



Physicochemical Properties as Driver of Odonata Diversity in Oil Palm Waterways

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Large-scale oil palm agriculture has caused deforestation in the tropics, but also degrades stream water quality and reduces aquatic biodiversity. Though the outcomes of industrial-scale oil palm plantations for biodiversity have been explored extensively, the consequences of small-scale oil palm agriculture for freshwater macroinvertebrate fauna are poorly understood. Here, we explored the impacts of small-scale oil palm agriculture on aerial adult Odonata (the dragonflies and damselflies), which, due to their inherent sensitivity to habitat degradation, represent useful indicators of wider ecosystem health. We surveyed riparian corridors of man-made waterways in natural habitats converted into agricultural lands in both peat swamp and mangrove forest, comprising a total of 60 sampling units across a region of Peninsular Malaysia where such small-scale agricultural practices are widespread. We hypothesized that physicochemical water quality of oil palm waterways together with riparian vegetation influence Odonata species richness and composition. Our results revealed that Odonata species richness increased with dissolved oxygen, water temperature and vegetation cover, but decreased with water level, pH, and total dissolved solids. Species composition was influenced by both dissolved oxygen and pH. The present study provides valuable insights into the effects of small-scale oil palm agriculture for water quality of associated aquatic habitats, and subsequent responses of adult Odonata. Therefore, smallholders should reduce the use of chemical pesticides and fertilizers to improve the conservation value of oil palm waterways for both Odonata and aquatic fauna more generally, in order to be certified as biodiversity-friendly agriculture.

Keywords: aquatic biodiversity, dragonflies, damselflies, habitat degradation, smallholdings, water quality

INTRODUCTION

Forest conversion to agricultural lands poses a major threat to biodiversity across terrestrial and aquatic ecosystems at multiple spatial scales (Mercer et al., 2014; Oliveira-Junior et al., 2015; Ghazali et al., 2016; Asmah et al., 2017). The expansion of oil palm plantations into tropical mixed-dipterocarp terra firma and fresh-water swamp forests affects terrestrial and river

ecosystems through altered hydrology and habitat availability (Luke et al., 2016, 2017). In Malaysia, agricultural land is estimated to cover 10.31 Mha of the total land area with oil palm plantation representing at least 5.74 M ha (Kushairi, 2017). These major changes of land use characteristics have contributed to different species composition from the original composition of the community (Che Salmah et al., 1998, 2014; Kadoya et al., 2009; Wong et al., 2016; Yahya et al., 2017).

Despite the loss of natural ecosystems, human-modified landscapes are still often capable of sustaining considerable biodiversity (Koch et al., 2014; Luke et al., 2016). However, the occurrence of Odonata species in tropical agricultural lands, particularly oil palm production landscapes, is currently understudied. The expansion of oil palm plantations into tropical forests alters physical and biogeochemical inputs to streams, thereby modifying hydrological function (Carlson et al., 2014). Agriculture degrades streams by increasing non-point source (NPS) pollution from agrochemical applications runoff, impacting riparian and stream channel habitat, and altering water flow and quality, with wide-ranging implications for biological communities and ecosystems (Allan, 2004; Ouyang et al., 2014; Wu and Lu, 2019). For instance, low dissolved oxygen concentrations associated with organic pollution and eutrophication can reduce the survival of many aquatic fauna (Breitburg et al., 2003; Jones et al., 2006).

The key role of dragonflies and damselflies (the Odonata) as predators and their interactions with different organisms and habitat types makes them good ecological indicators (Knight et al., 2005; Miguel et al., 2017; Brito et al., 2018). In addition, the complex life-histories of the Odonata—wherein the larval stages are aquatic and the adult stages terrestrial—makes them vulnerable to anthropogenic stressors in both ecosystem types (Samways and Steytler, 1996; Cleary et al., 2004; Ferreras-Romero et al., 2009; Kutcher and Bried, 2014). Stressors such as variation in water quality can reduce species richness of Odonata, as most taxa are confined to small forest remnants that are under threat from a myriad of human activities (Orr, 2004; Kalkman et al., 2008). Odonata density is highly dependent on the type and structure of aquatic and terrestrial vegetation for their foraging sites (Remsburg, 2011; Dolní et al., 2012; Dolný et al., 2014). Odonata fitness, however, is also associated with warming and contaminants during the aquatic larval stage with carry-over effects to adults stage (Stoks and Córdoba-Aguilar, 2012; Janssens et al., 2014). Agricultural practices on land adjacent to streams lead to soil erosion and subsequent runoff of fine sediments, nutrients, and pesticides, thus having major impacts on Odonata survival (Moore and Palmer, 2005).

Oliveira-Junior et al. (2015) suggested that agricultural activities appear to be the main factor determining changes in Odonata community composition and assemblages in the eastern Amazon, Brazil. Although Odonata are amphibiotic insects (Monteiro-Júnior et al., 2014), data from which to quantify the relationship between water quality and Odonata diversity are at present relatively scarce in the tropics. To date, only a few studies have indicated the importance of water quality for maintaining Odonata species, particularly aerial adult individuals in agricultural lands (Castillo et al., 2006; Rizo-Patrón et al.,

2013; Mercer et al., 2014; Mendes et al., 2019, 2020). Studies in aquatic ecology and/or biodiversity in oil palm production landscapes are limited to waterbirds (Sulai et al., 2015; Hawa et al., 2016), fish (Giam et al., 2015; Wilkinson et al., 2018), Anurans (Gillespie et al., 2012; Faruk et al., 2013; Gallmetzer and Schulze, 2015), and macroinvertebrates (Oppel, 2006; Mercer et al., 2014; Cunha et al., 2015). Ndaruga et al. (2004) reported that significant changes in aquatic macroinvertebrate assemblages were primarily due to water quality rather than prevailing climatic conditions. Thus, agricultural drainage can impact water quality variables that affect Odonata, either directly, or indirectly *via* reductions in the availability of their preferred food resources (Elo et al., 2015).

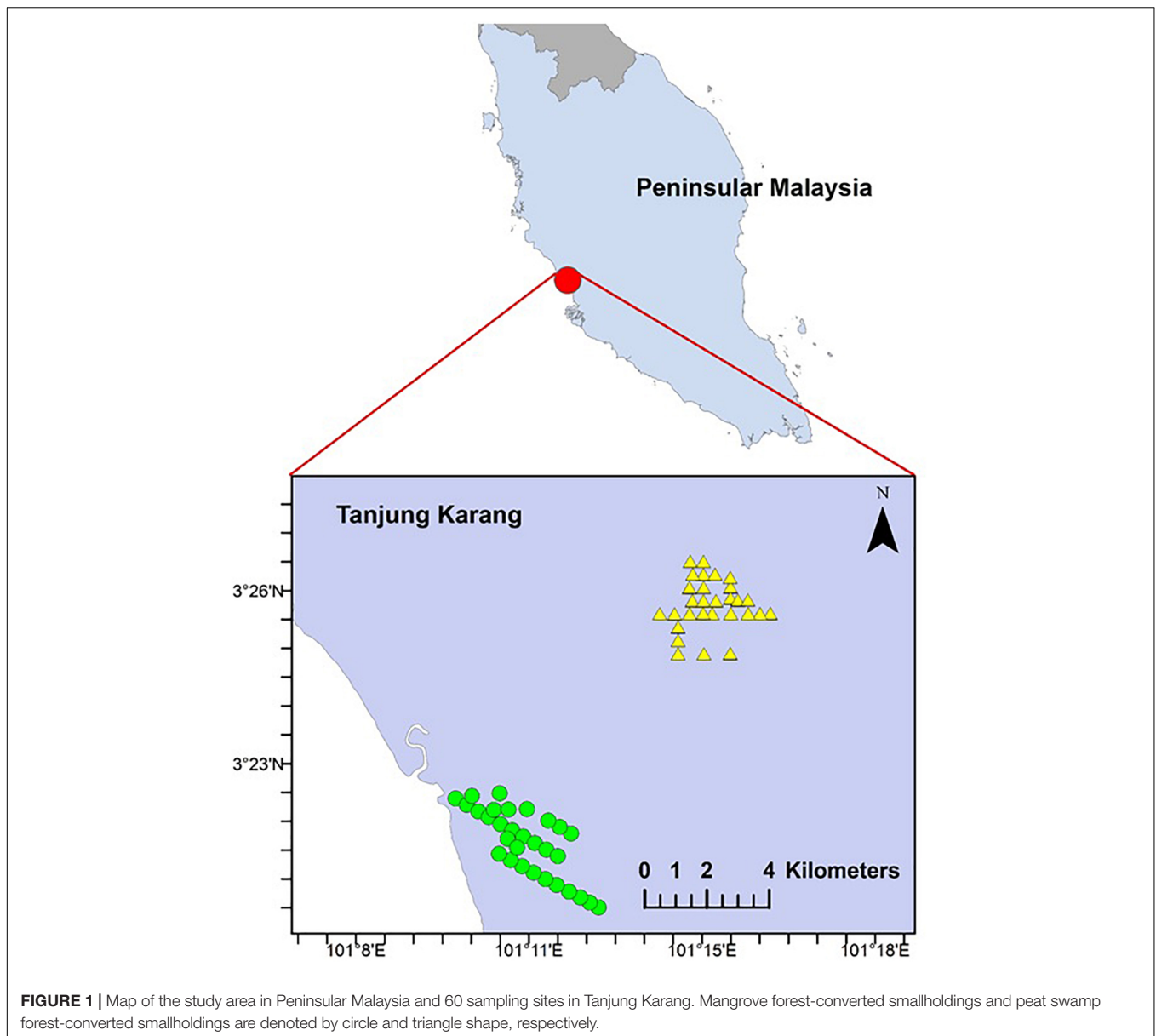
The aim of the present study was to investigate the relationship between adult Odonata species richness and physicochemical water quality and aquatic vegetation structure in oil palm smallholdings. We hypothesized that species richness and community composition of Odonata varies with respect to physicochemical water quality and vegetation structure in oil palm waterways. Specifically, we predicted that (i): reduced water quality (here characterized by low dissolved oxygen (DO), high total dissolved solid (TDS), high pH and altered thermal regimes) and disturbed in-stream habitat leads to diminished species-level diversity in this taxon; and (ii): Both peat-swamp-forest-converted and mangrove-forest-converted smallholdings supporting similarly reduced Odonata biodiversity (i.e., species richness and abundance), due to comparable habitat degradation in both ecosystem types.

MATERIALS AND METHODS

Study Area

The study was conducted in the municipality of Tanjung Karang (03°21.511'N, 101°13.163'E; area = 7,500 ha), west coast of Peninsular Malaysia (**Figure 1**). The daily temperature varies from 29 to 32°C and mean relative humidity of 65–70%. The highest temperature happened from April to June with the lowest relative humidity measured in June, July and September. Rainfall of about 58.6–240.0 mm per month was measured in the study area (Malaysian Meteorological Services Department). Permission to conduct fieldwork in smallholdings was granted by village heads and landowners. All study sites were located at <10 m above sea level, within coastal plain areas characterized by peat soil and flat terrain. The sizes of smallholdings in the study sites were less than 5 ha each and managed by independent smallholders. Man-made waterways have been established to prevent floodwater from entering cultivation areas during rainy seasons (primary monsoon, October to November; secondary monsoon, March to May) (**Figure 2**). The waterways were a common feature in the study area (Sulai et al., 2015). Oil palm has been commercially planted in this area since the 1970s (Sulai et al., 2015). Historically, the smallholding areas were converted from peat swamp (4439.67 ha) or mangrove forest (3097.71 ha).

We defined oil palm smallholdings as self-managed cultivation areas covering less than 50 ha that were owned by individual farmers (Azhar et al., 2011, 2015b; Oon et al., 2019a,b). Smallholdings typically support multiple-age stands of oil palm,



in which oil palms are planted alongside other commercial plants (e.g., banana, cassava, coconut, pineapple, mangoes, and tapioca) (Amoah et al., 1995; Azhar et al., 2014, 2017; Razak et al., 2020). Patches of oil palms of different heights are common in smallholdings (Azhar et al., 2011). Oil palm stands (>25 years) were rarely removed in smallholdings and instead left to naturally die and decompose. Hence, smallholdings tend to be more heterogeneous in terms of vegetation structure compared with plantation estates. Similarly, riparian vegetation can consist of remnants forest trees, replanted commercial plants and also weeds on streambank.

Sampling Design

We used a systematic survey design with a random start to ensure better spatial coverage and lower variance (Morrison

et al., 2008; Thomas et al., 2010). We established 60 sampling points alongside oil palm waterways. Thirty sampling points were established in each historical land cover type (i.e., peat swamp forest-converted or mangrove forest-converted smallholdings) (Figure 1). To ensure independence of observations, each point was spaced at least 400 m apart. Geographic coordinates were also recorded for each site. Sampling was undertaken from March to September 2015.

Aerial Adult Odonata Sampling

The presence of adult insects at each sampling point was assessed based on observations recorded during a discrete 20 min period following Bried et al. (2012). We recorded the number of individuals observed within a 10 m radius of the chosen sampling point. To identify adult Odonata, we used specialized taxonomic



FIGURE 2 | Typical man-made waterways at the study area. These waterways are built in oil palm smallholdings for flood-control and irrigation. Vegetation cover including non-aquatic and semi-aquatic weeds characterizes the waterways and provides places to perch from which Odonata can take off to capture prey and as a vantage point to patrol a territory.

keys for the region (Orr, 2003, 2005). We also captured individuals with an insect net when visual identification was not possible in the field. We recorded Odonata fauna encountered visually between 9 to 12.30 a.m. on a daily basis (during clear days). Sampling was repeated three times at each point.

Water Quality, Channel Morphology, and Vegetation Measurements

Physicochemical water quality variables were measured on the same day of Odonata sampling was done at each point. We used a Hanna Multimeter to measure temperature, salinity, pH, conductivity, dissolved oxygen (DO), turbidity, and total dissolved solids (TDS). Quadrats (25 m²) were established at each Odonata sampling point, to ensure every part of the sampling area had an equal chance of being sampled on each occasion (Sulai et al., 2015). We estimated the percentage of vegetation cover (inside the channel and on the bank) inside each quadrat. Similar to Odonata sampling, habitat sampling was repeated three times at each point. Water variables measured were summarized to provide descriptive statistical information (Table 1).

Statistical Analyses

All statistical analyses were performed in GenStat version 15 (VSN International). To assess the overall sampling effort, we

compared the observed species richness with the Chao 1 bias correction estimator for the species richness in Estimates version 9.1 (Colwell et al., 2004). To take into account imperfect detection of rare species, we also used ACE (Abundance Coverage-based Estimator) (Colwell and Coddington, 1994). Ten samples were used as the recommended upper limit for rare or infrequent species. Expected species accumulation curves were generated using Microsoft Excel. To contrast Odonata species richness and abundance between peat swamp forest-converted ($n = 30$) and mangrove forest-converted smallholdings ($n = 30$), we used two-sample t -test. Prior to the analysis, we conducted Shapiro-Wilk test and Bartlett's test to check for normality and homogeneity of variance, respectively. As species richness and abundance did not meet the assumptions of parametric statistical tests (i.e., data are not normally distributed and variances are not equal across groups), we square root-transformed both of them.

The relationship between Odonata species richness and habitat characteristics (e.g., physicochemical water quality and aquatic vegetation structure) was determined using Generalized Linear Models (GLMs) (Schall, 1991). To verify model assumptions, we plotted residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model. Water quality variables, vegetation cover, historical land cover and sampling month were registered as

TABLE 1 | Summary statistics for water quality and vegetation parameters.

Parameter	Habitat	Mean	Standard deviation	Range
Dissolved oxygen (mg/L)	Mangrove converted	2.162	1.541	0–6.27
	Peat swamp converted	2.001	0.743	0.79–4.07
Total dissolved solids (mg/L)	Mangrove converted	2,996	1,802	305–6,707
	Peat swamp converted	578.2	301.9	54–1,389
Water level (m)	Mangrove converted	0.429	0.228	0.11–1.12
	Peat swamp converted	0.278	0.118	0.07–0.58
Water temperature (°C)	Mangrove converted	27.09	0.846	25.67–29.48
	Peat swamp converted	27.33	1.349	25.49–32.46
pH	Mangrove converted	7.314	0.454	6.11–8.45
	Peat swamp converted	3.323	0.566	2.73–6.25
Vegetation cover (%)	Mangrove converted	58.63	35.28	0–100
	Peat swamp converted	38.87	36.45	0–100

explanatory variables in GLMs. Regression models predicting richness or diversity in aquatic habitats based on abiotic variables explained greater variance than did those predicting abundance (Therriault and Kolasa, 1999). We used a log-link function assuming a Poisson distribution to fit the models. Because the response variables (i.e., count data) exhibited over-dispersion, Poisson models were used as the preferred model. The dispersion parameter of Poisson models had been assumed to be fixed. In this case, the dispersion parameter was fixed at 1. We conducted Spearman correlation tests to determine multicollinearity among the predictor variables. Only one of each pair of highly correlated explanatory variables were included in the analysis, as collinearity can distort model estimation ($|r| > 0.7$) (Dormann et al., 2013). Conductivity (coefficient of correlation, $r = -0.725$) and salinity (coefficient of correlation, $r = -0.911$) were therefore excluded, while total dissolved solids remained in the model. We did not include historical land cover type (peat swamp forest-converted or mangrove forest-converted) as a predictor variable because it is obviously characterized by pH and salinity. Akaike Information Criterion (AIC) tests were conducted to select the most parsimonious models (Burnham and Anderson, 2002) and models with the lowest AIC scores were chosen. Because the number of samples/number of parameters = $24.86 < 40$ for our models, we used corrected AIC (Hurvich and Tsai, 1989; Burnham and Anderson, 2002). Under this criterion, the chosen model is the one that minimizes the Kullback-Leibler distance between the model and the truth (Burnham and Anderson, 2002). We also reported the percentage of explained deviance of each competing model (Burnham and Anderson, 2002). We computed Akaike weights to provide a measure of model selection uncertainty.

SIMPER analysis was used to determine the contribution of each species and differentiate Odonata assemblages (Clarke and Warwick, 2001). The cut-off for species contribution to each assemblage was fixed at 90%. BIO-ENV analysis was used to determine the environmental factors most associated with Odonata assemblages (Clarke and Warwick, 2001). Computation in this analysis was based on the Spearman-rank correlation method (Number of permutations = 999). SIMPER

and BIO-ENV analyses were conducted in Primer version 6 (PRIMER-E Ltd.).

RESULTS

Throughout the sampling period, we recorded a total of 1,217 adult Odonata, representing 24 species, 22 genera, and four families, comprising mostly dragonfly (Anisoptera) taxa (Table 2). Conversely, only five damselflies (Zygoptera) species were recorded. We recorded four forest species. These include *Rhyothemis phyllis*, *Lathrecista asiatica*, *Nannophya pygmaea*, and *Anax guttatus*. Based on the Chao 1 and ACE estimators of “true” species richness, our sampling effort yielded 94.90 and 91.03% of the “true” Odonata species richness, respectively (Figure 3). Our results revealed no significant difference in Odonata species richness ($t = -1.07$; $p = 0.285$) between peat swamp forest-converted (mean \pm SE = 2.90 ± 0.16) and mangrove forest-converted smallholdings (mean \pm SE = 2.60 ± 0.23). Similarly, we did not detect significant differences in Odonata abundance ($t = 1.53$; $p = 0.127$) between peat swamp forest-converted (mean \pm SE = 20.51 ± 1.37 individuals) and mangrove forest-converted smallholdings (mean \pm SE = 25.61 ± 3.03 individuals).

The most parsimonious model for Odonata was one that included dissolved oxygen, water temperature, vegetation cover, water level, pH, and total dissolved solids (Table 3). This model revealed that Odonata species richness increased with dissolved oxygen, water temperature, and vegetation cover (Figure 4). However, Odonata species richness decreased with increasing water level, pH, and total dissolved solids (Figures 5, 6). In total, the model accounted for 72.1% of the Akaike weights in the model set and explained 58.55% of the variation in Odonata species richness. Model validation indicated no problems. The following equation describes this model:

$$SP = 0.2565 \times DO - 2.375 \times WL - 0.1439 \times pH - 0.001 \times TDS + 0.116 \times WT + 0.004 \times VC - 5.120$$

where SP = Species Richness, DO = Dissolved Oxygen, WL = Water Level, pH = Water pH, TDS = Total Dissolved Solids, WT = Water Temperature, VC = Vegetation Cover.

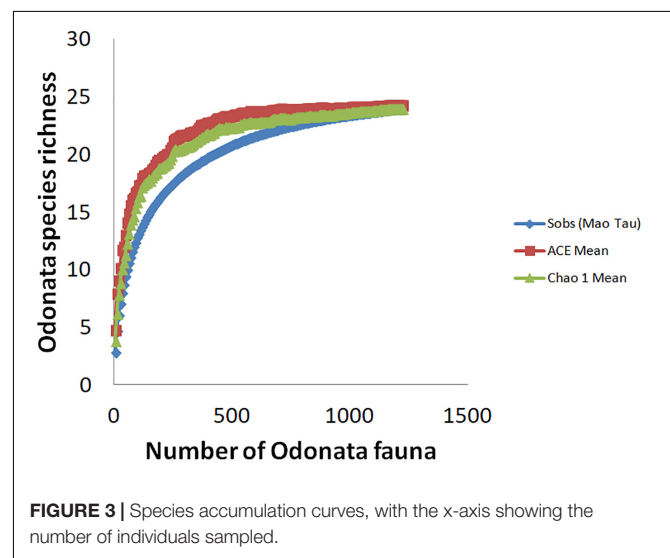
TABLE 2 | Species list of principal Odonata recorded at the study sites.

Suborder	Family	Species	Habitat	
Zygoptera	Coenagrionidae	<i>Ischnura senegalensis</i>	Disturbed open area	
	Coenagrionidae	<i>Pseudagrion australasiae</i>	Common on lakes, drains and lily ponds	
	Coenagrionidae	<i>Pseudagrion microcephalum</i>	Common on lakes, drains and lily ponds	
	Coenagrionidae	<i>Ceriagrion cerinorubellum</i>	Ponds, drains in disturbed open areas	
	Coenagrionidae	<i>Agriocnemis femina</i>	Ponds, drains in disturbed open areas	
Anisoptera	Libellulidae	<i>Neurothemis fluctuans</i>	Lakes, drains, marshes and paddyfields	
	Libellulidae	<i>Crocothemis servilla</i>	Disturbed open habitats, agricultural lands	
	Libellulidae	<i>Brachydiplax chalybea</i>	Ponds, drains, mangrove swamps in disturbed open areas	
	Libellulidae	<i>Orthetrum sabina</i>	Ponds, drains, marshes, forest margins & canopy, in disturbed open areas	
	Libellulidae	<i>Rhyothemis phyllis</i>	Marshy ponds, drains, brackish water	
	Libellulidae	<i>Brachythemis contaminata</i>	Margins of ponds, lakes, drains, sluggish river, tolerates polluted water	
	Libellulidae	<i>Diplacodes trivialis</i>	Open marshes, shallow drains, disturbed areas	
	Libellulidae	<i>Hylaeothemis clementia</i>	Lowland alluvial swamp	
	Libellulidae	<i>Lathrecista asiatica</i>	Coastal marshes and swamps, near forest margins in brackish water	
	Libellulidae	<i>Agrionoptera insignis</i>	Lowland forest marshes, sluggish streams, shady drains, disturbed areas	
	Libellulidae	<i>Potamarcha congener</i>	Disturbed open area, in slowly moving water	
	Libellulidae	<i>Acisoma panorpoides</i>	Disturbed open area, grassy swamps, drains, overgrown paddy	
	Libellulidae	<i>Tramea transmarna</i>	Well vegetated lakes, ponds, drains, in lowlands	
	Libellulidae	<i>Orthetrum glaucum</i>	Ponds, ditches in degraded open area	
	Libellulidae	<i>Orthetrum chrysis</i>	Lakes, ponds, marshes, in open area	
	Libellulidae	<i>Nannophya pygmaea</i>	Grassy lake borders, drains, marshes, in open area or forest margin	
	Libellulidae	<i>Trithemis aurora</i>	Ponds, lakes, weedy drains, sluggish streams, in open area	
	Aeshnidae		<i>Anax guttatus</i>	Drains, ponds, lakes, swamps, in disturbed open area, landward mangrove margins in brackish water
	Gomphidae		<i>Ictinogomphus decoratus</i>	Ponds, lakes margins, drains, in open areas

A relatively small number of species dominated the Odonata community in oil palm smallholdings, with ten out of a total of 24 of the species responsible for > 90% of the individuals recorded (Table 4). Species composition was significantly associated with dissolved oxygen and pH ($r = 0.387$; $p = 0.001$).

DISCUSSION

Our results reveal that, despite disturbance and habitat degradation, oil palm waterways still appear to contribute considerably to freshwater biodiversity within small-scale agricultural habitats. This finding reinforces the importance of maintaining man-made waterbodies for conservation outcomes in oil palm production landscapes (Sulai et al., 2015). Our data are comparable with Abdul et al. (2017) who recorded 22 Odonate species at larval stage, collected from a river which passes through an oil palm plantation in the northern part of Peninsular Malaysia. However, our study suggested that Odonata communities supported by oil palm waterways are impoverished in comparison to natural forests. Prior to forest conversion, as many as 78 Odonate species from 12 families were likely to exist in the study sites (Norma-Rashid et al., 2001), with Dow et al. (2012) reporting 50 Odonate species from nine families in comparable natural peat swamp forest on the east coast of Peninsular Malaysia. Despite considerably reduced diversity in the oil palm smallholding waterways studied here, Anisopteran diversity was still appreciable, though characterized by more



tolerant, generalist species compared to those recorded from undisturbed swamp habitats. Whilst we reveal that smallholdings may retain relatively high Anisoptera species richness despite extensive habitat disturbance, they host few species of typically more sensitive Zygoptera taxa (Júnior et al., 2015; Oliveira-Junior et al., 2015; Oliveira-Junior and Juen, 2019). Oliveira-Junior et al. (2015) suggested that Anisoptera are likely to be associated with degraded environments such as oil palm plantations. By contrast,

TABLE 3 | Model selection using Akaike weight.

Model	Number of variables, K	% explained deviance	AIC	Corrected AIC	Delta AIC ($\Delta_i = AIC_i - AIC_{min}$)	Relative likelihoods	Akaike weight, W_i
1	Water level + Dissolved oxygen + pH + Total dissolved solids+ Vegetation cover + Water temperature	58.55	190.82	191.32	0.00	1	0.721
2	Water level + Dissolved oxygen + pH + Total dissolved solids+ Vegetation cover + Water temperature + Sampling month	58.77	194.00	194.67	3.35	0.187	0.135
3	Water level + Dissolved oxygen + pH + Total dissolved solids+ Vegetation cover	57.06	194.37	194.73	3.41	0.182	0.131
4	Water level + Dissolved oxygen + pH + Total dissolved solids	55.23	199.23	199.46	8.14	0.017	0.012
5	Water level + Dissolved oxygen + pH	53.07	205.26	205.40	14.08	0.001	0.001
6	Water level + Dissolved oxygen	36.47	265.28	265.35	74.03	0.000	0
7	Water level	23.21	312.81	312.83	121.51	0.000	0

Model 1 is the most parsimonious model because it has the smallest AIC score. Using the cross-validation property of AIC, it is expected that under repeated sampling Model 1 would provide the best prediction of Odonata species richness 72.1% of the time.

Zygoptera are likely to indicate undisturbed environments such natural forests. With respect to land use modification, our findings are consistent with Sulai et al. (2015) who report that species richness and abundance did not differ significantly between peat swamp forest-converted and mangrove forest-converted smallholdings, with this likely associated with the comparable loss of original forest vegetation and associated habitat degradation in both ecosystem types.

Our regression models (i.e., GLMs) indicated that Odonata species richness was influenced by both physicochemical water quality variables and within-channel and bankside vegetation structure. This in contrast to a previous study (Jacobsen, 2008), where multiple regression analyses exploring the influence of several predictor variables revealed that oxygen saturation had the greatest (and the only statistically significant effect) on density-corrected richness. However, we did find that Odonata species richness and composition was positively related to dissolved oxygen, partially corroborating this finding. Similarly, previous studies (de Paiva Silva et al., 2010; Pryke et al., 2015) reported dissolved oxygen was an important determinant for Odonata species richness, and macroinvertebrate diversity indices more generally correlate inversely with TDS, pH and turbidity but positively with dissolved oxygen (Ndaruga et al., 2004). Some macroinvertebrates showed sensitivity to low oxygen conditions, and lethal effects were observed at low DO (i.e., <20%) saturation levels for a number of species (Connolly et al., 2004). The sensitivity to oxygen conditions is likely to be associated with the locations for oviposition and predation (Kietzka et al., 2017).

Our result indicated that Odonata species richness declined with increasing water level and pH. Williams et al. (2004) reported that water level was the main environmental factor linked to the gradual change in species assemblage between rivers, streams and ditches. Drainage may result in a decrease in pH (Laine et al., 1995). Indeed, pH is an important attribute affecting Odonata community composition more generally (Johansson and Brodin, 2003). Acidic waters with low pH values can cause adverse effects on dragonflies, particularly on the developmental time and hatching success of eggs (Punzo, 1988; Pollard and Berrill, 1992). Although Odonata are typically relatively tolerant to low pH, it may affect survival of some species (Corbet, 2004). In addition, acid-stressed regions are suitable habitats for specialists, which do not propagate in neutral waters (Hudson and Berrill, 1986). Rising water level may affect the zone where submerged plant roots form an important habitat type in oil palm waterways that become unavailable for Odonata and their prey specifically invertebrates.

Odonata species richness increased with rising water temperature in oil palm waterways. Many Odonates prefer warmer and shallow water for their ovipositional sites (Michiels and Dhondt, 1990), and higher water temperatures can promote increased rates of egg hatching and reduce predation on adult Odonata (Wolf and Waltz, 1988). Streams draining oil palm plantations often have markedly higher water temperatures compared to forest streams (Carlson et al., 2014). However, our findings are in contrast to patterns typically encountered in

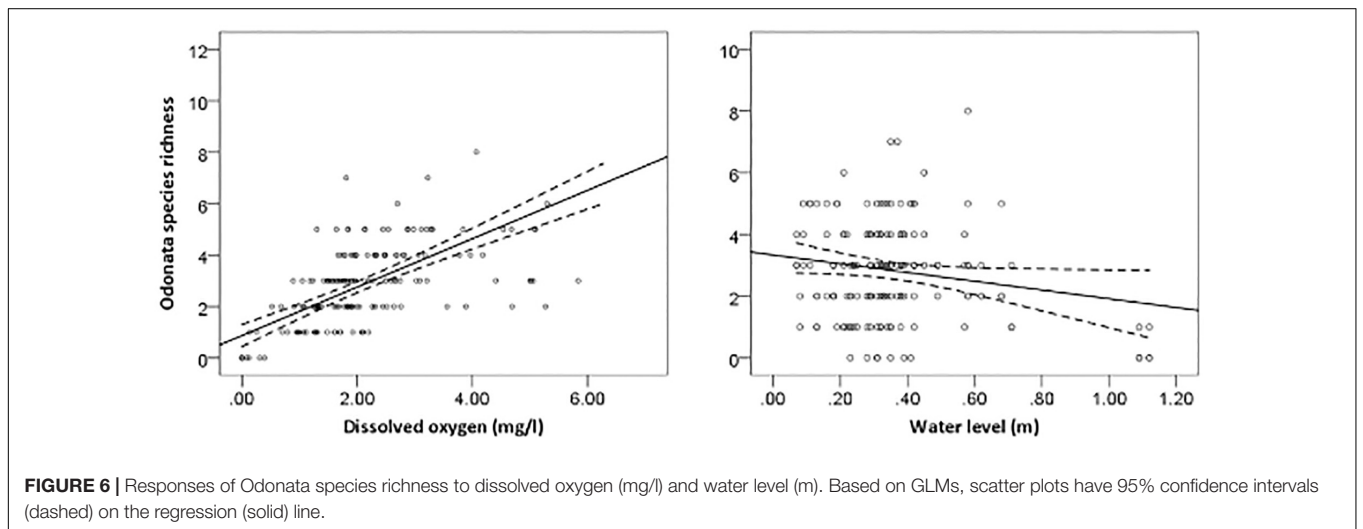
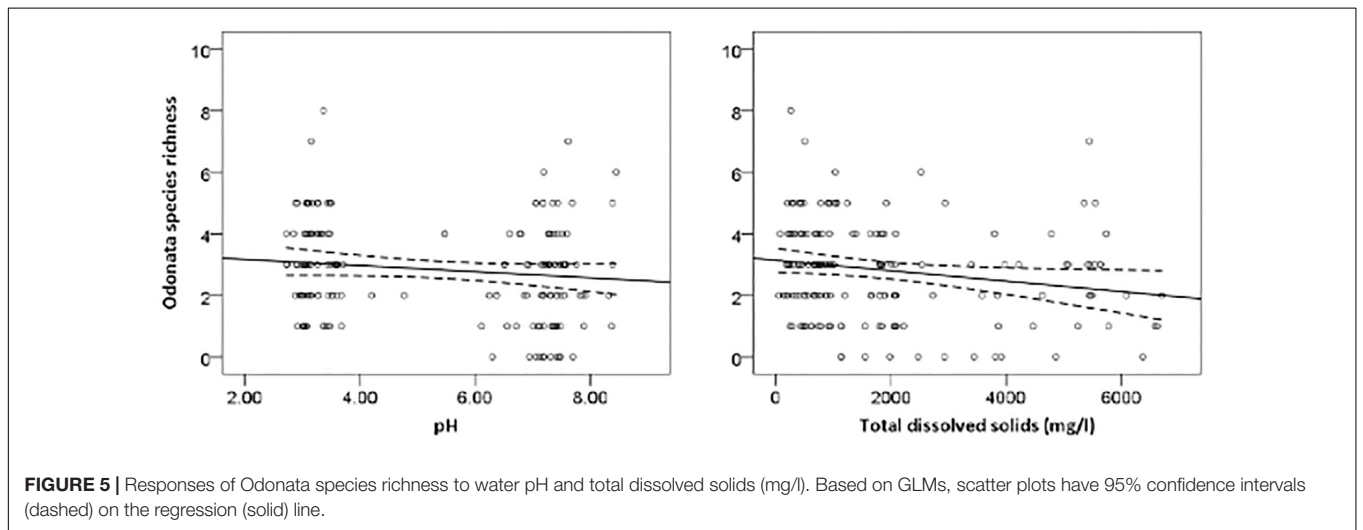
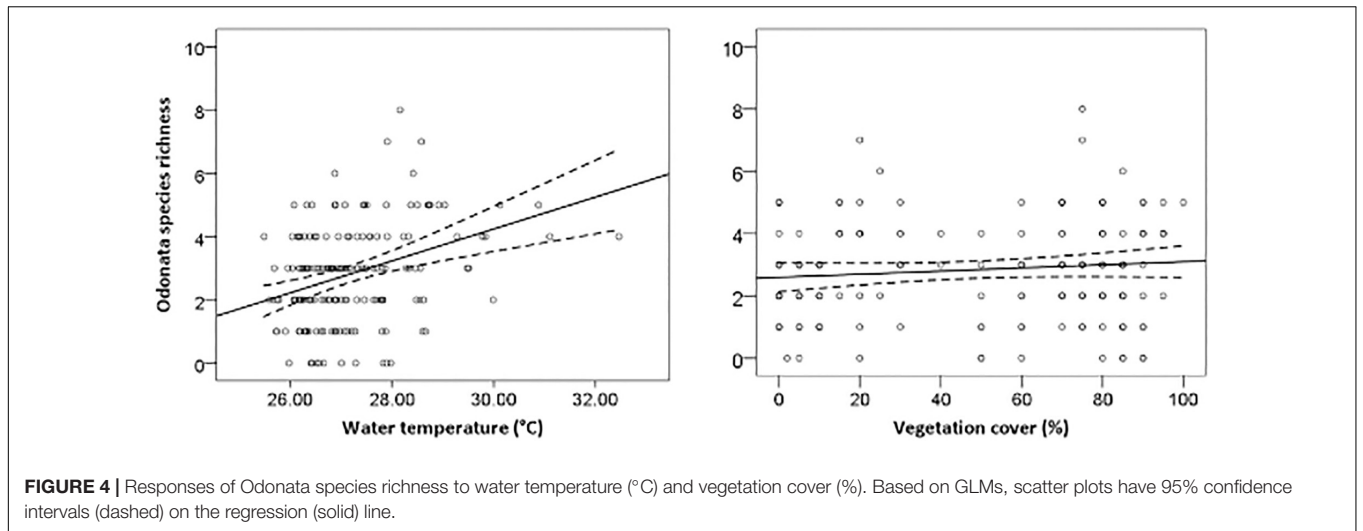


TABLE 4 | Odonata species that together composed over 90% of the assemblages (based on abundance) observed in sampled oil palm waterways.

Species	Contribution %	Cumulative contribution %
<i>Crocothemis servilia</i>	22.77	22.77
<i>Orthetrum sabina</i>	19.68	42.45
<i>Neurothemis fluctuans</i>	15.22	57.66
<i>Lctinogomphus decoratus</i>	6.41	64.08
<i>Ischnura senegalensis</i>	5.77	69.85
<i>Rhyothemis phyllis</i>	5.38	75.23
<i>Orthetrum chrysis</i>	5.30	80.52
<i>Brachydiplax chalybea</i>	4.89	85.41
<i>Tramea transmarina</i>	3.01	88.42
<i>Potomarcha congener</i>	2.16	90.58

temperate ecosystems with, for example, Durance and Ormerod (2009) reporting that the abundance of macroinvertebrate families can decline with increasing temperature. In addition to water quality, inevitable changes in vegetation patterns affect aquatic invertebrates (Elo et al., 2015). Vegetation structure served as a good indicator of habitat requirements for dragonflies and damselflies, thereby partially predicting species diversity (Remsburg and Turner, 2009). Vegetation structure benefits Odonata through resource availability and shelter (Buchwald, 1992), with positive relationships between Odonata and plant species richness observed at multiple spatial scales (Honkanen et al., 2011). Moreover, the height of key plant species also determines Odonate diversity, emphasizing the importance of vegetation structure for fliers and perchers (Lee Foote and Rice Hornung, 2005).

The use of agrochemicals (e.g., high rate of fertilizer application) to sustain crop productivity is one of the leading causes of water quality impairment in oil palm waterways (Khatun et al., 2017). Oil palm smallholders and plantation managers should be wary of eutrophication in oil palm smallholdings, due to consequent reductions in total dissolved oxygen in waterways. Moreover, eutrophication may limit sunlight availability for aquatic autotrophs due to the proliferation of heterotrophic fungi and the decay of algae on waterbody surfaces (de Paiva Silva et al., 2010; Burchett and Burchett, 2011). Excessive nutrient loads, primarily elevated nitrogen and phosphorus levels, can accumulate in slower moving waterways due to surface water run-off in poorly managed farmland (Burchett and Burchett, 2011). The present study recommended establishment of buffer strips to reduce the effects of eutrophication. Buffer strips greatly improve water quality of agricultural streams by reducing nutrient leaching in groundwater and surface water run-off, even though they comprise little of the total catchment area (Vought et al., 1995). Moreover, they may act to buffer streams from a host of catchment-wide anthropogenic stressors; even relatively small areas of near-stream forest cover may increase ecosystem resilience and stability, acting to boost aquatic macroinvertebrate diversity and production (Thomas et al., 2016). This may be especially important in structurally degraded monocultural landscapes, whereby the increased habitat complexity and resource availability facilitated by buffer

strips can help promote diversity in macroinvertebrate taxa, including Odonates.

Our results provide valuable information on which to assess the importance of man-made waterways as aquatic habitat for Odonata in oil palm production landscapes. Waterway management is particularly important to guarantee profitable agricultural production. Well-maintained waterways can increase yield while maintaining aquatic insect biodiversity, particularly in the case of sensitive groups such as Odonata. Most Odonata species encountered belong to the family Libellulidae as the larger-bodied adults can thermoregulate efficiently under warmer waterways condition in oil palm sites (Luke et al., 2017). The narrower channels in oil palm sites also lead to higher organic matter input through sediment deposition that promotes higher vegetation density (Singh et al., 2015). The applications of chemical pesticides and fertilizers in oil palm smallholding can, however, negatively impact Odonata, as chemical runoff can limit juvenile growth, development and survival (Dinh Van et al., 2014). Herbicide overuse removes undergrowth cover completely, which protects the soil against erosion caused by surface runoff in oil palm plantations (Tohiran et al., 2017; Darras et al., 2019). Another runoff carries away topsoil into the waterways, causing sedimentation and adversely affects the water quality. Odonata sensitivity to water quality thus provides a useful indicator for ecosystem quality more broadly. In return, biodiversity may help to buffer aquatic ecosystems against the ecological impacts of nutrient pollution (Cardinale, 2011). Despite the strength and consistency of our findings, our data are inherently limited to effects on adult Odonata taxa.

CONCLUSION

Our findings support evidence that human-induced disturbances such as oil palm expansion in the tropics resulted in pronounced changes in the taxonomical composition of the Odonata. Our data suggests that adult odonates have highly specific habitat requirements with respect to physicochemical water quality of oil palm waterways and riparian vegetation. Water quality appears to be key in driving resultant variation in Odonata biodiversity in oil palm production landscapes. By maintaining water quality in oil palm waterways, these man-made aquatic habitats may conserve Odonata communities in oil palm production landscapes. Future studies need to gather evidence related to improved waterway management. Unpolluted waterways in oil palm production landscapes may reduce ecological disturbances that affect odonate survival. It is essential to highlight that riparian vegetated buffer strips in oil palm smallholdings can differ depending on the type of farm management. Establishment of buffer strips along waterways can provide beneficial impact for soil and water quality while maintaining biodiversity in oil palm smallholdings. As there is no law enforcement in the study area, some smallholders consistently spray the buffer strips with chemical herbicides to clear them for oil palm planting.

In general, if agricultural practices intend to limit disturbances from oil palm cultivation, proper waterway management could help to improve the value of oil palm smallholdings as part of wider conservation-agricultural matrices (Azhar et al., 2015a; Sulai et al., 2015). As such, we suggest self-managed oil palm farming should aim to maintain water quality and physical habitat structure in plantation waterways, and minimize the use of chemical herbicides and fertilizers which flow into the river when it rained (Abdul et al., 2017), in order to be certified as biodiversity-friendly agriculture (e.g., Roundtable on Sustainable Palm Oil and Malaysian Sustainable Palm Oil). We recommend that smallholders should be given more information regarding biodiversity-friendly practices to help mitigate the negative impacts of intensive oil palm monoculture farming with respect to aquatic habitat management.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors upon request.

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AUTHOR CONTRIBUTIONS

MI and AG carried out the experiment. AN wrote the manuscript with support from ST. SN helped supervise the project. BA conceived the original idea and supervised the project. All authors contributed to the article and approved the submitted version.

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