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The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo

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SUMMARY

1. Dragonfly assemblages (Odonata: comprising damselflies, Zygoptera; and dragonflies, Anisoptera) in Southeast Asian rainforests are extremely diverse but increasingly threatened by habitat disturbance, including logging and conversion of forest to oil palm plantations.
2. Land-use change can affect dragonfly larval stages by altering within-stream environmental conditions, and adults by loss of perches, shade and hunting habitat. However, the extent to which dragonflies are affected by land-use change is not well known, and strategies for conservation are poorly developed.
3. We surveyed dragonfly adults and larvae, forest quality and stream environmental conditions across 16 streams in Sabah, Malaysia. Habitat surrounding the streams included pristine forest, selectively logged forest, oil palm with forested riparian buffer strips and oil palm without buffers.
4. Overall abundance and species richness of adult dragonflies stayed constant with habitat disturbance, but larval abundance and richness decreased with higher habitat disturbance, and larvae were largely absent from oil palm streams. There was also a clear shift in community composition of both adult and larval dragonflies. Anisoptera adults were more species rich and abundant, but Zygoptera adults were less species rich in more disturbed sites.
5. The presence of riparian buffers in oil palm plantations offered some protection for forest-associated dragonfly species, and streams with wider riparian buffers supported adult assemblages more similar to those found in logged forest. However, oil palm streams with riparian buffers still contained a depauperate larval assemblage compared to logged forest areas, and dragonfly assemblages in narrow riparian buffer streams were similar to those found in streams surrounded by continuous oil palm.
6. Our results provide clear evidence of the effect of land-use change on dragonflies. Conservation efforts to conserve forest communities should target the preservation of existing forest areas, but management within oil palm plantation landscapes to preserve riparian buffers can still have a marked beneficial effect on dragonfly communities.

Keywords: Odonata, oil palm, riparian buffer, selective logging, tropical streams

Introduction

Global agriculture is expanding rapidly to meet the demands of a larger and wealthier world population, and this is causing wide-scale loss of natural habitats (e.g. Tilman *et al*., 2001; Godfray *et al*., 2010; Ellis, 2011). This issue is particularly acute in tropical regions, where human populations are large and growing rapidly, where

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land is still available for conversion and where rapid development is being encouraged (Laurance, Sayer & Cassman, 2014). Mounting evidence suggests that nature in the tropics is being increasingly affected by agricultural expansion (e.g. Sodhi *et al*., 2004; Bradshaw, Sodhi & Brook, 2009; Laurance, Sayer & Cassman, 2014). Southeast Asia, which includes four 'biodiversity hotspots' (Myers *et al*., 2000), is experiencing widespread disturbance and degradation of rainforest by logging activities, and complete conversion of forests to cropland including rubber, forestry plantation and oil palm (*Elaeis guineensis*) for palm oil production. By 2010, the region had lost 70% of its lowland forest (Wilcove *et al*., 2013), while about 20% of Sabah was under oil palm plantation (Gunarso *et al*., 2013).

Odonata (including both dragonflies and damselflies, but henceforth shortened to dragonflies) are charismatic, culturally important, play important functional roles in ecosystems as both predators and prey and have the potential to provide valuable pest-control services to agricultural systems (Corbet, 1999). The Oriental region (including Southeast Asia from southern China to Java, Sundaland, and South Asia south of the Himalayas) has a highly diverse dragonfly fauna, with some of the highest numbers of described species and genera of all biogeographical regions. Several families are largely confined to the region (e.g. Chlorogomphidae, Euphaeidae, Devadattidae, Philosinidae and Pseudolestidae) and several others are mostly found there (e.g. Chlorocyphidae and Platystictidae) resulting in very high levels of endemism (Kalkman *et al*., 2008). Borneo is known to have approximately 357 species, of which 191 are endemic, and the true figure is likely to be in excess of 400 species (working list kept by Rory A. Dow). With currently available data, the highest levels of species richness and endemism occur in stream habitats in mixed dipterocarp forest in North Borneo (Kalkman *et al*., 2008); however, it must be acknowledged that data from Kalimantan are limited. It is thought that at least 70% of the dragonfly fauna, including over 80% of Zygoptera, are dependent on forest for survival (Orr, 2006), which suggests that current land conversion in the region could have pronounced negative effects on dragonfly populations.

Although a global assessment of the conservation status of dragonflies found that only one in 10 species were threatened globally, large numbers of species, particularly in the tropics, were 'Data Deficient' and so the authors acknowledge that the figure is likely to be much higher (Clausnitzer *et al*., 2009). They found that threatened species were clustered in tropical areas including the Indo-Malayan region, and North Borneo is particularly highlighted as a region with very high threat levels (Clausnitzer *et al*., 2009). The only study, of which we are aware, that considers the impacts of forest logging on Odonata in Borneo showed that species richness and taxonomic diversity declined, and community composition changed substantially along a gradient of forest degradation through to non-forest habitat in Kalimantan (Dolný *et al*., 2011, 2012). Similar results have been found in other sites around the world. Oppel (2006) found lower diversity in village compared to forest habitat in Papua New Guinea; Monteiro-Júnior, Juen & Hamada (2014) found changes in community composition in relation to degree of habitat disturbance in Amazonia; while Samways & Steytler (1996) found differences in abundance and community composition of adult dragonflies across different human-modified habitats in South Africa. However, we do not know of any studies that have yet assessed dragonfly assemblages in oil palm, and how they are affected by this highly modified land-use.

Odonata may be especially vulnerable to the effects of logging and conversion of forest to oil palm, because their larval and adult stages depend on distinctly different habitats. Dragonfly larvae are aquatic and so are affected by land-use change through its impacts on waterways. Land-use change can have substantial impacts on freshwater systems causing changes in inputs of water, sediment, organic matter and light (e.g. Allan, 2004; Burcher, Valett & Benfield, 2007) which can cause declines in the abundance and diversity of macroinvertebrates, and changes in community assemblage (Sponseller, Benfield & Valett, 2001; Benstead, Douglas & Pringle, 2003; Bojsen & Jacobsen, 2003; Iwata, Nakano & Inoue, 2003; Death & Collier, 2009; Lorion & Kennedy, 2009a). Dragonfly larvae are predators of other macroinvertebrates and are particularly affected by changes in benthos, water quality and aquatic vegetation structure (Corbet, 1999; Clausnitzer *et al*., 2009). Adult dragonflies are affected by the vegetation structure of the riparian zone for provision of perches and shade (Corbet, 1999; Clausnitzer *et al*., 2009), and by the quality of the surrounding habitat for hunting and dispersing, with many species spending much of their time away from streams and high in the canopy (Orr, 2006). Females make choices about where to lay their eggs according to habitat features such as water speed, dimensions of the water body and presence of aquatic vegetation (Corbet, 1999; Cordoba-Aguiler, 2008), and changes in these features may therefore also change dragonfly breeding behaviour and success. This sensitivity to conditions across both terrestrial and freshwater habitats means that dragonflies can be good indicators of habitat disturbance, with changes in assemblages and abundance giving information about habitat quality and, potentially, the status of a range of other taxa that are more difficult to sample (e.g. Chovanec & Waringer, 2001; Oppel, 2005; Simaika & Samways, 2009; Kutcher & Bried, 2014; Golfieri *et al.*, 2016).

Maintaining forested riparian buffer strips by the side of waterways has widely been suggested as a conservation strategy in agricultural areas. Riparian buffers help to regulate aquatic systems through control of water inputs, filtering out pollutants, stabilising banks, maintaining shade and inputs of organic matter, as well as by providing forested terrestrial habitat for a wide range of species (e.g. Naiman, Decamps & Pollock, 1993; Osborne & Kovacic, 1993; Machtans, Villard & Hannon, 1996). Riparian buffer strips are specifically listed in Principle 4 ('Use of appropriate best practices by growers and millers') of the sustainability Principles and Criteria of the Roundtable on Sustainable Palm Oil (RSPO) [Roundtable on Sustainable Palm Oil (RSPO) 2013], and Sabah law stipulates that all permanent water courses over 3 m wide should have 20 m wide riparian buffer strips (Sabah Water Resources Enactment 1998). Research has shown that forested riparian buffer strips in pasture help conserve stream macroinvertebrate and fish communities (Lorion & Kennedy, 2009a,b), while buffer strips in oil palm can increase fish (Giam *et al.*, 2015) and ant and dung beetle diversity (Gray *et al.*, 2014, 2015). However, it is uncertain how effective riparian buffers are for conserving dragonflies in oil palm plantations, particularly because their egg, larval and adult life stages may be affected by land-use change across a range of scales.

Surveys of Southeast Asian dragonfly assemblages in logged forest habitats are lacking, while assessments of species in oil palm plantations and riparian buffer strips are currently absent, despite the rapid recent expansion of these habitat types within the region. In this study, we aim to assess changes in abundance, richness and community composition of adult and larval dragonfly assemblages along a habitat disturbance gradient from pristine forest, to selectively logged forest and oil palm plantation. We also consider the role of forested riparian buffer strips in conserving assemblages of dragonflies, and discuss the potential of dragonflies as indicators in this system.

Methods

Stream sites

We surveyed 16 stream sites in Sabah, Malaysian Borneo. These were located at a mean altitude of 236 m asl ± SE 26 m, and had a mean slope across the whole catchment of 18.24° ± SE 0.81°. All sites have high annual rainfall (annual average 2883 mm at Danum Valley 1985–2012 (Walsh *et al.*, 2013), and 2455 mm at the 'Stability of Altered Forest Ecosystems' (SAFE) Project near Tawau 2012–2015 (R. P. D. Walsh, unpubl. data)), and little seasonality of climate, with drought only occurring in major El Niño Southern Oscillation years (Walsh & Newbery, 1999). Lowland dipterocarp rainforest is the natural vegetation type in the area (Marsh & Greer, 1992), and the geology is a mixture of sedimentary rocks such as sandstones, mudstones and tuff, with orthic acrisols as the main soil type (see Nainar *et al.* (2015) for more information).

Stream sites were spread across three research areas: the Danum Valley Conservation Area (117°48.75′E and 5°01′N), the Maliau Basin Conservation Area (116°54′E, 4°49′N) and the SAFE Project site in an area of the Kalabakan Forest Reserve (116°57′E to 117°42′E, 4°38′N to 4°46′N) (Fig. 1). The SAFE Project is a long-term, large-scale experimental project that is investigating the impacts of forest clearance, fragmentation and conversion of forest to oil palm on tropical ecosystems (see Ewers *et al.* (2011) for more information). At the time of our study, clearance had not yet been completed at the SAFE site, but the area still comprised a mixture of land-use types, typical of those in the wider region (Reynolds *et al.*, 2011). Our stream sites included:

1. Four streams within old growth lowland dipterocarp forest (old growth, OG). Two of these streams (OG-West and OG-Rhinopool) have never been logged, one stream (OG-Maliau) had been very lightly logged and one stream (OG-VJR) was within a Virgin Jungle Reserve and had suffered limited illegal logging (Ewers *et al.*, 2011) (Fig. 1). Although some logging had occurred at both the OG-Maliau and OG-VJR sites, this did not approach the extent of commercial selective logging that occurs in the region, and tree cover has been found to be similar to that in nearby undisturbed sites (data from Maliau, Tangki, 2014).

2. Seven stream sites within selectively logged forest (logged forest, LF) of different qualities. These sites were located in an area of continuous forest that had been selectively logged during the 1970s, with approximately 113 m^3 of timber removed per hectare, followed by multiple further rounds of logging between the late 1990s and early 2000s that removed another 66 m^3 ha^{-1} (LF-1, LF-2, LF-3, LF-4, LF-5 and LF-6), although in the case of one stream catchment (LF-7), there was only a single harvest of 37 m^3 ha^{-1} in this second time period (Fisher *et al.*, 2011; Struebig *et al.*, 2013; Pfeifer *et al.*, 2015).

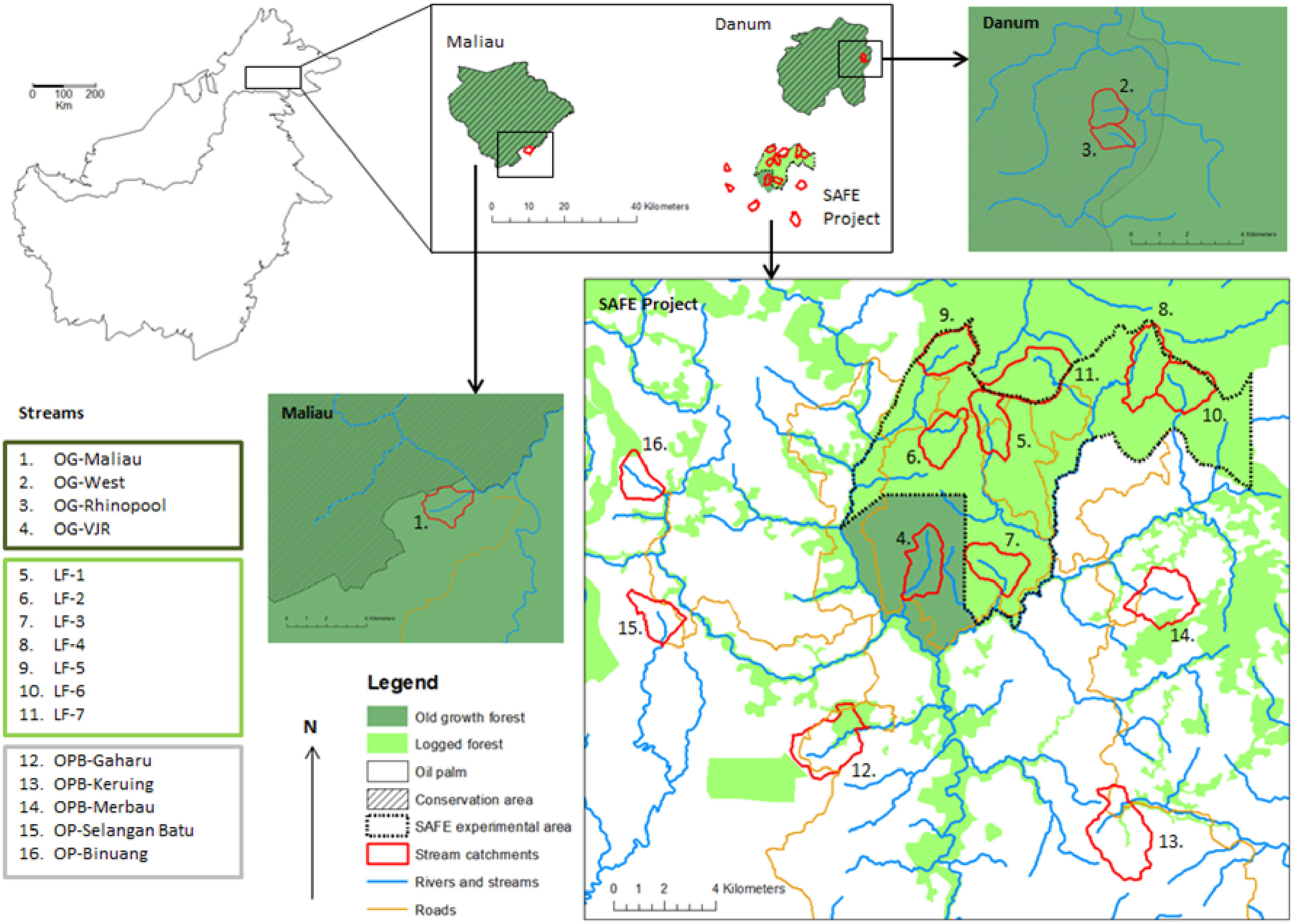

Fig. 1 Schematic and map showing the location of the 16 stream sites used in our study within Sabah, Malaysian Borneo. [Colour figure can be viewed at wileyonlinelibrary.com]

3. Three streams in oil palm plantations that had forested riparian buffer strips (oil palm with buffer, OPB). These streams were within areas of mature oil palm (planted 1999–2009) (Fig. 1), and varied in the amount of riparian vegetation and forest cover remaining within the wider catchment. OPB-Gaharu had the widest riparian buffer strip (mean *c.* 331 m, minimum *c.* 75 m on each side of the stream), OPB-Keruing had a medium width buffer (mean *c.* 68 m, minimum *c.* 33 m on each side of the stream), while OPB-Merbau had the narrowest buffer strip (mean *c.* 26 m, minimum *c.* 2 m on each side of the stream).

4. Two streams in oil palm plantations without any buffer strips (oil palm no buffer, OP). These streams (OP-Binuang and OP-Selangan Batu) were located in the same area as the oil palm buffer streams listed in (3) but had no forest remaining along their banks (Fig. 1).

Streams were distributed unequally across the four major habitat types (old growth forest, OG; logged forest, LF; oil palm with buffer, OPB; oil palm no buffer, OP) because we expected there to be greater habitat heterogeneity within the logged forest sites and we wanted to ensure that we surveyed the full habitat disturbance gradient. We therefore conducted analyses using continuous measurements of forest quality in addition to discussing differences between the four major habitat types.

In each stream, we started survey work at matched points that were approximately 2 km downstream of the stream source, with an upstream catchment size of 3.16 $km^2 \pm$ SE 0.31 km^2. We refer to these survey start points as the '0 m point' in each stream.

Forest quality

We measured riparian forest quality at 50 m intervals, for 500 m upstream of the '0 m point'. We measured canopy openness using a spherical densiometer (Lemmon, 1956), and tree density using a handheld relascope (Bitterlich, 1984). Vine cover and forest quality score [on the SAFE Project forest quality scale (Ewers *et al.*, 2011; Pfeifer *et al.*, 2015)] were assessed visually. We took measurements once at each site during June–December 2011–2013, again at all sites (except OG-Rhinopool and OG-West) during May–August 2014 and then averaged all values to give one value for each variable for each stream. We assessed forest quality across the whole of each stream catchment using maps of above-ground living biomass (AGB, t ha^{-1}), leaf area index (LAI, defined as leaf area per ground area) and percentage forest cover (FCover). These maps were developed by Pfeifer *et al.* (2016) using RapidEye^{TM} satellite images and ground measurements of forest quality. We used the library 'raster' (Hijmans, 2014) in R statistical software (R Core Team 2014) to clip the AGB, LAI and FCover forest maps to the shape of each catchment and then calculated the mean value (meanAGB, meanLAI and meanFCover) for each. For full details, please refer to Appendix S1.

Stream environmental conditions

Measurements were taken once at each stream during non-flood conditions, and included assessments of water chemistry, stream structure and habitat complexity. Water measurements included: point measurements of temperature, pH and conductivity, along with assessment of nitrate-N and phosphorous concentration within water samples. Stream structure and habitat complexity assessments included: point measurements of canopy openness in the middle of the stream, channel width and wetted width of the stream, maximum water depth and maximum water flow speed. We assessed percentage cover of different sediment sizes using a 5-point scale. We collected leaf material retained within the stream, oven-dried and then weighed it to determine levels of available leaf litter. We assessed percentage cover of dead wood, rapids, riffles and pools within 10 m transects along the stream. For all subsequent analyses, we used mean values for each environmental variable for each stream. For full details, please refer to Appendix S1.

Odonata sampling

We caught adult dragonflies using butterfly nets (Watkins and Doncaster, Leominster, http://www.watdon.co.uk/, 40 cm fourfold net, with white bag). Starting from the '0 m point', and travelling upstream, two people walked a 200 m transect during hot, sunny weather, between 10 am and 2 pm. We searched the stream and vegetation overhanging the stream, and we looked out for dragonflies in flight over the water. Once all dragonflies spotted in a location had been caught, we moved on. We re-surveyed the same transect between three and five times at each stream during 2012 and 2013, apart from at OG-West and OG-Rhinopool, where we conducted only two repeats of the transect at each, all during 2013. Sampling fell into three distinct collection periods (Time Block 1: April–August 2012; Time Block 2: November–December 2012; Time Block 3: April–June 2013).

We collected dragonfly larvae from stream bottom sediments using a Surber sampler (quadrat area 0.33 m^2, with 250 μm mesh net). Along the same 200 m transect used for adult dragonfly surveys, we sampled every 20 m, starting at 20 m. This gave a total of 10 samples per stream, apart from in OG-Rhinopool where only five samples were collected, and in OG-West, OPB-Gaharu, OPB-Keruing and OP-Selangan Batu where only nine samples were collected. At each sampling point, we placed the sampler at three randomly chosen points across the width of the stream bed. Two people then disturbed the sediment for 3 min at each point and flushed the net contents from all three points into white plastic trays. Dragonfly larvae were removed and stored for later identification in the laboratory. Sampling was conducted in non-flood conditions at multiple time points during 2012 and 2013.

We identified adult dragonflies and larvae using a light microscope and with reference to keys and literature for the region (e.g. Orr, 2003, 2005; Yule & Yong, 2004). We were able to identify adult dragonflies to species in most cases, and the larvae to genus or morphogenus. Individuals which we could not identify reliably are excluded from species/genus counts but included in overall abundance analyses. In the case of damaged larvae specimens, we counted the number of whole individuals and the number of halves and estimated overall abundance by summing the wholes, half of the halves and then rounding up to the nearest whole individual.

Statistical methods

Software used. We conducted statistical analyses using the R statistical package version 3.0.2 (R Core Team 2014). Unless stated otherwise, graphs were plotted using library 'ggplot2' (Wickham, 2009 with reference to Chang, 2013). The Borneo inset map in Fig. 1 was drawn using library 'maps' (Becker & Wilks, 2015). All other maps were drawn using ArcMap 10.2.1 GIS software [Environmental Systems Research Institute (ESRI) 2014)] using map layers developed from Landsat imagery (Ewers *et al.*, 2011), local maps and information from maps in Douglas *et al.* (1992) and Hansen *et al.* (2013).

Forest and stream quality. We used principal component analysis (PCA) to summarise variation in forest and stream quality across streams. We ran separate analyses for riparian forest quality, catchment forest quality and stream environmental variables, including the mean values from each stream in each case. We then used the principal components that summarised the largest portions of variation as summary metrics of riparian forest quality, catchment forest quality and stream conditions in further analyses.

Adult dragonfly abundance, diversity and community composition. We used the 'iNEXT' package (Chao *et al.*, 2014; Hsieh, Ma & Chao, 2014) to plot individual-based species accumulation curves for adult dragonflies in each of the broad habitat types (old growth forest, OG; logged forest, LF; oil palm with buffer, OPB and oil palm without buffer, OP) to assess the completeness of our sampling across streams.

To assess the relationship between forest quality and stream environmental conditions and adult dragonfly abundance, we ran negative binomial generalised linear mixed models (glmer.nb) in the package 'lme4' (Bates *et al.*, 2015). We used total abundance per transect, abundance of Anisoptera and abundance of Zygoptera as response variables, and environmental principal components as predictors and tested each combination singly. Stream and the collection time period (TimeBlock) were included as random effects (because group variance of Stream was 0.3345, and TimeBlock was 0.1768), and so the models took the form: Abundance per transect~Environmental principal component+(1|Stream)+(1|TimeBlock). We ran generalised linear mixed models (glmer) with Poisson family errors to assess the relationship between environmental conditions and adult dragonfly species richness, adult Anisoptera species richness and adult Zygoptera species richness. Models took the form: Species richness per transect~Environmental principal component+(1|Stream)+(1|TimeBlock). In all cases, models were checked for overdispersion and residuals were checked for homoscedasticity and normality. Model significance was assessed and *P*-values generated using log-likelihood ratio comparisons with null models.

We carried out canonical correspondence analysis (CCA) using the package 'vegan' (Oksanen *et al.*, 2014) to assess whether there were significant differences in community composition (in terms of presence and relative abundance of species) in relation to environmental conditions. We included all environmental variables (Catchment PC1, Riparian PC1, Stream PC1, Stream PC2) in the model, and used 999 random permutations to generate *P*-values to assess the significance of each variable. Results were plotted on ordination biplot diagrams to show the relationship between environmental variables, sites and species composition.

Dragonfly larvae abundance, diversity and community composition. As with adult dragonflies, we generated genus-level accumulation curves for dragonfly larvae in each of the broad habitat types to assess sample completeness using the 'iNEXT' package (Chao *et al.*, 2014; Hsieh *et al.*, 2014), and ran negative binomial generalised linear mixed models (glmer.nb) to compare larvae abundance per point and environmental conditions (Abundance per point~Environmental principal component+(1|Stream). It was not possible to test for differences in Anisoptera and Zygoptera separately because sample sizes were too low. For assessing the relationship between genus richness and environmental conditions, we used generalised linear mixed models (glmer) with a Poisson error structure. These were a better fit for the data than negative binomial models, but the model formula remained similar: Genus richness per point~Environmental principal component+(1|Stream). We used the same CCA analysis as described above to investigate trends in larvae genus-level community composition in relation to environmental conditions.

Results

Forest and stream quality

Principal component analysis summarised environmental variables into four key components: Riparian forest quality PC1 (Riparian PC1), Catchment forest quality PC1 (Catchment PC1), Stream PC1 and Stream PC2. Riparian PC1 explained 77.6% of the variation in measurements of riparian forest quality and Catchment PC1 explained 92.05% of the variation in measurements in catchment-scale forest quality across streams. Stream PC1 summarised 33.9% of the variation in stream variables, while Stream PC2 summarised a further 16.1%. For full details, please refer to Appendix S2, Figure S1, Tables 1 and 2.

Adult dragonfly abundance, diversity and community composition

Across our 16 stream sites, we caught 1650 individual adult dragonflies from 13 different families, and 49

Table 1 Loading scores showing how original forest quality variables correspond to the principal component summary variables (Catchment and Riparian PC1, PC2 and PC3) produced by the PCA, along with the variance in the original variables that is summarised by each component (note that all riparian loadings are multiplied by −1 to make them more readily interpretable).

	Principal components		
Riparian forest quality variables	Riparian PC1	Riparian PC2	Riparian PC3
Percentage cover vines	0.3970	−0.8339	0.3288
SAFE forest quality score	0.5538	0.1802	0.2517
Relascope tree density	0.5014	0.5188	0.3536
Canopy cover	0.5332	−0.0541	0.8388
Standard deviation	1.7620	0.8412	0.4050
Proportion of variance	0.7760	0.1769	0.0410
Cumulative proportion of variance	0.7760	0.9529	0.9939
Catchment forest quality variables	Catchment PC1	Catchment PC2	Catchment PC3
Above-ground biomass (AGB)	0.5527	0.8228	−0.1327
Forest cover (FCover)	0.5951	−0.2781	0.7540
Leaf area index (LAI)	0.5835	−0.4957	−0.6433
Standard deviation	1.6618	0.4806	0.0864
Proportion of variance	0.9205	0.0770	0.0025
Cumulative proportion of variance	0.9205	0.9975	1.0000

Table 2 Loadings of each stream variable onto first two principal components, Stream PC1 and Stream PC2. Scores >0.20, and therefore showing a high degree of association with that PCA axis, are shown in bold.

	Principal components	
Stream environmental variables	Stream PC1	Stream PC2
Leaves weight	**0.2135**	−0.1234
Water temperature	−0.1539	**0.2350**
pH	0.1214	0.1151
Conductivity	0.1190	0.1279
Flow average (time taken for ball to travel 2 m)	−0.0245	**−0.3565**
Canopy average	**−0.2733**	0.1190
Total width	**0.2514**	−0.0708
Wetted width	**0.2376**	−0.1990
Max depth	**0.2754**	−0.1570
% sediment bedrock	**0.2953**	0.0441
% sediment large rocks	**0.2429**	−0.0654
% sediment small rocks	−0.0592	**0.2019**
% sediment pebbles	−0.1415	−0.1338
% sediment sand	**−0.2456**	−0.0112
Nitrate	**−0.2572**	−0.1306
Phosphate	**0.2576**	0.1599
% of 10 m that was rock	**0.3091**	0.1893
% of 10 m that was pebbles	−0.1360	**−0.3515**
% of 10 m that was sand	−0.1673	0.1184
% of 10 m that was dead wood	0.0971	−0.0073
% of 10 m that was rapids	0.1131	**0.3580**
% of 10 m that was riffles	−0.1927	**0.2628**
% of 10 m that was connected pools	−0.0929	−0.4391
% of 10 m that was isolated pools	**0.2416**	−0.1354
Standard deviation	2.8506	1.9680
Proportion of variance	0.3386	0.1614
Cumulative proportion	0.3386	0.5000

different species. Twenty-two of these species are endemic to Borneo, and two are listed as 'Near Threatened' on the IUCN Red List, although based on a comprehensive dataset (literature and collections) for Borneo, many species would be Data Deficient if assessed today (R. A. Dow, pers. comm.). During the course of our work, we discovered a new species – *Phaenandrogomphus safei* (see Dow & Luke, 2015 for taxonomic description) at a logged forest site – and found several new records for Sabah across logged forest and oil palm sites: *Heliogomphus cf. blandulus, Macromia westwoodi* and *Onychothemis culminicola*. A list of families, species and their abundances within each of the major habitat types is shown in Table S1, while a summary of captures is given in Table 3.

There were no significant relationships between catchment and riparian forest quality, or stream conditions and total abundance of adult dragonflies per transect, but there were significantly more Anisoptera in low quality streams (low Stream PC1, Catchment PC1 and Riparian PC1 values) (Fig. 2). Abundance of adult Anisoptera was therefore significantly higher in more disturbed habitats with more individuals found in oil palm streams than in logged forest and old growth forest (Fig. 2). In contrast, there were no significant differences in Zygoptera abundance along the disturbance gradient.

The species accumulation curves for adult dragonflies in each of the habitats show levelling-off, suggesting that we sampled a substantial proportion of the species present in the area (Fig. 3). There were no significant trends in overall dragonfly species richness per transect in relation to forest quality or stream condition. However, Anisoptera species richness was significantly negatively correlated with Stream PC1, Catchment PC1 and Riparian PC1, with higher species richness in more disturbed forest and oil palm stream sites (Fig. 2). In contrast, Zygoptera species richness was significantly positively correlated with forest quality. Zygoptera richness was significantly higher in streams with high forest quality catchments (high Catchment PC1 scores) (Fig. 2), but they did not show a significant correlation with habitat quality at the riparian or stream scale (Riparian PC1 and Stream PC1).

Table 3 Summary abundance and species richness values of adult and larval dragonflies across the four major habitat types: oil palm no buffer (OP), oil palm with buffer (OPB), logged forest (LF) and old growth forest (OG). For adult dragonflies, number of 200 m transects (*n*) in each habitat is listed in the heading, while number of sampling points (*n*) is listed for larval dragonflies.

Adult dragonflies	Family	Oil palm no buffer (OP) *n* = 6	Oil palm with buffer (OPB) *n* = 13	Logged forest (LF) *n* = 32	Old growth forest (OG) *n* = 13
Adult dragonfly abundance per transect		20.67	23.92	18.91	47.38
Adult dragonfly species richness per transect		2.33	1.38	0.91	2.31
Adult Zygoptera abundance per transect	Platystictidae	0	0	0.44 (1 species)	0.46 (3 species)
	Calopterygidae	0	3.15 (3 species)	3.41 (3 species)	7.15 (5 species)
	Chlorocyphidae	2.5 (3 species)	4.77 (4 species)	1.41 (5 species)	6.23 (4 species)
	Devadattidae	0	0	0.19 (1 species)	0.46 (1 species)
	Euphaeidae	0	4.85 (1 species)	10.63 (1 species)	28.92 (4 species)
	Philosinidae	0	0	0	2.46 (1 species)
	Platycnemididae	1.50 (1 species)	3.77 (1 species)	0.50 (5 species)	0.69 (4 species)
	Coenagrionidae	8.5 (3 species)	1.85 (1 species)	0.31 (1 species)	0.15 (1 species)
Adult Anisoptera abundance per transect	Aeshnidae	0	0	0	0.08 (1 species)
	Gomphidae	0	0.08 (1 species)	0.09 (3 species)	0.08 (1 species)
	Macromiidae	0	0	0.03 (1 species)	0
	Synthemistidae	0	0.08 (1 species)	0	0.08 (1 species)
	Libellulidae	8.17 (7 species)	3.31 (6 species)	1.63 (8 species)	0.62 (4 species)

Larval dragonflies	Family	Oil palm no buffer (OP) *n* = 19	Oil palm with buffer (OPB) *n* = 28	Logged forest (LF) *n* = 70	Old growth forest (OG) *n* = 34
Larval dragonfly abundance per point		0.37	0.11	0.90	3.53
Larval dragonfly genus richness per point		0.16	0.11	0.19	0.38
Larval Zygoptera abundance per point	Calopterygidae	0	0	0.01 (1 genus)	0.06 (1 genus)
	Chlorocyphidae	0	0	0	0.09 (1 genus)
	Euphaeidae	0	0.04 (1 genus)	0.43 (1 genus)	1.24 (1 genus)
	Lestidae	0	0	0	0.03 (1 genus)
	Philosinidae	0	0	0.01 (1 genus)	0.03 (1 genus)
	Platystictidae	0	0.04 (1 genus)	0.03 (1 genus)	1.12 (1 genus)
Larval Anisoptera abundance per point	Chlorogomphidae	0	0	0.04 (1 genus)	0
	Gomphidae	0	0	0.34 (7 genera)	0.85 (5 genera)
	Libellulidae	0.21 (2 genera)	0	0.03 (1 genus)	0
	Macromiidae	0.16 (1 genus)	0.04 (1 genus)	0	0.12 (2 genera)

There were significant differences in community composition of adult dragonflies in relation to environmental conditions (Fig. 4). Species-level dragonfly community composition varied significantly with stream condition (Stream PC1), and in relation to riparian forest quality (Riparian PC1) (Fig. 4a). The CCA ordination shows that the unbuffered oil palm (OP) sites and two of the three buffered oil palm (OPB) sites differed substantially from the logged forest (LF) and old growth forest (OG) sites in terms of environmental conditions and adult dragonfly assemblages (Fig. 4b). The only oil palm site that appeared similar to forest sites is OPB-Gaharu, which had a very wide riparian buffer strip (mean *c*. 331 m and minimum *c*. 75 m on each side of the stream) (Fig. 4b). Only a relatively small number of species were associated with oil palm sites, while many more species were associated with forested sites (Table 3; Fig. 4).

Dragonfly larvae abundance, diversity and community composition

We caught 195 dragonfly larvae across 21 different genera/morphogenera, and 10 different families (Tables 3 and S2). There were several dragonfly families and genera for which we found larvae and no adults, and *vice versa*. The correlation between number of larvae and adults caught across the different families was poor (Spearman rank correlation = 0.18, $n = 14$, $P = 0.5357$). Many more Gomphidae, Platystictidae and Macromiidae larvae were caught than adults, while for all other

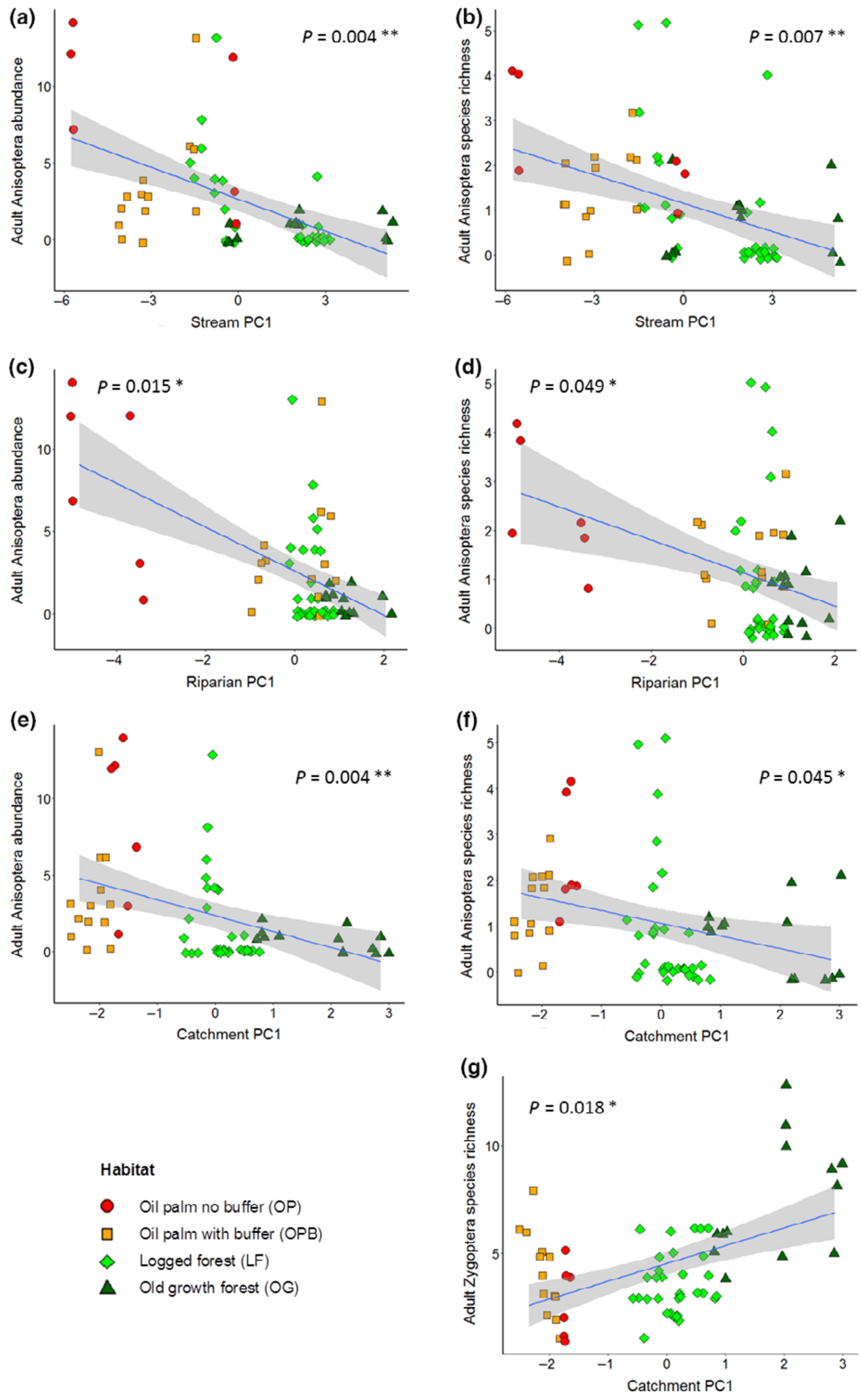

Fig. 2 Relationship between Stream PC1 and adult Anisoptera abundance (a) and adult Anisoptera species richness (b); between Riparian PC1 and adult Anisoptera abundance (c) and adult Anisoptera species richness (d); and between Catchment PC1 and adult Anisoptera abundance (e), adult Anisoptera species richness (f) and adult Zygoptera species richness (g). Each point represents one 200 m transect, and abundance and richness measures are per transect. Points have different shapes according to the broad habitat type of the stream: circle = oil palm no buffer (OP); square = oil palm with buffer (OPB); diamond = logged forest (LF); triangle = old growth forest (OG), as shown in the legend within the figure. Lines indicate the lm model fit ±95% confidence interval. *P*-values show results of log-likelihood ratio test comparison of mixed-effect models with null models. For *P*-values, $*P < 0.05$, $**P < 0.01$. [Colour figure can be viewed at wileyonlinelibrary.com]

families, many more adults were caught than larvae (Figure S2).

The individual-based accumulation curves for genera appear to be levelling-off, suggesting that we caught a substantial portion of the genera present across the area (Fig. 3). Very few larvae were found in oil palm sites, including the oil palm sites that had riparian buffer strips. We found significantly higher abundance and genus richness of dragonfly larvae in streams with higher surrounding catchment forest quality (higher Catchment PC1) (Fig. 5). The relationships between stream quality (Stream PC1), water speed (Stream PC2) and both larval abundance and richness were not significant. There were no significant trends in abundance and richness in relation to riparian-scale forest quality (Riparian PC1).

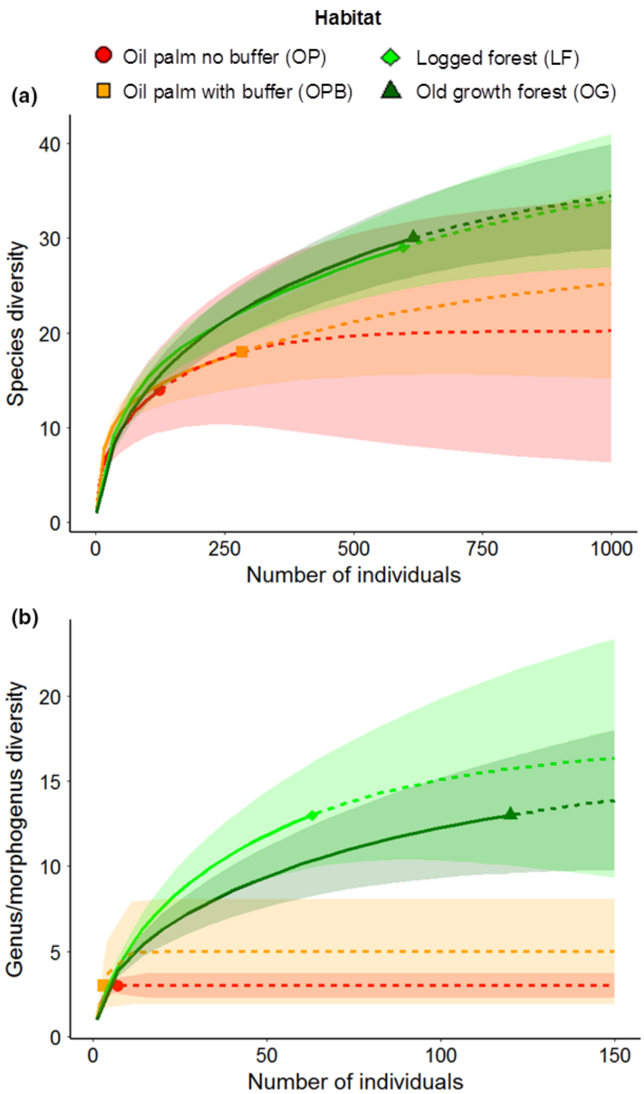

Fig. 3 Accumulation curves of the number of (a) species of adult dragonflies, and (b) genera of dragonfly larvae, found in relation to individuals sampled. Each line represents all streams within each of the broad habitat types combined, and is marked with a shaped symbol: circle = oil palm no buffer (OP); square = oil palm with buffer (OPB); diamond = logged forest (LF); triangle = old growth forest (OG). Solid lines represent interpolation from the samples actually collected, while dotted lines represent extrapolation. [Colour figure can be viewed at wileyonlinelibrary.com]

Dragonfly larvae genus-level community composition varied significantly with stream quality (Stream PC1) and near-significantly with catchment-scale forest quality (Catchment PC1) (Fig. 6a). As with adult dragonflies, the CCA biplot for larvae (Fig. 6b) shows that logged forest sites, old growth forest sites and the OPB-Gaharu site, which had a wide oil palm buffer, were associated with high catchment forest quality and stream quality (high Catchment PC1 and high Stream PC1) values and the occurrence of many of the larvae genera. The OP-Binuang oil palm site with no buffer, and the OPB-Merbau site with just a narrow buffer are spaced further away on the biplot, with only three larval genera associated with them – Libellulidae *Trithemis*, Libellulidae Unknown and Macromiidae *Macromia* (Fig. 6b). Two of the oil palm sites do not appear on the biplot because no larvae were found at these sites. The number of different genera found was substantially higher in forested sites (Table 3; Fig. 6c; Table S2).

Discussion

This study is the first to consider the impacts of oil palm plantations on dragonfly assemblages, and one of just a few that assesses the community composition of dragonflies across comparable stream sites in a range of land-use types in Southeast Asia. We found a rich and diverse assemblage comprising a wide range of families and endemic species, many of which were confined to forested sites. Although the overall abundance and total richness of adult dragonflies did not decline significantly with habitat disturbance, there was a significant change in community composition which included an increasing dominance of Anisoptera compared to Zygoptera with greater habitat disturbance. Many of the endemic species appear largely limited to forested habitats and were not found at oil palm sites. Unlike adults, dragonfly larvae showed significant declines in abundance and richness with increasing catchment disturbance, and significant changes in community composition in relation to stream environmental conditions. Larvae were almost completely absent from oil palm sites both with and without buffer strips.

Substantial changes in community composition along the habitat gradient, despite there being no change in the overall abundance or richness of adult dragonflies, indicates that there is species replacement within adult dragonfly assemblages as a result of land-use change and disturbance. Many of the species endemic to Borneo were present or abundant only in forest sites, and were absent from oil palm. For nearly all of its history Borneo has been forested: its dragonfly fauna, in particular the endemics, is therefore adapted to forest conditions (Orr, 2006). Many adult dragonflies may require forest for hunting, and it is known that many gomphids and females of other families spend much of their time in the canopy (Orr, 2006). There may also be species which depend on low overhanging vegetation beside waterways, or narrow twigs and branches for perches – structures which are largely absent in homogenous oil palm plantations. Additionally, degree of shading by vegetation has been recognised as a key factor affecting dragonfly

(a)

Predictor	Chi-square	F	p-value
Stream PC1	0.21553	2.6840	0.001 ***
Stream PC2	0.06895	0.8586	0.128
Catchment PC1	0.22573	2.8110	0.192
Riparian PC1	0.22541	2.8071	0.040 *

(b)

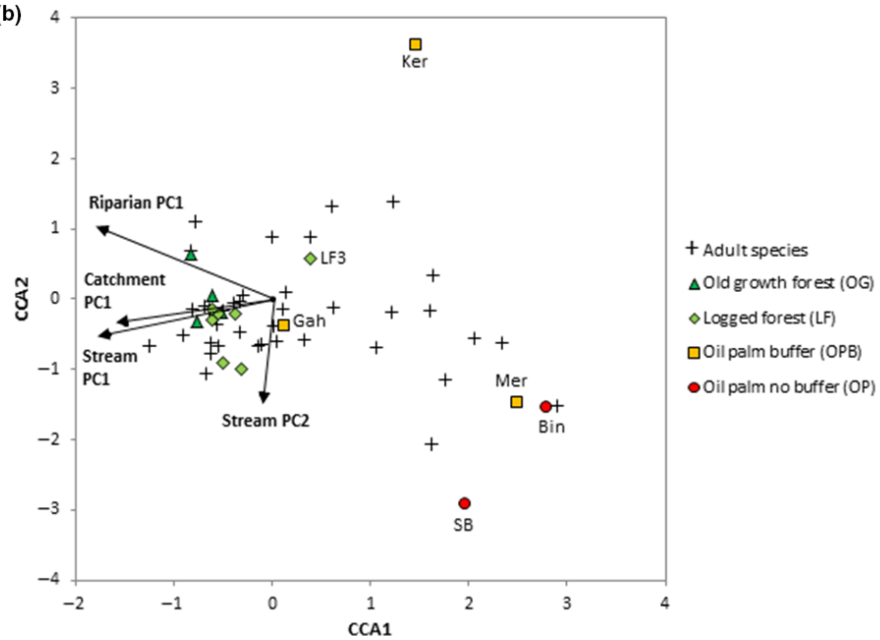

Fig. 4 Results of canonical correspondence analysis (CCA) to assess the relationship between environmental predictors (Stream PC1, Stream PC2, Catchment PC1 and Riparian PC1) and adult dragonfly species-level community composition across our 16 stream sites. *P*-values were generated by 999 random permutations. Streams are shown by different shapes according to broad habitat grouping [triangle = old growth forest (OG); diamond = logged forest (LF); square = oil palm with buffer (OPB); circle = oil palm no buffer (OP)] and the dragonfly species are shown as crosses. The closer stream and dragonfly points are on the diagram, the greater the likelihood of a species occurring at that site. For clarity of viewing, species names are omitted from the diagram. Site abbreviations Gah = OP-Gaharu; Ker = OPB-Keruing; Mer = OPB-Merbau; Bin = OP-Binuang; SB = OP-Selangan Batu. Environmental variables are shown by arrows. The direction shows the direction of increase in that variable, i.e. higher scores at the tip of each arrow. [Colour figure can be viewed at wileyonlinelibrary.com]

assemblages (Oppel, 2005). Many small stream species (particularly small-bodied Zygoptera) may be adapted to the relatively cool and near-constant temperatures of the forest understorey, and may be unable to thermoregulate effectively in streams in hot open areas that proliferate in degraded forest and oil palm sites (Data from the same site from Hardwick *et al*., 2015: Maximum temperature: old growth forest = 25 °C *cf.* oil palm = 30.5 °C; Daily temperature range: old growth forest = 4 °C *cf.* oil palm = 9 °C). Temperature-sensitive species could potentially be out-competed by larger gap-loving species if forest is cleared (De Marco Júnior, Batista & Cabette, 2015). Many of the species that were present in oil palm sites were large-bodied, sun-loving, cosmopolitan Anisoptera, including many within the Libellulidae family. It is thought that these would have originally been rare in forested areas, and relied on their long-distance dispersal abilities to travel between the few forest gaps available (Orr, 2006), but it may be that they are now expanding their range into open oil palm ecosystems and replacing forest-specialist species. Similar patterns of increased Anisoptera dominance have been found in disturbed forest sites in Kalimantan (Dolný *et al*., 2011, 2012), park and city habitats in South Africa (Samways & Steytler, 1996), and intermediate and degraded forest sites in Amazonia (Monteiro-Júnior *et al*., 2014).

Changes in the dragonfly fauna in disturbed sites are seen even more clearly in the larvae. Larval richness and abundance declined significantly in relation to forest disturbance at the catchment-scale, with only nine individuals from across just a few genera (*Euphaea, Rhinagrion, Macromia, Trithemis* and another unknown Libellulidae) found in oil palm streams, and no larvae at all in two out of the five oil palm streams. The drop in larval numbers in relation to disturbance may be because adults are choosing not to oviposit in the most disturbed, oil palm stream sites, perhaps because of an increase in abundance of open habitat species that use other standing or slow-flowing water nearby for reproduction (e.g. *Orthetrum* spp., *Trithemis aurora, Neurothemis ramburii* and *Pantala flavescens*). Alternatively, numbers may be low because females of species that lay eggs in streams may be assessing the stream conditions at disturbed sites and choosing not to oviposit. This could be because key features such as water speed and presence of vegetation (Corbet, 1999; Cordoba-Aguiler, 2008) have changed or been lost. Alternatively it could be that dragonfly eggs are being laid in oil-palm streams, but that eggs and larvae have lower survival rates. Air temperatures in oil palm are hotter than in forest (Hardwick *et al*., 2015) and Odonata eggs and larvae can be sensitive to high temperatures (e.g.

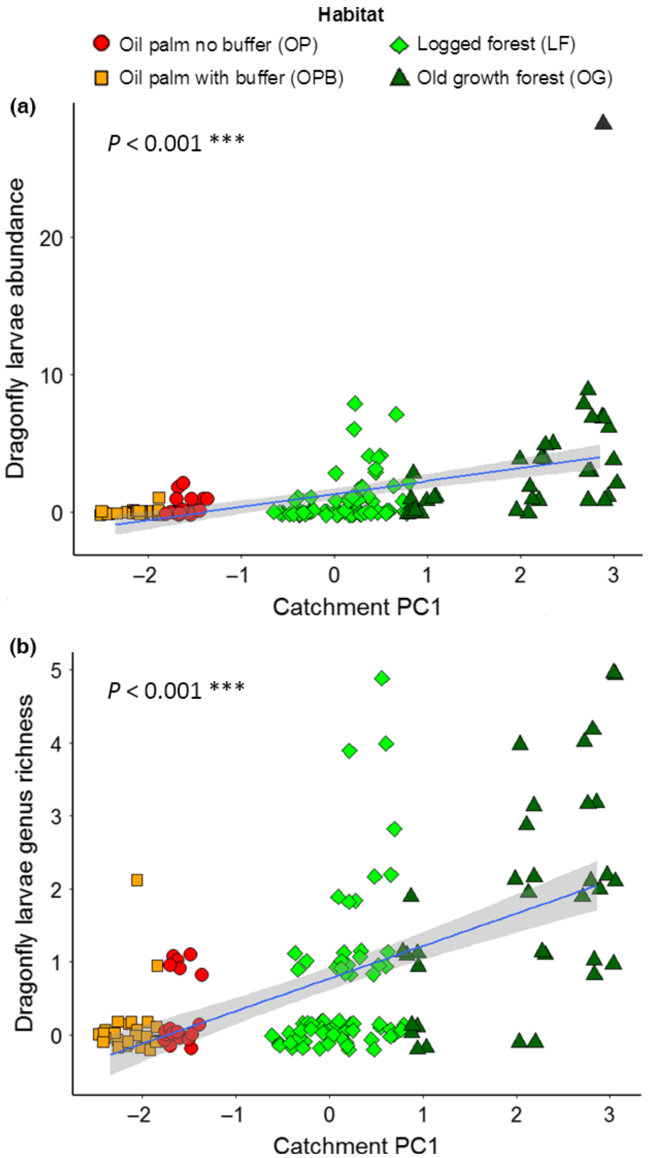

Fig. 5 Relationship between catchment forest quality (Catchment PC1) and (a) abundance, and (b) genus richness of dragonfly larvae per sampling point. Points have different shapes according to the broad habitat type of the stream: circle = oil palm no buffer (OP); square = oil palm with buffer (OPB); diamond = logged forest (LF); triangle = old growth forest (OG). Lines indicate the lm model fit ±95% confidence interval. *P*-values show results of log-likelihood ratio test comparison of mixed-effect models with null models. For *P*-values, ***$P < 0.001$. [Colour figure can be viewed at wileyonline library.com]

Corbet, 1999; Clausnitzer *et al*., 2009), potentially causing low survival.

Although adults and larvae showed broadly similar changes in abundance and community composition with habitat disturbance, we found a very different subset of the community in each case. Some families (e.g. Calopterygidae and Chlorocyphidae) were much more strongly represented in our adult surveys than in the larvae surveys, while others (e.g. Gomphidae, Platystictidae and Macromiidae) appeared mostly in larval samples. This is likely to represent differences in ease of capture of the adults, and relates to behaviour such as differences in perching and territory guarding; extent to which adults are using the stream for foraging or mate finding as well as for oviposition; and differences in egg-laying behaviour. Some species may rarely visit a stream except for oviposition, or be very inconspicuous and well hidden, resulting in the larvae being more numerous in our samples. It is known that Gomphidae, in particular, seldom visit streams except to oviposit, and spend much of their time foraging in the canopy, making adult catches rare (Orr, 2006). In addition, adult dragonflies disperse freely, and so it is also likely that some of the individuals we caught were at suboptimal sites and were just passing through, whereas presence of larvae in the water is a guarantee that they are living there (Valente-Neto *et al*., 2016).

The discrepancy between adult and larvae catches shows the value of surveying both life history stages in order to give a more complete picture of the assemblage (Orr 2006; Valente-Neto *et al*. 2016). Additional surveys of exuviae would also be highly desirable to be sure that species are successfully completing their lifecycle at a site (Cordoba-Aguiler, 2008; Raebel *et al*., 2010), but it is recognised that exuviae can be challenging to survey, and so can often under-estimate richness (Cordoba-Aguiler, 2008; Bried, D'Amico & Samways, 2012). Our results offer a potentially useful starting point for developing bioindicators of stream health for the region based on adults and larvae, as we found several clearly observable and easily measured changes in dragonfly communities with habitat disturbance. As has been observed in other studies (e.g. Oppel, 2005; Dolný *et al*., 2012), the relative abundance of adult Zygoptera to Anisoptera could provide a simple indicator of the health of a waterway. Alternatively, a count of larvae could also be a means of rapid assessment. If indicators were developed, they could be used to assess the health of streams in degraded forest areas to see how heavily they have been affected by disturbance, or to measure improvement following riparian restoration of an oil palm site, for example.

Our results give useful information about the effectiveness of riparian buffer strips in oil palm plantations for mitigating impacts of forest conversion. Although the oil palm stream with the widest riparian buffer strip appeared similar to logged forest sites in terms of adult dragonfly fauna, larvae were largely absent. The oil palm sites with narrower buffers were much more

(a)

Predictor	Chi-square	*F*	*P*-value
Stream PC1	0.45778	2.9660	0.001 ***
Stream PC2	0.18949	1.2277	0.295
Catchment PC1	0.36664	2.3755	0.064
Riparian PC1	0.30979	2.0071	0.159

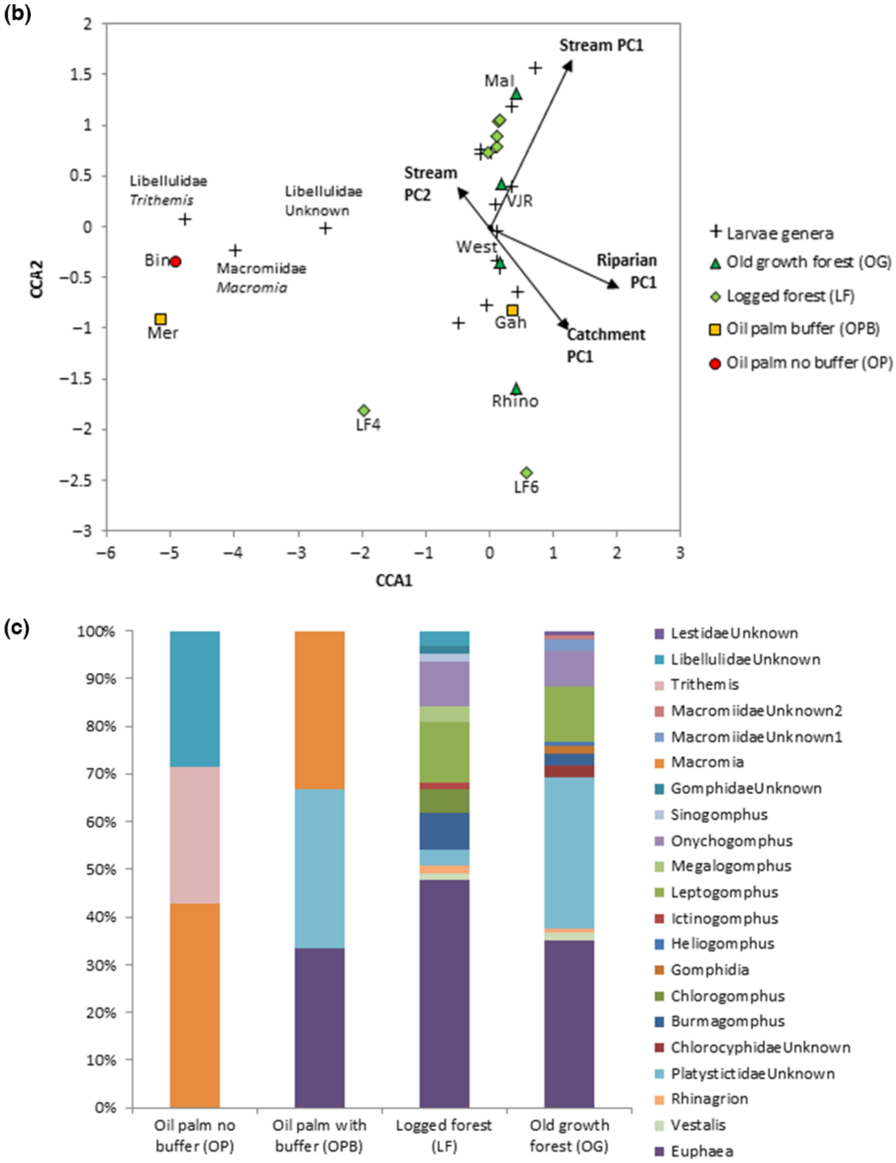

Fig. 6 (a and b) Results of canonical correspondence analysis (CCA) to assess the relationship between environmental predictors (Stream PC1, Stream PC2, Catchment PC1 and Riparian PC1) and dragonfly larvae genus-level community composition across our 16 stream sites. *P*-values were generated by 999 random permutations. Streams are shown by different shapes according to broad habitat grouping [triangle = old growth forest (OG); diamond = logged forest (LF); square = oil palm with buffer (OPB); circle = oil palm no buffer (OP)] and the dragonfly larvae genera are shown as crosses. The closer stream and dragonfly points are on the diagram, the greater the likelihood of a genus occurring at that site. For clarity of viewing, only the subset of genera that are mentioned in the main text, and a subset of stream sites are named on the diagram. Site abbreviations are: Rhino = OG-Rhino-pool; West = OG-West; VJR = OG-VJR; Mal = OG-Maliau; Gah = OP-Gaharu; Mer = OPB-Merbau; Bin = OP-Binuang. Environmental variables are shown by arrows. The direction shows the direction of increase in that variable, i.e. higher scores at the tip of each arrow. (c) shows the percentage contribution of each dragonfly larvae genus to the assemblage found in each of the major habitat types [old growth forest (OG); logged forest (LF); oil palm with buffer (OPB); oil palm no buffer (OP)]. [Colour figure can be viewed at wileyonlinelibrary.com]

similar to the non-buffered oil palm streams, suggesting that the narrow buffers (20 m) required by law in Sabah and other regions may do little to maintain forest stream-dependent dragonfly communities. A study of dung beetle communities in riparian buffer strips in Sabah also found that species richness increased with strip width (Gray *et al.*, 2014), suggesting that width of buffer may be important for maintaining populations of both aquatic and terrestrial species.

Dragonflies are a highly diverse, charismatic and a functionally important component of freshwater ecosystems in Southeast Asia, but Odonata communities appeared heavily altered in disturbed forest and oil palm plantation sites. Our study found significant declines in abundance, richness and substantial shifts in community composition of adult and larval dragonflies in relation to catchment-scale and more localised habitat disturbance, and riparian buffer strips appeared to offer only limited protection for forest stream-dependent dragonfly species in oil palm plantation. Larvae in particular were largely absent from oil palm streams. As dragonflies can often be indicators of wider ecosystem health, these changes in their assemblage could signal substantial impacts of habitat disturbance on other taxa as well. We suggest that wider scale landscape planning with inclusion of forest fragments and corridors in oil palm, should be trialled and investigated to help conserve dragonfly fauna. In addition, we encourage the development of dragonfly adult and larval indicators of habitat integrity at the within-stream, riparian and catchment-scale, to aid rapid assessment of riverine habitats and to direct targeted conservation action in the region.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details about methods.

Appendix S2. Additional details about results.

Table S1. Adult dragonfly species list.

Table S2. Larval dragonfly genera list.

Figure S1. Correlations between catchment, riparian and stream principal components.

Figure S2. Catches of adults *versus* larvae within different families.

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