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Riparian reserves in oil palm can protect forest bird communities

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Summary

1. Conversion of forest to oil palm agriculture is a significant and continuing 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 quantified bird community structure of 20 sites in an oil palm-forest mosaic in Sabah, Malaysia using 6104 detections from 867 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, riparian areas in continuous logged forest and non-riparian logged forest control sites.
3. Riparian reserves, oil palm waterways, continuous riparian forest and non-riparian control forest sites supported distinct avifaunal communities. Generalised linear models showed riparian reserve width, forest quality and the amount of surrounding forest cover to be the strongest predictors of bird species richness. For forest-dependent species, each of these predictors had stronger effect size when compared with all species. On average, reserves held 31% of all species and 30% of forest specialists, whereas continuous riparian forests 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 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 highest numbers of species were found in riparian forest with above-ground carbon densities exceeding 75 tC ha^{-1}, indicating the importance of habitat quality, as well as width, in supporting riparian bird communities.
5. *Synthesis and applications*. If designed and protected appropriately, riparian reserves support diverse bird communities including many species of conservation concern in oil palm estates. This can be achieved by designating large reserves (80-200 m total

width), but to maximize species numbers forest disturbance should also be minimised prior to conversion as well as during plantation operations.

Key-words: agriculture, riparian buffer, riparian zone, biodiversity, land-use change, fragmentation, landscape configuration, forest management.

Introduction

Human activities are causing biodiversity decline at an unprecedented pace globally (Pimm *et al.* 2014), with agricultural expansion being a primary cause of species loss in the tropics (Gibson et al. 2011; Costanza et al. 2014; Jantz et al. 2015). At least 522 Mha of tropical forest was converted to production between 1980 and 2000 (Gibbs et al. 2010) and a further 150 Mha was lost between 2000 and 2012 (Hansen et al. 2010). A major contributor to this problem has been cultivation of oil palm (*Elaeis guineensis*), with at least 3.7 Mha of palm plantation directly associated with deforestation on Borneo alone since 1973 (Gaveau et al. 2016). With a global coverage of over 16.4 Mha, oil palm agriculture is now one of the most profitable land-uses in the tropics, with demand expected to continue to rise with a growing global population (Sayer et al. 2012; Vijyay et al. 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). This pattern has been documented in many agricultural land-use types, including fruit orchards (Round et al. 2006), rubber plantations (Warren-Thomas et al. 2015), and oil palm under both smallholder cultivation (Azhar et al. 2011) and industrial production (Edwards et al. 2010). Retaining forest areas within human-modified tropical landscapes can therefore enhance biodiversity levels (Ewers & Didman, 2006), although crop yields are likely to be reduced as a consequence (Edwards et al. 2010; Phalan et al. 2011). Such remnant forest patches are maintained typically on slopes (Sheldon et al. 2010), floodplains, or along waterways (Foster et al. 2011).

Waterways and riparian areas are often afforded legal protection in tropical countries to mitigate flooding and sedimentation (Mayer et al. 2007). In Malaysia, for example, agricultural companies are required to maintain riparian reserves of between 5 and 50 m from each riverbank (Government of Malaysia, 2012). While reserve width requirements are dictated by the size of the river and administrative region, most are 20-30 m (Government of Malaysia, 2012). 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, voluntarily agree to retain riparian reserves, and there are ambitions to increase the width requirements (Luke et al. 2017).

While the main rationale for protecting riparian reserves is hydrological, these habitats may also be important for maintaining wildlife populations (Naiman et al. 1993). In Queensland, Australia, four out of six arboreal mammal species present in continuous forest used riparian areas of native vegetation (Laurance & Laurance, 1999) and, in Sumatra, riparian reserves in paper-pulp plantations supported large-mammal communities comparable to those in continuous forest (Yaap et al. 2016). Amazonian bird communities in large and undisturbed riparian reserves retain near-complete mammal and bird assemblages when compared to large forest patches (Lees & Peres, 2008; Zimbres et al. 2017). Similarly, in riparian reserves in Borneo, fish (Giam et al. 2015), dung beetle and leaf-litter ant (Gray et al. 2014, 2016) 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 remnant forest patches is likely to be influenced by many of the processes associated with conventional habitat fragmentation, such as area-mediated changes, isolation and edge effects (Wilcove, et al. 1986; Fahrig, 2003). However, riparian areas also exhibit several distinct ecological and geophysical characteristics that can affect their biodiversity value. In temperate regions, ecological communities sampled near rivers tend to be distinct from adjacent upslope areas (Naiman & Decamps, 1997), with terrestrial riparian specialists being more common (Naiman et al. 1998), and upslope species underrepresented due to habitat filtering (Weiher & Keddy, 2001) and niche competition (MacAuthur & Levins, 1967). Ecological assessments of remnant riparian habitat should therefore be contextualised through comparison with riparian areas within contiguous native habitat to be robust. However, this has not always been undertaken.

Although waterways are afforded protection in many tropical countries, few studies have provided recommendations to inform the design of riparian reserves for biodiversity conservation. Here, we explore the relationships between the reserve width, forest quality within the reserve, and the biodiversity present. Specifically, we characterised bird communities in riparian reserves within a typical forest-oil palm landscape of Southeast Asia to evaluate the relative value for riparian and non-riparian biodiversity. Reserve width, the main criterion stipulated in environmental policy, is expected to correlate positively with species diversity, with more species supported in wider reserves (Lees and Peres, 2008; Gray et al. 2014; Zimbres et al. 2017). However, the expected species numbers might not be supported if the riparian habitat is of insufficient quality (Luke et al. 2017, but see Gray et al. 2014). Given the role of fragment area in determining species richness and composition, it is also informative to understand how reserve width and habitat quality could influence biodiversity value in relation to other landscape covariates, and whether the largest reserves can support similar levels of biodiversity to continuous forest areas. This is also a fundamental policy question since protecting larger/wider reserves involves a trade-off between preserving biological communities and making land available for agriculture. As riparian reserves in oil palm are the focus of environmental policy in the certification sector, we also examine whether they are of value for forest-dependent species and species of conservation concern according to the IUCN Red List. In doing so, we elucidate possible management options within oil palm landscapes which should have the greatest benefit to species of conservation concern.

Methods

Study system

The study is set in and around the Stability of Altered Forest Ecosystems (SAFE) project site (117.5°N, 4.6°E) in Sabah, Malaysian Borneo (Fig.1, Ewers et al, 2011). The 80,000 ha area comprises both forest and plantations of oil palm and *Acacia*. 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 is comprised of multiple oil palm estates with trees aged between 8 and 12 years. Within this matrix, remnants of logged forest of varying quality are protected alongside watercourses as riparian reserves. These reserves typically extend ca. 30 m on each bank from the river channel, but across the landscape the reserve widths range from 15-500 m. Reserves also vary significantly in altitude (66–360 m.a.s.l.), topographic ruggedness and substrate (rocky through to sandy).

We sampled bird communities alongside 20 rivers. Ten of the rivers were within oil palm plantation and had riparian reserves (RR), two were in the oil palm with no riparian reserve and were used as controls (OPR), and a further eight rivers were used as controls within the logged forest (LFR). The rivers sampled in oil palm were selected to represent the range and distribution of reserve widths present across the study area (median=54 m, mean=95 m, SD=135 m) and plantations elsewhere in Southeast Asia. Forest quality, indicated by above-ground carbon density measured via LiDAR (Coomes et al. in review), also varied substantially across riparian areas in oil palm and forested controls. Finally, to document any differences between riparian and non-riparian bird communities, we also surveyed eight non-riparian continuous forest sites (CF).

Bird sampling

At each riparian site, birds were sampled at ten point count stations placed at 180-220 m intervals (Euclidian distance) along a 2 km transect that followed the course of the river. The stations were situated up to 10 m up the riverbank to minimise interference from the sound of running water. During each point count, a single experienced observer (SLM) recorded all bird species heard or seen within a 50 m radius of the point. Counts were conducted on days of clear weather between 05:50 and 11:00, and were repeated on three separate occasions at each site between 2014 and 2016. For non-riparian sites, the ten point counts were spatially configured at comparable distances along access trails. Sites were sampled at mean intervals of 72 days between visits. Three species of swift (*Aerodramus maximus*, *A. salangana* and *A. fuciphagus*) could not be reliably separated and so were considered together as *Aerodramus spp.* The bird sampling data from the three surveys were pooled across the ten stations at each site.

Environmental predictors of bird community structure

For each site, we calculated mean above-ground carbon density across the ten point count stations, using remotely sensed data. We used this as an index for overall habitat quality. Similarly, we also calculated canopy height, altitude and topographic ruggedness for each site as an average of values extracted within a 50 m radius of each of our ten point stations. Above-ground carbon density and canopy height were extracted from high-resolution (30 x 30 m and 5 x 5 m respectively) LiDAR datasets, which were gathered in November 2014 using a Leica ALS50-II sensor (Coomes et al. 2017). Altitude (30 x 30 m resolution) was estimated from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov). Likewise, topographic ruggedness was derived using the SRTM data, according to Wilson et al. (2007). Average values for each raster layer were calculated within a 50 m buffer radius of each station using the R 3.2.3 (R Core Development Team, 2015) packages ’raster’, ‘sp’, ‘rgdal’, ‘gtools’ ‘doMC’ and ‘maptools’ .

For each riparian reserve sampled, we estimated the reserve width at each station from the LiDAR canopy height layer (5m 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 tape measure or laser rangefinder (Leica Rangemaster CRF 1000). Subsequently, this value was subtracted from the LiDAR derived width estimate to determine the actual land surface within the riparian 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 1000 m radius of each point count station. All environmental predictors were averaged values across the ten point count stations per site.

Statistical analyses

Species accumulation curves were constructed for each site, and inspected for being close to asymptote, to confirm that sampling was adequate. To demonstrate differences in richness between habitats we also produced accumulation curves for each habitat type (Fig. 1). Rarefied curves, based on 100 iterations, were produced using the ‘vegan’ package. We used the number of bird encounters, rather than absolute numbers, to generate curves, as early morning roost flights of *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 as measured on our *x*-axis.

We used a generalised linear modelling (GLM) framework in ‘lme4’ to explore the partitioning of species abundance and richness by habitat type. GLMs used observed richness values from an equal sampling design. Spatial autocorrelation was assessed using a Moran’s I test on the residuals of our GLM for richness across all riparian sites in order to test for unforeseen associations between nearby sites. The package ‘multcomp’ was used to perform linear hypothesis Tukey tests between habitat combinations (LFR vs. CR, LF vs. RR, LFR vs. OPR, RF vs. RR, RF vs. OPR, RR vs. OPR). This procedure was repeated for two subsets of our community: forest-dependent species and species of conservation concern. Forest-dependent species were defined according to the consensus opinion of five expert ornithologists with extensive experience of Southeast Asian avifauna (Nick Brickle, Frank Rhiendt, Dave Bakewell, Craig Robson and Simon Mitchell), while species of conservation concern were defined as those on the IUCN Red List with a status of near-threatened through to critically endangered (IUCN, 2017).

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 pooled species abundances at each site and non-metric multidimensional scaling (NMDS) ordinations generated using PC-ORD 6.07, to organise 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 randomised 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 (the abundances of which were square-root transformed) following Struebig et al. (2013). Non-parametric permutations tests (ADONIS) 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 (Dufrene & Legrandre, 1997).

GLMs were used to determine whether species richness was driven by our potential environmental predictors (river channel width, riparian reserve bank 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. As ruggedness and altitude were correlated, one of the environmental predictors had to be excluded from the modelling process. Ruggedness was retained in the riparian reserve models, because the range of values was greater than for altitude, and vice versa for modeling across all sites.

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

Results

Species abundance and diversity

Across the 28 sites, we detected 6104 individual birds of 202 species, including 133 forest-dependent species (3838 individuals) and 62 (821 individuals) species of conservation concern (Table 1). Our species accumulation curves approached an asymptote for both each site and each habitat type and followed the same trajectory, confirming that we had sampled the avifauna well enough to assess differences in richness and assemblage structure between them (Fig. 2).

Birds were more abundant in riparian reserves than in forest and oil palm control rivers, but significantly less abundant than in non-riparian forest sites (Fig. 3; mean site-level abundance: LFR=264.0, CF=165.7, RR=226.1, OPR=172.5). Riparian reserves supported similar levels of bird species richness to riparian forest controls, and double that recorded of oil palm control rivers (Fig. 3; mean site-level species richness: CR=61, RR=64.27, OPR=30.5).

Forest-dependent species accounted for 65% of all individuals across the whole community (54% in RR; 74% of LFR; 20% in OPR; and 70% in CF). They were significantly less abundant outside of the both continuous forest and logged riparian forest control sites (Fig 3; mean total site-level abundance: CF=186.6, LFR=172.9, RR=124; OPR=34.4). Forest-dependent species richness was highest in continuous forest controls and riparian logged forests and significantly lower in oil palm (Fig 3; mean site-level species richness: CF=52.5, LFR=44.6, RR=35.8; OPR=6.0).

Species of conservation concern comprised 13% of all individuals across the landscape. They made up a larger component of the bird community in riparian (18%) and non-riparian (16%) controls in continuous forest, compared to those in riparian reserves (11%) and oil palm river controls (2%). There was no significant difference in the number of species of conservation concern found in riparian reserves and logged riparian forest sites in terms of either abundance or richness (Fig 3; mean site-level abundance: CF=41.3, LFR=29, RR=25.3; OPR=3; mean site-level richness: CF=20.1, LFR=16, RR=13.5, OPR=3). 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 riparian width).

Species community composition

Our NMDS ordination of community composition performed better than those based on randomised data (Monte Carlo test: observed stress=12.4; simulated stress=28.7; *P*=0.004; Fig.4a), and showed four clear habitat groupings. The most divergent of these were the oil palm riparian controls, which supported an almost entirely different bird community. Communities in riparian reserves were more similar to those in riparian and non-riparian control sites, but still distinct from both habitat types in terms of species composition (Fig. 4). Since the oil palm riparian controls 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 highly abundant species (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 (Fig. 4; forest-dependent species: R^2=0.125 *P*=0.01; species of conservation concern: R^2=0.1403 *P*=0.01).

Indicator species analyses revealed 13 significant associations between particular bird species and habitat types. *Pelargopsis capensis* and *Enicurus ruficapillus* were indicative of riparian reserves and riparian control forests, respectively. We also found several species, including *Malacopteron magnirostre*, were indictors for continuous forests, and a suite of generalist species, including *Lonchura fuscans*, were significant indicators for oil palm rivers (Table 1).

Environmental predictors of riparian reserve communities

Our models demonstrated that riparian reserve width was an important predictor of bird species richness and avian community composition (Table 2; Fig. 5). Observed and estimated levels of richness responded to changes in riparian width and above-ground carbon density in a consistent manner.

Riparian reserve width, above-ground carbon density and forest cover were all important predictors of observed species richness for the full community (Table 2). This pattern was the same for forest-dependent species though did not apply to species of conservation concern. Across all riparian habitats, above-ground carbon was a significant 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 the richness of all species and of forest dependent species, as well as of assemblage structure reflected by 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 riparian width at which richness was equal to that found in continuous riparian forests (Fig. 5). Trend lines intersected mean richness levels for riparian controls at ca. 40 m for all species. 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 magnitude of the relationship with above-ground carbon density also varied between community subsets. (Fig. 5)

Discussion

We found that oil palm riparian reserves supported comparable levels of bird diversity to continuous forest, especially when reserves are wide and comprise high carbon forest, but they contained fewer forest-dependent taxa and species of conservation concern. By contrast, other studies show riparian reserves sustain intermediate levels of diversity between monoculture tree plantations and control forest sites for dung beetles (Gray et al. 2014) and large mammals (Yaap et al. 2016). Our appraisals of forest-dependent taxa and species of conservation 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 best promote biodiversity. For birds in oil palm, we find that riparian reserve width is an important predictor of overall biodiversity levels, with forest remnants at least 40 m wide (i.e., 80 m total width) supporting comparable numbers of species to continuous forest riparian sites. Nonetheless, to support equivalent numbers of forest-dependent taxa and species of conservation concern, riparian reserves would need to be at least 100 m wide (200 m total width), based on extrapolation of observed trend lines (Fig. 4d, g). 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 would actually use riparian reserves even if they were of substantial width.

Uniquely for oil palm landscapes, our results demonstrate the influence of forest quality (as measured by above-ground carbon density), as well as reserve width, on the riparian reserve avifauna. This suggests that protecting reserves of poor forest quality is unlikely to offer 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 predictors of forest species richness in riparian reserves (Lees & Peres, 2008; Zimbres et al. 2017). This result supports the idea that wildlife-friendly 'land-sharing' approaches to management may be less successful than 'land-sparing' (Gilroy et al. 2014), especially because small areas of non-continuous forest, such as riparian reserves, are more susceptible to degradation through edge effects (Helzer & Jelinski, 1999). Disentangling this relationship is difficult, however, as both larger fragments and reserves tend to be of higher habitat quality than smaller ones (e.g., Lees et al. 2009).

Previous studies have only compared riparian reserves with the communities of continuous non-riparian forest. We show that, while overall richness remains comparable to continuous non-riparian forests, bird community composition in reserves is intermediate between that of continuous riparian and oil palm riparian habitats (Fig 3a). While there were many species shared between riparian reserves and continuous riparian forest habitat, reserves also had some generalist species *Spilopelia chinensis*, *Geopelia striata, Copsychus saularis*, and *Pycnonotus analis* that were rare or absent in both riparian and continuous control forests. 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 (Ewers & Didman, 2006; Benedick et al. 2006).

We found that bird communities in oil palm rivers without a reserve were highly depauperate, supporting only ca. 40 species, which is consistent with species richness observed in previous oil palm research (Edwards et al. 2010). The presence of rivers therefore 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 buffers can still have a significant positive effect on bird community structure albeit a small one. Crucially, degraded reserves still held more forest-dependent taxa and species of conservation concern than did oil palm, although at much lower richness and abundance than in continuous riparian 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 & Haddad (2005) demonstrated that *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 et al. 2007), which can result in extinction cascades long after fragmentation has taken place (Kitzes & Harte, 2015). Nevertheless, riparian reserves could be acting as movement corridors between larger, higher quality, areas of forest. In the context of land-use change, assisting species dispersal in this way could be vital in maintaining viable populations in otherwise isolated remnant habitat fragments (Brown and Kodric-Brown 1977; Capon et al. 2013), particularly for interior forest bird species (Gillies & St. Clair, 2008).

Riparian areas in our study held different species to continuous forest. For instance, green heron (*Butorides striatus*) and blue-eared kingfisher (*Alcedo meninting*) were only noted in riparian habitats, while threatened species such as chestnut-naped forktail and yellow-bellied bulbul (*Alophoixus phaeocephalus*) were only found in continuous forest.

While the former three species are river specialists, feeding on either fish or stream invertebrates, the latter is ostensibly a forest specialist (Eaton et al. 2016). Microclimate, vegetation structure and prey abundance have been found to differ between riparian and non-riparian habitats in Hong Kong, and these changes correlated with differences in bird species richness and abundance (Chan et al. 2008). This emphasises the value of including a riparian forest as a comparator, rather than just non-riparian continuous forest, as has been done in previous studies. It also demonstrates that spatial turnover in species composition between riparian and non-riparian 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). From a policy perspective, this underscores the importance of ensuring that riparian areas are captured within tropical forest protection designations, even if legislation is not geared towards specifically protecting them.

Management recommendations

Based on our results, several recommendations for the improved management of riparian reserves are possible. These are not mutually exclusive, but each would have different outcomes for bird communities within riparian reserves if adopted. First, increasing minimum widths to 40 m on each bank would improve bird diversity in riparian reserves to levels typical of contiguous riparian forests. In tandem with the 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 width and species richness is logarithmic, so the highest gains in richness are at small widths. However, this would only maximise 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 degraded habitat in existing plantations, but also by ensuring that contractors follow legislation while salvage logging and establishing new ones. In countries such as Malaysia, these restrictions already exist for conventional logging operations (Forest Enactment for Sabah, 1968). Although these are generally followed on a landscape-wide scale, narrow riparian reserves are difficult to define and map prior to clearance and may suffer from the opportunistic removal of valuable timber as a result. Once land is re-designated after salvage logging and preparation for plantation, this can result in legal reserves of substandard forest habitat quality. By improving the enforcement of riparian reserve policy prior to and during salvage logging, reserves of higher habitat quality can be maintained. This will not only benefit threatened biodiversity, but is also likely to have knock on benefits to other wildlife, hydrological regimes, and water quality downstream.

Author contributions:

SLM, MJS, DPE, HB and ZGD conceived the ideas and designed the methodology; SLM collected, processed and analyses bird encounter data; DC provided LiDAR data; SLM, MJS, ZGD and DPE led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Bird abundance data and LiDAR-derived environmental data will be available through the NERC online archive DOI: XXXX

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Figures

Figure 1. Twenty-eight bird sample sites in riparian (n=20) and non-riparian (n=8) habitat types in the Stability of Altered Forest Ecosystems (SAFE) landscape and surrounding agricultural matrix in Sabah, Malaysian Borneo. A site comprised ten 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.

Figure 2. Rarefied bird species accumulation curves for each riparian and control habitat type based on 100 iterations. Grey buffers denote one standard deviation either side of mean richness values.

Figure 3. 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 (*P*<0.05) between all habitat types except for those cases marked non-significant (n.s)

Figure 4. Nonmetric multidimensional scaling ordination of bird community structure across riparian and non-riparian 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 7 forest-dependent species and 3 species of conservation concern, and therefore could not be plotted within the same ordination space.

Figure 5. Observed (cyan triangles) and estimated species richness (orange circles) for riparian reserve sites were directly related to reserve width (on each bank) for all species; forest-dependent species; and species of conservation concern (a, d, g). Centre panels indicate

the average estimated and observed richness from the eight logged riparian control sites. Observed and estimated species richness were also significantly associated with above-ground carbon density (b, d, f). The relationships were examined using generalised linear mixed models (see Table 2). Error bars demonstrate the first and third quartile in the distribution of mean species richness across all riparian control sites.

Table 1. Thirteen indicator bird species showing significant associations ($p<0.05$) with different habitat types (continuous forest, CF; logged riparian forest, LFR; riparian reserves, RR; oil palm riparian controls, OPR), according to the INDVAL algorithm (Dufrene & Legrandre, 1997). Relationships with non-metric multidimensional scaling axes (Axis 1=A1, Axis 2=A2) for each species are shown as R^2 and Tau correlation coefficients.

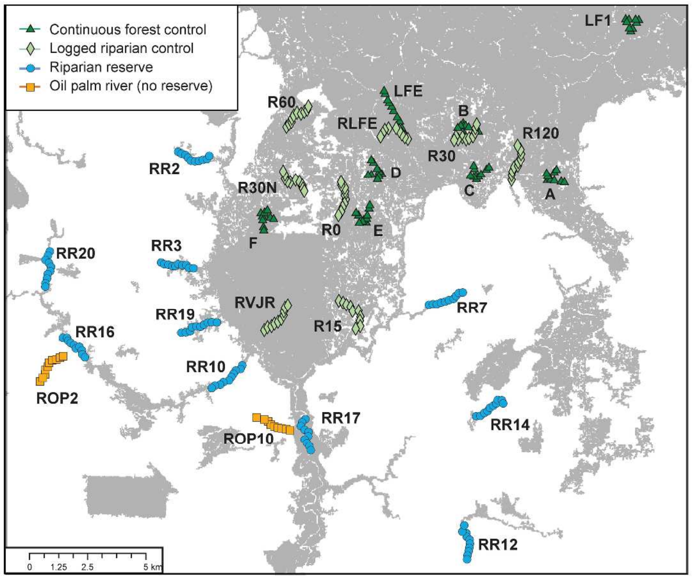
Species	**Habitat**	**IV**	**Mean**	**SD**	**A1 R^2**	**A1 Tau**	**A2 R^2**	**A2 Tau**
Malacopteron magnirostre	CF	61.4	29.1	10.43	0.242	-0.48	0.32	-0.46
Pycnonotus simplex	CF	54.7	29.4	9.65	0.015	-0.03	0.31	-0.43
Copsychus pyrropygus	CF	50.0	20.6	12.46	0.774	0.69	0.003	-0.04
Phaenicophaeus diardi	CF	43.1	21.5	11.66	0.028	-0.15	0.30	-0.44
Enicurus ruficapillus	LFR	61.6	25.1	12.08	0.212	-0.46	0.00	0.06
Pelargopsis capensis	RR	40.0	20.7	12.12	0.017	0.22	0.10	0.22
Geopelia striata	OPR	100	16.3	12.43	0.503	0.36	0.00	0.08
Cinnyris ornatus	OPR	88.9	18.9	13.02	0.279	0.21	0.00	0.14
Lonchura fuscans	OPR	70.6	27.8	12.99	0.358	0.47	0.00	-0.14
Egretta garzetta	OPR	41.7	18.8	12.23	0.303	0.37	0.02	0.14

Actitis hypoleucos	OPR	45.5	16.2	12.28	0.252	0.28	0.02	0.16
Chrysocolaptes validus	OPR	46.9	16.7	11.82	0.28	0.30	0.01	0.15
Centropus bengalensis	OPR	40.8	18.9	12.12	0.21	0.26	0.01	0.076

Table 2. Outputs of generalised linear mixed models, showing model averaged parameter estimates for important predictors, standard error and confidence intervals for predictors of observed species richness and assemblage structure. The ΔAIC<4 model set was used to estimate the averaged outputs. n represents the number of sites included in each model.

Predictor	**Parameter estimate**	**SE**	**Lower 95% CI**	**Upper 95 % CI**
All species, riparian reserves (n=10)				
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, riparian reserves (n=10)				
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, riparian reserves (n=10)				
Intercept	13.4	0.9	11.4	15.4
All species, all riparian sites (n=19)				
Intercept	59.6	2.5	54.3	64.9
Forest-dependent species, all riparian sites (n=19)				
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 , all riparian sites (n=19)				
Intercept	13.3	0.8	11.6	15.0

Above-ground carbon density	5.2	2.6	1.8	10.0
Assemblage structure: All species				
NMDS axis 1, All Habitats (n=26)				
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
Assemblage structure: Forest-dependent species				
NMDS1 All Habitat (n=26)				
Intercept	0.1	0.4	-0.7	0.9
Assemblage structure: Species of Conservation Concern				
NMDS1 All Habitats (n=26)				
Intercept	-0.0	0.1	-0.2	0.1
Forest cover	-1.1	0.2	-1.6	-0.7



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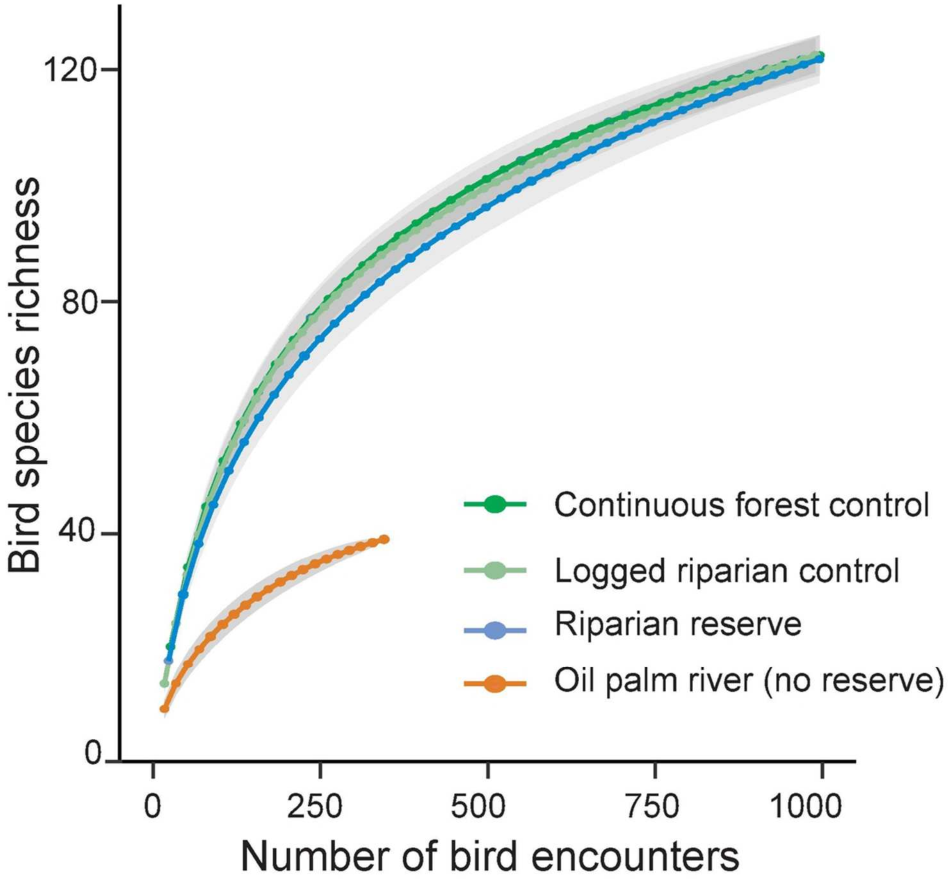

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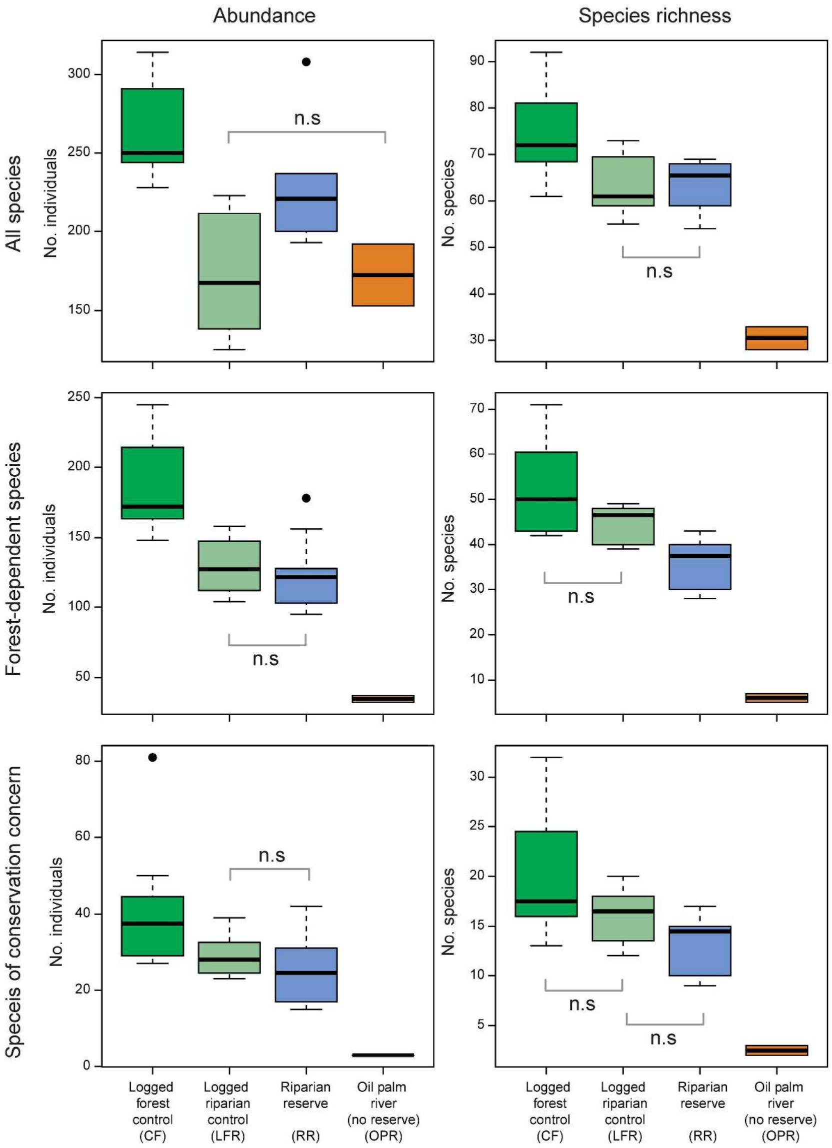

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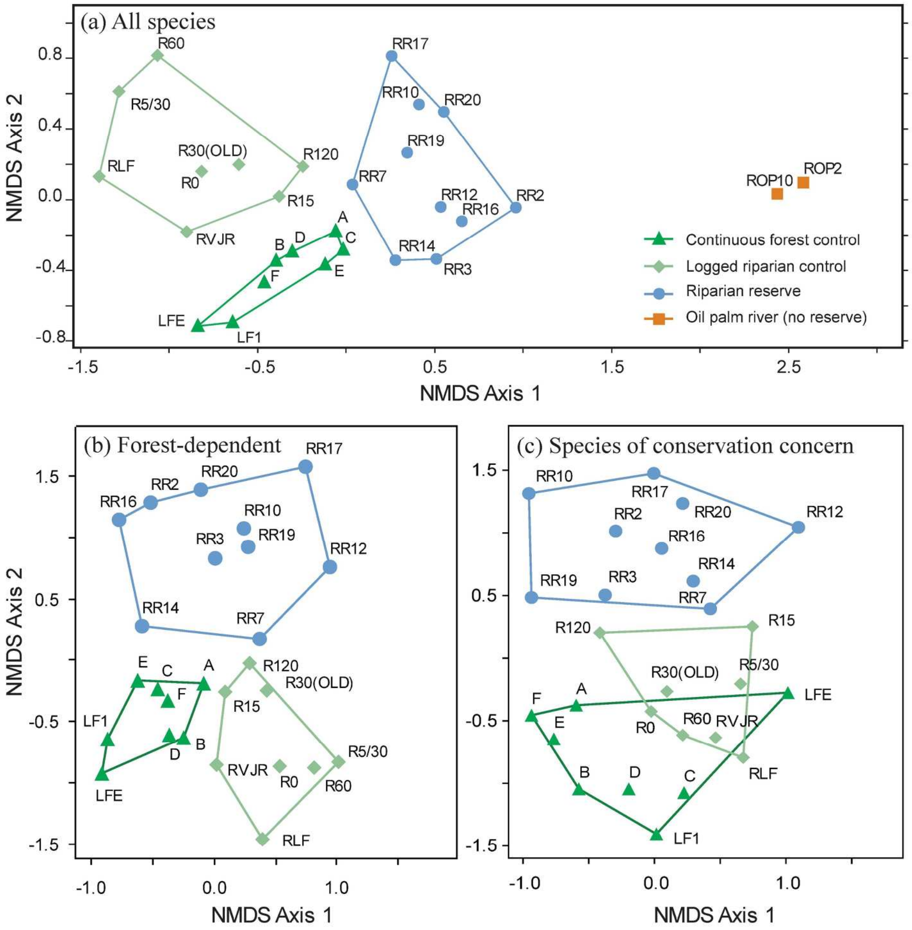

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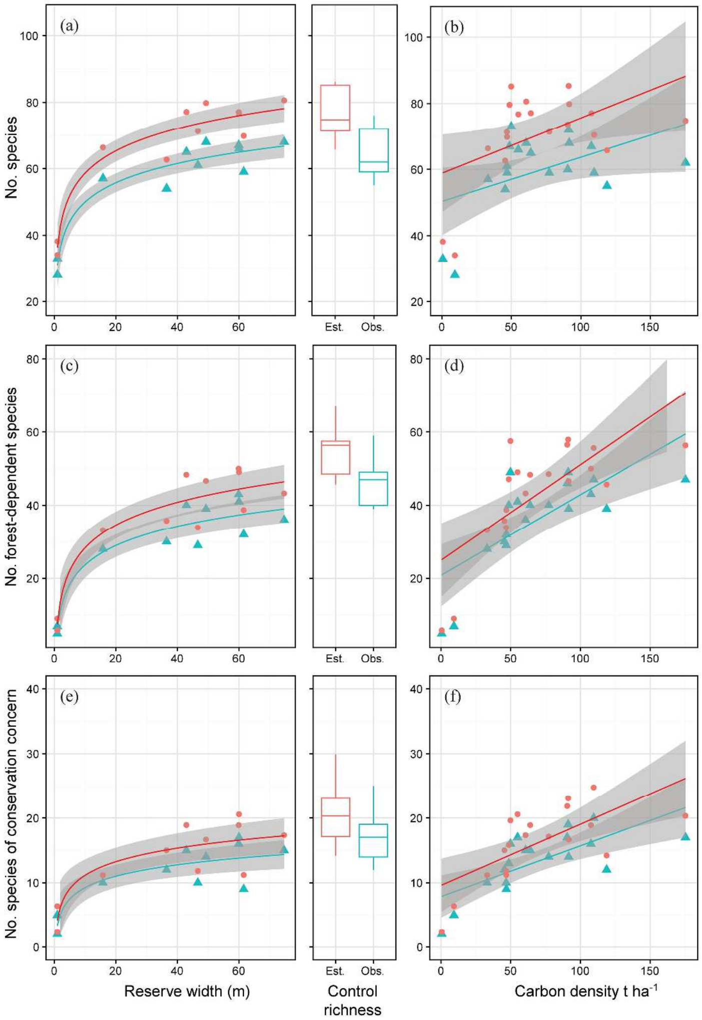

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