



## Article

# Odonata (Insecta) Communities in a Lowland Mixed Mosaic Forest in Central Kalimantan, Indonesia

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**Abstract:** Assessing a taxon's response to change in environmental variables is fundamental knowledge to understanding trends in species diversity, abundance, and distribution patterns. This is particularly needed on Borneo, where knowledge on Odonata populations in different habitats is poor. To address this gap, we present the first study investigating the relationship between morphology and species distribution of Odonata communities in a heath (kerangas)-dominated mixed-mosaic-lowland forest in southern Borneo. We sampled 250-m line transects in three habitat types: mixed peat swamp, kerangas, and low-pole peat swamp, with weekly surveys from December 2019 to February 2020. A total of 309 individuals were detected from 25 species. Anisoptera and Zygoptera diversity was the highest in mixed peat swamp and lowest in low pole, while abundance was the highest in low pole and lowest in kerangas; with kerangas notably harboring a very small sample size. Odonata community assemblages differed most between mixed peat swamp and low pole. Morphological data were compared between suborders and habitats. Anisoptera showed significantly larger thoraces, hindwings, and hindwing-to-body ratio than Zygoptera. Anisoptera in low pole were significantly smaller in body, thorax, and hindwing compared to both kerangas and mixed peat swamp. Anisoptera showed a strong association with pools and Zygoptera with flowing water. Heterogeneity, habitat characteristics, presence of specialists, body size, and the interaction between species' morphological traits and habitat characteristics likely explained the trends observed.

**Keywords:** anisoptera; abundance; ecophysiology; dispersal; diversity; habitat-heterogeneity; heath; kerangas; morphology; zygoptera



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## 1. Introduction

Much ecological research is dedicated to understanding the causes of variation in species richness across habitats and regions [1,2]. Species richness is a consequence of characteristics, conditions, and processes that occur at both local and regional scales [3,4]. At a local scale, i.e., within a single habitat or microhabitat [5], species richness is shaped by habitat characteristics and species interactions [2,6]. At larger (regional) scales, evolutionary processes, historical changes in environmental conditions, and climate appear to shape species richness [2,7,8]. Understanding the causes of these patterns has taken on a new urgency, as species are experiencing a precipitous decline because of anthropogenic

activities [9]; despite the fact that many extant species are yet to be described and their role in the ecosystem understood [10,11].

The ‘habitat heterogeneity hypothesis’ postulates that more heterogeneous environments support a larger number of species than homogeneous environments, because they support a larger quantity and variability in micro-climatic gradients and micro-habitats [12,13]. Consequently, there exists a greater variability of ecological niches and resource availability, which supports a higher alpha and beta diversity by allowing species with differing resource acquisition, life-history, and habitat selection strategies to co-exist [13–15]. For habitat heterogeneity to enhance faunal species diversity, each habitat type (and its connected patches) must be sufficiently large to support viable populations [16]. Further, as species assemblages are also shaped by biotic interactions such as predator–prey interactions and competition, large enough habitats are also required to allow populations of species to persist [16,17]. However, although there is an overarching consensus that a positive relationship exists between habitat heterogeneity and species diversity [17–19], this relationship can also be negative [18,20,21].

It is crucial to understand a taxon’s response to changes in environmental variables, as it is fundamental to understanding a taxon’s trends in species diversity, abundance, and distribution patterns [22,23]. Here, we investigate this in Odonata, as they are relatively easy to sample, taxonomically well resolved, inhabit a wide range of biotopes, occupy higher trophic position as predators, adopt a biphasic lifecycle, and are of importance to the scientific community due to their ecological indicator potential [24–26].

Habitat characteristics are thought to shape and influence Odonata species diversity, abundance, and distribution patterns. The plethora of literature suggests that shade [27–29], vegetation structure [30] and water [19,25] are primary drivers in shaping Odonata species assemblages. This is because shade (canopy cover) influences in-water characteristics and the amount of light reaching the forest floor, thus influencing thermoregulation; the presence/absence of water limits Odonata reproduction; and because vegetation structure has a strong influence on predator–prey interactions, thermoregulatory opportunities, dispersal ability, mate detection, shelter and roosting, and breeding and oviposition sites [30–32].

In Odonata, body size is strongly associated with thermoregulation [23,33,34] and dispersal ability [23,35]; two co-evolved traits that result from a complex interplay of evolutionary history and the selecting forces of habitat variables (biotic and abiotic); the strength of which is determined by the dependency of species on those habitat variables [23]. Thermoregulatory requirements and dispersal ability may therefore not only form the basis for understanding behavioral and distribution patterns in Odonata but may also be important in determining how environmental tolerance and resource use patterns evolved [23]. Moreover, it is expected that species that exhibit low dispersal abilities will tend to be more affected by small-scale environmental changes and are more likely to be resource specialists [23]. Thus, it is increasingly important in regions of widespread habitat loss and fragmentation to understand the interplay between morphology, dispersal, and thermoregulation in odonates [36,37].

The Odonata fauna of Central Kalimantan, Indonesia remains poorly understood [38], with the majority of records from this region originating from just four short periods of field work [38,39]. Research on Odonata has also been conducted in East Kalimantan, focusing on investigating changes in taxonomic structure and functional diversity in response to environmental perturbations (e.g., [40–42]). However, the methods employed in those studies included study sites that differed in their degree of disturbance. This study, on the contrary, will investigate Odonata communities in intact habitats spatially distributed in a mosaic structure.

Heath forests (also known locally as kerangas and will hereafter be referred to as kerangas) occur on sandy soils and are relatively poorly studied on Borneo. Here they range from stunted forests with high pole density, to more structurally and species diverse ecosystems [43], that may harbor a wealth of wildlife including many rare and endemic species [44]. Yet, this landscape is threatened through mining, timber concessions, and

conversion to oil palm and agriculture [44], making the study of Odonata here particularly pertinent. The literature investigating Odonata communities in kerangas is sparse, with only three studies, as per our knowledge, previously conducted. Orr [45,46] found that the kerangas forest in Brunei harbor only few species of Odonata, but none were found strictly limited to the habitat, whereas Purwanto et al. [47] provided a short list of species associated with kerangas habitat in Belitung Timur. However, no prior study has been conducted investigating Odonata communities in a heath (kerangas)-dominated-mixed-mosaic habitat structure in southern Borneo, with neither also looking at the relationship between morphology and distribution.

This study will be the first to investigate the relationship between Odonata community morphology and distribution within a heath-dominated mosaic habitat structure on Borneo. We tested the hypothesis that Odonata species richness and abundance would differ between the three habitat-types studied, and that these diversity and abundances patterns would be influenced by varying biotic characteristics such as canopy cover, and abiotic characteristics such as light intensity and surface water characteristics. In line with this, we also tested the hypothesis that morphological characteristics—body length, thorax size, and hindwing length of species assemblages would differ between habitat specific communities.

## 2. Materials and Methods

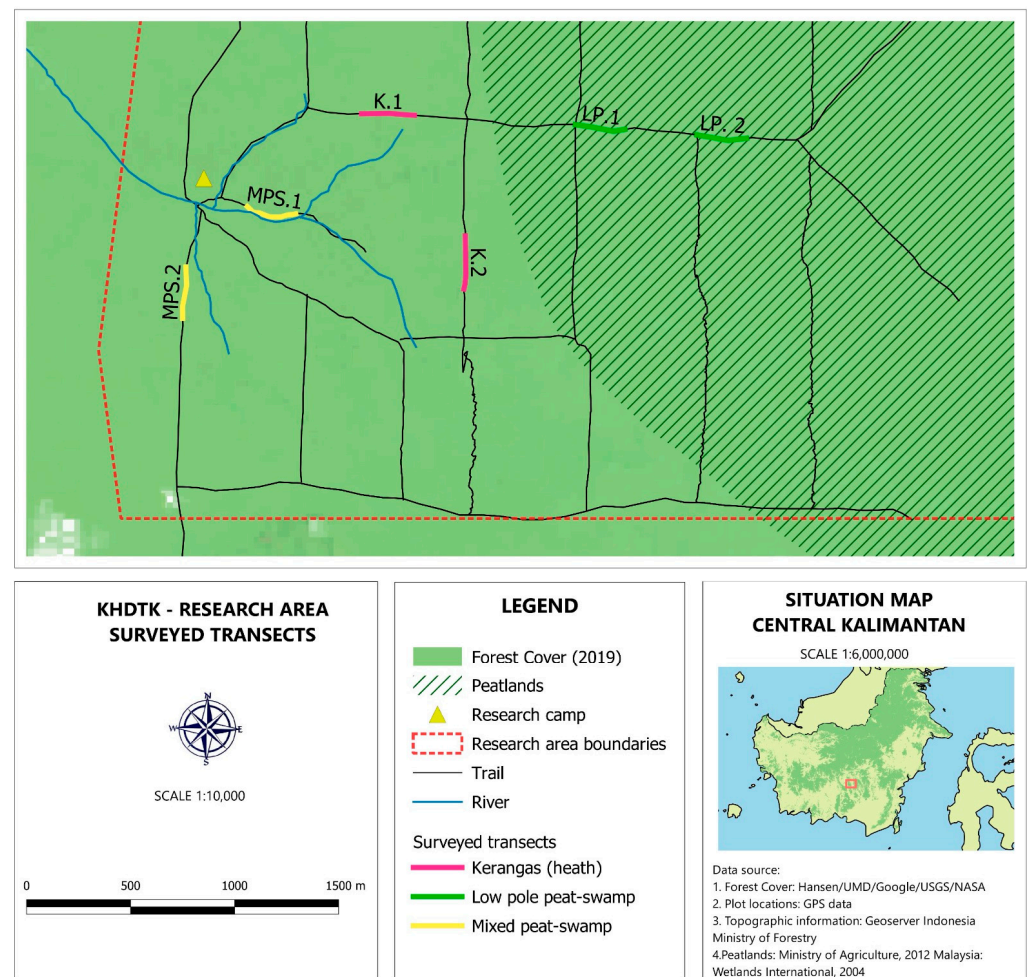
### 2.1. Site Description

This study was conducted in the 4910-ha Mungku Baru Education Forest (Kawasan Hutan Dengan Tujuan Khusus—KHDTK), which is near the Mungku Baru village and lies between palm oil and timber concessions in the heart of the unprotected Rungan landscape in Central Kalimantan, Indonesia (Figure 1; Central Coordinates  $-1.64169^{\circ}$   $113.77505^{\circ}$ ) [44]. The undulating topography creates a mosaic of habitat types, which are intersected and drained by black water streams [44,48]. We sampled three habitat types within KHDTK; kerangas (also known as heath), low-pole peat swamp forest (here after referred to as low-pole), and mixed-peat swamp (here after referred to as mixed-peat), which includes riverside forest primarily occurring in narrow strips along the stream banks [44]. See [44] (pp. 11–15) for details on soil and tree characteristics in each habitat.

### 2.2. Odonata Sampling and Sampling Design

Line transect surveys were implemented as they are considered a useful and reliable method for quantitative sampling of flying insects [49–51]. A total of six transects, two per habitat, were established across the three different habitat-types using an existing transect system (Figure 1). Each transect was 250-m in length and 0.5-m in width, which allows for a good representation of odonate diversity and abundance [52]. Surveys were carried out between 0900h and 1430h Western Indonesian Time (WIT) to coincide with the period of highest Odonata activity [51].

Odonata sampling occurred during the wet season (7 December 2019 to 2 February 2020). Surveys were conducted by the same observer (Jorian A Hendriks) to limit bias. Each habitat type was surveyed 16 times, 8 times per transect, over the course of eight weeks. Surveys were conducted by slowly walking the length of each transect. Using an aerial net, any odonate seen was caught, measured, marked, photographed, and released at the point of capture. No samples were taken. The location of capture of each individual along each transect was determined using a hand-help GPS device (Garmin GPSMAP® 64s). The length of the body (BL), thorax (TS), and hindwing (HWL) were measured with a vernier caliper. Photographs of their lateral, dorsal, and ventral view, and anal appendages were taken and served as the basis for individual identification. To identify recaptures of an individual, each individual captured was marked on its abdomen with a black spot using a permanent marker [53] as marking wings has been suggested to be negatively correlated with survival and mating success [54,55].



**Figure 1.** An overview of the established transect structure in the Mungku Baru Education Forest (Kawasan Hutan Dengan Tujuan Khusus), Central Kalimantan, Indonesia. Transects locations used for Odonata surveys are shown in respective colours: yellow—mixed peat swamp (MPS), red—kerangas (heath) (K), and green—low pole peat swamp (LP). Map provided by The Borneo Nature Foundation.

Odonates that were feeding, mating or teneral were not captured or disturbed and were identified to species-level from a distance. In cases of recapture, the date, type of habitat, suborder, distance along the transect, and species were noted. Only captured Odonata, and those individuals seen feeding and mating were included in analysis. Teneral, sighted individuals, and recaptured individuals were excluded from analysis. Sighted individuals included those that were seen and identified to genus or species level, but that were not captured and measured.

### 2.3. Environmental Variables

Light intensity, pH and temperature of the surface water, and the presence of lotic or lentic water sources or dry ground, were recorded within a 5-m diameter at the point of capture of each individual. Light intensity was used as a proxy of canopy cover and was measured using a lux meter (AS823 SMART SENSOR). The area occupied by surface water was estimated visually using a template of reference photographs of varying degrees of surface water extents. pH and temperature were measured using a pH 009 (I) A pen type meter (Hinotek) and a digital water thermometer (TPM-10), respectively. Regular assessments of habitat parameters using the above methods were also made at 25-m intervals on each transect to analyze potential habitat use and selection by Odonata.



## 2.4. Data Analysis

Species diversity was calculated using the Shannon–Wiener Index ( $H'$ ) [56] and was further elucidated using the effective number of species (ENS) [57,58]. Species–effort curves were calculated by generating interpolation/extrapolation curves to estimate species richness for each habitat [59]. Species relative abundance was calculated and plotted to find which species were more represented within each habitat-type. We considered a species to be relatively abundant when it exceeded the relative abundance (RA) threshold of 15%. Rank-abundance graphs (Whittaker plots) were constructed to identify dominant species using the formula: number of individuals of species  $x$  / total number individuals in habitat type and were constructed using ggplot2 [60]. Dissimilarity in species assemblages between habitat types was calculated using the Renkonen Percent Similarity Index.

To evaluate the influence of habitat type controlling for suborder—which we did by taking the interaction effect into account—we created generalized linear models (GLMs) for each of the relevant morphological measurements: body length (mm), wing length (mm), thorax length (mm), and hindwing-to-body ratio. We plotted the distribution of each dependent variable to verify the appropriate distribution and visually inspect for outliers. The dependent variable distributions were continuous with a long right tail, so we fitted each model with a Gamma distribution and a log link. The resulting equations are of the form: measurement value  $\sim$  habitat type \* suborder. All estimates were calculated by computing pairwise marginal means separately for each suborder, adjusting the  $p$  value using the Tukey method for multiple comparisons [61]. It was not possible to include species as a random effect due to small sample sizes (Table A1).

As is common for ecological community data, each dependent variable had several extreme outliers. To reduce the effect of leverage on the model from these outliers, we removed outliers outside of three standard deviations from the mean for each dependent variable by suborder before fitting the model. Because we are interested in determining the typical morphological characteristics in each habitat type, such outliers are not especially informative given that each of the dependent variables are nearly normally distributed and unimodal.

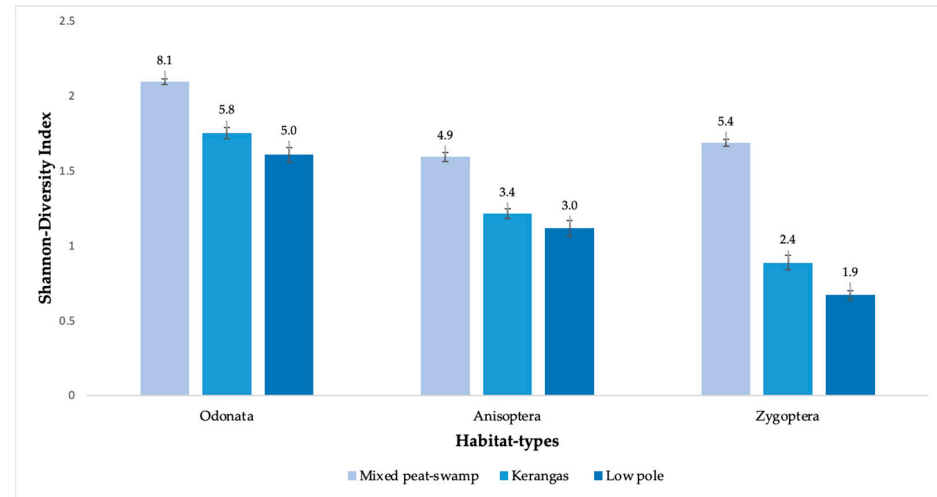
To test whether there was an association between suborder and habitat type we used a GLM with a binomial distribution of the form suborder  $\sim$  habitat type. All statistical analyses were conducted in R 4.1 [62] with an alpha of 0.05. For each GLM, we evaluated model fit by comparing fitted residuals to expected simulated residuals in a Q-Q plot along with conducting dispersion and outlier tests [63].

## 3. Results

A total of 306 individuals were captured representing 9 families, 21 genera, and 25 species (Table A2), and 7 individuals were recaptured throughout the study but were excluded from analysis. Of the total Odonata individuals captured, 53.3% belonged to the suborder Anisoptera, representing 2 families, 8 genera, and 10 species. The remaining 46.7% of individuals captured belonged to the suborder Zygoptera, representing 7 families, 13 genera, and 15 species. The most dominant Anisopteran and Zygopteran families were *Libellulidae* and *Platycnemididae*, respectively. Out of the total captured, 82.8% were male and 17.2% female, with more males than females captured across all habitats: mixed peat swamp (M = 66, F = 7); kerangas (M = 15; F = 9); low pole (M = 177, F = 32). However, in kerangas, there were significantly fewer males proportional to females (Est =  $-1.73$ ; se = 0.579;  $p < 0.001$ ; nA = 160, nZ = 149). Of the total individuals captured, 40 are yet to be identified to species level: *Coelliccia* sp., (one individual), *Prosticta* sp., (one individual), *Unknown* sp., (one individual), *Prodasinieura* spp., (34 individuals) and *Vestalis* sp. (three individuals). One capture (belonging to the genus *Ceriagrion*, and hereafter referred to as *Ceriagrion* sp.) is suspected as being potentially new to science (Figure A1; see the same figure for a small collection on other sampled odonates).

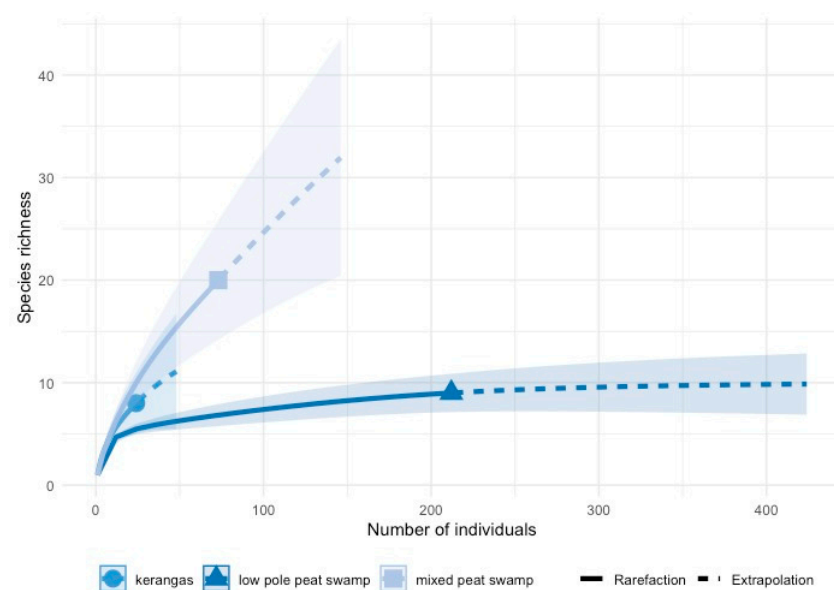
### 3.1. Diversity and Abundance

Species diversity was highest for mixed peat swamp, intermediate for kerangas and lowest for low pole (Figure 2). The species diversity for each suborder was the highest in mixed peat swamp and the lowest in low pole (Figure 2).



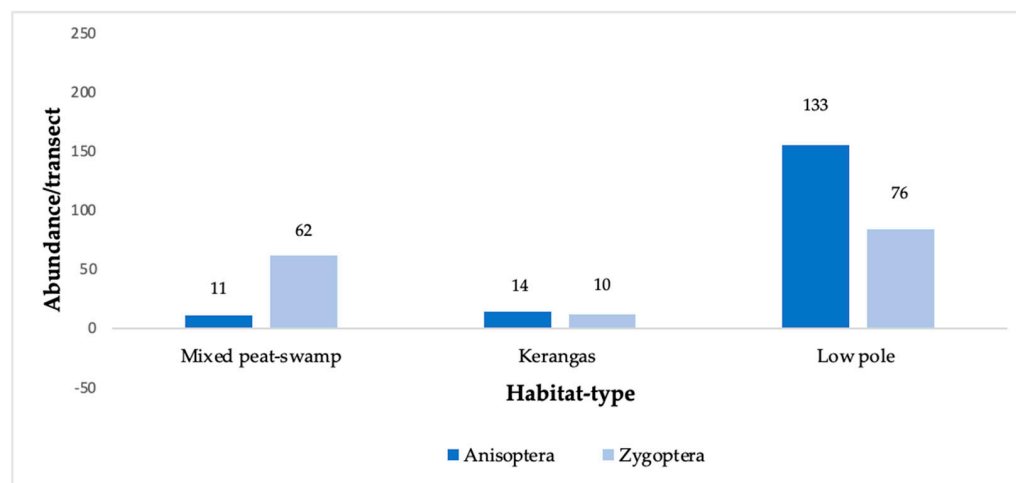
**Figure 2.** Shannon-diversity Index ( $H'$ )—Odonata (which includes both Anisoptera and Zygoptera) (left), Anisoptera (middle), and Zygoptera (right) for habitat-types mixed peat swamp, kerangas, and low pole forests. Effective number of species (ENS) values are given above each respective bar.

A species–accumulation curve showed that sampling effort inadequately represented the Odonata species richness in mixed peat swamp and kerangas, as indicated by the absence of an asymptote (Figure 3). This contrasts with the low pole, where sampling effort adequately represented the Odonata communities as indicated by the presence of an asymptote (Figure 3). The lack of an asymptote for kerangas is partially due to the few individuals observed in the habitat, while the lack of an asymptote in mixed peat swamp is almost certainly due to a higher species richness.



**Figure 3.** Species accumulation curve of Odonata (dragonflies and damselflies) for the three studied habitat types: mixed peat swamp, kerangas (heath), and low pole peat swamp. The solid line represents observed values while the dotted line presents extrapolated estimates of species richness with continued sampling.

Expressed as a percentage of total captures across all habitats, the highest number of Odonata captures were in low pole (68.3%), followed by mixed peat swamp (23.8%), and then kerangas (7.84%). Anisoptera abundance, in terms of total captures, was the highest in low pole (86.1%) and the lowest in mixed peat swamp (6.1%), whilst Zygoptera abundance was the highest in low-pole (53.2%) and the lowest in kerangas (7.6%) (Figure 4).

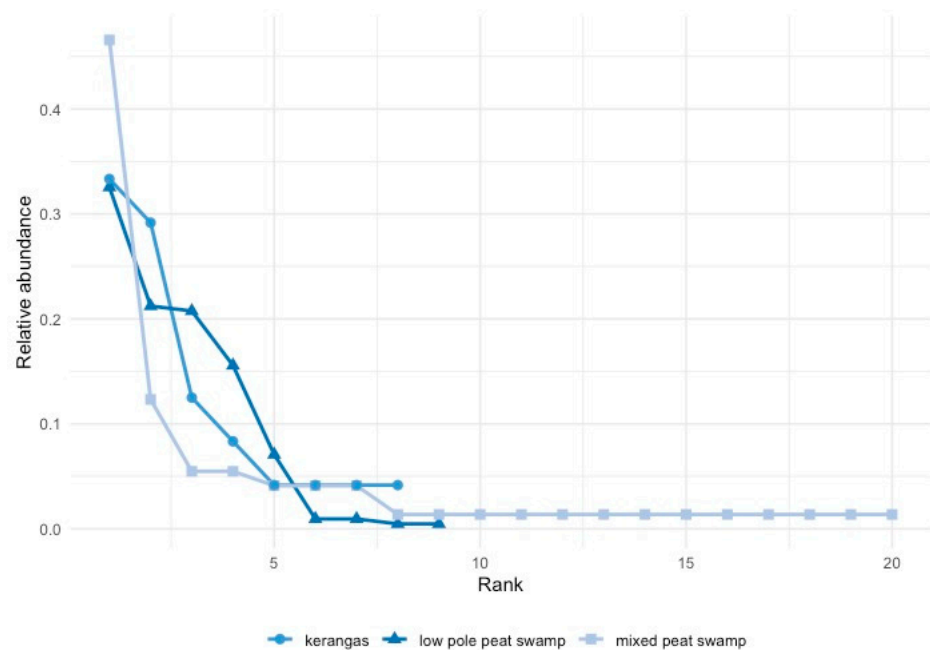


**Figure 4.** Suborder abundance with standard errors (SE) for habitat-types mixed peat swamp, kerangas, and low pole peat swamp forests.

A rank–abundance graph shows high dominance at higher ranks across all habitats, as illustrated by a steep gradient (Figure 5), due to the dominance of certain species relative to other species present. However, at lower ranks, dominance is low, with mixed peat swamp exhibiting a large number of rarer (low dominant) species (Figure 5). Across habitat types, the rank abundance graph follows a similar trend, although a less steep drop from dominant to rare species; which we would expect for the entire study area, clearly showing how some species are abundant (proliferating) while others appeared relatively rare as indicative by the presence of many singletons (one individual of a species) (Figure 5). Each habitat harbored a different set of dominant species (between  $1 \leq n \leq 3$  species). In mixed peat swamp, *Prodasineura* spp. (RA = 0.5), in kerangas—*Orchithemis xanthosoma* (RA = 0.3), *Amphicnemis triplex* (RA = 0.3) and *Ellatoneura aurantiaca* (RA = 0.2), and in low pole—*Brachygonia oculata* (RA = 0.4), *Brachygonia puella* (RA = 0.2) and *Ceriagrion* sp. (RA = 0.2) exceeded the 15% RA threshold (Figure A2). The Renkonen Percent Similarity Index from least to most similar, was in the order: mixed peat swamp vs. low-pole (6.73%), mixed peat swamp vs. kerangas (20.28%), and kerangas vs. low-pole (26.44%). Out of the 25 species captured, four species: one Zygoptera (*Amphicnemis triplex*) and three Anisoptera (*Brachygonia puella*, *Orchithemis xanthosoma*, and *Tyriobapta laidlawi*) were captured across all habitat types.

### 3.2. Environmental Variables

The average temperature and pH of the surface water across all habitat-types was 27.14 °C (SE =  $\pm 0.4$ ) and 4.3 (SE =  $\pm 0.56$ ), respectively. Canopy cover, from most dense to least dense was mixed peat swamp (M (lx) = 793.0, SE =  $\pm 104.5$ ), followed by kerangas (Mlx = 964.6, SE =  $\pm 82.0$ ), and then low pole (Mlx = 2916.9, SE =  $\pm 172.0$ ). A chi-square test of independence showed significant association between suborder and use of lotic (flowing water) or lentic (forest pools) habitats ( $n = 222$ ,  $df = 1$ ,  $X^2 = 53.0$ ,  $p < 0.001$ ; Phi ( $\phi$ ) = 0.5,  $p < 0.001$ ), where 95% of Anisoptera sampled showed strong association with forest pools and 5% of Anisoptera for flowing water. However, within the suborder Zygoptera, no significant difference was found between selection of forest pools (49.6%) or flowing water (51.4%).



**Figure 5.** Rank-abundance graph (Anisoptera and Zygoptera) for the three studied habitat types: mixed peat swamp, kerangas, and low pole peat swamp. The steep slopes observed at lower ranks are due to the presence of dominant species, while the long tails observed at lower ranks are due to the presence of singletons (single individuals of a species).

### 3.3. Species Characteristic Data

The results of GLMs comparing morphological characteristics between habitat type for each suborder are provided in Table 1. Controlling for variation across habitat types, Anisoptera had shorter body length than Zygoptera (Est =  $-0.512$ ; SE =  $0.020$ ;  $p < 0.001$ ;  $n_A = 101$ ,  $n_Z = 122$ ). However, Anisoptera showed significantly larger thoraxes than Zygoptera (Est =  $0.286$ ; SE =  $0.254$ ;  $p < 0.001$ ;  $n_A = 103$ ,  $n_Z = 124$ ), and a significantly greater hind wing to body ratio (Est  $0.498$ ; SE =  $0.0174$ ;  $p < 0.001$ ;  $n_A = 102$ ,  $n_Z = 122$ ). There was no significant difference in hind wing length between suborders.

**Table 1.** The statistical test results of the generalized linear models (GLMs) for morphological traits body length, thorax length, hind wing length, and hindwing-to-body ratio compared across habitat types—mixed peat swamp (MPS), low pole (LP), and kerangas (K), and controlling for suborder—Anisoptera (A) and Zygoptera (Z). The estimate is the marginal difference between the first habitat compared to the second. Significant differences found are bolded.

Morphological Trait	Habitat Comparison	Suborder	Estimate	Standard Error	df	t Ratio	p Value
Body	LP-MPS	Z	0.025	0.022	217	1.16	0.478
	LP-K	Z	$-0.053$	0.041	217	$-1.293$	0.4
	MPS-K	Z	$-0.079$	0.042	217	$-1.883$	0.146
	LP-MPS	A	$-0.217$	0.046	217	$-4.753$	<b>0.001</b>
	LP-K	A	$-0.255$	0.035	217	$-7.37$	<b>0.001</b>
	MPS-K	A	$-0.038$	0.054	217	$-0.703$	0.762
Thorax	LP-MPS	Z	$-0.005$	0.028	221	$-0.186$	0.981
	LP-K	Z	0.088	0.054	221	1.632	0.235
	MPS-K	Z	0.093	0.054	221	1.711	0.203
	LP-MPS	A	$-0.141$	0.053	221	$-2.668$	<b>0.022</b>
	LP-K	A	$-0.198$	0.045	221	$-4.4$	<b>0.001</b>
	MPS-K	A	$-0.057$	0.065	221	$-0.869$	0.66



Table 1. Cont.

Morphological Trait	Habitat Comparison	Suborder	Estimate	Standard Error	df	t Ratio	p Value
Hindwing	LP-MPS	Z	−0.012	0.028	216	−0.421	0.907
	LP-K	Z	−0.086	0.053	216	−1.622	0.238
	MPS-K	Z	−0.074	0.053	216	−1.39	0.348
	LP-MPS	A	−0.248	0.055	216	−4.531	<b>0.001</b>
	LP-K	A	−0.256	0.044	216	−5.807	<b>0.001</b>
	MPS-K	A	−0.008	0.066	216	−0.126	0.991
Hindwing:Body	LP-MPS	Z	−0.068	0.019	218	−3.55	<b>0.001</b>
	LP-K	Z	−0.051	0.035	218	−1.481	0.302
	MPS-K	Z	0.017	0.035	218	0.479	0.881
	LP-MPS	A	0.039	0.036	218	1.084	0.525
	LP-K	A	0	0.03	218	−0.004	1
	MPS-K	A	−0.039	0.044	218	−0.882	0.652

In comparing habitat types, Anisoptera assemblages in low pole were significantly smaller by body, thorax, and hindwing measurements compared to Anisoptera assemblages in kerangas and mixed peat swamp. These patterns did not hold for Zygoptera assemblages, in which the only significant difference across habitats was that the hind wing-to-body ratio for Zygoptera assemblages in low pole was lower than the ratio for the Zygoptera assemblage in mixed peat swamp (Table 1).

#### 4. Discussion

##### 4.1. Diversity, Abundance, and Communities

Our results of the present study indicate that Odonata diversity, abundance, and distribution patterns, and composition observed are shaped by a number of interplaying factors such as habitat characteristics, undergrowth vegetation, ecosystem productivity, body size and body size induced ecophysiological constraints, and the presence of habitat specialists.

The divergence observed between trends in species diversity and abundance was unexpected, i.e., species diversity from greatest to lowest was in the order: mixed peat swamp > kerangas > low pole, whilst abundance, from greatest to lowest, was in the order: low pole > mixed peat swamp > kerangas. Given the importance of vegetation to Odonata and its role as a structural constituent [18,31,32], we expected species diversity to be positively related with increased undergrowth vegetation. Instead, based on data from a previous study [44], undergrowth vegetation was most abundant in low pole, which showed the lowest species diversity, but the highest abundance in both suborders. According to Hykel et al. (2020) [32], only certain habitats with specific physical structure can provide suitable conditions for perching. Building on this, we can suggest that the abiotic conditions (or habitats structural features) in low pole were suitable in providing sufficient perching structures, given that 62% of the captures in low pole can be described as characteristic perchers, which are typically small odonates [14,64]. This is coherent with our results in that the Anisoptera assemblage in low pole showed significantly smaller body, hind wing, and thorax lengths, as compared to the Anisopteran assemblages in kerangas and mixed peat swamp habitat.

Another factor potentially limiting species diversity and abundance is that of ecosystem productivity. Typically, there exists a relationship between species diversity and ecosystem productivity, with more productive ecosystems supporting a higher species diversity and abundance [65]. Based on previous studies in the region, ecosystem productivity was found to be the highest for mixed peat swamp and the lowest for low pole [44,66]; a trend consistent with that of Odonata species diversity observed herein. However, the dissonance observed between species diversity and abundance implies that other factors in addition to vegetation and productivity are at play in determining the species diversity and abundance between the habitat types in the study area.

Body size is the nexus that links shade and thermoregulatory behavior in odonates. The difference in size between dragonflies and damselflies, with, generally speaking, the former being larger than the latter [14,64], leads to contrasting ecophysiological requirements related to thermoregulation and varying propensities for dispersal [23,26,35]. This results in different distribution patterns and habitat choice between the suborders. Most damselflies are small “thermal conformers” that exchange their heat with their environment via convective heat exchange [64], which is dependent on their surface-to-volume ratio and leaves them susceptible to overheating and dehydration. Therefore, in our lowland site close to the equator, lower temperatures, such as in areas covered by dense forest canopy, as observed in mixed peat swamp habitat, are likely to favour many species of Zygoptera [23,67,68], with over 80% of damselfly species confined to and living around streams covered by dense vegetation [68]. Furthermore, the restriction of species of this suborder to one area or habitat is not uncommon, as many species show high degrees of habitat specialization [14,69,70]. Thus, ecophysiological constraints and the tendency of the damselfly species found in mixed peat swamp to remain confined to mixed peat swamp habitat (i.e., showing high degrees of habitat specialization), likely explained the low homogenization in species assemblages observed between mixed peat swamp and low pole, and the five-fold increase in damselfly species recorded in mixed peat swamp habitat.

On the contrary, despite the ecophysiological constraints many species of the suborder Zygoptera face [23], low pole supported two species—*Amphicnemis triplex* and *Ceriagrion* sp., which were abundantly present. This is because within the suborder Zygoptera, there exists a continuum in families that are true habitat specialists to families that are true habitat generalists. Both *A. triplex* and *Ceriagrion* sp. represent the family Coenagrionidae, known to include the most ubiquitous species that are highly abundant and dominant in open, highly illuminated habitats with stagnant water [71]. Interestingly, although both species belong to the same ubiquitous family, *A. triplex* was captured across all habitat types, whereas *Ceriagrion* sp. was exclusively confined in its distribution to low pole peat swamp habitat. Therefore, it is likely that other species-specific factors such as resource preference [23], may explain the observed distribution pattern in *Ceriagrion* sp. Unlike Anisoptera, there was no consistent patterns across morphological traits in Zygopteran species assemblages between habitat-types. However, it is uncertain what explains the significant differences found in the hindwing-to-body ratio between the Zygopteran assemblages found in low pole and mixed peat swamp; with this not being further investigated in this study.

Anisoptera are largely endotherms or heliotherms [14,64]. Heliotherms exchange heat with their environment via irradiation heat exchange, which is dependent only on the surface area exposed to the sun [64]: a mechanism characteristic of many percher species [64]. Increased luminosity favors species of this suborder, as they require high ambient temperatures to become active, while shaded environments are found to restrict and reduce the occurrence and abundance of many species of dragonfly [27,72,73]. The greater relative abundance of Anisoptera in low pole is thus likely to be attributed to the accentuated luminosity that arises from the characteristic low forest canopy [44,74], and also likely explains the reduced abundance of Anisoptera in the more shaded mixed peat swamp and kerangas habitats. Additionally, the uneven peaty forest floor and permanently high water-table in low pole [14,74] leads to the formation of forest pools of varying depths and sizes, a habitat characteristic ideal for many species of Anisoptera [18,75].

The degree of similarity observed between Odonata species assemblages in kerangas and low pole was due to the overlap in Anisoptera species, with all species sampled in kerangas also being found in low pole. This is perhaps surprising, considering how different kerangas and low pole habitats are in terms of their biotic and abiotic characteristics [44,48,74]. However, the ability to tolerate a wide range of environmental conditions is not uncommon within the suborder Anisoptera, as many species are generalists [23,67,73]. The dissimilarity in species assemblages found between low pole and mixed peat swamp is likely to be primarily due to the presence of habitat specialists. Specialists increase the diversity and abundance found within a habitat type as they show distinct habitat prefer-

ences [76]. The most abundant species in low pole—*Brachygonia oculata* and *Brachygonia ophelia* (Libellulidae)—are peat swamp specialists, along with *Brachygonia puella* (Libellulidae), another species that favors open and marshy low pH habitat [38]. These species accounted for ~62% of the total captures of Odonata (Anisoptera and Zygoptera) in low pole, a substantial amount, considering that nine species were found all together. This argument is further substantiated given that both habitat types – mixed peat swamp and low pole, differed greatly in their suborder ratio, in line with the well-established thesis that both Anisoptera and Zygoptera show contrasting ecophysiological requirements [23]. The significantly smaller Anisoptera in low pole compared to mixed peat swamp likely indicates that Anisoptera species between these two habitat-types exhibit differing thermoregulatory abilities, and thus different habitat selection strategies [23,26,35]. These results align with those of many studies showing variations in community structure and composition between suborders because of their contrasting ecophysiological requirements [14,23,69,72].

#### The Role of Mixed-Mosaic Habitat Structure on the Odonata Community in Kerangas

Kerangas occupies the largest proportion of the forest area in the KHDTK study site (33.8%) [44]. Yet, the species diversity and abundance of Odonata was relatively low here, with no species sampled unique to the habitat-type. A similar result was found by Orr [46], where only 4.4% of the total Odonata identified were represented in kerangas, with none found strictly limited to the habitat-type. Orr [77] found that kerangas formations neighboring swamp forests often harbor swamp species which establish feeding territories at high abundance. This was also observed in our study, in which species such as *Brachygonia puella* (Libellulidae) and *Brachygonia ophelia* (Libellulidae) were found in high abundance in adjacent low pole peat swamp habitats in addition to their presence in kerangas.

The rarity of surface water and undergrowth vegetation may explain the low abundance of Odonata observed in kerangas [25,32,44], although fleeting surface water may attract some species [45]. The dense forest canopy of kerangas likely further discourages the presence of many Anisoptera species [27]. Most female Odonata must be close enough to water to lay their eggs, but they do not typically remain near water throughout most of their adult life, while males of many species establish and defend territory near water to find prey and mates [32]. It is likely that this role differentiation in sexes of Odonata explains the relatively higher proportion of females sampled relative to males in Kerangas [32]. However, the question remains as to whether these species would be present if not for the mosaic nature of the landscape? For example, species such as *Elatoneura aurantiaca* (Protoneuridae) and *Vestalis* sp. (Calopterygidae) were found associated with mixed peat swamp habitat interspersed along the kerangas transect and were not captured anywhere outside of these zones. Similarly for species such as *Brachygonia puella* (Libellulidae) and *Brachygonia Ophelia* (Libellulidae). Furthermore, according to Orr [40], kerangas tends to support shade-loving stenotopic Odonata species with a high number of Bornean endemics. The species with the highest abundance in kerangas were *Orchithemis xanthosoma* (Libellulidae), *Amphicnemis triplex* (Coenagrionidae), and *Brachygonia puella* (Libellulidae): the first two are Bornean endemics, with the latter being endemic to Indonesia [78]. Thus, it appears from the previous literature and from our results, that kerangas is likely to function more as a tertiary habitat type. Alternately, kerangas could be suitable to support species such as those that oviposit in phytotelmata (for example *Lyriotheis cleis*—which was spotted outside of survey transects). However, for the majority of the species that lay their eggs in water or aquatic plants, kerangas is likely to provide refuge or shelter sites, or areas for roosting or breeding—for example, almost 50% of the *O. Xanthosoma* females captured had eggs at their abdomen (personal observation); thereby explaining the higher degree in similarity of Odonata assemblages between low pole and mixed peat swamp, and kerangas.

#### 4.2. Morphology, Dispersal, and Habitat Selection

Here we find that morphological traits associated with increased dispersal and larger range size were in accordance with suborder habitat selection, with Odonata that showed

larger morphological traits selecting for more lentic habitats, while Odonata that showed smaller morphological traits selecting for more lotic habitats.

Odonata species are either associated with lentic or lotic habitats, and those species in unpredictable habitats need a greater ability to disperse to ensure the survival of populations [79,80]. Therefore, Odonata species adapted to lentic habitats would require larger thorax and wing morphology, which would allow them to disperse better than species adapted to more lotic (reliable) habitats [37,80]. Within the Odonata communities in KHDTK, Anisoptera showed a greater use of forest pools (lentic sources), while Zygoptera showed a greater use of flowing water (lotic sources). As lentic sources are considered more uncertain habitats than lotic sources [80], this was in accordance with the differences in morphological traits observed between the suborders in our study. An increased thorax size implies better dispersal capacity as a larger thorax has more space available for thoracic musculature, and therefore greater power output [81]. This is also coherent with hindwing lengths observed, in which Anisoptera showed larger hindwings relative to Zygoptera, given that wing morphology is also an important determinant of dispersal capacity [35]. However, Rundle et al. [82] suggested that when hindwing length relative to body length was used (HWL/BL), it was more indicative of range size (i.e., distributional range or site occupancy), as a greater HWL/BL ratio is positively associated with enhanced flight performance and dispersal [37,82]. This, we also found, in that Anisoptera exhibited significantly larger HWL/BL ratios as opposed to Zygoptera, which was in line with suborder habitat selection patterns observed.

There is very little published information available on the migration patterns of southern Asian Odonata [83] and on the ecology of Borneo Odonata species. Due to this we have been unable to consider the potential influence of (seasonal) migrations in our study. Although, we expect this to be relatively low, given Borneo's relatively aseasonal climate and that many Borneo Odonata species are endemic to the island [38]; we did, however, notice over the duration of the study, potential community shifts which may be an indication of migration. Thus, we would nevertheless recommend that future Odonata researcher in the area attempt to address this topic.

## 5. Conclusions

Diversity, abundance, and distribution patterns, and composition observed in KHDTK are shaped by a number of interplaying factors such as contrasting habitat characteristics, undergrowth vegetation, ecosystem productivity, body size and body size induced ecophysiological constraints, and the presence of habitat specialists. These factors are further exemplified due to the heterogeneity of the lowland mixed mosaic kerangas forest studied herein—in that, despite habitat type being so closely located with each other strong Odonata population dynamics exist—with KHDTK thereby supporting a greater species diversity and abundance of Odonata than one habitat alone could harbor. This in turn led to different habitat selection strategies and resource use patterns observed in the Odonata fauna in KHDTK. Furthermore, despite kerangas being the most dominant habitat in KHDTK, this habitat type appears to largely serve as a tertiary habitat. We hypothesize that poor undergrowth vegetation and a scarcity of water restricts many species of Odonata from thriving in this habitat. Lack of water, combined with proximity to other habitats, also likely explained the higher proportion of females to males sampled in this habitat relative to low pole and mixed peat swamp habitats. These variables also likely explain why kerangas not only showed similar degree in overlap in species assemblages with low pole and mixed peat swamp, but also as to why this habitat type lacked a unique subset of dominant species; thereby advancing our knowledge on the association between Odonata fauna and kerangas (heath) habitat type.

Considering how poorly researched and under-represented kerangas are, in addition to the rapid threats that kerangas-dominated mosaic habitats face on Borneo, the findings of this study suggest that heterogeneous areas such as these are worth protecting given the substantial biodiversity it supports. We thereby urge policy to protect the larger Rungan

landscape, as except for KHDTK, the landscape continues to have an unprotected status. We suggest that more extensive research into Odonata communities and their association with kerangas (heath) habitat types need to be carried out to further understand the role of Kerangas within the wider heterogeneous habitat structure. A factor not accounted for in this study but could be of relevance is the relationship between Odonata species diversity and riparian vegetation, which includes aquatic, emergent, and marginal vegetation, and macrophytes, as the literature suggests there to be a positive relationship between Odonata and riparian vegetation; considering the presence of such vegetation in mixed peat swamp. Further, a full year survey analysis with more transects over a larger spatial extent could better take seasonality and spatial correlations into account, thereby also accounting for potential migrations. This could lead to a better representation of the Odonata diversity within KHDTK, as this heterogeneous landscape undoubtedly supports a higher species richness and abundance than sampled herein.

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## Appendix A

**Table A1.** The rationale behind as to why it was not possible to include species as random effect due to small sample sizes recorded across all habitat types: Kerangas (heath), low pole peat swamp, and mixed peat swamp.

Habitat Type	Suborder	Number of Species with at Least 5 Measured Records
Kerangas	Z	1
	A	1
Low pole peat swamp	Z	2
	A	3
Mixed peat swamp	Z	2
	A	0

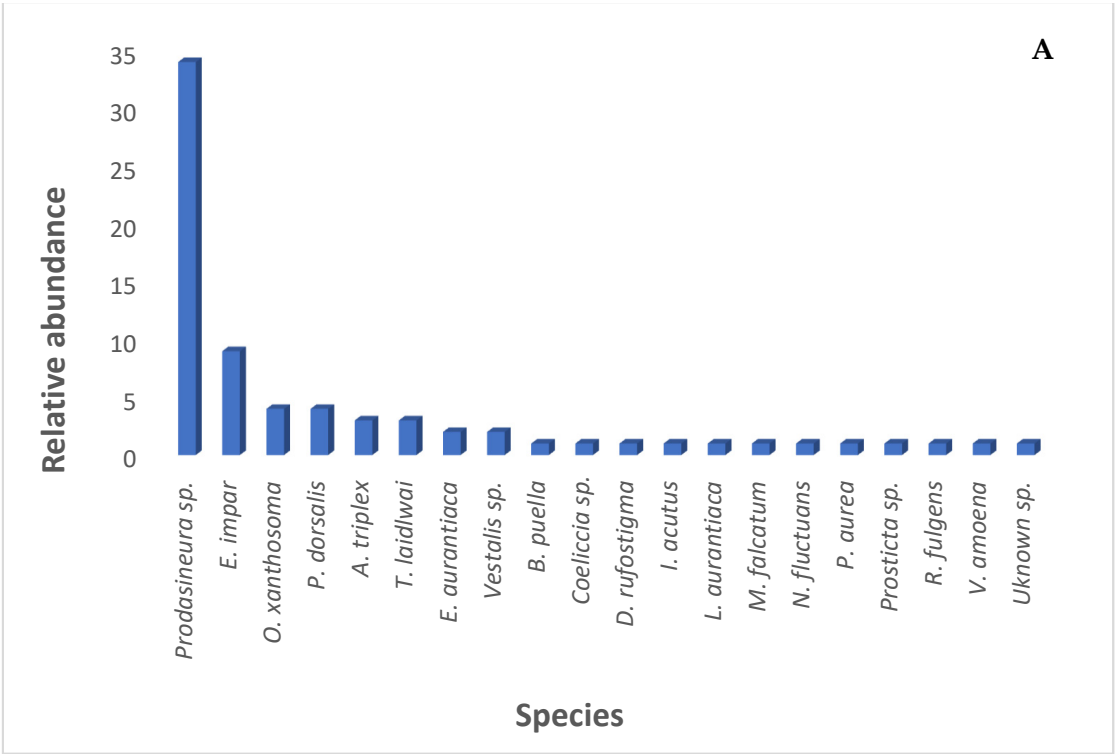


**Table A2.** A complete species list of all Odonata captured within Kawasan Hutan Dengan Tujuan Khusus. This list includes species captured within surveyed transects (\*) and those captured outside of surveyed transects.

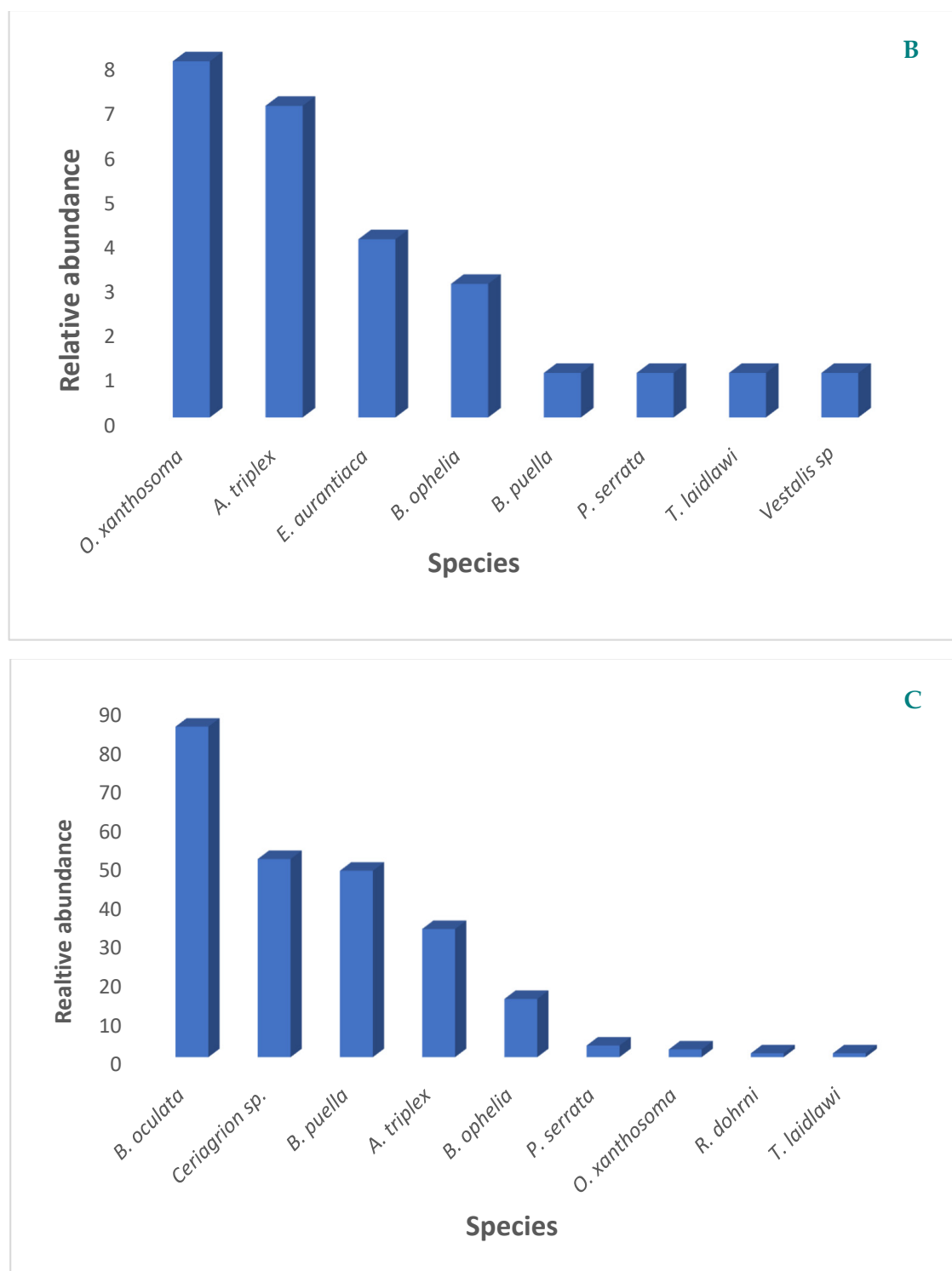
No	Suborder	Family	Genus	Species	Mixed Peat Swamp	Kerangas	Low Pole Peat Swamp
1	Anisoptera	Gomphidae	<i>Ictinogomphus</i>	<i>acutus</i> *	x		
2	Anisoptera	Gomphidae	<i>Leptogomphus</i>	<i>coomansi</i>			
3	Anisoptera	Libellulidae	<i>Agrionoptera</i>	<i>sexlineata</i>		x	
4	Anisoptera	Libellulidae	<i>Brachygonia</i>	<i>oculata</i> *			x
5	Anisoptera	Libellulidae	<i>Brachygonia</i>	<i>ophelia</i> *		x	x
6	Anisoptera	Libellulidae	<i>Brachygonia</i>	<i>puella</i> *	x	x	x
7	Anisoptera	Libellulidae	<i>Lyriothemis</i>	<i>cleis</i>		x	
8	Anisoptera	Libellulidae	<i>Nannophya</i>	<i>pygmaea</i>	x		
9	Anisoptera	Libellulidae	<i>Neurothemis</i>	<i>fluctuans</i> *	x		
10	Anisoptera	Libellulidae	<i>Orchithemis</i>	<i>xanthosoma</i> *	x	x	x
11	Anisoptera	Libellulidae	<i>Orthetrum</i>	<i>chrysis</i> *			
12	Anisoptera	Libellulidae	<i>Orthetrum</i>	<i>sabina</i>			
13	Anisoptera	Libellulidae	<i>Pornothemis</i>	<i>serrata</i> *		x	x
14	Anisoptera	Libellulidae	<i>Raphismia</i>	<i>inermis</i>			
15	Anisoptera	Libellulidae	<i>Rhyothemis</i>	<i>obsolescens</i>		x	
16	Anisoptera	Libellulidae	<i>Rhyothemis</i>	<i>fulgens</i> *	x		
17	Anisoptera	Libellulidae	<i>Risioephlebia</i>	<i>dohrni</i> *			x
18	Anisoptera	Libellulidae	<i>Tramea</i>	<i>phaeoneura</i>			
19	Anisoptera	Libellulidae	<i>Tramea</i>	<i>transmarina</i>			
20	Anisoptera	Libellulidae	<i>Tyriobapta</i>	<i>laidlawi</i> *	x	x	x
1	Zygoptera	Calopterygidae	<i>Vestalis</i>	<i>amoena</i> *	x		
2	Zygoptera	Calopterygidae	<i>Vestalis</i>	sp. *	x	x	
3	Zygoptera	Chlorocyphidae	<i>Libellago</i>	<i>aurantiaca</i> *	x		
4	Zygoptera	Chlorocyphidae	<i>Pachycypha</i>	<i>aurea</i> *	x		
5	Zygoptera	Coenagrionidae	<i>Aciagrion</i>	<i>borneense</i>			
6	Zygoptera	Coenagrionidae	<i>Agriocnemis</i>	<i>minima</i>			
7	Zygoptera	Coenagrionidae	<i>Amphicnemis</i>	<i>triplex</i> *	x	x	x
8	Zygoptera	Coenagrionidae	<i>Archibasis</i>	<i>melanocyana</i>			
9	Zygoptera	Coenagrionidae	<i>Ceriagrion</i>	<i>cerinorubellum</i>			
10	Zygoptera	Coenagrionidae	<i>Mortonagrion</i>	<i>falcatum</i> *	x		
11	Zygoptera	Coenagrionidae	<i>Pseudagrion</i>	<i>coomansi</i>			
12	Zygoptera	Coenagrionidae	<i>Ceriagrion</i>	sp. *			x
13	Zygoptera	Euphaeidae	<i>Dysphaea</i>	<i>dimidiata</i>			
14	Zygoptera	Euphaeidae	<i>Euphaea</i>	<i>impar</i> *	x		
15	Zygoptera	Megapodagrionidae	<i>Podolestes</i>	<i>atomarius</i>			x
16	Zygoptera	Platycnemididae	<i>Coeliccia</i>	sp. *	x		
17	Zygoptera	Platystictidae	<i>Drepanosticta</i>	<i>rufostigma</i> *	x		
18	Zygoptera	Platystictidae	<i>Protosticta</i>	sp. *	x		
19	Zygoptera	Protoneuridae	<i>Elatoneura</i>	<i>aurantiaca</i> *	x	x	
20	Zygoptera	Protoneuridae	<i>Prodasineura</i>	sp. *	x		
21	Zygoptera	Protoneuridae	<i>Prodasineura</i>	<i>dorsalis</i> *	x		
22	Zygoptera	Not known	Unknown	sp. *	x		



**Figure A1.** A photo plate of a few sampled species: (A) *Amphicnemis triplex* (male) (B) *Rhyothemis obsolescens* (male), (C) *Vestalis amoena* (male), (D) *Pachycypha aurea* (female), (E) *Neurothemis fluctuans* (male), (F) *Ceriagrion* sp.; one of the two species of damselfly captured in low pole peat swamp and present in high abundance, and which is potentially new to science.



**Figure A2.** Cont.



**Figure A2.** Relative-abundance of Odonata species in habitat-types (A) mixed peat swamp, (B) kerangas, and (C) low pole peat swamp habitat.

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