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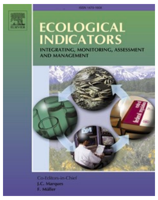

Original Articles

Damselflies and dragonflies in distress: The impact of forest fires and logging on odonate assemblages

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ABSTRACT

We assessed the impact of logging and forest fires on the species richness, evenness, and structure of odonate assemblages located on the island of Borneo. Landscape-scale species richness was highest in unburnt and once-burnt landscapes and lowest in two landscapes subjected to multiple burn events. These landscapes also had lower evenness compared to primary and once-burnt landscapes, highlighting the detrimental effects of repeated burn events on odonate species assemblages. There was significant geographic distance dependence in three of the six landscapes studied including primary and burnt landscapes. Odonate assemblages, furthermore, did not significantly deviate from Hubbell's neutral model predictions at metacommunity and local scales in any of the landscapes. Finally, we identified a significant association between species traits and environmental conditions, which appeared to be largely driven by disturbance. Landscapes subjected to multiple burn events in particular were largely populated by species associated with standing water bodies and with large geographical distributions. Our study emphasises how disturbances like burning and logging are associated with shifts in species composition, favouring species associated with disturbed environments, while reducing the prevalence of endemic species.

1. Introduction

Tropical rainforests are among the most diverse ecosystems on earth (Novotny et al., 2006; Fujii et al., 2018; Pillay et al., 2022). Forests in general, and tropical rainforests in particular, furthermore, play critical roles in the global water cycle and influence local and regional precipitation patterns (Ellison et al., 2017). Deforestation can disrupt this cycle, leading to reduced rainfall and increased droughts in surrounding areas, which can affect agriculture and water availability (Lawrence and Vandecar, 2015; Lapola et al., 2023). Many modern medicines are, furthermore, derived from rainforest plants, including treatments for cancer, heart disease, and malaria (Newman & Cragg, 2016). Beyond ecosystem services, tropical rainforests contribute to the global economy through timber, non-timber products, and ecotourism (Kirkby et al., 2011). Despite their importance, tropical rainforests face severe threats from agriculture, logging, mining, and forest fires. In the Amazon, Southeast Asia, and Central Africa, large areas of rainforest have been, and are being, cleared for palm oil plantations, cattle ranching, and commercial logging (Foley et al. 2007; Laurance, 2010).

Once believed to be relatively fire-resistant due to their high humidity, tropical rainforests are increasingly experiencing devastating fires (Uhl & Kauffman 1990; Barlow & Peres 2004; Nepstad et al., 2004; Aragão et al., 2008; Field et al., 2009; Gaveau et al., 2014; Brando et al., 2020). Intense El Niño-Southern Oscillation (ENSO) events (Cochrane 2003; Brando et al., 2020), logging and other human activities, which open up the forest, have contributed to the rise in tropical forest fires (Lindenmayer et al. 2009). These fires have severe consequences for both the environment and local communities. When tropical forests burn, they release vast amounts of noxious compounds into the atmosphere (Kunii et al. 2002; Radojevic 2003). Once tropical forest fires are ignited during ENSO events, they create feedback loops that further enhance fire risk. Fires reduce forest canopy cover, increasing sunlight

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penetration, which in turn dries out the forest floor, making it more flammable (Cochrane and Laurance, 2008). While ENSO events and fires are natural phenomena, human activities amplify their effects and impacts. Logging, deforestation, land-use change, and the intentional use of fire for agricultural purposes increases the vulnerability of forests to fire during ENSO events (Cochrane, 2003). The loss of forests also disrupts ecosystems, leading to biodiversity loss, and soil erosion (Foley et al. 2007; Guillaume et al. 2015).

The island of Borneo, which hosts one of the most biodiverse tropical rainforests in the world (de Bruyn et al., 2014), has been significantly impacted by forest fires during ENSO events (Siegert et al., 2001). The interplay between human activity and ENSO-induced climate variability has, furthermore, created a cycle of recurrent fires in Borneo, with lasting ecological and environmental impacts. Fires in Borneo, especially during strong El Niño years including 1982–1983, 1997–1998, 2015–2016, and 2019, have devastated large tracts of tropical rainforest (Siegert et al., 2001; Chen et al., 2016; Sloan et al., 2017; Grosvenor et al., 2019). For example, the 1997–1998 fires destroyed approximately 5 million hectares of forest in the Indonesian province of East Kalimantan alone (Siegert et al. 2001; Page et al., 2002).

Odonates, commonly known as dragonflies and damselflies, are important bioindicators in tropical ecosystems due to their sensitivity to environmental conditions, particularly water quality and habitat structure (Suh and Samways, 2005; Butler and deMaynadier, 2008; Clausnitzer et al., 2009; Dolný et al., 2012; Simaika and Samways, 2012; da Silva Monteiro et al., 2015; de Moor 2017; Perron et al., 2021). Both larvae and adults rely on water for critical stages of their life cycle. Odonates can, therefore, provide valuable insights into the health of freshwater habitats and surrounding terrestrial environments. Many tropical odonate species are habitat specialists, with some showing preference for shaded forest streams while others thrive in open, sunlit ponds (Corbet, 1999). The habitat preferences of odonate species, whether for lotic (fast- or slow-flowing streams), or lentic (pools, ponds, or stagnant water) water bodies, furthermore, influence how they respond to environmental disturbances. While species richness and abundance generally decline in heavily polluted or degraded water bodies (Rueger et al., 1969), some odonate species show greater tolerance for disturbed habitats or poor water quality (Perron et al., 2021). They, furthermore, display high species richness and endemism, particularly in regions like Southeast Asia (Clausnitzer et al., 2009).

Odonates play a crucial role in tropical ecosystems as both predators and prey. As larvae, they are important predators of other aquatic organisms, including mosquito larvae, making them valuable in controlling vector populations (Akram et al., 2016; Córdoba-Aguilar et al., 2021). Despite their ecological importance, tropical odonates face several conservation challenges. Habitat loss due to deforestation, and pollution are major threats (Sánchez-Bayo and Wyckhuys 2019). The destruction of freshwater habitats, such as streams and wetlands, can lead to declines in odonate populations, especially those species that are habitat specialists (Clausnitzer et al., 2009). Odonates, for example, that prefer fast-flowing, oxygen-rich, brooks and rivers in forested habitat (Gibbons and Pain 1992; Kalkman et al., 2008; Letsch et al., 2016) are often more vulnerable to environmental disturbances (Doeg and Milladge, 1991; Jonsen and Taylor, 2000; Bilotta and Brazier, 2008; Luke et al., 2017; Cheri and Finn, 2023).

Another important habitat for odonates are the slow-flowing streams characteristic of lowland and marsh forest, which provide essential breeding, feeding, and resting areas (Szanyi et al. 2023). These habitats offer a rich variety of aquatic plants for egg-laying and the development of nymphs, as well as a high abundance of prey. Slowly-moving lowland forest and marshland streams also often have higher levels of productivity and biodiversity, contributing to complex food webs that benefit odonates (Juen et al., 2007). In addition to more permanent lotic habitat, certain species prefer ephemeral water sources such as forest pools or phytotelmata. Temporary pools are generally characterised by fluctuating water levels, low oxygen concentrations, and a lack of permanent predators, making them a specialised but attractive habitat for certain species (Corbet, 1999).

Odonates can also be found in association with a wide range of standing (lentic) water bodies including ponds, lakes, stagnant waters and artificial habitats such as drains and reservoirs. These habitats can vary greatly in terms of size, depth, and vegetation, making them suitable for a diverse array of odonate species, but are mainly found in open habitat with direct exposure to sunlight. Ponds also offer abundant marginal vegetation, which can be used for oviposition (Kalkman et al., 2008) and offer a balance between predator presence and resource availability, with elevated productivity and the prevalence of submerged and emergent vegetation, which provide suitable habitat for both adult odonates and their aquatic larvae (Juen et al., 2007). The transient and fragmented nature of standing water bodies may encourage dispersal among species with a preference for these habitats. This may reduce geographical isolation among populations and species occupying these water bodies may have large distributional ranges (Letsch et al., 2016). Because of their role as ecological indicators, odonates are increasingly being integrated into conservation and management strategies (Simaika and Samways 2011; Bush et al., 2013; Kalkman et al., 2018). Odonates are also easy to observe and comparatively easy to identify (although this does not apply to all odonate taxa) with numerous guides available from various locations.

Borneo is home to a rich variety of odonates (Orr, 2003). The diverse freshwater ecosystems of Borneo, from slow-moving lowland rivers to fast-flowing montane streams, provide a wide range of distinct habitats that support this high species diversity. Of the 371 species found on the island, 51 % are endemic (Dow et al. 2022). The percentages of endemics vary from 23 % for the Anisioptera (dragonflies) to 73 % for the Zygoptera (damselflies). Odonates in Borneo occupy a wide range of habitats, from peat swamp forests to montane streams. Some species are highly adaptable and can be found in disturbed habitats, such as agricultural fields and urban areas, whereas others are more restricted to intact forest environments (Luke et al. 2017).

In the present study, we sampled odonates from differentially-disturbed landscapes in Indonesian Borneo. The landscapes were sampled in a 5.2 million ha area, which has been severely affected by ENSO-induced drought and forest fire. Two large fragments of unburnt forest remained following the 1997/98 fires including a large unburnt fragment of 138 000 ha and a smaller fragment of 3 500 ha. In the larger fragment, we sampled one logged and one primary forest landscape. In the small fragment we sampled primary forest and three differentially-disturbed (once-, twice-, and frequently-burnt) landscapes surrounding this fragment. Having previously studied odonate beta diversity over a large spatial scale across multiple landscapes (Cleary et al., 2004), here we focused on landscape-scale patterns of beta diversity and alignment with neutral model predictions in addition to relating odonate species traits to environmental variables. The following hypotheses were tested. 1. We predicted lower diversity (species richness and evenness) in landscapes subjected to multiple disturbance (burn) events. 2. We predicted a significant association between geographic distance and odonate dissimilarity (geographic distance dependence) in disturbed (logged and burnt) landscapes, 3. we predicted significant deviations from Hubbell's neutral model predictions (Hubbell 2001) in disturbed (logged and burnt) landscapes, and 4. we predicted a significant association between odonate species traits (habitat preference, global distribution and size) and environmental conditions (forest structure) largely driven by disturbance (logging and forest fires). Hubbell's (2001) neutral model is a theoretical framework in ecology that proposes that individuals within a community, regardless of species, are functionally equivalent in terms of their fitness, birth, death, and dispersal rates. This means that ecological differences between species, which are central to niche theories, do not play a role in determining species abundance and distribution. Instead, stochastic processes, such as random births, deaths, speciation, and dispersal, drive the dynamics of biodiversity and species composition.

2. Material and methods

The field study took place from January to November 2000 in the Indonesian province of East Kalimantan (Borneo). Six landscapes were sampled, of which three were unburnt (two primary and one logged) and three subjected to previous burn events. All landscapes were situated between −0.9 and −1.2 decimal degrees latitude and 116 and 117 degrees longitude. See Supplementary data 1 for the location of all plots. Supplementary data 2 contains the raw data for all odonates recorded during the study. Supplementary data 3 contains information about the landscapes and plots.

The original vegetation of all landscapes was predominantly moist lowland dipterocarp forest in generally hilly terrain located less than 500 m above sea level. The landscapes were sampled in two main areas, namely, a 138 000 ha large unburnt isolate and a small 3 500 ha unburnt isolate in the Sungai Wain nature reserve and surrounding burnt forest (Cleary, 2003). In the small unburnt isolate, we sampled one primary forest landscape (P1S) and three burnt forest landscapes surrounding this isolate. The landscapes consisted of gentle hills and valleys, including areas of swamp forest, at relatively low altitudes (23 – 124 m asl). The landscapes surrounding the small unburnt isolate consisted of once-burnt forest in the burnt part of the Sungai Wain nature reserve (B1S; burnt for the first time during the 1997/98 ENSO event), twice-burnt forest in the proximate Wanariset research forest (B2S; burnt during the 1982/83 and 1997/98 ENSO events) and a frequently-burnt, predominantly grassland area located at Km 30 along the Balikpapan to Samarinda highway (B3S; Cleary, 2016). The frequently-burnt forest (B3S) was burnt so often that it mainly consisted of alang-alang (*Imperata cylindrica*) grasslands with a few remnant forest patches. In the large unburnt isolate, we sampled primary forest in the Gunung Meratus protected forest (P2L) and adjacent logged forest (L1L) (Cleary, 2017). The landscapes in the large unburnt fragment consisted of relatively steep hills at altitudes ranging from 146 – 236 m asl with faster-flowing small streams and rivers. L1L was logged in 1993/94. Logging was selective, extracting mainly dipterocarp species with a cutting cycle of 35 years. Detailed maps and spatial analyses of the impact of the 1997/98 ENSO event in eastern Borneo can be found in Siegert et al. (2001). The burnt forests in B1S and B2S were not uniformly burnt but had networks of remnant unburnt forest in the burnt forest matrix. These networks made up an estimated 10.6 % (B1S) and 8.1 % (B2S), respectively, of the total area in each landscape (Eichhorn, 2006) and were primarily found along the flood plain. Vegetation in these remnants was visually similar to unburnt forest (pers obs. DFRC).

2.1. Sampling

Sampling took place along 300-m transects demarcated with ironwood poles (Cleary, 2003). Transects were located in the field with compass and clinometer and georeferenced with a handheld GPS device (Garmin 12XL). Elevation was determined with an altimeter and the slope/inclination measured using a clinometer from a base position (Suunto, Vantaa, Finland). 16 randomly-allocated transects were sampled in each landscape. Odonates were sampled when encountered within 15 m on either side of the transect. The transect was traversed repeatedly on foot from one end to the other at a steady pace, which was only halted to collect specimens (Cleary, 2003). It is very difficult, if not impossible to identify many Bornean odonates on the wing. Individuals were, therefore, hand-netted and subsequently identified in the field. Sampling took place between 9:00 and 16:00 h, except during rain, using nets and with two people catching per plot. The date of capture and location were noted for each individual. Voucher specimens of all odonate species were placed in glassine envelopes and preserved (using silica gel) in an airtight container and later rechecked in Leiden by Jan van Tol. These have been deposited at Naturalis Biodiversity Center, Leiden, the Netherlands.

2.2. Environmental variables

In addition to sampling odonates in each 300-m transect plot, a single 200 m^2 (20 × 10 m) subplot was established and demarcated with ironwood poles along each transect. Trees (including all saplings greater than 1 cm dbh [diameter at breast height]) and lianas (greater than 1 cm dbh) higher than 1.3 m were sampled in the whole 200 m^2 plot following Cleary (2016, 2017). Herbaceous ground covering plants were sampled in a 2 × 2 m subplot nested within each larger 200 m^2 subplot and the percentage cover was estimated for each herbaceous species. The diameter at breast height (dbh) was measured and the height was estimated for all sampled trees and lianas. The following variables were included as environmental predictors: percentage grass cover, percentage herb cover, percentage fern cover, liana bamboo abundance, large liana abundance ($>$ 5 cm DBH), small liana abundance ($<$ 5 cm DBH), sapling abundance ($<$ 5 cm DBH), pole abundance (5 cm $<$ DBH $<$ 10 cm), tree abundance ($>$ 10 cm DBH), mean DBH, mean basal area, altitude (Alt) and percentage of the plot burnt (Fire).

2.3. Species traits

Odonate species were assigned to four habitat preference categories, namely species mainly found in lentic water bodies including ponds, drains, lakes, stagnant and other standing water bodies (Stand), species mainly found in forest pools (Pools), species mainly found in slow-moving forest streams in marsh and lowland forest (SlowSt), and species mainly found in fast-moving forest streams (FastSt). An example of an odonate species associated with marshland and slow-moving streams, *Tyriobapta torrida*, is shown in Supplementary data 4. Information on the habitat preferences of odonates was based on personal observations and validation using a wide range of sources including Laidlaw (1917), van Tol and Rashid (1995), Orr (2003), Dow (2010), and Orr et al. (2010). In addition to habitat preferences, species were categorised based on size (small: forewing length $<$ 25 mm *versus* large: forewing length $>$ 25 mm) and on geographic distribution (EndBor: endemic to Borneo, EndSun: Endemic to Sundaland, Moderate: distribution extending to Southeast Asia, Eastern Indonesia or the Philippines, and Wide: distribution extending to East Asia, Australia, India, Africa or beyond).

2.4. Statistical analyses

2.4.1. Diversity and geographic distance dependence

Odonate species, traits, geographic and environmental data matrices were imported into R (R Core Team, 2022). The number of species and Pielou's J evenness were assessed for each plot. Evenness was calculated using the diversity function from the vegan package and the log of observed species. For the odonate species data, a distance matrix was constructed using the Bray-Curtis index with the vegdist function in the vegan package in R (Oksanen et al., 2022). For geographic distance, a distance matrix was obtained using the earth.dist function from the fossil package. This creates a distance matrix of pairwise distances in kms between all pairs of plots within a landscape. Variation in odonate species composition among plots was visually assessed for each landscape with plots of pairwise dissimilarity as a function of the geographic distance between plots. The MRM function from the ecodist library in R was used with 1000 permutations to carry out regressions on distance matrices with the Bray-Curtis dissimilarity matrix as response variable and geographic distance as predictor variable. Species accumulation curves of species richness *versus* the number of individuals sampled were obtained for each landscape using the specaccum function from the vegan package with the method argument set to "rarefaction".

2.4.2. Neutral model

Hubbell's neutral model is often applied to a "metacommunity", which consists of multiple local communities connected by dispersal. Species are distributed across these local communities, and their presence in any particular community is determined by both local birth–death dynamics and the immigration and emigration of individuals from the broader metacommunity (Hubbell, 2001). The model posits that local biodiversity reflects the combined effects of local ecological drift and immigration from the metacommunity. Our study used a method developed by Harris et al. (2017) to test for deviations from neutral model predictions. This approach uses Bayesian inference to analyse data and test for significant deviations from neutral community predictions. The method of Harris et al. (2017) uses a hierarchical Dirichlet process and provides estimates of the fundamental biodiversity number θ and immigration rates (I). The parameter θ can be considered as the rate at which new species enter the metacommunity due to speciation (Harris et al., 2017). With higher values of θ, the more species accumulate in the metacommunity and the distribution becomes skewed towards species with lower abundances. Concomitantly, lower θ values indicate fewer species in the community because the balance tips towards fewer new species being formed or existing species going extinct. This can lead to a community with lower species richness and potentially more dominance by a few species because there are fewer opportunities for new species to establish. The method of Harris et al. (2017) provided more reliable estimates of θ and immigration rates than previous methods, e.g., Etienne (2009). To apply the Harris et al. (2017) method to our data, we first downloaded the NMGS-master folder, which can be obtained from https://github.com/microbiome/NMGS (last checked: 2024 09 05). For each landscape, comma-delimited species (rows) by sites (columns) tables were generated in R. These were used as input for NMGS. The output files consisted of simulated estimates of θ for the metacommunity of each landscape and immigration estimates for each plot. These were imported into R and mean, median, and standard deviations were calculated for θ and the immigration values of each plot. The output files also consisted of '_m' and '_s' files. We tested for deviations from neutral model expectations at the metacommunity and local scale for each landscape using the Sig.pl script from the Scripts folder in the C folder of the NMGS-master folder with./Scripts/Sig.pl 1 3 and./Scripts/Sig.pl 2 3, respectively, with the _m files as input.

In addition to the method of Harris et al. (2017), we also followed the approach of Maaß et al. (2014) where they developed a method to predict beta diversity and to test for deviations from neutral model predictions. In the present study, 999 simulated communities were generated. Beta diversity was assessed following Legendre and De Caceres (2013) and Maaß et al. (2014). If the observed beta diversity of a landscape fell outside the range of the simulated data sets, it was considered to have a higher (more dissimilar) or lower (more similar) beta diversity than expected by chance. Observed communities within the simulated range were considered to be consistent with neutral model dynamics. The results of these analyses are interpreted in the context of expected assembly processes resulting from the observed disturbance regimes. Mean beta diversities were calculated for each landscape and the histogram of these values plotted against observed beta diversity following Maaß et al. (2014).

2.5. RLQ analysis

RLQ analysis, as detailed by Dolédec et al. (1996), was used to link environmental conditions with species traits. This analysis integrates three separate ordinations of environmental variables (R), species composition (L), and species traits (Q). The method is implemented in R using the ade4 library (Dray and Dufour 2007). Here, species abundance data was analysed using correspondence analysis (CA) with the dudi.coa function. This was followed by principal components analysis of environmental variables using the dudi.pca function whereby the row.w argument consisted of a vector of row weights obtained from the species composition analysis. Species traits data were analysed using multiple correspondence analysis with the dudi.acm function whereby the row.w argument consisted of a vector of column weights obtained from the species composition analysis. Finally, the rlq function was used to perform a double inertia analysis of the R and Q arrays. This analysis maximises covariation between environmental factors (R) and species traits (Q) relating environmental variables to species traits symmetrically. The significance of the results was tested using the randtest function from the ade4 library, which performs permutation tests assessing the statistical significance of observed patterns by comparing them against random permutations of the data. In the present study, we tested models 2 (permutation of sites) and 4 (permutation of species). Unlike traditional approaches that link functional diversity to taxonomic diversity indirectly, RLQ analysis allows direct association between habitat differences and functional diversity. This makes RLQ analysis useful for conservation management, enabling the monitoring and prediction of land-use changes based on species traits and RLQ scores (Dolédec et al., 1996; Ribera et al., 2001, Dray et al., 2002; Hausner et al., 2003).

3. Results

We sampled a total of 96 plots across 6 differentially-disturbed landscapes. A total of 5633 odonate individuals and 85 species belonging to 13 families were sampled. Landscape scale species richness was highest in the landscapes P1S, L1L and B1S and lowest in the highly perturbed B3S (Fig. 1). Landscape richness was also higher in the logged L1L than the adjacent primary forest P2L. Landscapes subjected to multiple burn events (B2S and B3S) also had lower evenness than proximate primary and once-burnt landscapes (P1S and B1S) (Table 1). Evenness was also relatively low in the primary landscape P2L. There was significant geographic distance dependence in three of the six landscapes (B1S, B3S, and P1S) (Fig. 2 and Table 1). The variance in dissimilarity values between pairs of plots was, furthermore, greater in logged (L1L) than proximate primary forest (P2L).

None of the odonate communities deviated significantly ($p_N < 0.05$) from neutral model predictions at metacommunity or local scales although the odonate community in P2L was marginally non-significant

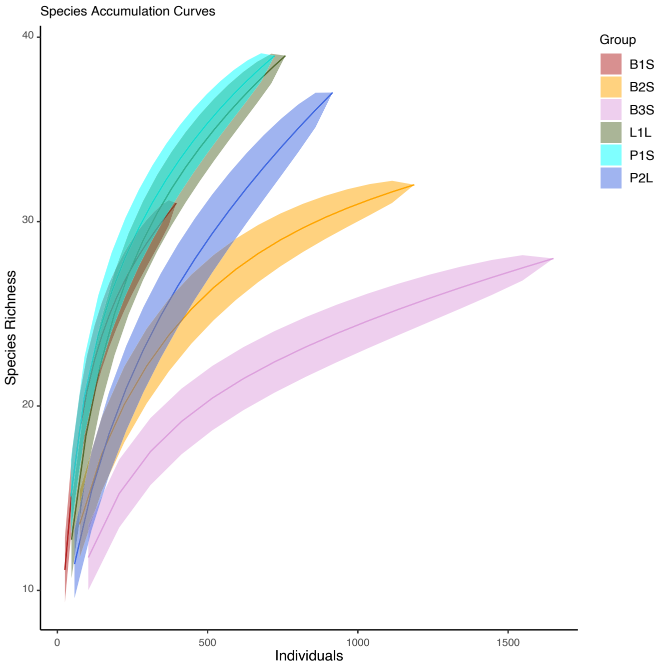

Fig. 1. Odonate species accumulation curves as a function of increasing numbers of individuals sampled. The curves represent once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in Meratus logging concession (L1L), primary forest in Sungai Wain nature reserve (P1S), and primary forest in Meratus logging concession (P2L).

Table 1

Summary statistics of the number of species, individuals, plots, species density, evenness, beta diversity, results of the MRM analyses, estimates of θ, immigration (I), and tests for significant deviations from neutral model predictions at metacommunity and local scales for once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in Meratus logging concession (L1L), primary forest in Sungai Wain nature reserve (P1S), and primary forest in Meratus logging concession (P2L).

	Variable	Reference	B1S	B2S	B3S	L1L	P1S	P2L
Total	Individuals		399	1630	1653	776	723	920
Total	Plots		16	16	16	16	16	16
Total	Observed species		32	36	30	41	39	39
Mean	Evenness		0.86	0.77	0.69	0.77	0.79	0.66
sd	Evenness		0.09	0.08	0.08	0.11	0.07	0.12
	Beta diversity		0.328	0.288	0.149	0.350	0.452	0.209
	MRM – F		**10.61**	4.76	**13.40**	1.94	**7.46**	0.02
	MRM – p		**0.006**	0.092	**0.008**	0.306	**0.026**	0.902
	MRM – R^2		**0.083**	0.039	**0.102**	0.016	**0.059**	0.000
Mean	θ	Harris	9.1	7.7	6.2	11.1	10.9	9.8
sd	θ	Harris	1.9	1.5	1.3	2.1	2.1	1.8
Mean	Immigration 'I'	Harris	46.5	29.9	40.4	40.3	27.0	42.3
sd	Immigration 'I'	Harris	21.9	25.8	29.5	30.3	18.5	40.0
median	Immigration 'I'	Harris	47.3	21.8	31.2	34.0	23.2	29.3
min	Immigration 'I'	Harris	1.4	0.6	9.9	5.5	5.2	1.8
max	Immigration 'I'	Harris	81.4	110.8	108.4	85.4	70.2	147.0
	Metacommunity p_N	Harris	0.420	0.389	0.151	0.194	0.503	0.053
	Local p_L	Harris	0.612	0.665	0.612	0.501	0.751	0.503

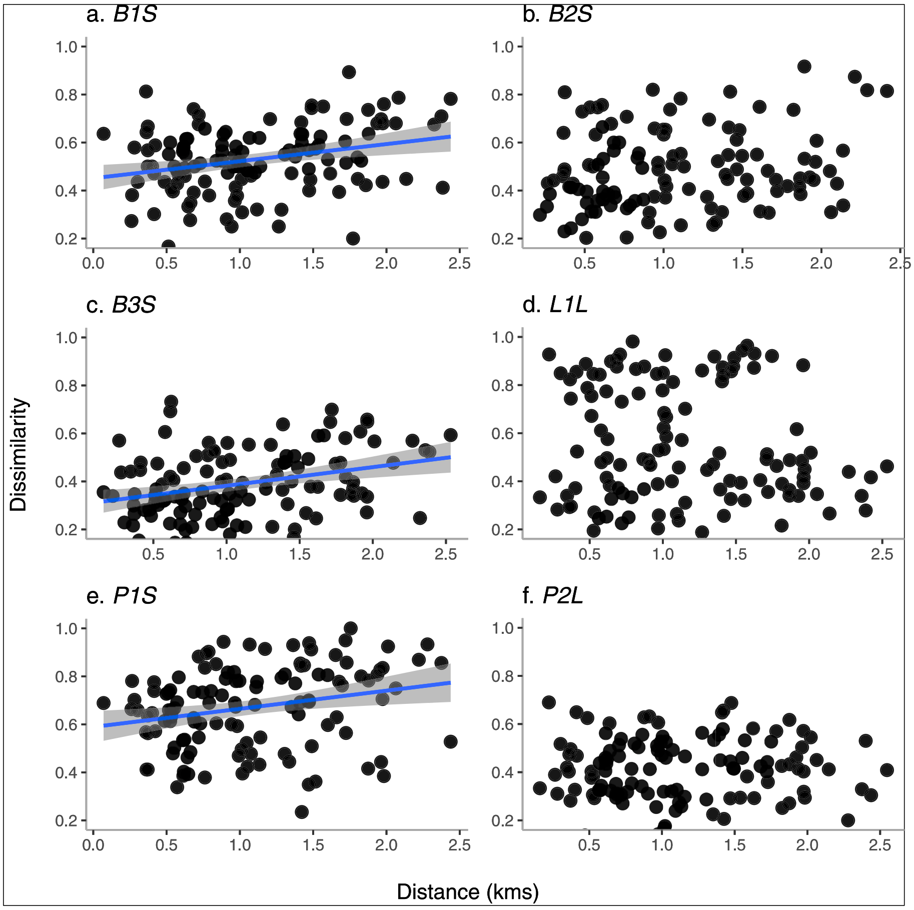

Fig. 2. Variation in dissimilarity as a function of geographic distance between sample plots for a. once-burnt forest (B1S), b. twice-burnt forest forest (B2S), c. frequently-burnt forest (B3S), d. logged forest in Meratus logging concession (L1L), e. primary forest in Sungai Wain nature reserve (P1S), and f. primary forest in Meratus logging concession (P2L).

($p_N = 0.053$; Table 1); θ values ranged from 6.2 ± 1.3 in B3S to 11.1 ± 2.1 in the logged L1L landscape (Table 1). The low θ values in B3S suggest lower richness and greater dominance, both of which are in line with the results pertaining to species richness and evenness. The number of species and evenness were both higher in the proximate unburnt landscape P1S, which had the second highest θ value. In and around the small unburnt fragment, θ declined from a high of 10.9 ± 2.1 in P1S to the previously mentioned low in B3S. Mean immigration values ranged from 27.0 ± 18.5 in P1S to 46.5 ± 21.9 in B1S (Table 1). Mean beta diversity values ranged from 0.149 in B3S to 0.452 in P1S (Fig. 3 and Table 1). In line with the results of the Harris et al. (2017) test, the results of the simulation analysis indicated that the odonate community of the P2L landscape was closest to significant deviation from neutral model predictions followed by the B3S landscape. The observed beta diversities of the other landscapes fell well within neutral model predictions.

Results of the RLQ analysis are presented in Fig. 4. The first axis of the species compositional and environmental analyses separated plots sampled in burnt landscapes from plots sampled in unburnt landscapes (Fig. 4a,b). The second axis separated unburnt plots sampled in the small unburnt fragment from those sampled in the large unburnt fragment. Two models were tested (with 999 permutations) permuting the rows of the R array (model 2) and permuting the rows of the Q array (model 4) (Fig. 4c,d). Both yielded highly significant results ($P < 0.001$) showing a strong association between odonate species traits and environmental parameters related to vegetation structure in addition to altitude and the percentage of a plot that burnt. The first two axes of the RLQ analysis (Eigenvalues: 2.1997 and 0.0497, respectively) explained 96.86 % and 2.19 %, respectively, of the total variance from the data matrix that crossed the site environmental characteristics and the species traits. In order to permit a detailed examination of the covariation of species traits and environmental variables, these are graphically displayed along the first two RLQ axes (Fig. 4e,f). At low RLQ axis-1 values, species, which were Bornean or Sundaic endemics or had a preference for slow-flowing streams or marshes were associated with forested areas with a greater abundance of palms, higher mean tree DBH and basal area. Species mainly found in pools (at low RLQ axis-2 values) were associated with greater numbers of saplings, poles, small lianas and trees whereas species mainly found around fast-flowing streams (at high RLQ axis-2 values) were associated with forested areas with greater numbers of larger lianas at greater altitudes. At high RLQ axis-1 values, species associated with standing water bodies and with a wide geographical distribution were associated with burnt plots, and a greater cover of grass and bamboo lianas.

The percentages of the 50 most abundant odonate species in each landscape are presented in Fig. 5. There are several interesting observations with respect to these species and their distributions across landscapes, which largely align with the results of the RLQ analysis. Restricting ourselves to the landscapes inside and outside the small unburnt fragment (B1S, B2S, B3S, and P1S), there was a clear loss of

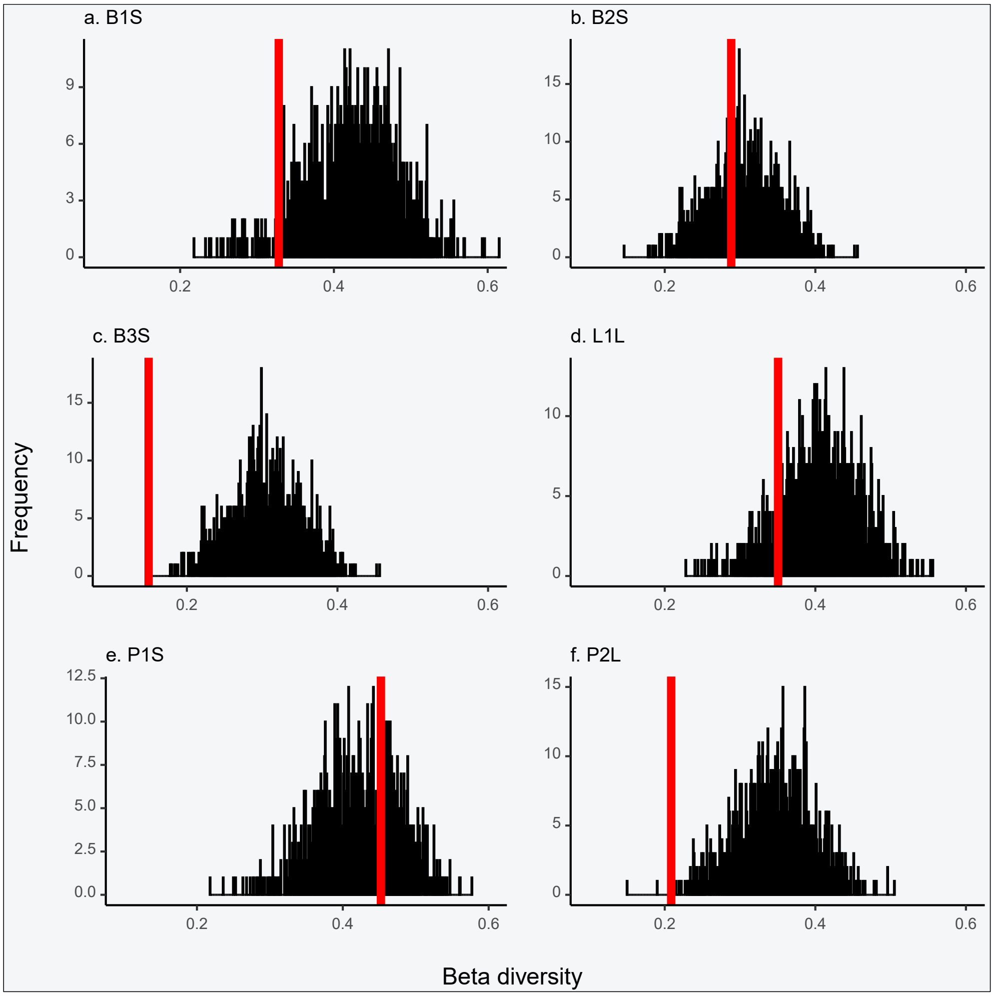

Fig. 3. Observed (red line) and simulated (histograms) beta diversity values for a. once-burnt forest (B1S), b. twice-burnt forest forest (B2S), c. frequently-burnt forest (B3S), d. logged forest in Meratus logging concession (L1L), e. primary forest in Sungai Wain nature reserve (P1S), and f. primary forest in Meratus logging concession (P2L).

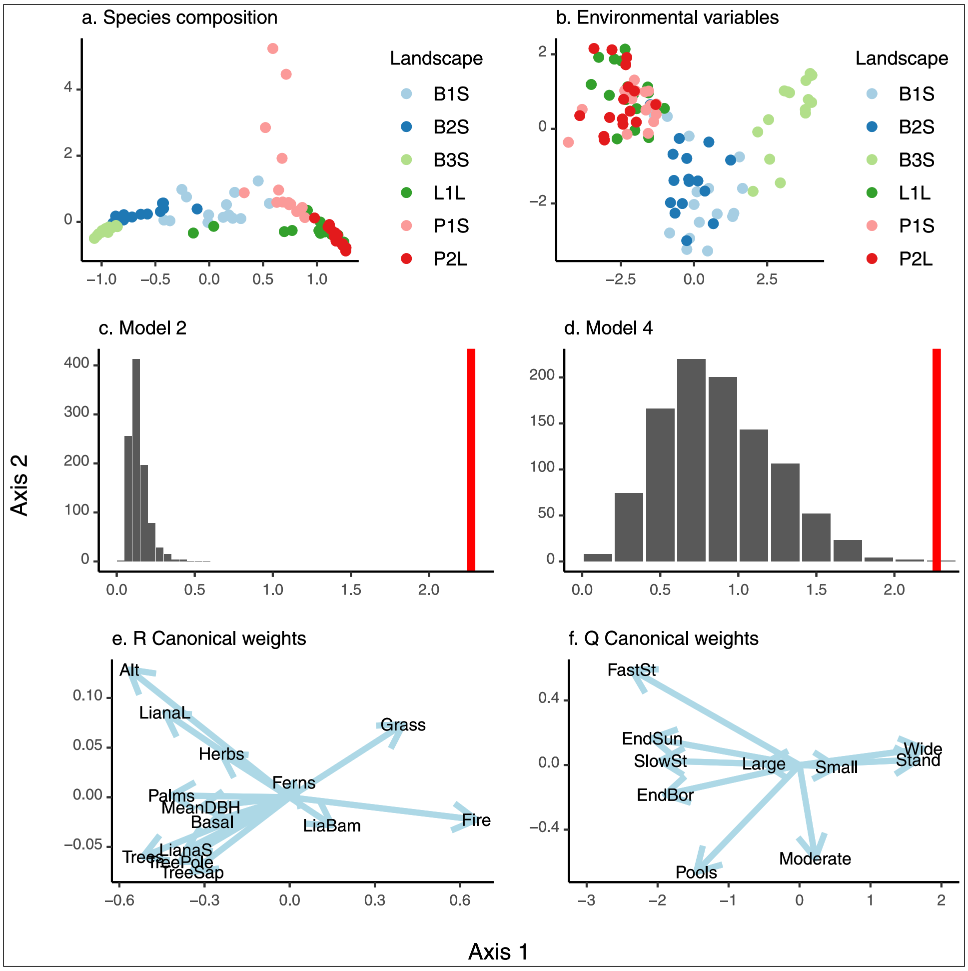

Fig. 4. Results of RLQ analysis. a. correspondence analysis of odonate species, b. principal component analysis of environmental data, c. results of randomisation test permuting the rows of the R array (model 2), d. results of randomisation test permuting the rows of the Q array (model 4), e. R Canonical weights (environmental variables), and f. Q Canonical weights (trait variables).

species associated with pools and slow streams from primary to burnt forest. In the severely-perturbed B3S, all of the abundant species were associated with standing water with the exception of *Libellago hyalina* (Selys, 1859). The species *Tyriobapta torrida* Kirby, 1889 was abundant in the primary forest landscape PS1, but was not recorded in any of the burnt landscapes. Species associated with fast flowing streams (e.g., *Euphaea subcostalis* Selys, 1873 and *Rhinocypha humeralis* Selys, 1873) were more diverse and relatively abundant in landscapes within the large unburnt fragment (L1L and P2L) in line with the greater prevalence of fast-flowing streams. Both logged and burnt forest landscapes were enriched with species associated with standing water bodies when compared to proximate primary forest landscapes. This included species not observed in primary forest landscapes such as *Rhyothemis phyllis* (Sulzer, 1776) and *Orthetrum sabina* (Drury, 1770). Other species such as *Neurothemis terminata* Ris, 1911 and *Neurothemis fluctuans* (Fabricius, 1793), which were observed in all landscapes, were particularly abundant in burnt landscapes. *Vestalis amaryllis*, the most abundant species in unburnt landscapes and the once-burnt landscape, was not observed in landscapes subjected to multiple burn events (B2S and B3S). Supplementary data 5 and 6 present the percentages of the 50 most abundant species identified by odonate family and geographical distribution. These results show a loss of Bornean and Sundaic endemics in disturbed habitat and an increase in widespread species. At the family level, we see that most of the widespread species associated with standing water bodies belonged to the Libellulidae family.

4. Discussion

With respect to our hypotheses, we confirm hypothesis 1 with respect to lower odonate diversity in landscapes subjected to multiple burn events, partially reject hypothesis 2 with respect to an association between geographic distance and odonate dissimilarity, and reject hypothesis 3 with respect to deviations from Hubbell's neutral model predictions in disturbed landscapes. We observed significant distance dependence in three of the four landscapes in and around the small unburnt fragment, including burnt and primary landscapes, but no significant distance dependence in the logged and primary landscapes within the large unburnt fragment. There was also significant distance dependence in the once-burnt and frequently-burnt landscapes, but not in the twice-burnt landscape. With respect to the neutral model, none of the landscapes deviated from neutral model predictions although deviation was closest to significance in the primary forest landscape P2L and the frequently-burnt landscape B3S. In line with hypothesis 4, we found a highly significant association between odonate species traits and environmental conditions, which appeared to be largely driven by disturbance, particularly in relation to burning.

Previous studies have highlighted the importance of geographic distance dependence across a range of different assemblages including butterflies, odonates, plants, prokaryotes and vertebrates, and habitats (Nekola and White, 1999; Cleary et al., 2004; Soininen et al. 2007; Clark et al., 2021; Cleary et al., 2022). These results are, however, often scale-dependent with a greater prevalence of geographic distance dependence

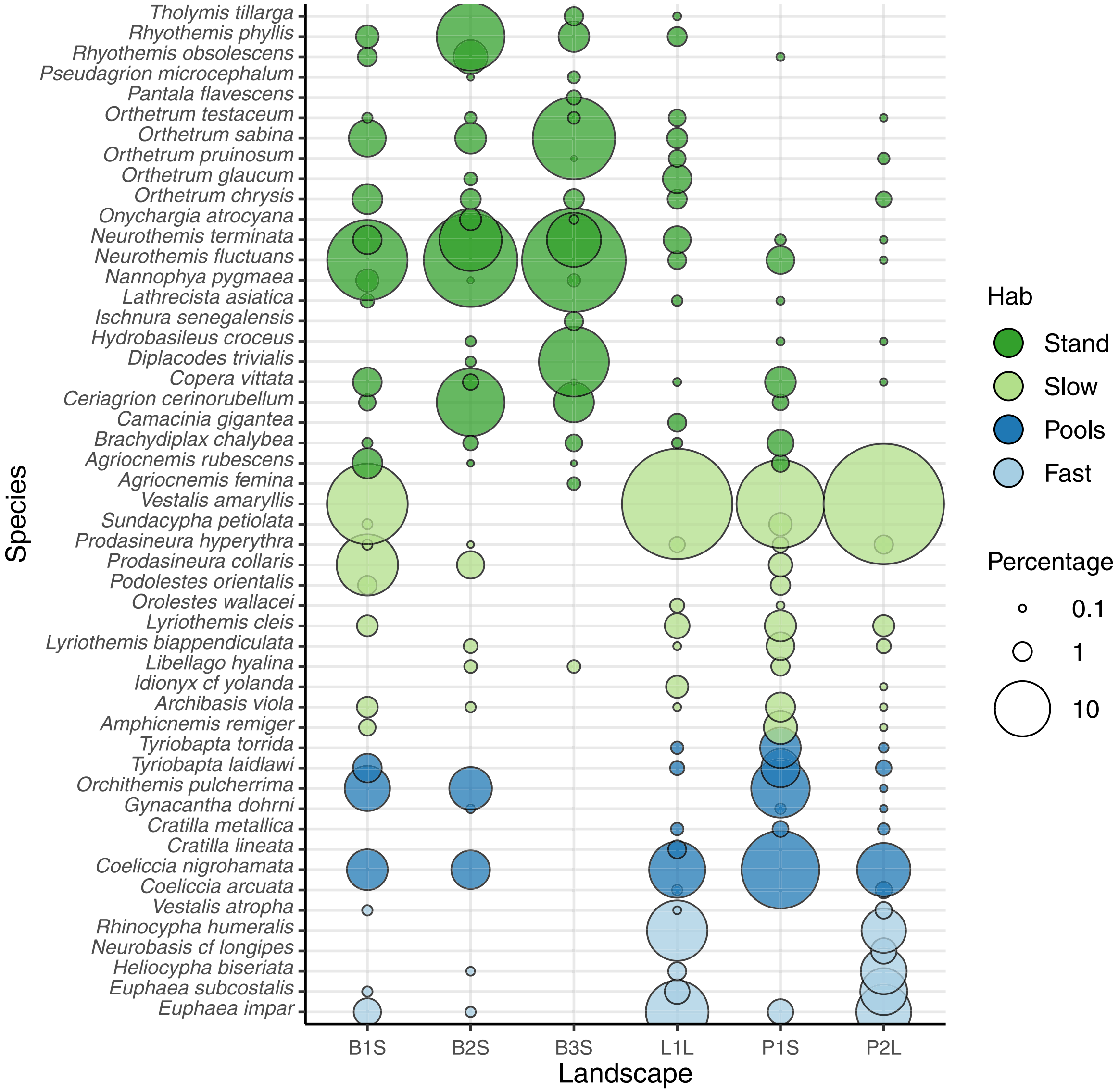

Fig. 5. Percentages of the 50 most abundant odonate species (shown along the y-axis) recorded in burnt, logged and primary forest landscapes. The symbols are colour-coded according to habitat preference. The circle size of the symbol is proportional to the mean percentage of odonate individuals per landscape as indicated by the symbol legend in the upper right corner of the figure. The x-axis codes refer to once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in Meratus logging concession (L1L), primary forest in Sungai Wain nature reserve (P1S), and primary forest in Meratus logging concession (P2L).

at larger spatial scales (Soininen et al., 2007; Clark et al., 2021). In a previous study taken over a large spatial scale (Cleary et al. 2004), we showed that spatial and environmental variables explained more than 60 % of the variation in composition of odonates and more than 70 % of the variation in composition of butterflies. With respect to odonates, most of the variation was explained by the environmental and spatially-structured environmental components with only ~ 9 % due to the purely spatial component. Our results show that geographic distance dependence also appears to play a role at smaller spatial scales in structuring odonate communities in primary and burnt landscapes surrounding the small unburnt fragment although there was not a clear association with landscape disturbance.

In addition to habitat differences, the sampling strategy applied in the present study may also have influenced the results. We sampled relatively large, 300-m long, transects, which were randomly allocated to large 450 ha landscapes (Cleary, 2003; Eichhorn, 2006). Random sampling, as used in the present study, is widely applied in field surveys for its ability to provide an unbiased representation of communities or assemblages, minimising selection bias and enhancing result validity (Sokal and Rohlf, 1981; Zar, 2010; Levy and Lemeshow, 2013). The sampling approach can also have an important influence on the study results. For example, Diekmann et al. (2007) found that random sampling yielded more common species but fewer rare species compared to non-random sampling. For smaller plot sizes, species richness was, furthermore¸ higher in non-randomly placed plots compared to randomly placed ones. For example, Dolný et al. (2011) observed 88 odonate species in primary and degraded areas of the Sungai Wain protected forest in comparison to 47 species in the present study. Dolný et al. (2011), furthermore, noted that their goal was to find the maximum number of species and not to follow a transect. Random sampling also produced fewer significant correlations between ordination scores and soil parameters, highlighting biases in non-random methods (Diekmann et al., 2007). However, random sampling has some limitations. It can be time-consuming and challenging in heterogeneous or inaccessible environments (Lewis, 2004; Diekmann et al., 2007). In highly variable environments, random sampling may over- or under-sample certain areas, distorting results (Thompson, 2012). Stratified random sampling, which divides populations into subgroups, can address such challenges by ensuring adequate representation of diverse conditions. Despite these drawbacks, the results of the present study likely provide an unbiased representation of the odonate community and allow for meaningful landscape comparisons.

In line with hypothesis 4, we found a highly significant association between odonate species traits and environmental conditions. This also appeared to be largely driven by disturbance, particularly burning, but also logging as previously demonstrated with bird (Cleary et al., 2007) and butterfly (Cleary et al., 2009) assemblages. Odonate assemblages within a given landscape type, however, appeared to follow neutral model predictions. One possible reason for this seeming contradiction and lack of deviation from neutral model predictions in disturbed habitats could be that these environments act as filters, allowing only certain species to survive while excluding others (Sieber et al., 2019). Neutral processes can operate at different scales. For example, specific habitats or biotopes may only be colonised by a limited range of species from the surrounding ecosystem. This colonisation may occur through passive dispersal mechanisms like wind or water or through active dispersal, depending on the species. Once established in a new or disturbed habitat, these 'filtered' species form a local community where neutral dynamics may or may not apply. If neutral processes are at play, changes in species populations, determining which species thrive and which decline, occur randomly rather than through selective pressures (Hubbell, 2001). Additionally, new species that can pass through the habitat filters may join the community from the broader metacommunity, enhancing diversity. However, the neutral model does not take into account how environmental factors, such as light, temperature, salinity, or pH, limit which species can colonise a habitat or how those species interact within the established community (Sieber et al. 2019). Habitat disturbance, whether logging or burning, appears to allow certain species, particularly those associated with standing water, to enter the disturbed landscape and form part of the odonate community. Concomitantly, other species appear no longer able to survive in these disturbed landscapes.

In the present study, odonates associated with fast-flowing streams were mainly found in unburnt landscapes within the large unburnt fragment, landscapes at higher elevations than those of the small unburnt fragment. Most of the species observed in the primary forest landscape were also observed in logged forest suggesting that logging did not appear to have a seriously adverse effect on these species. The same applied for species associated with slow-flowing streams and pools. The result was very different with forest fires. Several species associated with pools and slow-flowing streams in primary forest (P1S) were not observed in landscapes subjected to multiple burn events (B2S and B3S), e.g., *Tyriobapta torrida* and *Vestalis amaryllis* Lieftinck, 1965. *Tyriobapta torrida* individuals can be relatively abundant in lowland and marsh forests in the vicinity of slow-flowing streams and have been known to exhibit territoriality at breeding sites (Norma-Rashid, 1999; Aziz and Mohamed, 2018).

In contrast to the above, odonates inhabiting lentic water bodies, such as ponds, rice fields, ditches, and floodplains, tend to be generalists with greater resistance to disturbances (Renner et al. 2018). In the present study, these species were more abundant and prevalent in logged and burnt forest and formed the majority of individuals and species in the frequently-burnt landscape. Two of the most abundant species associated with lentic water bodies were *Orthetrum sabina* and *Neurothemis fluctuans*. *Orthetrum sabina*, commonly known as the Slender Skimmer or Green Marsh Hawk, is a widespread dragonfly species with a geographic range spanning Africa, Asia, and Australia. It is highly adaptable and can be found in a variety of freshwater habitats, including ponds, lakes, slow-moving rivers, rice paddies, and even temporary pools (Orr, 2003). *Orthetrum sabina* prefers areas with abundant vegetation around water bodies, which provide perching sites for adults and suitable habitat for larvae. It, however, can also be found in grassland habitat far from water bodies. The species is frequently observed in disturbed environments, including urban areas and agricultural fields, highlighting its adaptation to human-altered landscapes (Pavithran et al. 2020). *Neurothemis fluctuans* is another widespread dragonfly species although not to the same extent as *Orthetrum sabina*. The species thrives in disturbed habitats, particularly areas near slow-moving or stagnant water bodies such as ponds, ditches, marshes, and rice fields (Norma-Rashid et al., 2001). Its tolerance to human-altered environments, including urban areas, makes it one of the most frequently encountered dragonfly species in the region (Aziz et al., 2018).

Large-scale disturbances, such as logging and forest fires, can have different impacts on endemic *versus* widespread species (Charrette et al., 2006; Cleary and Mooers, 2006). The impact of disturbance on endemic species is a crucial area of study, especially in biodiversity hotspots where species often have limited ranges and specific habitat requirements. Endemic species are particularly vulnerable to large-scale disturbances because of their restricted distributions and specialised ecological roles (Myers et al., 2000; Charrette et al., 2006; Cleary and Mooers, 2006). One of the main consequences of disturbance on endemic species is habitat loss, which reduces their available living space and can drive local extinctions. Loss of habitat may be a particularly pertinent problem for Bornean odonates given the rapid loss of habitat and the high degree of endemicity (Miettinen et al. 2011; Dow et al., 2022). In tropical rainforests, logging, forest fires, and agricultural expansion have fragmented habitats, isolating endemic species populations and reducing gene flow (Cleary et al., 2006; Fauvelot et al., 2006; Broadbent et al., 2008; Radespiel and Bruford, 2014). In contrast to endemic species, widespread species often benefit from large-scale disturbances (Alroy, 2017). Their broader distribution across multiple regions and habitats allows them to escape localised disturbances and persist in unaffected areas.

When chronic and severe, disturbances such as forest fires can homogenise landscapes, removing forest cover and riparian vegetation, and polluting waterways (Pettit and Naiman, 2007). This process, which transforms structurally complex forested habitats into uniform environments, adversely impacts biodiversity. When habitats become more similar, they can no longer support the same range of species leading to a decline in species richness (Tabarelli et al., 2012). Habitat homogenisation can also impair ecological services such as pollination, water purification, and weather regulation leading to negative consequences for human well-being (Nobre et al., 2016; Kovács-Hostyánszki et al. 2017). This process appeared to be well underway in landscapes subjected to multiple burn events in the present study with a loss of endemic species and species associated with lotic habitats.

CRediT authorship contribution statement

Daniel F.R. Cleary: Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anna M. Bijlmer:** Writing – review & editing, Methodology, Investigation. **Dille Wielakker:** Writing – review & editing, Methodology, Investigation. **Nicole J. de Voogd:** Writing – review & editing, Writing – original draft, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data 1. KML file showing the locations of the plots. Supplementary data 2. Long format raw data containing observations of odonate species per plot and landscape. Column labels refer to: Ident (Individual identifier), Plot (Plot identifier), Landscape (Landscape identifier), Include (Included in present study), Num (Individual number), Number (Number of individuals; all 1 in present study), Date (Date of capture), Suborder (Taxonomic status), Family (Taxonomic status), Species (Taxonomic status), and Code (Species code), Author (Species authority), and Remarks. The other columns refer to species size (SizeMin, SizeMax, SizeNum, and Sze), habitat preference (Hab, Habitat_full, Stream and Breeding), Dst (Distribution class category), number of areas recorded (Numb) and areas recorded (Borneo, Sundaland, SE Asia, Palawan, East Asia, India, IndPhil, Pacific, Africa, Australia, Europe and the Americas). Supplementary data 3. Locations of all plots in the present study. Column labels refer to: Plot (Plot identifier), Code, Location (Location of plot), Landscape (Landscape in which plot is located), type2 (Other code for landscape), Long (Longitude), Lat (Latitude), Trees (Number of trees with DBH > 10 cm), MeanDBH (Mean diameter at breast height), Basal (Basal area), Alt (Altitude), Incl (Inclination), Include (Include in present study), Fire (Percentage of plot burnt), FragUnb (Size of largest unburnt fragment), Logging (Logged or not), Year (Year of sampling), CodeKarl (Karl Eichhorn's plot code), and Flood (Area of plot in floodplain). Supplementary data 4. Photograph of *Tyriobapta torrida* taken by DFR Cleary. Supplementary data 5. Percentages of the 50 most abundant odonate species (shown along the y-axis) recorded in burnt, logged and primary forest landscapes. The symbols are colour-coded according to geographic range. The ranges are EndBor: endemic to Borneo, EndSun: endemic to Sundaland, Moderate, and Wide: widespread. The circle size of the symbol is proportional to the mean percentage of odonate individuals per landscape as indicated by the symbol legend in the upper right corner of the figure. The x-axis codes refer to once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in Meratus logging concession (L1L), primary forest in Sungai Wain nature reserve (P1S), and primary forest in Meratus logging concession (P2L). Supplementary data 6. Percentages of the 50 most abundant odonate species (shown along the y-axis) recorded in burnt, logged and primary forest landscapes. The symbols are colour-coded according to plant family classification. The circle size of the symbol is proportional to the mean percentage of odonate individuals per landscape as indicated by the symbol legend in the upper right corner of the figure. The x-axis codes refer to once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in Meratus logging concession (L1L), primary forest in Sungai Wain nature reserve (P1S), and primary forest in Meratus logging concession (P2L). Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113382.

Data availability

All the raw data has been included as supplementary data.

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