

Riparian buffers can help mitigate biodiversity declines in oil palm agriculture

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Agricultural expansion is a primary driver of biodiversity decline in forested regions of the tropics. Consequently, it is important to understand the conservation value of remnant forests in production landscapes. In a tropical landscape dominated by oil palm (*Elaeis guineensis*), we characterized faunal communities across eight taxa occurring within riparian forest buffers, which are legally protected alongside rivers, and compared them to nearby recovering logged forest. Buffer width was the main predictor of species richness and abundance, with widths of 40–100 m on each side of the river supporting broadly equivalent levels of biodiversity as compared to logged forest. However, width responses varied markedly among taxa, and buffers often lacked forest-dependent species. Much wider buffers than are currently mandated are needed to safeguard most species. The largest biodiversity gains are achieved by increasing relatively narrow buffers. To provide optimal conservation outcomes in tropical production landscapes, we encourage policy makers to prescribe width requirements for key taxa and different landscape contexts.

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Conversion of natural habitats to agriculture has adverse impacts on biodiversity (Tilman *et al.* 2017), particularly in the tropics, where agricultural expansion accounts for 73% of deforestation (Curtis *et al.* 2018). Among the main crops linked to tropical biodiversity decline is oil palm (*Elaeis guineensis*), which currently occupies 19.5 million ha of formerly forested land (Meijaard *et al.* 2020). Although most oil palm production is concentrated in Southeast Asia, new frontiers are emerging across the tropics. To minimize the impacts of future oil palm expansion on biodiversity, it is imperative to develop conservation strategies that make production landscapes more hospitable to biodiversity.

Species loss due to conversion of tropical forests to oil palm can potentially be mitigated by setting aside remnants of

natural vegetation. Forested “riparian buffers” – areas of natural habitat alongside rivers, sometimes also called “riparian reserves” – could help achieve this goal if they support species typical of intact forest. Many countries already have measures for protecting riparian buffers in place, but predominantly for maintaining hydrological processes, water quality, and other ecosystem functions (Luke *et al.* 2019). However, the role that buffers play in supporting biodiversity is garnering increasing attention among environmental scientists and practitioners, particularly with the growth of agricultural sustainability standards and eco-certification schemes.

To a large extent, the effectiveness of riparian buffers in safeguarding biodiversity will depend on habitat area and quality, as with other habitat fragments (Haddad *et al.* 2015). Area, reflected by the width of the riparian buffer, will mediate the impacts of adverse environmental conditions at habitat edges (Pfeifer *et al.* 2017) and is expected to be a key predictor of the number of species supported (Mitchell *et al.* 2018). Habitat quality, and therefore the microhabitat conditions and resources present (Williamson *et al.* 2020), is also likely to play an important role (Zimbres *et al.* 2017; Deere *et al.* 2020a). Despite the increasing amount of research effort on riparian buffers, few studies have examined the influence of both buffer width and habitat quality on biodiversity, and many of these are restricted in their capacity to inform optimum buffer properties due to limited taxonomic scope and/or confounding landscape effects arising from study design (Luke *et al.* 2019).

Here, we provide a multi-taxon assessment of the biodiversity value of riparian forest buffers in oil palm agriculture. Biodiversity surveys were implemented in a single

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human-modified landscape following a replicated design. Using a matched analytical framework across datasets, we compared different riparian habitat types and estimated the optimum width and habitat quality needed to maximize the biodiversity value of a buffer, providing an evidence base that is directly comparable across a range of taxa.

Methods

Research was undertaken around the Stability of Altered Forest Ecosystems project area (www.safeproject.net) in Sabah, Malaysian Borneo (Figure 1), across an 80,000-ha landscape comprising lowland dipterocarp forest and plantation agriculture. Most remaining forest was selectively logged between 1970 and 2008, mirroring trends elsewhere in Southeast Asia. Although large tracts of forest are recovering following formal protection, certain areas in the landscape were heavily disturbed by salvage logging prior to further plantation development. The surrounding landscape is dominated by oil palm (up to 18 years since first planting) and contains remnant forest on hilltops and alongside rivers.

We collected data at 35 rivers (ranging from 3–10 m in width and up to 1.2 m in depth) surrounded by recovering logged forest ($n = 4$), heavily disturbed forest ($n = 7$), or oil palm plantations. Rivers within plantations either were completely devoid of forest vegetation (that is, palms planted to river edge; $n = 4$) or included a riparian buffer of remnant vegetation ($n = 20$). Riparian treatments (heavily disturbed forest and the plantation rivers) therefore captured variation in the intensity of human habitat modification, which we compared to reference rivers in recovering logged forest. Across the tropics, logged forests occupy more land than old growth forests, and retain a high proportion of the animal species found in pristine habitats (Putz *et al.* 2012). Despite

their inherent conservation value, logged forests are particularly susceptible to agricultural conversion (Bicknell *et al.* 2015), and therefore reflect the forest habitat typically impacted by oil palm expansion.

We conducted surveys across eight taxonomic groups: aquatic insect larvae, adult Odonata (dragonflies and damselflies), dung beetles, fish, anurans, birds, small mammals, and large mammals (WebPanel 1). We observed 377 species across 322 sampling locations. Taxa were not surveyed across all rivers/sampling locations, resulting in variation in sample size among datasets.

We gathered data on buffer width and forest quality to characterize the availability and structure of habitat on plantation rivers. We estimated terrestrial buffer width from Light Detection and Ranging (LIDAR)-derived canopy height (5-m resolution; Swinfield *et al.* 2020) and field measurements. For consistency with riparian policy documents, buffer width was expressed as the average width on each bank of the river (range: 10–325 m). We used LIDAR-derived aboveground biomass (metric tons per hectare [$t\ ha^{-1}$]) estimated from regionally specific models (Jucker *et al.* 2018) as a measure of forest quality. Following criteria established by the High Carbon Stock Approach (HCSA; <http://highcarbonstock.org>), the principal land-use planning tool adopted by sustainability standards to delineate forest cover in oil palm plantations, we defined “forest” as stands with $>75\ t\ ha^{-1}$ biomass. We extracted biomass as mean values from radii selected using scale optimization methods (WebTables 1 and 2) around each taxon-specific sampling location: mean recovering logged forest biomass, $216\ t\ ha^{-1}$ (range: $156\text{--}298\ t\ ha^{-1}$); riparian buffer, $143\ t\ ha^{-1}$ ($78\text{--}275\ t\ ha^{-1}$); oil palm, $40\ t\ ha^{-1}$ ($0\text{--}167\ t\ ha^{-1}$).

We also quantified forest extent at the water catchment scale as a potentially important predictor of terrestrial and aquatic communities (Erős and Lowe 2019). Twenty-four upstream catchments were delineated from spatially explicit

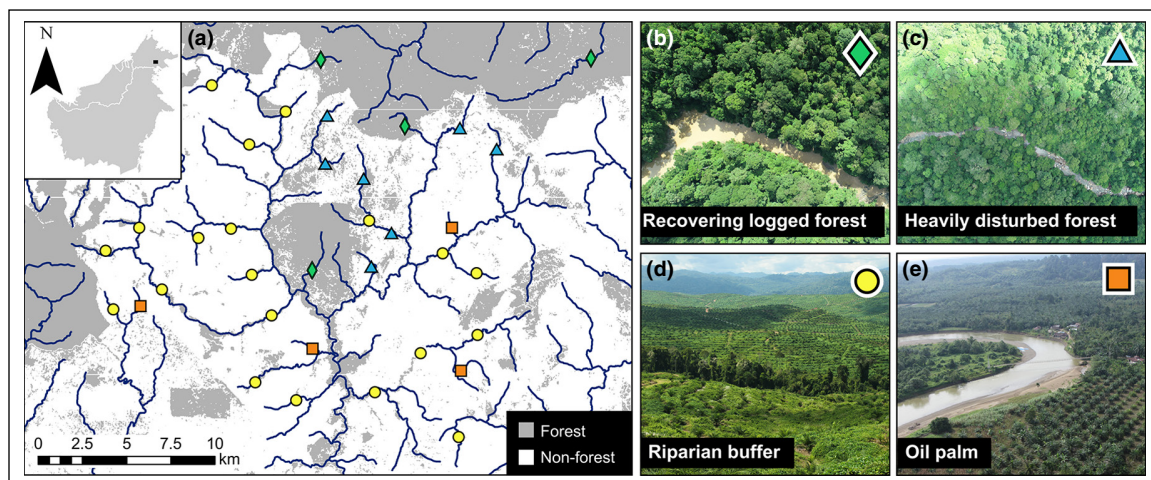


Figure 1. (a) Riparian study sites ($n = 35$), encompassing reference rivers (recovering logged forest) and human-modified riparian treatments (heavily disturbed forest, riparian buffer, and oil palm). Forest and non-forest habitats are denoted in gray and white, respectively. Inset shows the island of Borneo and the Stability of Altered Forest Ecosystems project area (black square), situated in Sabah, Malaysian Borneo. (b–e) Legend provides a visual representation of riparian habitat types relative to color-coded symbols. Image credits: (b and c) S Milne, (d) MJ Struebig, and (e) ConservationDrones.

surfaces of river flow direction and accumulation, developed from elevation data (30-m resolution, taken from the US National Aeronautics and Space Administration Shuttle Radar Topography Mission). Forest extent was derived from reclassified biomass maps and expressed as the proportion of catchments that comprised forest (mean = 0.12; range = 0.006–0.68).

Data analysis

We compiled biodiversity metrics to characterize how communities and populations varied across the sampling locations for each taxon. To describe community composition, we calculated species richness (family richness for aquatic insect larvae) across all treatments and sampling locations. As richness estimates accumulate with survey effort, we corrected for sampling bias using sample-based extrapolation (Hsieh *et al.* 2016). Community intactness in plantation rivers was quantified in two ways, both representing the difference between each sampling location and the average across reference sites in the recovering logged forest: namely, (1) the percentage of species found in plantation rivers compared to reference sites (hereafter, relative species richness) and (2) application of the Sørensen similarity index to account for species identity. Throughout, community intactness was expressed using relative measures, acknowledging that reference sites may have lost some disturbance-sensitive species due to a legacy of habitat modification. To understand the processes driving compositional differences both between and within plantation rivers and reference forest, we disaggregated the Sørensen index into components of turnover (species replacement) and nestedness (species loss/gain; Baselga 2010).

Abundances were expressed as raw or mean counts across spatial replicates for taxa (aquatic insect larvae, Odonata, dung beetles, and fish) that could be reliably identified and counted and had been sampled with equal survey effort among rivers. For taxa sampled using temporally replicated surveys, and where field methods precluded individual identification (anurans, birds, small mammals, and large mammals), we estimated abundance as a function of per-capita detection using hierarchical multi-species Bernoulli/Poisson N -mixture models (WebPanel 2; Royle and Nichols 2003).

We constructed pairwise comparisons of richness and abundance in riparian treatment sites relative to reference forest sites. For each pairwise comparison, we calculated the effect size using standardized mean differences, adjusted to account for heteroscedasticity between treatments (Bonett 2009). Positive effect sizes were interpreted as biodiversity gains (ie increases in richness or abundance) in riparian treatments relative to reference forest.

Effect sizes were summarized using hierarchical mixed-effects meta-analyses at the level of treatments (to assess how habitat modification intensity impacted riparian biodiversity) and taxon (to understand taxon-specific responses

treatments). This framework controls for higher precision of datasets with greater replication. Across all models, we specified random effects for (1) individual observations, to model residual variance explicitly; (2) biodiversity datasets, to account for pseudoreplication associated with multiple riparian treatments for each taxonomic group; and (3) species, to control for non-independence in species responses (Sánchez-Tójar *et al.* 2020).

Generalized linear mixed-effects models (GLMMs) were constructed to quantify the influence of buffer width, habitat quality, and catchment-scale forest cover on richness and abundance in plantation rivers. Across models, buffer width was described using a second-order polynomial term to allow for nonlinear associations. Count data (species richness and raw abundance) were described using a Poisson distribution and log-link function, modified to account for zero inflation where necessary. GLMMs based on modeled abundance were specified using a gamma distribution and log-link function, given that data were characterized by non-negative, continuous values clustered around zero. GLMMs based on richness leveraged the entire dataset, while abundance models were fitted separately for each taxonomic group (WebPanel 2).

We applied nonlinear mixed-effects models (NLME), described using a Gompertz function, to identify the optimum buffer width and forest quality that maximized community intactness in plantation rivers. By resolving the asymptote of the sigmoidal function, we were able to identify the width at which intactness stabilized in riparian buffers for each taxon (WebPanel 2).

Since biodiversity in forest remnants may have been experiencing extinction debts due to a legacy of disturbance (Rosa *et al.* 2016), we implemented GLMMs to assess temporal responses of biodiversity relative to years since forest conversion to plantation. We found no evidence to suggest declining richness or abundance across taxonomic groups (WebFigure 1), suggesting that communities had reached an equilibrium following forest conversion over the timescales investigated (up to 18 years).

Analyses were undertaken separately for all species in a taxonomic group combined and forest-dependent species only. We defined forest-dependent species as those affiliated with forest and demonstrating sensitivity to habitat conversion according to published studies and/or expert opinion (WebPanel 1). Aquatic insect larvae could not be identified to species level; therefore this group was excluded from assessments of forest-dependent taxa.

Results

Riparian buffers and heavily disturbed forests retained similar richness to reference forest sites, but species abundances tended to be higher (Figure 2). Conversely, plantation river communities, where there were no buffers, contained relatively few taxa present at low abundances

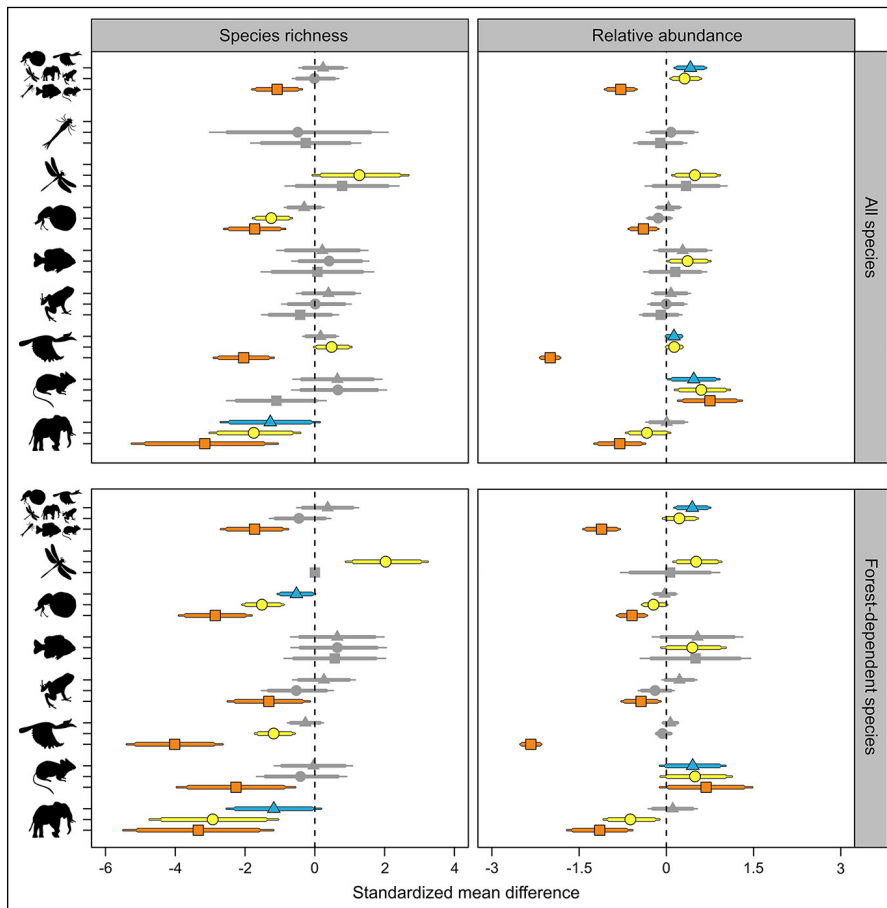


Figure 2. Standardized mean differences for species richness (family richness for aquatic insect larvae) and abundance in riparian treatments (symbols shown in Figure 1) relative to reference forest (vertical dashed black line) for (top to bottom) all taxa combined, and separately for taxonomic groups (aquatic insect larvae, Odonata, dung beetles, fish, anurans, birds, small mammals, and large mammals). Points denote posterior means, whereas line widths represent 75% (thick horizontal lines) and 95% (thin horizontal lines) Bayesian credible intervals (BCIs). Points and credible intervals for influential parameters are color-coded to reflect riparian treatments. Statistical differences are considered substantial if the 95% BCIs do not overlap zero and moderate if the 75% BCIs do not overlap zero. Non-influential parameters are presented in gray.

and lacked forest-dependent species (Figure 2). Yet these impacts varied substantially by taxon (Figure 2). Dung beetle and large mammal richness and abundance were lower in all riparian treatments than in the reference forest. However, riparian buffer sites supported comparably more species of Odonata and birds, and a greater abundance of fish and small mammals, than the recovering logged forest. Across most taxa, effect sizes confirmed that forest-dependent species were highly sensitive to landscape modification.

Wider buffers supported more species overall, particularly when only forest-dependents were considered (WebFigure 1). These trends were consistent across taxa, underpinned by substantial positive diversity–width relationships for birds, dung beetles, and mammals. Likewise, wider buffers were associated with higher fish and bird abundances (WebFigure 1),

but width-mediated increases were weaker for anurans, dung beetles, and forest-dependent Odonata. The patterns for birds and dung beetles were nonlinear, indicating an inflection point beyond which larger buffer widths did not result in species gains.

The effects of habitat quality and catchment-scale forest cover were highly variable across taxa (WebFigure 1). Overall, riparian habitats with higher aboveground biomass supported more species, reflecting the responses of birds, anurans, and mammals. Species abundances were less affected by habitat quality, with only birds and mammals occurring at greater densities in high biomass forests. In general, vertebrates, along with dung beetles that depend on them, were more diverse and abundant in plantation rivers where a larger proportion of forest was retained in the catchments, but this was not the case for other taxa.

When all taxa were considered collectively, communities in plantation rivers were comparable in richness to those in the reference forest when buffer widths reached ~110 m (95% Bayesian credible interval [BCI]: 78–183 m) on each side of the river and forest biomass approached 180 t ha^{-1} (93–455 t ha^{-1}). However, there were marked differences among taxa. Odonata, fish, anuran, bird, and small mammal communities reached equivalent species richness when buffers were ~45 m wide on each side of the river (Figure 3) and forest biomass was up to 86 t ha^{-1} (WebFigure 3). Conversely, aquatic insect larvae, dung beetle, and large mammal communities were typically depleted, with buffers only supporting 75–91% of the species found in the reference forest even where buffers were wide (>420 m) or comprised high biomass forest (> 190 t ha^{-1} ; Figure 3; WebFigure 3).

These patterns were more pronounced for forest-dependent species, with buffer widths of ~370 m on each side of the river (193–521 m) and forest biomass of ~ 290 t ha^{-1} (134–652 t ha^{-1}) required across taxa. For those taxonomic groups where equivalent species numbers could be achieved between the plantation rivers and reference forest (Odonata, fish, anurans, and small mammals), buffers would need to be up to 170 m wide on each side of the river (Figure 3) and comprise high forest biomass (up to 320 t ha^{-1} ; WebFigure 3). However, representation of forest-dependent dung beetles, birds, and large mammals was considerably lower in buffers overall, with extensive widths (426–595 m) and structurally intact forest (324–471 t ha^{-1}) required to retain these species (Figure 3; WebFigure 3).

The Sørensen similarity index for community intactness in plantation rivers stabilized at 0.49 (0.41–0.56) for all taxa combined, corresponding to a buffer width of ~230 m (85–682 m) on each side of the river and a forest biomass of ~340 t ha⁻¹ (132–630 t ha⁻¹). This reflects considerable compositional shifts across individual taxa (0.29–0.67 in buffer widths 114–915 m with biomass of 128–623 t ha⁻¹; Figure 4). The curves for most taxonomic groups lacked a distinct asymptote, indicating that neither buffer width nor forest quality had a substantial impact on community similarity.

Compositional shifts between the recovering logged forest and plantation rivers were mainly driven by species turnover, accounting for between 65% and 94% of the observed differences in community structure across taxa (Figure 4). Conversely, variation in aquatic insect larvae communities was a product of nestedness (65%), likely reflecting the coarse taxonomic classification of this group. Reference rivers had a high degree of community similarity across taxa (Sørensen similarity: 0.61–0.85), whereas composition was more variable across plantation rivers (similarity: 0.15–0.44 across taxa) owing to a high degree of species turnover (75–87% of observed compositional differences).

Conclusions

Our multi-taxon assessment provides crucial insights into the biodiversity value of forested riparian buffers in tropical agriculture. High numbers of species, including forest-dependents, can be found in these remnant forests if these areas are sufficiently wide. Optimal buffer widths vary substantially among taxa, but for each animal group at least 75% of the number of species found in recovering logged forest could be retained in buffers up to 500 m wide on each side of the river. The minimum width commonly prescribed in Sabah is 20 m, which would support 59–146% of the species numbers observed in recovering logged forest, depending on the taxon. Crucially, given that the greatest gains in richness were observed when the width of the smallest buffers was increased, doubling this prescription to 40 m would deliver substantial biodiversity gains in our study system (eg 28% more bird species, 14% more small mammals). However, for certain taxonomic groups (ie aquatic insect larvae, dung beetles, large mammals), and particularly forest-dependent species, much larger widths would be needed to support a community comparable

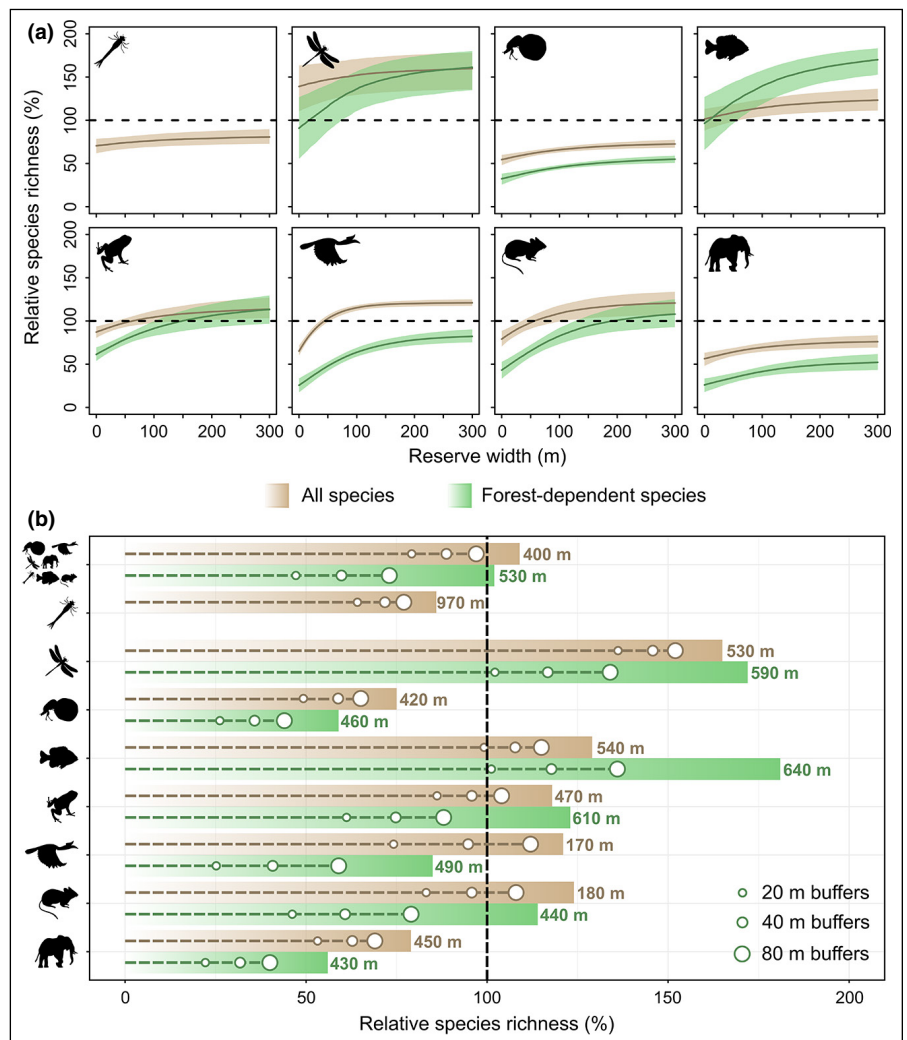


Figure 3. Relative species richness (percentage of species present in plantation rivers compared to reference forest sites) for all species (brown) and forest-dependent species only (green) relative to buffer width. (a) Solid lines indicate the mean of the posterior distribution, whereas shaded areas denote uncertainty, expressed using 95% BCIs. (b) Horizontal bars show the relative species richness (family richness for aquatic insect larvae) at which riparian buffer communities stabilize. Corresponding buffer widths are denoted adjacent to the bars. Open circles represent relative species richness at 20-m, 40-m, and 80-m buffer widths, to visualize the potential conservation gains associated with amendments to current buffer width policies/guidelines. For aquatic insect larvae, we present findings for all species only due to the coarse taxonomic classification of this group.

to the reference forest (420–970 m), demonstrating that buffers are not a substitute for continuous forest habitat. Similar findings have arisen from studies of neotropical mammals and birds, for which >100-m riparian forest buffer widths are recommended (Lees and Peres 2008; Zimbres *et al.* 2017).

There is increasing recognition that maintaining and enhancing forest quality in riparian buffers improves prospects for biodiversity in tropical agriculture (Zimbres *et al.* 2017; Luke *et al.* 2019), yet clear guidelines for restoration are lacking. For example, the Roundtable on Sustainable Palm Oil (RSPO) encourages plantation managers to restore degraded buffers but does not provide detailed guidelines for

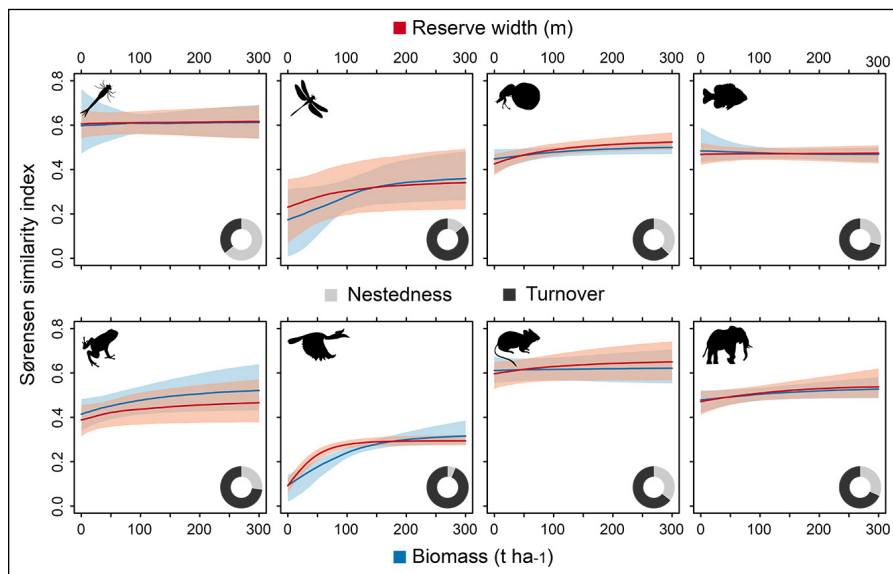


Figure 4. Riparian community composition relative to buffer width (red shades) and forest quality (blue shades). Compositional variation between plantation rivers compared to reference forest sites is expressed using the Sørensen similarity index (range 0–1, indicating complete taxonomic separation through to identical community structure). Solid lines indicate the mean of the posterior distribution, whereas shaded areas denote uncertainty, estimated from 95% BCIs. Donut charts (insets) demonstrate the mechanisms underpinning compositional differences (light and dark gray represent nestedness and turnover, respectively).

enhancing biodiversity (Barclay *et al.* 2017). Across taxa, we identified thresholds in aboveground biomass of 180–220 t ha⁻¹ in the forest buffer, which would support 76–164% of the species numbers found in recovering logged forest. However, to retain forest-dependent species, forest biomass in the buffer would need to be much higher. These thresholds could be implemented within existing land-use planning frameworks adopted by oil palm certification standards, such as HCSA, to help prioritize restoration activities in production landscapes.

Species responses to riparian buffers are highly specific, resulting in considerable variation within and between taxa. Riparian buffers are often highly disturbed remnant habitats, typically logged long before surrounding forest is cleared. Therefore, wildlife communities in buffers may have already passed through an extinction filter resulting in the loss of some of the most disturbance-sensitive species (Betts *et al.* 2019), after which buffers support only a subset of conservation-priority species. Many species that occur in buffers, particularly narrow ones, are disturbance-tolerant generalist taxa, including wide-ranging species with broad dietary or habitat requirements that are typical of fragmented landscapes (Ewers and Didham 2006). Buffers provide a cooler and more humid environment than oil palm plantations, and wider buffers mitigate the microclimatic edge effects of habitat fragmentation (Williamson *et al.* 2020). Many of the terrestrial species detected in narrow buffers are likely transient, using them for short-term refuge (Rodríguez-Mendoza and Pineda 2010), seasonal resources (Keuroghlian and Eaton 2008), or dispersal (Gray *et al.* 2019). Nevertheless, transient use of buffers may

still help populations to persist in the long term, particularly in areas where the landscape matrix is inhospitable (eg orangutans [*Pongo spp.*]; Seaman *et al.* 2021).

The most substantial effect sizes were for terrestrial taxa, with freshwater fauna appearing to be more resilient to habitat modification (see Wilkinson *et al.* 2018). Freshwater impacts tended to be strongest for larvae, suggesting that invertebrates may be more vulnerable to disturbance if the early stages of their lifecycle are aquatic (Luke *et al.* 2017). Freshwater fauna are heavily influenced by their immediate aquatic environment, conditions of which are often driven by upstream processes that impact substrates, particulate matter, and water quality (Leal *et al.* 2018). Nevertheless, we found little evidence of these catchment-level impacts on the freshwater taxa in our analysis. Downstream processes that affect aquatic connectivity can be important but often overlooked determinants of freshwater biodiversity, and require careful consideration during conservation planning in riparian systems (Leal *et al.* 2020).

The importance of strengthening riparian buffer protection is being increasingly recognized across the tropics, as policy makers, practitioners, and agricultural industries seek ways to minimize their environmental impacts. The RSPO provides additional riparian management guidelines that extend beyond the regulatory requirements of some countries, focusing primarily on buffer width (Luke *et al.* 2019). Indeed, our study confirms that buffer width should be a principal criterion underpinning the conservation value of forested remnants. We found that 20 m – the minimum width prescribed in Malaysia – is inadequate for many taxa, and that a “one-size-fits-all” approach is poorly supported by our data. As such, biodiversity outcomes will likely be enhanced if policy makers and practitioners advocate different sized buffers in different situations. For example, a 30–40-m buffer width might be sufficient for many taxa, but in certain landscape contexts much larger widths (eg 100–200 m) could be needed, especially to facilitate species movement and connectivity. Across the tropics, calls for context-dependent riparian guidelines are emerging (Dala-Corte *et al.* 2020), emphasizing the need to define target taxa when prescribing buffer widths for conservation purposes. In particular, to ensure that the benefits of riparian policy adjustments are distributed across realms, the response of both terrestrial and aquatic taxa should be considered during environmental decision making (Leal *et al.* 2020). Given that biodiversity responses to oil palm are broadly consistent across the tropics (Meijaard *et al.* 2020), the recommendations offered here should be transferrable to oil palm contexts in other tropical countries. However, this would benefit from further validation in areas other than Southeast Asia and in different agricultural contexts.

Riparian habitats support distinct faunal communities (eg Sabo and Soykan 2006; Mitchell *et al.* 2018) and should be considered part of an integrated strategy of forest retention alongside remnant patches of high conservation priority (Deere *et al.* 2020b). However, we should be realistic about conservation outcomes that can be achieved by riparian buffers in highly modified landscapes. Across all taxonomic groups, community structure was fundamentally altered in buffers and independent of key riparian properties, demonstrating clear limits to the biodiversity that can be retained in forest remnants. Community composition varied substantially between riparian sites, which is characteristic of tropical systems in general (Solar *et al.* 2015; Leal *et al.* 2018). Riparian networks should therefore be managed as cohesive conservation units to support landscape-level processes and ensure that biodiversity is better represented in human-modified tropical landscapes. Nonetheless, simply expanding riparian buffer widths represents an important step toward enhancing the biodiversity value of agricultural landscapes dominated by oil palm.

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■ Data Availability Statement

Biodiversity data used in this manuscript are available in the Stability of Altered Forest Ecosystems Zenodo online repository (<http://doi.org/10.5281/zenodo.6477764>).

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