain characteristics. In particular, the abundance of bugs was lower within streams with more rapid flow speeds and higher percentage cover of rapids and riffles, and in those with lower percentage cover of connected pools and deadwood (StreamPC2). The richness of bugs was lower within streams which had more rapid flow speed, and higher water temperature and average canopy openness, as well as higher percentage cover of rapids and riffles, and those with less steep slopes, lower percentage cover of rocks, and lower percentage cover of isolated pools and deadwood (StreamPC1 and StreamPC2). Average abundance and richness of semi-aquatic bugs in oil palm plantations were lower than forest sites, regardless of the presence of riparian buffer strips. There was clustering in the community composition of bugs associated with disturbance, with catchment forest quality, and with stream characteristics mainly associated with flow speed, canopy openness, and percentage deadwood. In contrast, we found no significant differences in the total biomass of semi-aquatic bugs in relation to catchment-, riparian-, or stream-scale differences in environmental conditions. We also found no effect of environmental disturbance at any scale on the proportion of juveniles to adults or winged to wingless adult individuals for all species, or female to male *Ptilomera* sp.

Abundance, richness, and community composition of semi-aquatic bugs was sensitive to land-use change. Previous studies in the Amazon basin also found lower richness (although not abundance) and altered community composition of semi-aquatic bugs in streams surrounded by oil palm compared to those surrounded by forest (Cunha et al., 2015; Cunha & Juen, 2017; Dias-Silva, Brasil, Juen, et al., 2020). Similarly, other studies investigating the impact of forest logging and conversion to oil palm plantations on other freshwater taxa found lower species richness in the absence of forest (Kano et al., 2019; Konopik et al., 2015; Luke, Dow, et al., 2017; Mercer et al., 2014), and therefore also altered local community composition (Faruk et al., 2013).

One OG site (Rhinopool) had particularly high abundance and richness, and therefore had considerable influence on overall trends. Indeed, the removal of Rhinopool from the analyses caused different factors at the stream level to have significant effects on bugs, although this was not the case at the catchment and riparian scales. In particular, characteristics of streams associated with flow (flow speed and percentage cover of riffles), as well as canopy openness and percentage cover of deadwood, that were main significant contributing factors when Rhinopool was included, became
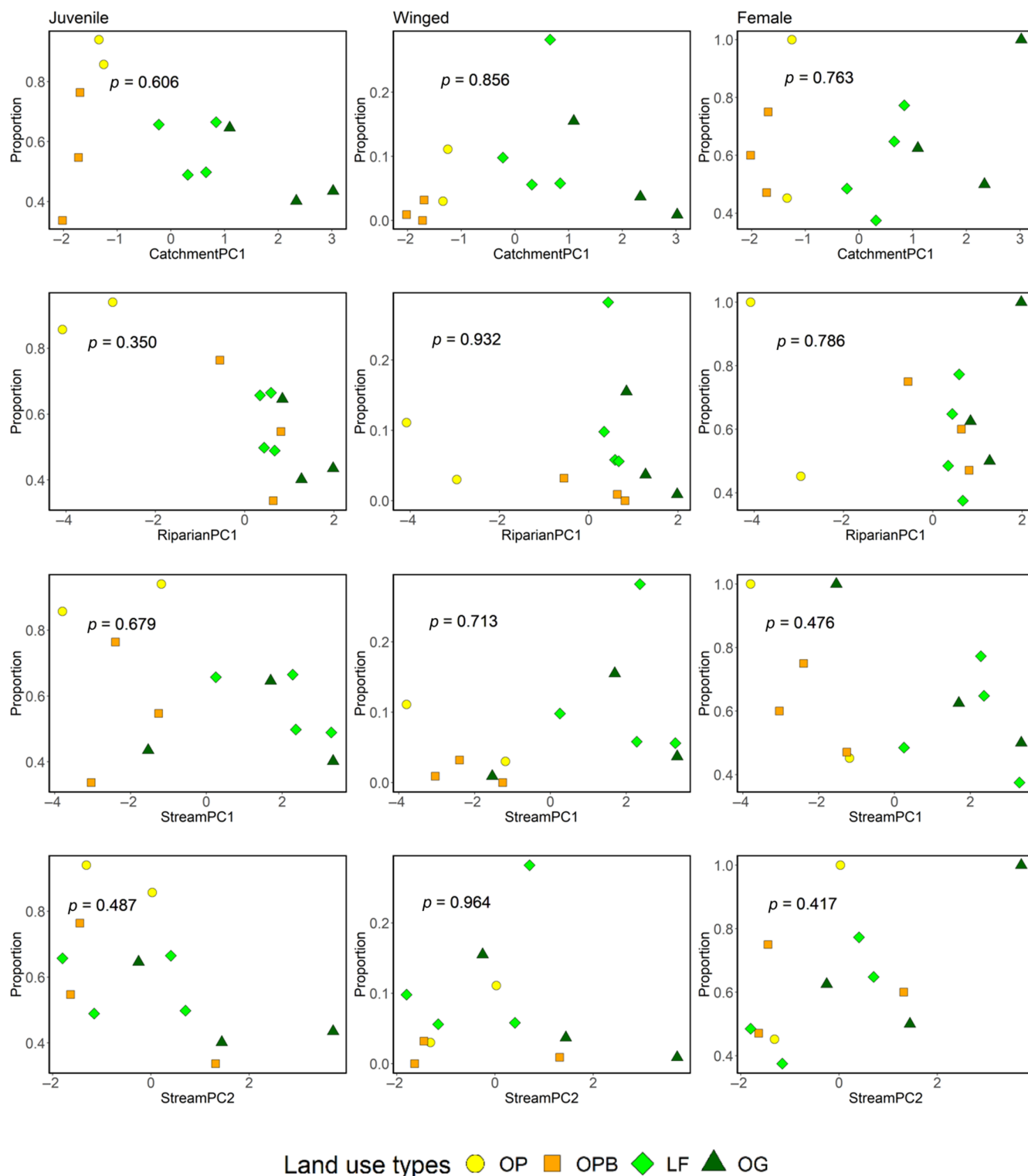
FIGURE 4 Correlations between environmental conditions across three scales (catchment, riparian, and stream) on the proportion of juveniles (left-hand side panels) and winged individuals (middle panels) of semi-aquatic bugs (Gerromorpha), as well as on the proportion of female *Ptilomera* sp. (right-hand side panels). OP, oil palm no buffer; OPB, oil palm with buffer strips; LF, logged forest; OG, old growth forest. Different points showing different habitat types are included for illustrative purposes only and were not included as a factor in the analyses. Data used for analyses in this study came from transects at each stream.

non-significant after the removal of this stream site. The change in the trend after removal of Rhinopool could be related to higher variability in the within-stream variables and reduced overall effects

or because of the distinct characteristics of the Rhinopool at the stream scale. Furthermore, since Rhinopool was the only site that had never undergone any logging, it is difficult to be certain whether

this value represents unusually high levels of diversity at this particular site or is representative of the bug assemblage across a range of pristine forest sites. However, after removal of Rhinopool from analyses, differences between the bug abundance and richness at lightly logged old growth sites and the more disturbed LF sites still indicated a clear relationship with forest quality, albeit over a reduced range of abundance and richness values, suggesting that the trends we detected were robust. It is important to note that this study only included 12 streams across the habitat change gradient. Therefore, it is possible that trends were heavily influenced by individual stream characteristics. Additional studies in other streams will help to assess how general the patterns were that we observed in our study.

At the catchment scale, change across habitat types could include altered inputs (e.g., nutrients, sediments, herbicides, and pesticides) to streams through runoff, together with changes in the intensity of impacts of extreme events such as heavy rain. As this study indicated and as identified in previous research, at the riparian scale, sites that had no forested margins could have experienced hotter microclimate and lower input of food sources (Hardwick et al., 2015; Luke, Dow, et al., 2017; Spence & Andersen, 1994). In particular, stream margins provide food sources for semi-aquatic bugs both directly (e.g., terrestrial invertebrates that accidentally fall into the water surface [Spence & Andersen, 1994]) and indirectly (provision of litter supply for aquatic macroinvertebrates which are prey items for the bugs [Chellaiah & Yule, 2018; Luke, Dow, et al., 2017]). Therefore, the loss of input from stream margins might have reduced the availability of prey items for semi-aquatic bugs. In addition, the reduced amount of litter might have reduced egg laying sites for bugs (Bush & Hu, 2005; Sweeney, 1993). Finally, at the stream-scale, changes in stream physical and chemical features may also have affected the movement of some species (Crumière et al., 2016; Ditrich et al., 2008; Spence & Andersen, 1994).

Effects of habitat disturbance were more consistent and marked at catchment and riparian scales than at stream scales. This is probably because catchment and riparian scales themselves impact stream-scale characteristics and may therefore have more profound and widespread effects. Additionally, catchment and riparian-scale characteristics were largely based on structure and factors that are unlikely to vary in the short term, while chemical and physical characteristics of streams are likely to vary with rainfall levels and short-term effects (De Pauw & Roels, 1988), potentially adding variability to the data that was unrelated to land-use. A related point, and caveat of our study, is that sampling occurred at only a single time-period for each stream. Therefore, environmental variables and indeed bug communities that change over time may not be adequately sampled in a single period or be representative of longer-term trends. However, comparison of the sites where we measured more than once did not show temporal change in semi-aquatic bug communities, suggesting that this may not be an important factor at these sites.

The lack of consistent effects for stream level variables is also reflected in our sensitivity analyses. The relatively greater impact of larger scales of disturbance is also likely to be a key factor in explaining why bug communities in oil palm sites with buffers did not differ markedly from oil palm sites without buffers. Although the presence of buffers may have increased shading and reduced runoff into the streams (Luke et al., 2019), it is likely that the large-scale differences in catchment characteristics dwarfed these effects, leading to similar communities across oil palm streams (Wilkinson et al., 2018). Finally, it should be noted that we used PCAs to reduce the dimensionality and summarise environmental data (Jolliffe, 1986) in this study, owing to our limited number of sample points. Although the PCA axes at the stream scale represented the majority of variation in the data (c. 65%) and although commonly used in ecological studies of this kind, this approach does mean that some of the variation in the environmental variables was not captured, meaning that the potential impact of this variability on bug communities was not detected.

Two species were found in all or almost all streams, *Ptilomera* sp. and *Rhagovelia* sp.1. These are both well adapted to fast-flowing water, which can be found naturally in pristine sites, but also in degraded sites linked to higher runoff and streamflow (Hurkmans et al., 2009). Additionally, there were two species of veliid bugs (*Microvelia* sp.1 and sp.2), which were found in relatively high abundance in only logged and OG, suggesting that they are sensitive to forest conversion. Contrastingly, several morphospecies were only found in oil palm streams (either with or without buffer strips), such as those in the genera *Cylindrostethus* and *Limnogonus*, with the latter being relatively rare (only two individuals were found in this study). These results accord with those from previous studies, which have found that species in the genus *Microvelia* were associated with forest, while bugs in the genus *Cylindrostethus* were associated with degraded habitats in Brazilian streams (Cunha et al., 2015). Studies conducted in peninsular Malaysia found *Cylindrostethus* bugs in streams close to oil palm plantations (Mohd Ishadi et al., 2014), while *Limnogonus* bugs were found in secondary forest or protected area streams, but in extremely low abundance compared to the overall abundance found across taxa (eight out of 19,928 individuals in Al-Shami et al., 2011 [this study was conducted at streams polluted by industrial, agricultural, and domestic sectors, with streams passing through a local recreational area as a reference site], and two individuals out of 849 individuals in Mohd Ishadi et al., 2014), in line with this study.

In contrast to abundance and richness, total biomass of semi-aquatic bugs was more robust to land-use change, with no environmental variables being significantly associated with changes in total biomass at any scale. This lack of measurable impact of disturbance on total biomass was probably related to species turnover. Even though some species were lost from sites with lower catchment, riparian, and stream qualities, common large-bodied species (such as *Ptilomera* sp. [Gerridae]) persisted, with the highest average abundance of this morphospecies recorded in LF streams followed by oil palm with and without buffer strips, while OGs supported the lowest total biomass, resulting in no discernible difference in total biomass across sites. The robustness of this and other species in disturbed sites may have been due to its adaptability to environmental change,

such as being able to cope with fast-flowing water (Kim et al., 2022). Additionally, the two old-growth sites with the highest abundance of semi-aquatic bugs (Maliau and Rhinopool streams) were dominated by Veliidae, which were generally smaller than the Gerridae and would contribute less to total biomass.

The lack of impacts on the proportion of juveniles/adults, and female/male *Ptilomera* sp. indicates that disturbance did not affect the reproduction of populations. If disturbance had a disproportionate effect on one sex, we might expect the sex ratio to be biased in more disturbed conditions, potentially affecting reproduction. Consequently, we might expect the proportion of juveniles to adults to decline. Additionally, since *Ptilomera* can be considered as disturbance tolerant due to its commonness across land-use types in this study, further research is required to confirm if there will be similar findings on species that are sensitive to anthropogenic disturbance. We also detected no difference in the proportion of winged/wingless individuals, suggesting that dispersal was also not affected by disturbance. Other studies have found that populations tend to develop wings when conditions are unfavourable or sites dry up (Spence, 1989). The lack of differences in the proportion of winged and wingless individuals in this study therefore indicates that conditions did not stimulate bugs to develop wings, perhaps because, despite changes in condition, streams in the study sites were permanent habitats. It is possible that, since we sorted samples only to genus and morphospecies level, some morphospecies might have contained more than one species. If these showed different or opposing trends in response to environmental changes, then this might have masked real differences. However, this limitation would not affect the results obtained for the abundance or total biomass aspects of the study, and so should not substantially affect community-level analyses.

4.1 | Implications for conservation and land management

Our study has important implications for land management and conservation. We found that a change in land-use from forest to oil palm plantation was associated with much lower abundance and species richness of semi-aquatic bugs, as well as changes in community composition. Indeed, the sensitivity of some species in this group to habitat degradation may make them potentially valuable indicators of change (particularly *Microvelia* sp.1 and sp.2 [Microveliinae]). This has potential implications for the functioning of stream ecosystems, since semi-aquatic bugs are predators of aquatic and terrestrial invertebrates as well as being eaten by a range of animal species, which may lead to reductions in related functions (Marschalek & Deutschman, 2022). In contrast to abundance and richness, total biomass was robust across the gradient of environmental conditions, perhaps indicating maintenance of food resources for the predators of semi-aquatic bugs despite habitat degradation. Other studies have found that, compared to richness or abundance, total biomass can be more important in determining ecosystem functions supported by an insect group in rainforests in Southeast Asia (Slade

et al., 2011). Therefore, the lack of effects of degradation on total biomass of semi-aquatic bugs may indicate some stability in functions supported by this group. More work is needed to confirm this, particularly in terms of the effects on the whole food web and ecosystem functions associated with semi-aquatic bugs.

Taken together, this study emphasises the importance of protecting remaining forest for conserving the full biodiversity of this group, as has been emphasised by another recent study (Cunha et al., 2022). Perhaps because the logging operations at LF sites in this study were selective, the sites contained more abundant and richer species assemblages than oil palm streams. Outside of these areas, more degraded habitats could be managed in ways that support existing species which provide functions in the ecosystem. For example, clearcut logging may not be able to provide the same level of support for biodiversity as selective logging, particularly because clearcutting can alter microclimatic conditions (canopy removal increases air and water temperatures) and hence causes changes in the density (Noel et al., 1986) or composition (Wallace & Ely, 2014) of local aquatic species. Different stream management practices could be trialled to maintain cool water temperature, canopy cover, as well as high proportions of rocks and deadwood in these systems. However, our results indicate that maintaining forested river margins (buffers) had only marginal effects on semi-aquatic bugs. As we only studied five oil palm streams in this study, we call for more studies assessing factors related to land-use management in catchments and riparian areas that could be manipulated to better support semi-aquatic bugs.

thank Jakob Damgaard, Lars Vilhelmsen, and Henrik Enghoff who helped S.H.L. with the sample identification in Copenhagen; Mick Webb based in the London Natural History Museum who helped M.F.H. to make connection with Herbert Zettel and obtained access to semi-aquatic bug collections in the Museum; and Herbert Zettel who provided guidance with semi-aquatic bug identification for M.F.H. We are grateful for the feedback from Dr Konstans Wells, Dr James Herbert-Read, as well as two anonymous reviewers which has improved the manuscript.

CONFLICT OF INTEREST STATEMENT
We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT
Data set and analytic codes are available at 10.5281/zenodo.7516680 (Harianja, Turner, et al., 2023).

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How to cite this article: Harianja, M. F., Turner, E. C., Barclay, H., Chey, V. K., Aldridge, D. C., Foster, W. A., & Luke, S. H. (2024). The effects of land-use change on semi-aquatic bugs (Gerromorpha, Hemiptera) in rainforest streams in Sabah, Malaysia. *Freshwater Biology*, 00, 1–17. https://doi.org/10.1111/fwb.14229