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RESEARCH ARTICLE

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Riparian reserves help protect forest bird communities in oil palm dominated landscapes

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Abstract

1. Conversion of forest to oil palm agriculture is a significant and ongoing threat to tropical biodiversity. Despite this, little is known about the value of riparian reserves in oil palm and how these conservation set-asides might best be managed to maintain biodiversity.
2. We characterized bird communities of 28 sites in an oil palm-forest mosaic in Sabah, Malaysia using 6,104 encounters from 840 point counts. Sites included oil palm riparian reserves of various vegetation quality and reserve widths, which were compared to oil palm streams without a riparian reserve as well as riparian and nonriparian control areas in continuous logged forest.
3. Riparian reserves, oil palm waterways, and control sites in riparian and nonriparian forest supported distinct avifaunal communities. Riparian reserve width, forest quality, and amount of forest cover were the strongest predictors of bird species richness. For forest-dependent species, each of these predictors had a stronger effect size when compared with all species. On average, reserves held 31% of all species and 30% of forest specialists, whereas riparian forest controls averaged 32% of all species, but 38% of forest species.
4. Riparian reserves with >40 m of natural vegetation on each bank supported similar bird diversity to riparian forest control habitats found in continuous forest. However, to support equivalent numbers of forest-dependent species and species of conservation concern, reserves would need to be at least 100-m wide on each bank. The largest numbers of species were found in riparian reserves with above-ground carbon densities exceeding 75 tC/ha, highlighting the importance of forest quality, as well as width, in supporting riparian bird communities.
5. *Synthesis and applications*. If designed and protected appropriately, riparian reserves in oil palm estates support diverse bird communities, including many species of conservation concern. This can be achieved by designating large reserves (80–200 m total width). But, to maximize species numbers, forest disturbance should also be minimized prior to conversion as well as during plantation operations.

KEYWORDS
agriculture, biodiversity, forest management, landscape configuration, land-use change, oil palm, riparian reserve, riparian zone

1 | INTRODUCTION

Human activities are causing an unprecedented biodiversity decline (Pimm et al., 2014), with agricultural expansion being a primary cause of tropical species loss (Gibson et al., 2011). At least 522 Mha of tropical forest was converted between 1980 and 2000 (Gibbs et al., 2010) and a further 150 Mha was lost between 2000 and 2012 (Hansen, Stehman, & Potapov, 2010). A major contributor to this problem has been oil palm cultivation (*Elaeis guineensis*), which is now one of the most profitable land uses in the tropics, with continued demand (Vijay, Pimm, Jenkins, & Smith, 2016). Meeting this demand will require improved productivity on existing estates, as well as expansion of the crop into new areas.

Tropical production landscapes harbour significantly less biodiversity than native forest (Gibson et al., 2011); a pattern documented in many agricultural land-uses, including fruit orchards (Round, Gale, & Brockelman, 2006), rubber plantations (Warren-Thomas, Dolman, & Edwards, 2015), and oil palm under both smallholder cultivation (Azhar et al., 2011) and industrial production (Edwards et al., 2010). Retaining forest remnants within human-modified tropical landscapes can therefore enhance biodiversity levels (Laurance et al., 2018), although crop yields are likely to be reduced as a consequence (Edwards et al., 2010). Forest patches are maintained typically on slopes, floodplains, or along waterways.

Waterways and riparian areas are often afforded legal protection in tropical countries to mitigate flooding and sedimentation (Mayer, Reynolds, McCutchen, & Canfield, 2007). In Malaysia, for example, agricultural companies are required to maintain riparian reserves of between 5 and 50 m from each riverbank, with most being 20–30 m (Government of Malaysia, 1965). In Brazil reserves can be 30–500 m wide depending on channel width, but recent policy changes drastically reduce the prescribed widths (da Silva et al., 2017). In addition, oil palm companies that adhere to guidelines under the Roundtable for Sustainable Palm Oil (RSPO), the primary environmental certification scheme for this crop, agree to retain riparian reserves, and there are ambitions to increase the width requirements (Luke et al., In preparation).

While the main rationale for protecting riparian reserves is hydrological, these habitats may also be important for maintaining wildlife populations. In Sumatra, riparian reserves in paper pulp plantations support large-mammal communities comparable to those in continuous forest (Yaap et al., 2016), and in Amazonia large and undisturbed riparian reserves retain near-complete mammal and bird assemblages when compared to large forest patches (Lees & Peres, 2008; Zimbres, Peres, & Bom, 2017). In Borneo, fish (Giam et al., 2015), dung beetle and leaf-litter ant (Gray, Simmons, Fayle, Mann, & Slade, 2016; Gray, Slade, Mann, & Lewis, 2014) assemblages in oil palm riparian reserves are more similar to those in contiguous logged forests than the surrounding oil palm matrix in terms of composition, species diversity, and functional group diversity.

The species composition of riparian remnants is likely to be influenced by many of the processes associated with habitat fragmentation, such as area, isolation, and edge effects (Laurance et al., 2018). Area, or width of the riparian remnant, is expected to be a primary determinant of diversity, yet few researchers have documented this in tropical regions, and even fewer provide explicit width recommendations to inform riparian reserve design (Luke et al., In preparation). In the neotropics, riparian zones are reported to extend to 60–250 m for plants (Schietti et al., 2014), 100 m for snakes (de Fraga, Lima, & Magnusson, 2011), and 140 m for understorey birds (Bueno, Bruno, Pimentel, Sanaiotti, & Magnusson, 2012), but since these studies were undertaken in forested areas it is unclear whether the same width thresholds would apply in fragmented habitats or agricultural systems, or indeed to other tropical regions (van der Hoek, Zuckerberg, & Manne, 2015).

Here, we explore the relationships between riparian reserve width, forest quality, and the birds present in a modified tropical landscape of Southeast Asia. Specifically, we characterized bird communities in riparian reserves set in forest or oil palm to evaluate the relative value for riparian and nonriparian biodiversity. Reserve width, the main criterion stipulated in environmental policy, is expected to correlate positively with species richness, with more species supported in wider reserves (e.g., Gray et al., 2014; Lees & Peres, 2008; Zimbres et al., 2017). However, the expected levels of species richness might not be supported if the habitat quality is low (Luke et al., In preparation). Given the roles of other confounding variables in the fragmentation literature (Laurance et al., 2018), it is important to understand how measures of patch size (i.e., width) and quality affect riparian remnant biodiversity in the context of the wider landscape covariates (e.g., elevation, isolation). There is also fundamental policy interest in establishing whether the largest riparian reserves can support similar levels of biodiversity to continuous forest sites, since protecting larger/wider reserves involves a trade-off between conservation interests and making land available for agriculture. We sought to address these questions, while also examining whether riparian reserves are valuable for forest-dependent species and species of conservation concern, since these taxa are the focus of environmental policy in the certification sector.

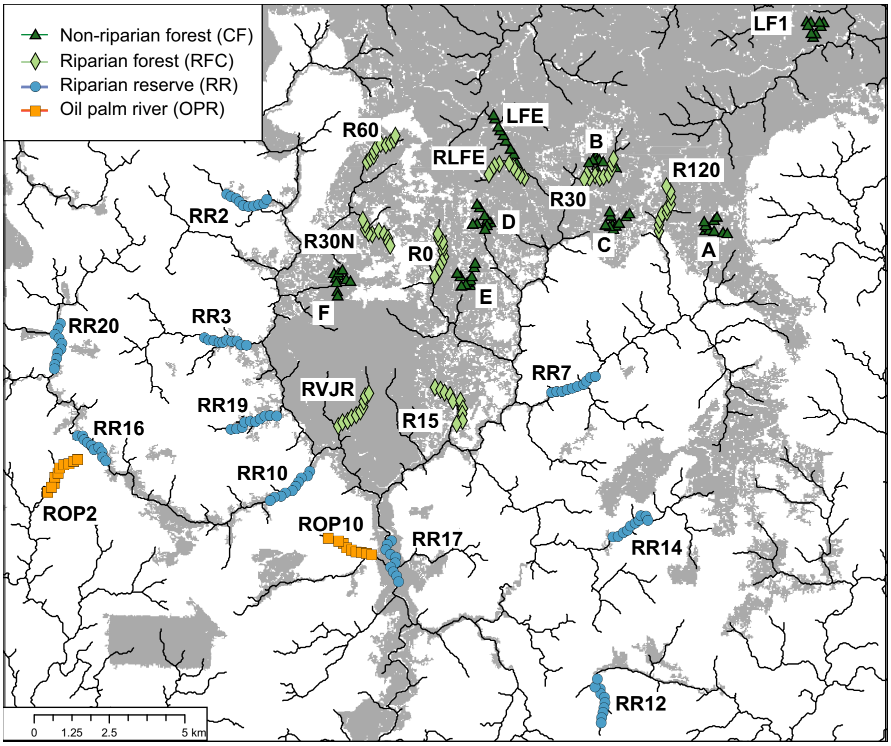

FIGURE 1 Twenty-eight bird sample sites in riparian (*n* = 20) and nonriparian (*n* = 8) habitat types in the Stability of Altered Forest Ecosystems (SAFE) landscape and surrounding agricultural matrix in Sabah, Malaysian Borneo. A site comprised 10 point count stations (indicated by points on the map), each of which were sampled for birds on three separate occasions. Forest is shown in grey; tree plantations (predominantly oil palm), and cleared areas in white. Forest cover was derived from Hansen et al. (2013) and updated to represent the landscape in 2014 accurately. Black lines denote the river courses

2 | MATERIALS AND METHODS

2.1 | Study system

The study was set in and around the Stability of Altered Forest Ecosystems (SAFE) project (117.5°N, 4.6°E) in Sabah, Malaysian Borneo (Figure 1, Ewers et al., 2011). The 80,000 ha area comprises both forest and plantations of oil palm and *Acacia*, with all matrix study sites surrounded by oil palm. Most of the remnant forest has been logged two to four times over 30 years and contains few mature trees (Struebig et al., 2013), although some parts are less disturbed and are formally protected. The surrounding agricultural matrix comprises multiple oil palm estates with trees planted 8–12 years before the study. Within this matrix, remnants of logged forest are protected alongside watercourses as riparian reserves. Reserves typically extend *c*. 50 m on each bank from the river channel, but vary between 10 and 470 m (median = 54 m, *SD* = 135 m) across the landscape. Reserves also vary in altitude, topographic ruggedness, and substrate (rocky to sandy).

We sampled bird communities alongside 20 rivers. Ten of the rivers were within oil palm plantations and had riparian reserves (RR), two were in the oil palm plantation with no riparian reserve and were used as controls (OPR), and a further eight rivers were used as controls within the logged forest (hereafter riparian forest control; RFC). The rivers sampled in oil palm were selected to represent the range and distribution of reserve widths present across the study area and plantations elsewhere in Southeast Asia. Larger riparian reserves were scarce and only one site of >100 m was available in our study area (RR17, width = 470 m). Forest quality, indicated by aboveground carbon density measured via LiDAR (Jucker et al., 2018), also varied substantially across the landscape. Finally, to document any differences between riparian and nonriparian bird communities, we also surveyed eight nonriparian control sites in continuous forest (hereafter forest control; CF), all of which had also been previously logged, reflecting the dominant remnant forest type in lowland Southeast Asia.

2.2 | Bird sampling

At each riparian site, birds were sampled via 10 point counts set at 180–220-m intervals (Euclidian distance) along a 2-km transect following the course of the river. The stations were situated up to 10 m up the riverbank to minimize interference from the sound of running water. During each count, a single experienced observer (SLM) recorded all bird species heard or seen within a 50 m radius of the point for 15 min including fly-overs. Average river width ranged between 5 and 13 m, meaning that the detection radius encompassed both terrestrial vegetation and the river. However, the river itself never accounted for more than 5% of the total point count area. Counts were conducted between 05:50 and 11:00 in clear weather, and were repeated on three separate occasions at each site between 2014 and 2016. For nonriparian sites, the 10 point counts were spatially configured at comparable distances along access trails. Sites were sampled at mean intervals of 72 days between visits (Supporting Information Table S1). Three species of swift (*Aerodramus maximus*, *A. salangana* and *A. fuciphagus*) could not be reliably separated and are considered as *Aerodramus* spp. The bird sampling data from the three surveys were pooled across the 10 stations at each site. Taxonomic nomenclature follows Eaton, van Balen, Brickle, and Rhiendt (2016).

2.3 | Environmental predictors of bird community structure

For each site, above-ground carbon density (mean values across the ten point counts sites) was derived from remotely sensed data, and used as a proxy for overall forest quality, since lower carbon densities were evident in areas that experienced the most degradation via logging (Jucker et al., 2018). Similarly, we also calculated altitude and topographic ruggedness for each site as an average of values extracted within a 50-m radius of each of our 10 point stations. Above-ground carbon density was extracted from LiDAR-derived datasets (30 × 30 m), which were gathered in November 2014 using a Leica ALS50-II sensor (Jucker et al., 2018). Altitude (30 × 30 m) was estimated from the Shuttle Radar Topography Mission (SRTM; https://www2.jpl.nasa.gov/srtm/). Likewise, topographic ruggedness was derived using the SRTM, according to Wilson, O'Connell, Brown, Guinan, and Grehan (2007). Average values for each raster layer were calculated within the buffer radius of each station using the R 3.2.3 (R Development Core Team, 2008) packages "raster", "sp", "rgdal", "gtools," "doMC," and "maptools" (Analytics Revolution, 2014; Bivand & Lewin-Koh, 2013; Bivand & Rowlingson, 2016; Hijmans & van Etten, 2002; Pebesma & Bivand, 2005).

For each riparian reserve sampled, we estimated reserve width at each station from the LiDAR canopy height layer (5-m resolution). The width of the river channel was included in this remote measurement as vegetation often obscured the riverbanks. River channel width was recorded in the field, between the high water marks of the two banks, using a laser rangefinder (Leica Rangemaster CRF 1000). Subsequently, this value was subtracted from the reserve width estimate to determine the actual land surface within each reserve. Mean bank reserve width is typically referenced within environmental policy documents, so we use this metric throughout the paper.

As a measure of landscape-scale forest availability, we also calculated percentage forest cover within a 1,000-m radius of each point count station, capturing the availability of forest in the landscape without overlapping forest associated with other sample sites. All environmental predictors were average values across the 10 point count stations per site.

2.4 | Statistical analyses

Species accumulation curves were constructed for each site and habitat type, and inspected for being close to asymptote to confirm that sampling was adequate (Supporting Information Figure S1). Rarefied curves, based on 100 iterations, were produced using the "vegan" package in R (Dixon, 2003). We used the number of bird encounters, rather than absolute numbers, to generate curves, as early morning roost flights of Sunda yellow-vented bulbul (*Pycnonotus analis*) occasionally resulted in >100 individuals recorded from a single point. In this case, large numbers of a single species recorded within one visit were treated as a single encounter.

We used a GLM framework in "lme4" to explore the partitioning of species abundance and richness by habitat type. Spatial autocorrelation was assessed using a Moran's *I* test on the residuals of the GLM for richness across all riparian sites to test for unforeseen associations between nearby sites. The package "multcomp" was used to perform Tukey tests between pairwise habitat combinations (RFC vs. CF, RFC vs. OPR, etc.), and the procedure repeated for two subsets of our community: forest-dependent species (defined by consensus of five expert ornithologists in Southeast Asia, Nick Brickle, Frank Rhiendt, Dave Bakewell, Craig Robson and Simon Mitchell), and species of conservation concern (status of near-threatened through to critically endangered, IUCN, 2017).

To visually demonstrate the associations between both carbon density and reserve width, and community structure we plotted the relationships graphically. Community integrity was measured using the Bray–Curtis dissimilarity index on an abundance matrix (sensu Banks-Leite et al., 2014). We used mean differences in species composition between riparian reserves (RR) and each of the riparian forest controls (RFC) to reflect reductions in community integrity.

Ordinations were used to explore bird species composition in relation to habitat type and our environmental predictors. Pairwise Bray–Curtis dissimilarity coefficients were calculated between species abundances pooled from across the three visits at each site and nonmetric multidimensional scaling (NMDS) ordinations generated using PC-ORD 6.07 (McCune & Mefford, 2011) to organize sites by similarity in species composition. The reliability of the ordinations was determined by comparing NMDS solutions produced from 250 runs of real data, with those produced from randomized species-site matrices using a Monte Carlo test. The ordinations were then repeated to ensure that they reflected representative signals in community data and were not being disproportionately impacted by either rare (by removing species recorded only once within the dataset) or highly abundant species (by square-root transformation of all abundances) following Struebig et al. (2013). Nonparametric permutations tests (ADONIS, in "vegan") were used to examine compositional differences between habitat types. We also investigated which species were most associated with particular habitat types using the indicator species analysis INDVAL in PC-ORD (Dufrene & Legendre, 1977).

The GLMs were used to determine whether species richness was driven by our potential environmental predictors (river channel width, riparian reserve width, landscape-scale forest cover, and above-ground carbon density) at our 20 riparian sites. We selected Gaussian family models, as this best reflected the probability distribution of species richness. All predictor variables were tested for collinearity. As ruggedness and altitude were correlated ($r > 0.18$), ruggedness was retained in the riparian reserve models, because the range of values was greater than for altitude, and altitude was retained in the other models for the same reason.

To examine the influence of the environmental predictors on species composition, we constructed GLMMs for our two NMDS axes for all habitat types. Habitat type was included as a random variable. Oil palm river communities were excluded from these analyses as species composition was very different from that in other habitat types and this signal obscured any other potential patterns of interest. Parameters were model-averaged across all models within ΔAIC < 4 of the best model. The modelling process was repeated for forest-dependent species and species of conservation concern separately.

3 | RESULTS

3.1 | Species abundance and richness

Across the 28 sites, we detected 8,784 individual birds (6,104 encounters), of 202 species, including 133 forest-dependent species (3,838 encounters, 4,939 individuals) and 62 (821 encounters, 1,094 individuals) species of conservation concern. Our species accumulation curves approached an asymptote for both site and habitat type, confirming that we had sampled the avifauna well enough to assess differences in richness and community structure between them (Supporting Information Figure S1).

Birds were more abundant in riparian reserves than riparian forest controls and oil palm rivers, but similar to those in nonriparian forest controls (Figure 2a). Riparian reserves supported similar levels of bird species richness to riparian forest controls, and double that recorded in oil palm rivers (Figure 2b).

Forest-dependent species accounted for 65% of all individuals across the whole community, and were significantly more prevalent in both nonriparian and riparian forest controls than in riparian reserves or oil palm rivers (70% in CF; 74% in RFC; 54% in RR; 20% in OPR; Figure 2c). Forest-dependent species richness was highest in both forest control types and significantly lower in oil palm rivers (Figure 2d).

Species of conservation concern comprised 13% of all individuals across the landscape, and formed a larger component of the bird community in riparian (18%) and nonriparian forest controls (16%), compared to those in riparian reserves (11%) and oil palm rivers (2%). There was no significant difference in the number of species of conservation concern found in riparian reserves and riparian forest control sites in terms of either abundance or richness (Figure 2f,g). Species richness was not influenced by spatial autcorrelation (Moran's *I* test; observed = −0.04, $p = 0.80$ of GLM residuals for model including habitat type, above-ground carbon density, and reserve width).

3.2 | Bird community composition

Our NMDS ordination of community composition performed better than those based on randomized data (Monte Carlo test: observed stress = 12.4; simulated stress = 28.7; $p = 0.004$; Figure 3a), and showed four clear habitat groupings. The most divergent were the oil palm rivers, which supported an almost entirely different bird community to other sites. Communities in riparian reserves were more similar to those in riparian and nonriparian controls, but still distinct from both habitat types in terms of species composition. Since the oil palm rivers had such a strong influence on the landscape-wide ordination, we removed them in our subsequent analyses to better discriminate between the remaining habitat types. Our subsequent NMDS represented 89% of the variation in bird community structure (stress = 14.8). None of the models were improved significantly after removal of singletons and square-root transformation of species abundance; as indicated by an increase in stress (16.35).

Species composition was significantly different across all four habitat types (ADONIS: $R^2 = 0.11$, $p = 0.01$). The same pattern was evident when restricted to just forest-dependent species and species of conservation concern (Figure 3; forest-dependent species: $R^2 = 0.13$, $p = 0.01$; species of conservation concern: $R^2 = 0.14$, $p = 0.01$).

Community integrity in riparian sites showed similar patterns to our ordinations, in that riparian reserves were intermediate to riparian forest controls and oil palm rivers (Figure 2c,e,h).

Indicator species analysis revealed 13 significant associations between particular bird species and habitat types, including four species associated with nonriparian forest controls, seven of oil palm rivers, and one each for riparian reserves and the riparian forest controls (Supporting Information Table S2).

3.3 | Environmental predictors of riparian reserve communities

Our GLMMs demonstrated that riparian reserve width was an important predictor of bird species richness and avian community composition (Table 1; Figure 4). Reserve width and above-ground carbon density affected bird richness in a consistent manner. None of the other environmental metrics we tested had a demonstrable effect in our final models.

Riparian reserve width, above-ground carbon density, and forest cover were all significant positive predictors of observed species richness for the full community (Table 1). This pattern was the same for forest-dependent species, but did not apply to species of conservation concern. Across all riparian habitats, above-ground carbon was a significant positive predictor of species richness for both forest-dependent taxa and species of conservation concern. However, our final model for riparian habitats did not reveal any significant predictors across all species. Forest cover was an important predictor of community structure as reflected by the NMDS axis 1 for species of conservation concern. The second axes of our NMDS analyses exhibited no significant relationship with the environmental predictors.

Community subsets for all species, forest-dependent species, and species of conservation concern differed in the reserve width at which richness was equal to that found in riparian forest controls (Figure 4). Trend lines intersected mean richness levels for riparian controls at *c.* 40 m when all species were examined. However, for forest-dependent taxa and species of conservation concern, riparian reserves did not reach equivalent richness levels to that found at control sites. The extent of this pattern with above-ground carbon density also varied between community subsets (Figure 4d,e,f). Notably, reserve richness reached equivalent levels to control

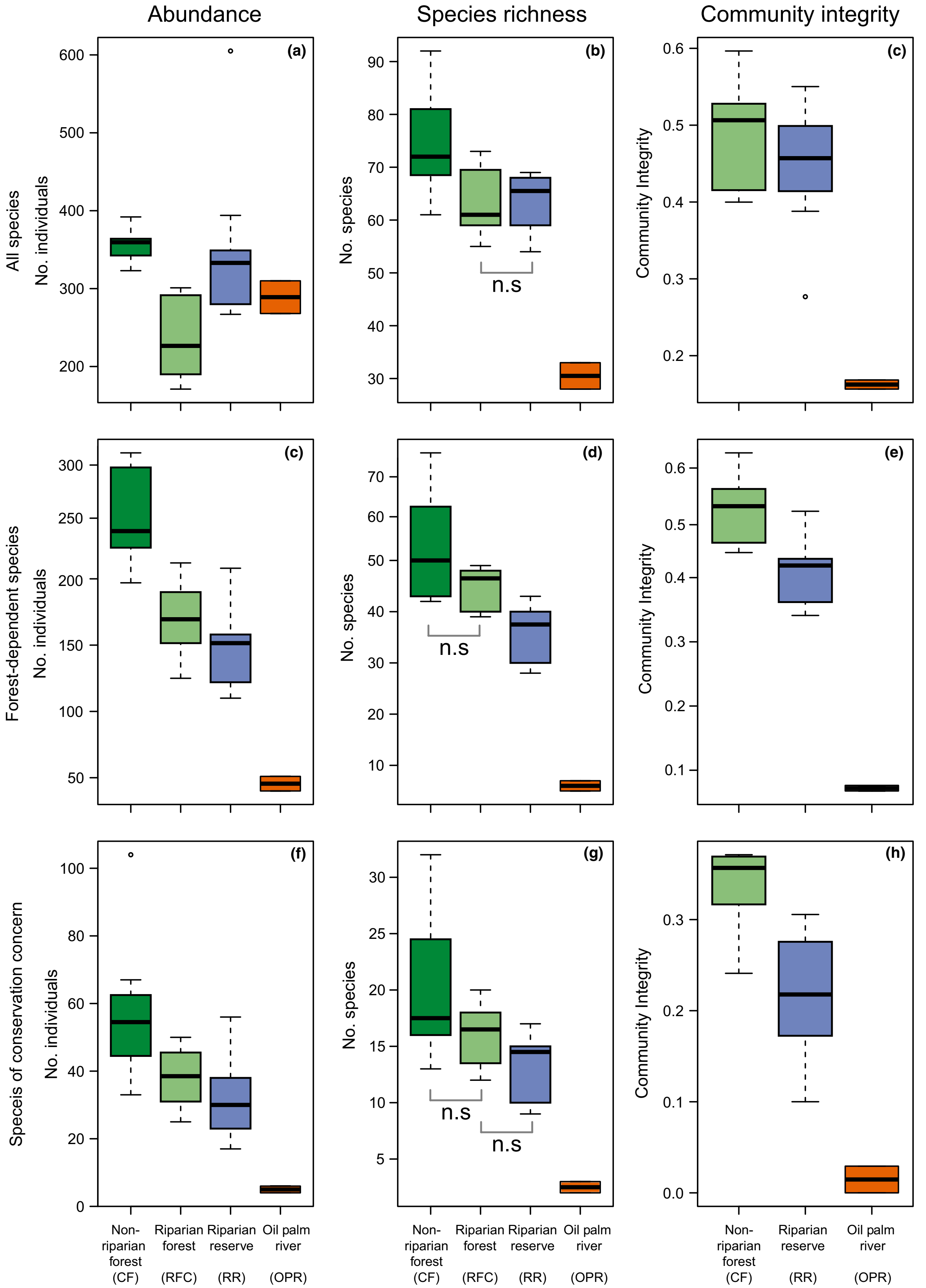

FIGURE 2 Boxplots of site-level bird abundance and species richness across the different habitat types for: all species; forest-dependent species; and species of conservation concern. General linear model-derived linear hypothesis Tukey tests revealed significant differences in richness ($p < 0.05$) between all habitat types except for those cases marked nonsignificant (n.s)

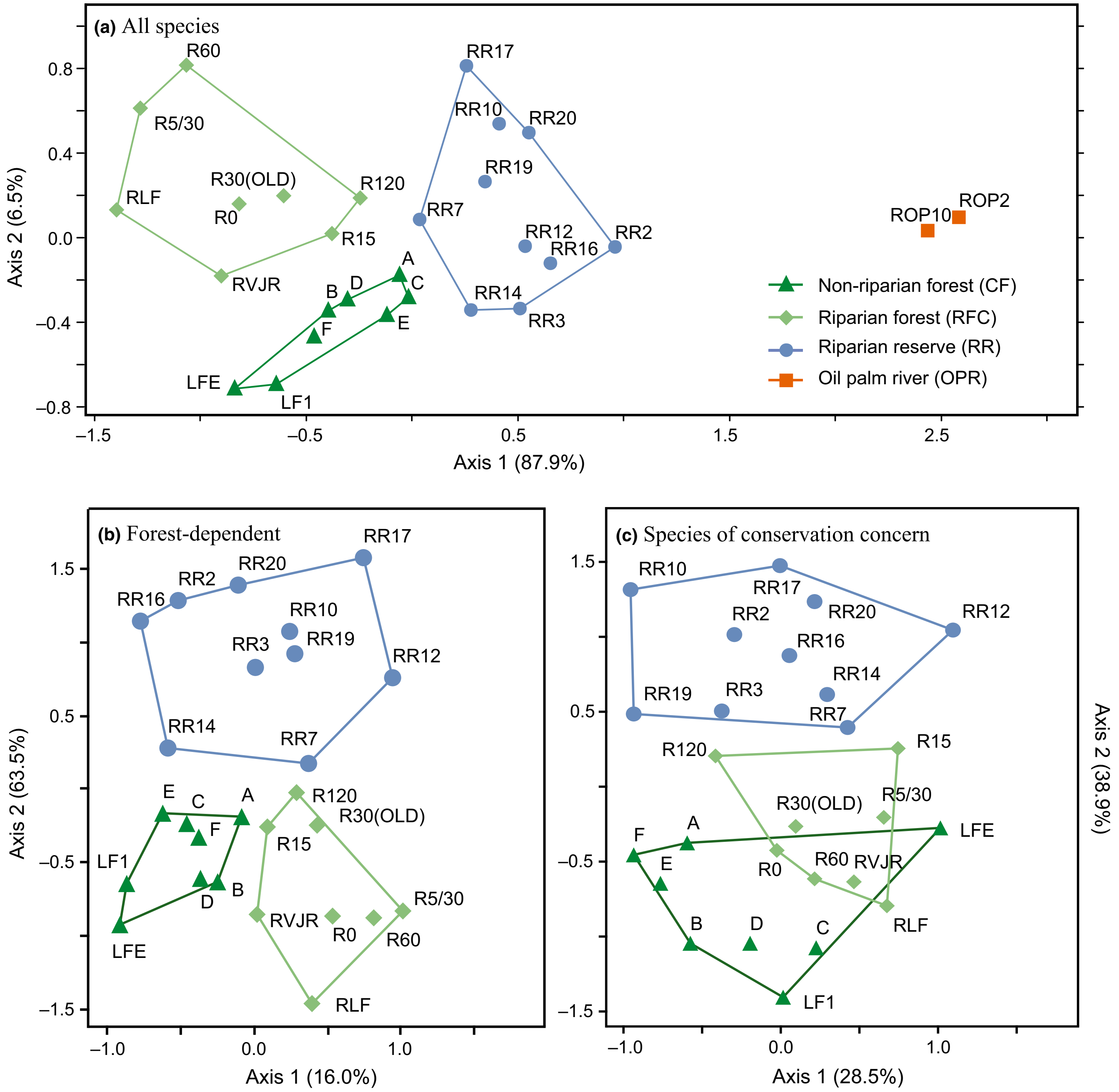

FIGURE 3 Nonmetric multidimensional scaling ordinations of bird community structure across riparian and nonriparian habitat types. Plots show dissimilarity across (a) all species; (b) forest-dependent species; and (c) species of conservation concern. Oil palm river sites were excluded from (b) and (c) because they included only seven forest-dependent species and three species of conservation concern, and therefore could not be plotted within the same ordination space. Axis scores denote R^2 values

sites at around 65 tC/ha for all species, but at around 100 tC/ha for forest-dependent and species of conservation concern subsets.

4 | DISCUSSION

We found that riparian reserves in oil palm, supported comparable levels of bird diversity to sites in continuous forest (both CF and RFC), especially when reserves are wide and comprise high carbon forest. However, these reserves contained fewer forest-dependent taxa and species of conservation concern, which likely require larger tracts of continuous forest for long-term population viability. These results suggest that the mandated reserve width in many tropical countries should be increased. In tandem, forest quality in riparian reserves should be improved: in new plantations by delineating reserves prior to clearance and preventing additional logging within them; in existing heavily degraded reserves via vine cutting and planting with native trees, plus by replanting in areas where crops were planted to river banks and no riparian reserves retained. Our appraisals of forest-dependent taxa and species of conservation

TABLE 1 Outputs of GLM and GLMM showing model averaged parameter estimates, *SE*, and confidence intervals for important predictors of observed species richness and community structure. The ΔAIC < 4 model set was used to estimate averaged outputs. *n* represents the number of sites included in each model. One riparian reserve (RR17) was excluded several environmental predictors were missing for this site

Predictor	Parameter estimate	*SE*	Lower 95% CI	Upper 95% CI
GLM: richness in riparian reserves and oil palm rivers (RR, OPR, *n* = 11)				
All species				
Intercept	63.8	1.1	61.2	66.4
Above-ground carbon density	6.1	2.2	0.9	11.3
Forest cover	8.3	2.3	2.9	13.8
Riparian reserve width	8.6	2.5	2.9	14.3
Forest-dependent species				
Intercept	36.7	1.3	33.6	39.8
Above-ground carbon density	6.6	2.6	0.5	127
Riparian reserve width	10.3	3.0	3.4	17.2
Forest cover	8.9	3.0	1.9	15.9
Species of conservation concern				
Intercept	13.4	0.9	11.4	15.4
GLM: richness in riparian habitats (RR, OPR, RFC, *n* = 19)				
All species				
Intercept	59.6	2.5	54.3	64.9
Forest-dependent species				
Intercept	36.1	2.0	31.9	40.3
Above-ground carbon density	156.0	5.3	5.0	27.0
Species of conservation concern				
Intercept	13.3	0.8	11.6	15.0
Above-ground carbon density	5.2	2.6	1.8	10.0
GLMM: community structure (NMDS axis 1) in all forest or riparian reserve (RR, RFC, CF, *n* = 26)				
All species				
Intercept	0.0	0.0	−0.1	0.0
Above-ground carbon density	−0.2	0.1	−0.3	−0.1
Forest cover	−0.4	0.1	−0.5	−0.3
Forest-dependent species				
Intercept	0.1	0.4	−0.7	0.9
Species of conservation concern				
Intercept	−0.0	0.1	−0.2	0.1
Forest cover	−1.1	0.2	−1.6	−0.7

concern also demonstrate that not all species are well represented in riparian reserves and it is likely that these taxa require larger tracts of continuous forest for long-term population viability.

Despite a growing number of ecological studies on tropical riparian reserves, there is still little information regarding which features have the greatest benefit for biodiversity (Luke et al., In preparation). For birds in oil palm, we find that riparian reserve width is an important predictor of overall number of species, with reserves at least 40 m wide (i.e., 80 m total width) supporting comparable numbers of species to riparian forest controls. Nonetheless, to support equivalent numbers of forest-dependent taxa and species of conservation concern, riparian reserves would need to be much larger—at least 100 m wide (200 m total width), based on extrapolation of observed trend lines (Figure 4b,c). We can only extrapolate, as large riparian reserves are scarce in our study system and oil palm landscapes in general. It therefore remains to be seen whether all forest-dependent taxa and species of conservation concern present in logged forest would actually use riparian reserves even if they were of substantial width and close to continuous forest.

Uniquely for oil palm landscapes, our results demonstrate the influence of forest quality (as measured by above-ground carbon

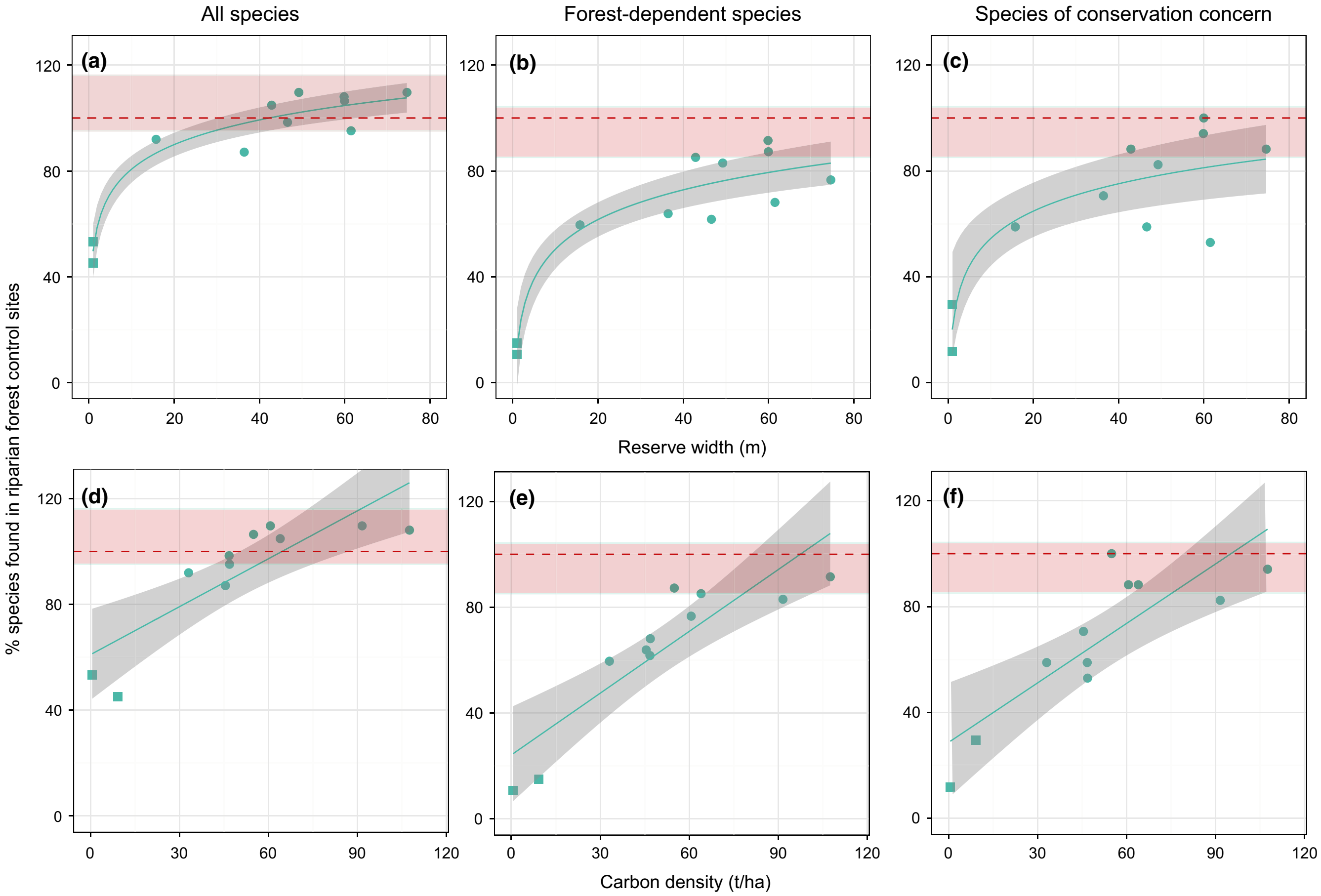

FIGURE 4 Observed species richness for riparian reserve (circles) and oil palm river (squares) sites in relation to reserve width (on each bank) for all species; forest-dependent species; and species of conservation concern (a, b, c). Richness values are expressed as percentages of the median richness from the eight riparian forest control (RFC) sites. Observed species richness was also significantly positively associated with above-ground carbon density (d, e, f). Horizontal red shading demonstrates the first and third quartile in the distribution of species richness across all RFC contol sites, with median shown as the black dotted line. Grey shading around trend lines denotes 95% confidence intervals. One riparian reserve (RR17) was excluded from the models because of missing environmental data for the site

density), as well as reserve width, on the riparian reserve avifauna. These findings suggest that protecting reserves of poor forest quality will offer few conservation gains without habitat restoration. Similar findings have been reported from cattle ranching areas in Amazonia, where riparian reserve width and percentage canopy cover were both positively related to bird and mammal richness (Lees & Peres, 2008; Zimbres et al., 2017). This result implies that approaches to restore biodiversity in agricultural areas may be less successful than sparing areas for conversion in the first place, especially because small forest patches, such as riparian reserves, are susceptible to further degradation via edge effects (Laurance et al., 2018). Disentangling this relationship is difficult, however, as both larger fragments and reserves tend to be of higher forest quality than smaller ones (e.g., Lees & Peres, 2008).

Many previous studies have only compared riparian reserves with the communities of continuous nonriparian forest controls (e.g., Gray et al., 2014). We show that, while overall richness remains comparable to nonriparian control sites in continuous forest, bird community composition in riparian reserves is intermediate between that of riparian controls (RFC) and oil palm rivers (OPR) (Figures 2 and 3). While there were many species shared between riparian reserves and riparian forest habitat, reserves also had some generalist species (e.g., *Spilopelia chinensis* [spotted dove], *Geopelia striata*, [zebra dove] *Copsychus saularis*, [oriental magpie robin], and *Pycnonotus analis* [Sunda yellow-vented bulbul]) that were rare or absent in both riparian and nonriparian forests' controls (i.e., CF and RFC). These matrix-dwelling species are known to be abundant in both industrial oil palm plantations (Edwards et al., 2010) and mixed smallholder cultivation (Azhar et al., 2011). Riparian reserves also lacked several forest-dependent taxa and species of conservation concern, in accordance with previous studies, which found small forest fragments to support few specialist species (Laurance et al., 2018). Across all riparian reserves, we recorded over 70% of the community found in nonriparian forests and over 80% (Supporting Information Figure S1) of the community found in riparian forest control areas. However, the highly different community composition (Figure 3) and lower site-level species richness (Figure 2) suggests that such forest species are found in greatly reduced numbers in riparian reserves.

We found that bird communities around oil palm rivers without a reserve were highly depauperate, consistent with species richness observed in previous oil palm studies (Azhar et al., 2011; Edwards et al., 2010). Thus, the presence of rivers per se appears to have little effect on bird diversity in the absence of significant amounts of natural vegetation. This stark difference was clear even for sites with degraded reserves, highlighting that narrow, low-quality riparian reserves can still have a significant positive effect on bird community structure albeit a small one. Crucially, narrow and degraded reserves still held more forest-dependent taxa and species of conservation concern than oil palm on its own, although at much lower numbers than in large riparian forest areas.

It is possible that species recorded in riparian habitats are not part of a viable population and that the reserves are sinks (Gilroy & Edwards, 2017). For example, Weldon and Haddad (2017) demonstrated that indigo buntings (*Passerina cyanea*) in small fragments continued to nest in patches with greater forest edge despite increased mortality. Likewise, small fragmented areas of habitat are far more susceptible to further perturbations and edge effects than large continuous forests (Ewers, Thorpe, & Didham, 2007), which can result in extinction cascades long after fragmentation has taken place (Kitzes & Hartle, 2015). Alternatively, riparian reserves could act as movement corridors between larger, higher quality, areas of forest. In the context of land-use change, facilitating species dispersal in this way could be vital in maintaining viable populations in otherwise isolated remnant habitat fragments (Capon et al., 2013), particularly for interior forest bird species (Gillies, Cassady, & Clair, 2008).

Riparian forest in both riparian controls and riparian reserves held distinct bird communities to other sites. For instance, *Butorides striatus* and *Alcedo meninting* were only recorded in riparian habitats, while *Enicurus ruficapillus*, a species of conservation concern (near-threatened), was identified as an indicator of riparian forest controls (Supporting Information Table S2). Microclimate, vegetation structure, and prey abundance have been found to differ between riparian and nonriparian habitats in Hong Kong, and these changes correlated with differences in bird species richness and abundance (Chan, Chan, Yu, Zhang, & Dudgeon, 2008). This emphasizes the value of including a riparian forest as a comparator, rather than just a nonriparian continuous forest. It also demonstrates that spatial turnover in species composition between riparian and nonriparian sites is greater than that within just one habitat type, indicating that riparian areas have an additional effect on regional species richness (Sabo et al., 2005).

4.1 | Management recommendations

Our results warrant several recommendations for the improved management of riparian reserves in the tropics. These are not mutually exclusive, but each would have different outcomes for bird communities if adopted. First, increasing minimum reserve widths to at least 40 m on each bank would improve bird diversity to levels typical of riparian areas in large forest blocks. In tandem with the vine cutting and replanting of native tree species, this could also benefit forest-dependent species, since reserve width showed a stronger relationship with forest species richness than it did for overall community richness.

Second, the greatest gains in species richness for the smallest loss of cultivated area could be achieved by replanting vegetation in reserves narrower than 30 m to meet existing legislative guidelines. This is because the relationship between reserve width and species richness is nonlinear, with the greatest gains in richness occurring at small widths. However, this would only maximize species richness at the level of individual rivers, whereas effects on landscape-scale richness and the benefit to forest-dependent species would be less significant.

Finally, the biodiversity protection of any future riparian reserves could be greatly improved by increasing the quality of reserve habitat. This is not just achieved by restoring a degraded habitat in existing plantations but also by ensuring that contractors follow environmental regulations while forests are being converted. In countries such as Malaysia, these restrictions already exist for conventional logging operations (Forest Enactment for Sabah, 1968). However, narrow riparian reserves are difficult to define and map prior to clearance and may endure opportunistic removal of valuable timber as a result. Once land has been redesignated after logging for plantation, this can result in riparian reserves of substandard forest quality. By improving the enforcement of riparian reserve policy prior to and during conversion operations, riparian areas of higher forest quality could be maintained. This is likely to not only benefit threatened biodiversity but could also have knock on benefits to other wildlife, hydrological regimes, and water quality downstream.

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AUTHORS' CONTRIBUTIONS

S.L.M., M.J.S., D.P.E., H.B., and Z.G.D. conceived and designed the methodology; S.L.M. collected, processed and analysed bird encounter data; D.C. and T.J. processed LiDAR data; S.L.M., M.J.S., Z.G.D., and D.P.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Species richness and abundance as well as relevant environmental data analysed in this paper are available at the Dryad Digital Repository https://doi.org/10.5061/dryad.kn251r8 (Mitchell et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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