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RESEARCH ARTICLE

Riparian reserves protect butterfly communities in selectively logged tropical forest

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Abstract

1. Selective logging is the most widespread habitat disturbance in tropical forests. Primary forest set-asides along riparian zones are mandated in many countries and a key question is whether these riparian reserves provide biodiversity conservation benefits.
2. We characterise butterfly communities in fixed-width riparian reserves of 30m on each bank along narrow streams (<10 m) paired with interior logged forest transects, and in primary forests within a selective logging concession in the south-western Brazilian Amazon.
3. We found that primary forest species richness was more similar to riparian reserves than to paired interior logged forest points, whereas abundance remained higher in both riparian reserves and interior logged points, likely due to the intrusion of canopy-dwelling species in disturbed habitats, as previously reported in the literature. Butterfly assemblages within riparian reserves were more similar to unlogged primary forests than interior logged points, and canopy height in riparian reserves was associated with increased assemblage similarity to primary forest points.
4. Changes in abundance relative to primary forest were of a larger magnitude in interior logged points than in riparian reserves within logged forests, highlighting the role of riparian reserves in maintaining primary forest-like communities. We found no particular primary forest butterfly clades to be more sensitive to changes in abundance than other clades.
5. *Synthesis and applications.* Mandatory conservation set-asides around streams or rivers (riparian buffers) have an important role in protecting the abundance and composition of primary forest butterfly assemblages within selective logging concessions in tropical rainforests. This study highlights the need to assess the conservation value of protecting unlogged riparian forest strips in other taxa to inform policy.

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KEYWORDS

Amazon, biodiversity, conservation set-aside, lepidoptera, reduced impact logging, riparian buffers, riparian corridor, selective logging

1 | INTRODUCTION

Over 400 million hectares of tropical forest have been designated for commercial timber production, an area twice the size of Mexico (Blaser et al., 2011), highlighting the need to reconcile the timber industry with biodiversity conservation. Selectively logged forest can retain many species, including a host of threatened or endemic species (Fimbel et al., 2001). Nevertheless, extraction of valuable tree species leads to the disruption of the canopy, hotter microclimates in the short term, soil compaction and secondary impacts through road networks and skid trails, resulting in the reduction of forest interior specialists and increase in edge-tolerant generalists (Edwards, Tobias, et al., 2014). Harvesting intensity and practices determine the severity of these environmental changes and thus the impacts on biodiversity (Bicknell et al., 2014; Burivalova et al., 2014). Understanding which logging practices reduce forest degradation and maximise biodiversity retention is thus key to tropical conservation while meeting global demand for timber.

Riparian zones around streams are often the only forest that is legally required to be left unlogged within logging concessions. For instance, the Brazilian Forest Code requires the protection of intact vegetation as 'areas of permanent preservation' around ephemeral and permanent streams, springs and hilltops to protect hydrological ecosystem services, in both logging concessions and agricultural lands (Biggs et al., 2019). In Brazil, a strip of 30m of riparian forest should be protected on both sides of small streams (<10 m wide) and 50m around springs (Brasil, 2012; Zimbres et al., 2018), while in mainland Malaysia and in Sabah (Malaysian Borneo) riparian buffer zones of 5 m and 20m, respectively, are required by law, although regulations are poorly enforced (Chappell & Thang, 2007). Research into the value of riparian zones has traditionally focused on the retention of water quality and availability in agricultural landscapes (Luke et al., 2017), revealing that even narrow buffers (c. 5–10m) can help regulate hydrology, although overall forest quality likely affects their benefits (Luke et al., 2019).

In agricultural landscapes, particularly in oil palm plantations, many studies have shown the potential of protected riparian strips in safeguarding biodiversity and reducing the impacts of fragmentation via increased connectivity (Paolino et al., 2018) and that wider buffers (typically those >80m) and those that retain microclimatic refugia protect the most biodiversity (Williamson et al., 2020). Species assemblages in riparian reserves tend to resemble primary or secondary forest more than assemblages in adjacent plantations or cattle ranches, particularly for birds (Hawes et al., 2008; Keir et al., 2015; Mitchell et al., 2018) and some insects (Brito et al., 2017; Gray et al., 2016).

Whereas agricultural landscapes typically present a highly dissimilar matrix to the riparian reserves, little research has investigated the impacts of riparian reserves embedded within timber concessions, but points to important contributions to biodiversity conservation. In selectively logged subtropical and warm-temperate forests of Australia, riparian reserves maintained bat activity similar to that of mature forests (Lloyd et al., 2006). Within intensively managed timber plantations in the United States, 30–50m old-growth forest buffers along streams support communities of birds, amphibians and reptiles typically associated with mature forests (Guzy et al., 2019), while webs of riparian grassland strips in South Africa maintained the abundance and species richness of dragonflies (Kietzka et al., 2021). However, insect species richness does not always correlate well with the level of disturbance (Bonebrake et al., 2010). For instance, the loss of vertical stratification in logged forest can lead to inflated numbers of species detected with understorey or ground-based sampling, as shown for dung beetles (Davis & Sutton, 1998) and butterflies (Willot, 2004). In contrast, studying community assemblage and phylogenetic changes between habitats can point towards ways of protecting biodiversity as a whole and help identify clades particularly vulnerable to habitat degradation (Burivalova et al., 2015; Cardoso et al., 2021). Thus, this approach is needed to accurately assess the benefits of riparian reserves for biodiversity within tropical forest logging concessions.

Here, we assess the effectiveness of riparian reserves in protecting primary forest species within selectively logged forest. We do so by studying fruit-feeding butterfly (Family: Nymphalidae) communities in a logging concession in south-western Amazonia (Rondônia, Brazil). We sampled butterflies along riparian and paired interior forest points in both unlogged and selectively logged primary forest. We addressed three questions: (a) what are the impacts of riparian reserves on species abundance and richness in logged forest; (b) are butterfly assemblages in riparian reserves more similar to those in primary forest than those in their interior logged forest counterparts; and (c) are any changes in abundance across habitat types phylogenetically conserved.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was set in the 46,184-hectare logging concession within the Jamari National Forest, Rondônia, Brazil. The region's climate is hot and humid, with a relatively constant mean annual temperature (25.8°C) and precipitation (2,200–2,600mm/year). There is a well-defined dry season during the Austral winter months from

June to September. The concession is split into three sections, the southern-most 46,184 ha of which was managed by AMATA Brasil SA, a company that has been Forest Stewardship Council certified since 2010. They use a Reduced-Impact Logging (RIL) strategy, including digital mapping of all timber trees >40cm in trunk diameter and planned road networks (Mollinari et al., 2019; Montejo-Kovacevich et al., 2018). Timber extraction in our logged points took place between 2012 and 2015, with mean yield of 10.13 m³/ha (range = 0–35.2 m³/ha). As part of their RIL strategy, perennial and ephemeral streams were also digitally mapped prior to logging. Following Brazilian law (Zimbres et al., 2018), 60 m wide riparian buffers were kept unlogged along streams (30 m on each side), plus a 50-m diameter buffer around the stream headwater source (grey areas, Figure 1a).

2.2 | Butterfly sampling

We sampled butterfly communities in the dry season of 2016 (May–June) at 64 points alongside eight streams, six located in recently selectively logged areas and two in nearby unlogged primary forest (Figure 1a). Two transects of four points each were located on each stream: a riparian transect along the stream and an interior forest

transect 250 m away parallel to the riparian transect (Figure 1c). Points were 125 m apart from each other, which is sufficient to ensure spatial independence in butterfly assemblages (Montejo-Kovacevich et al., 2018; Ribeiro & Freitas, 2012; see Note S1 recapture data, Supplementary Information). As streams may be either ephemeral, that is, with an above-ground water channel during the rainy season, or small perennial, each logging area or Annual Production Unit (APU) was sampled at two locations, one along an ephemeral stream and one along a permanent stream (the mean width of channels measured at 12 points varying from 2.06 to 3.38 m; mean = 2.80 m).

Each point consisted of three baited traps ~5–10 m apart from each other, hung from the nearest tree branch available 1 m above the ground. We sampled fruit-feeding butterflies (Nymphalidae) using Van SomerenRydon cylindrical traps baited with a standardised mixture of mashed bananas and sugarcane juice that had been left fermenting in closed containers in the sun for 12 hr. Traps were operated for 10 full days in cycles of 16 points (two streams and interiors) at a time, with a total of 1,920 trap-days. Traps were visited every 48 h between 06:00 and 15:00 hr to record all butterflies captured and replace the bait with fresh mixture. We photographed, marked and released every individual on the same point they were captured. Species identifications were made from the photographic collection by experienced lepidopterist G.M.K., using

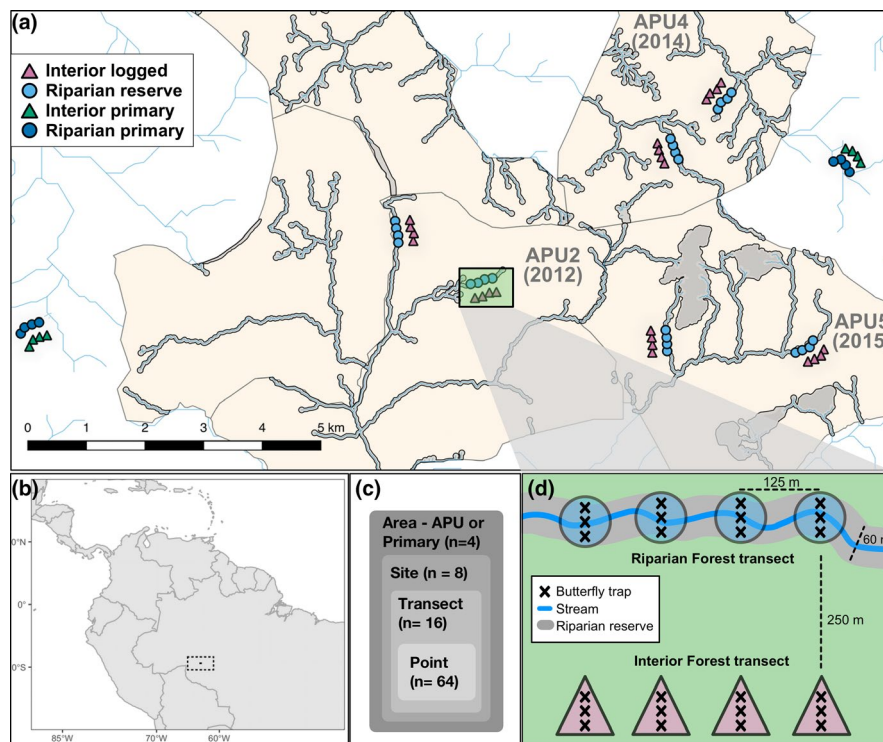


FIGURE 1 (a) Sixty-four sampling points in riparian forest ($n = 8$) and interior forest ($n = 8$) transects in both unlogged primary forest sites (dark blue and dark green points) and selectively logged forest sites (light blue and pink points). Streams are depicted in thin blue lines and in grey are protected riparian and stream headwater reserves, covering 30 m on both sides of the Centre of the stream (total 60 m width). Logging concession highlighted in beige, divided into annual production units (APUs) by grey lines (two streams sampled per APU) and with logging year in brackets. (b) Map of South America; the dotted rectangle highlights the wider area of the sampling points and the small black point within it the exact location of the map. (c) Schematic of hierarchical sampling. (d) Site sampling configuration within two APU forest transects in which riparian reserve points and interior forest points are indicated by circles and triangles, respectively

literature and online reference collections. This sampling approach did not require ethical approvals.

2.3 | Habitat variables

For each point, we measured variables relating to the surrounding environment for each of the three traps and then summarised these values per point. Stream width was measured at the nearest point along the stream to each of the three traps per point and the mean per point used for analyses. We measured the number and diameter at breast height (DBH) of all trees ≥ 10 cm within a 5 m radius of each trap and summed the values for each point. We estimated the mean and maximum canopy height directly above each trap, as well as the canopy openness estimated from a hemispherical photograph using a Sigma 4.5 mm circular fisheye lens, following Mollinari et al. (2019), and averaged the three estimates of each per point.

2.4 | Statistical analyses

All analyses were run in R V3.6.1 (R Development Core Team, 2019) and graphics were generated with the package `GGPLOT2` (Ginestet, 2011). Packages are specified below and all data and R scripts for carrying out analyses and producing results figures are publicly available in an open-access repository (Montejo-Kovacevich et al., 2022).

2.4.1 | Species abundance and richness

We compared overall species richness between habitat types (i.e. primary forest, riparian reserve and interior logged) with individual-based rarefaction and extrapolation curves, using the `iNEXT` package (Hsieh et al., 2016). We refer to primary forest habitat type as the combination of primary interior and riparian transects (i.e. four transects in total), as riparian reserves within logged forest aim to protect communities from both interior and riparian primary forest, and because we did not find large differences between the two. Extrapolation was obtained by doubling the initial reference sample size, interior logged forest ($n = 1,166$). We calculated 95% confidence intervals (CI 95%) using bootstrapping (Hsieh et al., 2016).

2.4.2 | Community integrity and environmental predictors

Changes in community composition were examined at the transect level, that is, at each stream we collated species abundances of the four points in the riparian transect, and separately the four points in the parallel interior forest transect (Figure 1, $n = 16$). This is to ensure that all representative species of a forest area are captured and avoid spatial autocorrelation issues in ordination analyses. We

computed the Whittaker beta-diversity index between all transects with the function `betadiver()` of the `VEGAN` package (Oksanen et al., 2013), performed an Adonis test to test for differences between habitat types (primary forest, riparian reserves within logged forest and interior logged forest), and Principal Coordinate Analysis (PCoA) to visualise community composition clustering across forest transects and habitats.

We evaluated the drivers of community dissimilarity between protected riparian or interior logged habitats and primary forest by calculating the Bray–Curtis dissimilarity index between all sampled points and obtaining the mean dissimilarity of each point to all primary forest points (Banks-Leite et al., 2014), implemented with the function `vegdist()` of the `VEGAN` package (Oksanen et al., 2013). We fitted two separate generalised linear mixed models with dissimilarity to primary forest points in protected riparian or interior logged habitats as response variables and 'site' as a random effect (Figure 1). For both models, explanatory variables were standardised to a mean of zero and unit variance to improve model convergence and included canopy cover and canopy height interacting with mean tree diameter. Additionally, in the riparian reserves model, stream width was included. These were implemented with the package `GLMMTMB` and a binomial family with logit link to adjust for proportion response variables and overdispersion (Brooks et al., 2017).

2.4.3 | Phylogeny construction and phylogenetic signal

To examine changes in primary forest species abundance within logged forest and riparian reserve communities across the phylogeny, we first constructed a phylogeny based on published sequences of three genes for representative species from 50 *Nymphalidae* genera included in our sample, with nine genera of *Riodinidae* as our outgroup (accessions in Table S1) and excluding two genera due to lack of data. Details of the phylogenetic reconstruction methods are found in the Supporting Information (Note S2, Supplementary Information).

We added species polytomies to the resulting genus-level phylogeny for analysis and visualisation, leading to a genus-level tree for 116 species. To study the effectiveness of riparian reserves in protecting primary forest species, we estimated the percentage of conspecific individuals found in each point type (unlogged primary, riparian reserve, interior logged forest) for those species found at least once in unlogged primary forest. We then calculated the absolute change (percentage points) between primary forest % abundance and riparian reserves or interior logged % abundance. Abundances were first standardised to account for the number of points sampled in each habitat. We plotted changes in proportional abundance across the phylogeny with the package `GGTREE` (Yu et al., 2018) and tested for phylogenetic signal with an Abouheif's test based on Moran's I , implemented with the `ADEPHYLO` package (Jombart & Dray, 2010).

3 | RESULTS

3.1 | Species abundance and richness

We collected a total of 2,751 individuals representing 139 species across 64 points. Point-level abundance was highest in logged areas compared to primary forest, in both riparian reserves and interior forests, but did not vary between riparian and interior points within primary or logged forest (Figure 2a). Point-level species richness was, on average, 33% higher in logged forest interior points compared to unlogged primary forest points, but there were no significant differences between interior and riparian points nor between riparian forests whether they were within logged ('riparian reserve logged') or within unlogged primary forest ('riparian primary', Figure 2b). Since the aim of riparian reserves within logged forest is to protect all primary forest species and we found no differences in richness or abundance between primary interior and riparian points, we hereafter refer to both primary forest transect types as 'primary forest'.

The overall number of species recorded was highest for interior logged forest (96 species in 24 points), followed by riparian reserves (89 species in 24 points) and primary forest (71 species in 16 points, which include primary interior and riparian points). Individual-based rarefaction curves reached an asymptote for all habitats, with extrapolations indicating we had sampled 80% of all species in both logged forest and in riparian reserves within logged forest (predicted richness 120 and 111, respectively), and 85% in primary unlogged forest (predicted richness 84; Figure S1, Supplementary Information).

3.2 | Butterfly community composition

At the transect level, species composition was significantly different between transects located across primary forest, riparian reserves within logged forest and interior logged forest (Figure 3a; ADONIS: $R^2 = 0.22$, $p = 0.003$). There was a strong overlap between riparian reserves and primary forest, and between riparian reserves and interior logged transects across the first and second PCoA axes, respectively (Figure 3a). At the point level, mean Bray-Curtis dissimilarity of butterfly communities between riparian reserves and primary forest points (Figure 3b, 0.65 ± 0.05) was similar in magnitude to the background dissimilarity between non-adjacent primary forest points (i.e. on different 'sites'; Figure 1; 0.65 ± 0.6), regardless of whether the primary forest points were located in riparian zones (Figure 3b, empty circles) or in interior primary forest (Figure 3b, empty triangles; Figure S2, Supplementary Information). In contrast, dissimilarity between points located in interior logged forest and primary forest (Figure 3b, 0.67 ± 0.03) was significantly higher than dissimilarity between riparian reserves and primary forest (paired t-test: $t[47] = -2.18$, $p = 0.03$), indicating that riparian reserves tend to be more similar to distant primary forest than to their closest interior logged forest points (250m away, Figure 1d).

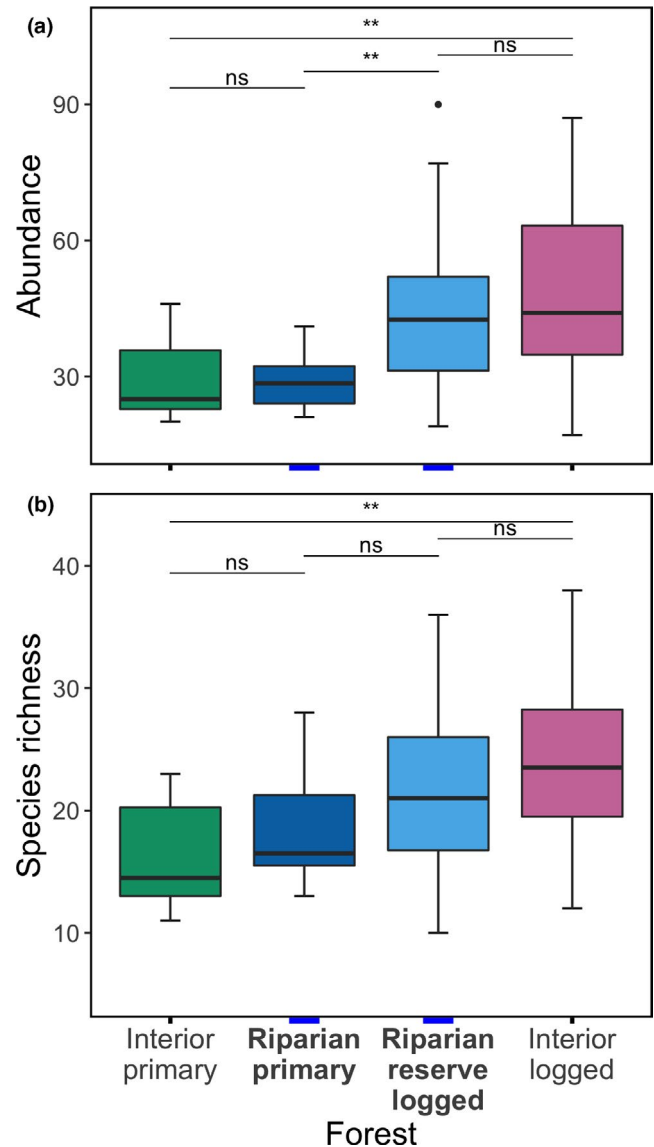


FIGURE 2 Point-level butterfly abundance (a) and species richness (b) across all habitat types. General linear model-derived post-hoc Tukey pairwise tests revealed significant pairwise differences (significant values: $p < 0.05^*$; $p < 0.01^{**}$; ns: Not significant) in abundance and species richness between habitat classes. The bottom and top of the boxes represent the first and third quartiles, respectively; the bold line represents the median, the point represents an outlier (a), and the vertical line delimits maximum and minimum non-outlier observations

We also examined whether the riparian reserve point or the interior logged point was more similar in community composition to primary forest communities. To account for the natural distance-decay in community similarity (i.e. points further apart may show more dissimilar communities regardless of habitat), we directly compared pairs of adjacent interior and riparian points (i.e. points 250m apart in the parallel transects in Figure 1d). There were more pairs of points that showed greater dissimilarity between primary forest sites and the interior logged forest point than against primary forest

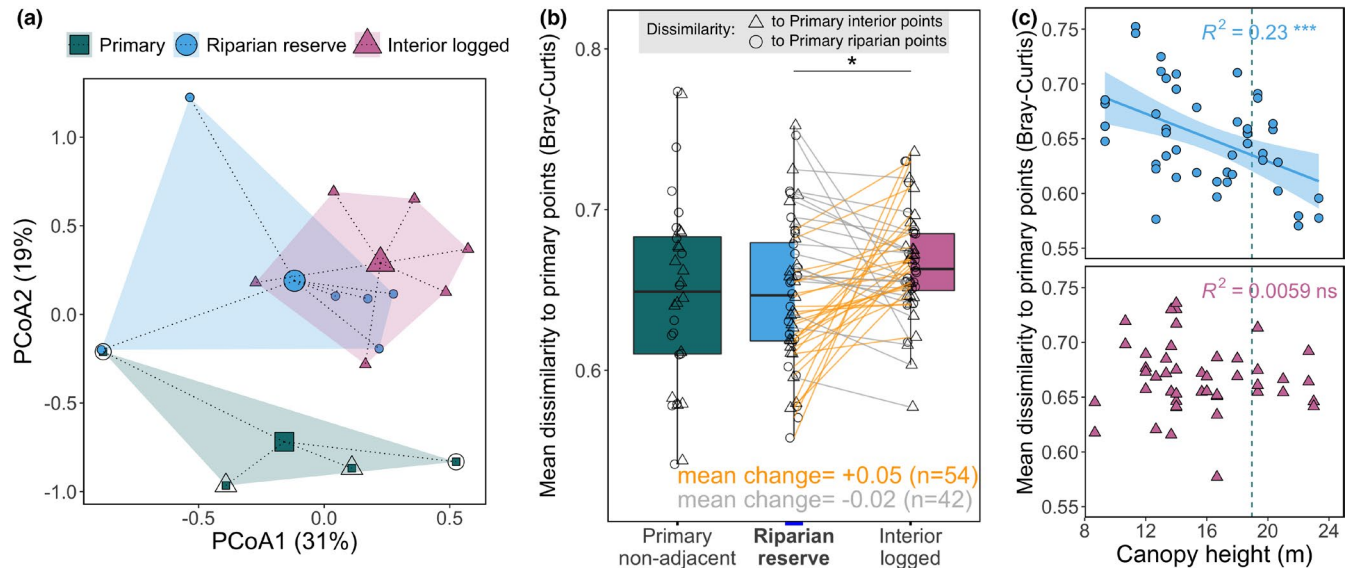


FIGURE 3 (a) Homogeneity of variance in beta diversity across primary forest (riparian and interior combined: Teal squares, with circle and triangle outlines for riparian and interior transects, respectively), riparian reserves (blue circles) and interior logged (pink triangles) forest transects. Centroids for each group represented by large symbols. (b) Mean pairwise Bray–Curtis dissimilarity to primary forest points in riparian (circles) or in interior transects (triangles). Lines join closest points across transects and are orange if dissimilarity to primary forest points is lower in riparian reserves compared to interior logged points (paired t-test significance $*p < 0.05$). (c) Regression of mean pairwise Bray–Curtis dissimilarity and mean canopy height between primary forest points (both interior and riparian) and riparian reserves within logged forest (blue circles) and primary forest points and interior logged forest points (pink triangles). Vertical green dashed lines show mean canopy height in unlogged primary forest points

sites and the riparian reserve point (Figure 3b: orange lines, mean change = 0.05, $n = 54$) than vice versa, where the mean change was also weaker (Figure 3b: grey lines, mean change = -0.02, $n = 42$). In other words, communities in riparian reserves were generally more similar to those found in primary forest than communities in interior logged forest were, even when the riparian reserve point was only 250m away from the interior logged forest point, further demonstrating the value of riparian reserves in buffering composition changes.

In riparian reserves, mean canopy height was a significant predictor of dissimilarity to butterfly communities in primary forest points while accounting for point location (i.e. with site as a random effect; Table 1), and explained 23% of the variation in dissimilarity in a linear beta-regression model (estimate = -0.25, $SE = 6.6 \times 10^{-3}$, $p < 0.001$; Figure 3c). By contrast, in interior forest points, none of the environmental variables measured explained community dissimilarity to primary forest points (Table S2; Figure 3c), indicating that timber removal through logging may distort these relationships. There were no significant differences in forest structure variables measured between habitat types, indicating that point-by-point variation in canopy height within riparian reserves is a major predictor of similarity to primary forest assemblages (Figure S2).

3.3 | Changes in abundance of primary forest species

Overall, many species that were found in primary forest at least once ($n = 72$) changed less in abundance in riparian reserves than in

TABLE 1 Environmental predictors of Bray–Curtis dissimilarity between riparian reserve and unlogged primary forest points. Output of GLMM showing parameter estimates and standard errors for predictors with 'site' as a random effect. All fixed effects were scaled and centred. Significant values $p < 0.05^*$; $p < 0.01^{**}$; $p < 0.001^{***}$

Predictor	Parameter estimate	SE
(Intercept)	0.66***	0.022
Canopy cover	0.04	0.023
Stream width	0.02	0.018
Mean tree diameter	0.03	0.023
Canopy height	-0.13***	0.022
Canopy height \times Mean tree diameter	-0.12***	0.022

interior logged points when compared to their primary forest abundance (36 species, orange lines, Figure 4a). Some species showed the opposite trend or had similar changes in abundance between riparian reserves and interior logged sites with respect to primary forest abundances (29 species, grey lines, Figure 4a), but these were lower in magnitude (mean change -14 compared to +27). On average, the difference in percentage abundance of primary forest species between primary and interior logged forest was 8.5% higher than between riparian reserves and interior logged forest points (paired t-test: $t[64] = -2.5$, $p = 0.015$; Figure 4c).

There was no phylogenetic signal in the degree of change in species abundance between primary forest and riparian reserves within

FIGURE 4 Change in abundance of primary forest species across riparian reserves and interior logged forest. (a) Percentage change in abundance in riparian reserve and interior logged forest relative to primary forest for all species (Box-Whisker plots) and individual species (lines). Orange lines indicate that the change in abundance in a given species was stronger in interior logged than in riparian reserves, and grey lines indicate the opposite trend. p -value shown for paired t -tests between habitats. (b) Genus-level phylogeny of primary forest species and the percentage difference in abundance of the total number of individuals captured in riparian and interior logged forest compared to unlogged primary forest. Darker green indicates an increasingly similar percentage abundance compared to unlogged primary forest; paler green indicates a stronger percentage change relative to unlogged forest (i.e. either a strong loss or gain); and white cells represent the loss of a primary forest species. (c) Examples of abundance distributions across habitats and genera, each line corresponding to one species and shading to absolute percentage change with respect to unlogged forest

logged forest or interior logged forest (change in riparian reserves: Abouheif Moran's $I = 0.04$, $p = 0.3$; change in logged forest: Abouheif Moran's $I = 0.0006$, $p = 0.5$; Figure 4a). Some genera, like the abundant *Morpho* spp. or the majority of *Chloreuptychia* spp., had similar abundances across all habitats, with no marked changes in either riparian reserves or logged forest areas (Figure 4a,b, dark shades of green). However, other species, such as *Pyrrhogyra stratonicius* or *P. edocla*, exhibited stronger changes in abundance in interior logged forest than in riparian reserves compared to primary forest (Figure 4b). When assessing all species, including those only found in logged areas, abundance changes in interior logged forest points compared to primary forest showed a significant phylogenetic signal (Abouheif Moran's $I = 0.15$, $p = 0.01$), but not when comparing riparian reserves and primary forest (Abouheif Moran's $I = 0.04$, $p = 0.2$). This highlights that community composition differences between logged and unlogged forest are stronger in some clades, but that overall butterfly assemblages in riparian reserves are more similar to primary forest than assemblages in logged points.

4 | DISCUSSION

Riparian forest reserves are legally mandated in many tropical logging concessions, but their value for biodiversity is unknown. We found that remnant unlogged riparian forests in an otherwise selectively logged forest landscape protect most of the butterfly diversity and abundance found in undisturbed primary forest, buffering community change compared to interior logged forest. In particular, we found four key differences between the butterfly communities in riparian reserves compared to communities in interior logged forests: (a) riparian reserve communities were more similar to distant primary forest communities than to communities in interior logged forest points 250m away; (b) primary forest communities were more similar to riparian reserve communities than to interior logged forest communities; (c) canopy height variation within riparian reserves is a major predictor of similarity to primary forest assemblages; and (d) differences in community composition between logged and unlogged forest are stronger in some clades than others.

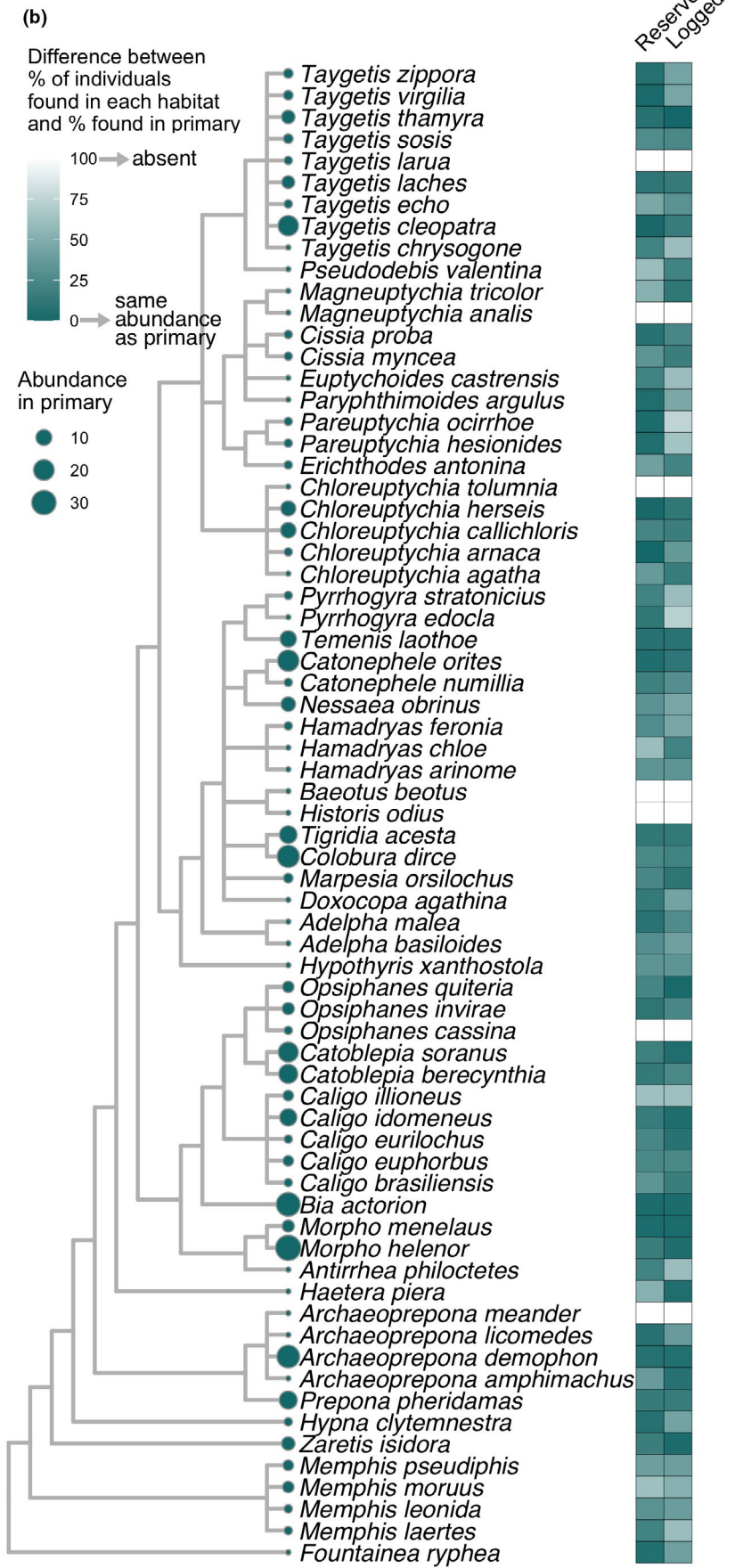
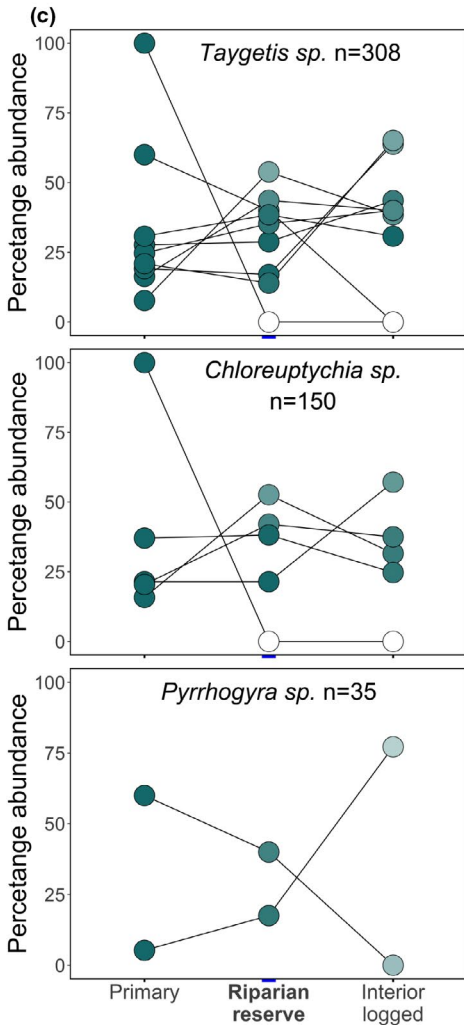
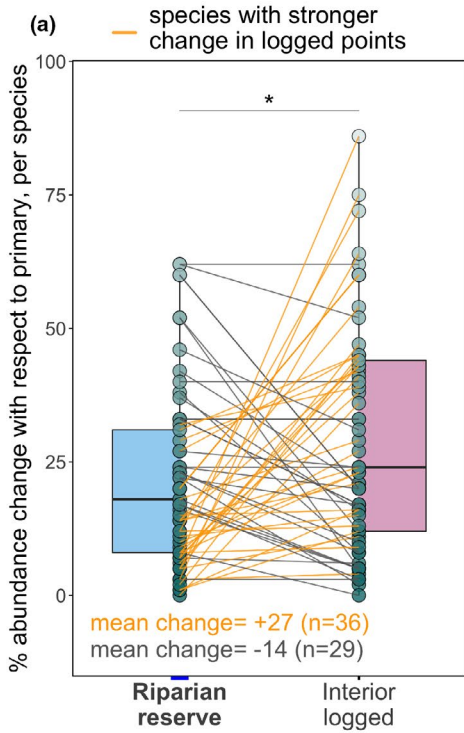
However, there were seven primary-forest species that were completely absent from logged forest, even within riparian reserves, indicating an important role of intact primary forest in protecting the entire species assemblage (Edwards et al., 2011). These species may require larger tracts of protected forest around riparian strips, well beyond the 60-m-wide buffer mandated by Brazilian laws for

streams narrower than 10 m. Canopy height in riparian reserves was correlated with compositional similarity of butterfly communities compared to unlogged forest, stressing the importance of protecting intact old-growth riparian zones and areas with large emergent trees within selectively logged concessions. Overall, our results demonstrate that riparian reserves within selectively logged Amazonian forests are protecting butterfly species and thus should remain a priority in sustainable logging planning.

4.1 | Riparian reserves protect butterfly communities

Retention of intact forest in logged landscapes can be due to regulatory constraints, that is, 'set-asides', as is the case with riparian reserves, or due to avoidance of rocky, steep or inaccessible points by loggers (Putz et al., 2019). Together, these patches of intact forest could greatly diminish the environmental impacts of logging (Griscom et al., 2019), while riparian buffer strips can also enhance corridors for wildlife (Lees & Peres, 2008). We have uniquely shown that riparian reserves within a large Amazonian logging concession protect virtually entire assemblages of primary forest-affiliated species. This supports findings from selectively logged sub-tropical and warm-temperate forests in Australia, where riparian reserves maintained bat activity similar to that of mature forests (Lloyd et al., 2006), and more broadly the biodiversity value of native riparian forest within intensively managed timber plantations (Guzy et al., 2019), oil palm (Mitchell et al., 2018), cattle pastures (Lees & Peres, 2008) and fast-growing tree monoculture (Hawes et al., 2008).

Butterfly abundance was generally higher in logged areas and unlogged riparian reserves compared to unlogged primary forest, but species richness was only significantly higher in logged interior points. Increased overall butterfly abundance in logged forest could be due to generalist or canopy-dwelling species benefitting from the loss of vertical stratification in canopy gaps following the removal of large trees, which has been widely reported in the literature (e.g. Ribeiro & Freitas, 2012). That riparian reserves retained a species composition more similar to undisturbed primary forest than core logged points and a comparable overall species richness compared to unlogged primary forest indicate that these protected areas are playing an important role as reservoirs of primary forest species, as demonstrated for many vertebrate and invertebrate taxa in oil palm plantations (Luke et al., 2019). We did not find a phylogenetic signal in the abundance changes of primary forest species retained in



riparian reserves and interior logged forests relative to unlogged primary forests, highlighting variation in responses between closely related species. Within oil palm plantations, riparian zones connected to primary forests protect high levels of avian phylogenetic diversity (Cardoso et al., 2021). Thus, riparian forest reserves in southwestern Amazonia are apparently effective in protecting primary forest lepidopteran species.

4.2 | Habitat characteristics of riparian reserves

We found that butterfly assemblages in riparian reserves with taller canopies were more similar to those in unlogged primary forest. Logged tropical forests significantly recover their understorey structure and microclimates a few years after reduced-impact logging (Mollinari et al., 2019; Senior et al., 2018), which could allow some biodiversity to recover as well. Butterflies can 'spillover' short distances from rainforests into adjacent oil palm plantations, indicating the importance of proximity to undisturbed habitats for dispersal (Lucey & Hill, 2012), and can facilitate movement of moths away from continuous forests, potentially enabling population re-establishment in regenerating habitats (Cardoso et al., 2021; Gray et al., 2019). Thus, preserving some intact and high-statured forest stands along riparian reserves may increase connectivity between protected unlogged forest areas and facilitate the re-colonisation of logged areas by taxa that depend on old-growth forest.

Long-term protection of riparian reserves is critical, especially with increased access enabled by logging roads and skid trails. In temperate clear-cut silviculture, selective logging within riparian buffers has negatively affected plant communities and microclimates (Mäenpää et al., 2020), even 30 years after logging (Flaspohler et al., 2002), although a small-scale study of low-intensity logging around an ephemeral stream in Bolivia found no effects on amphibian abundance after 1 year (Fredericksen & Fredericksen, 2004). The permanent protection of old-growth set-asides could safeguard tropical taxa that do not fully recover even 35 years after selective logging (Burivalova et al., 2015).

4.3 | Study limitations

This study has three key caveats. First, we only sampled one taxonomic group in one forest stratum. Fruit-feeding butterflies (Family: Nymphalidae) have been widely used in studies assessing the impacts of habitat disturbance on biodiversity, as they are taxonomically well resolved, easy to sample in a standardised manner, and diversity tends to correlate with species richness of butterflies as a whole in the Neotropics (Bonebrake et al., 2010). Sampling uniquely in the understorey could lead to an increase in species richness in logged areas, as the gaps left by logging facilitate the incursion of canopy-dwelling butterflies into the understorey (Montejo-Kovacevich et al., 2018; Ribeiro & Freitas, 2012). We found that total

species richness only differed significantly between interior unlogged and logged forest points, but not between riparian reserves and any other point type. Nevertheless, for the abundance change analyses across habitats and the phylogeny, we focused on species found at least once in primary forest, thereby reducing the effect of canopy or open-habitat species sampled in logged areas.

Second, our points were logged recently (1–4 years prior to the study) and thus butterfly communities may not have recovered fully. Nevertheless, the impacts of the burgeoning selective logging industry on Neotropical faunal diversity have been assessed with concessions logged <3 years prior (Azevedo-Ramos et al., 2006; Bicknell et al., 2015; França et al., 2016; Ribeiro & Freitas, 2012). Third, remnant riparian buffer strip width did not vary across the concession, being fixed to 30 m on both sides of the stream by law (Brasil, 2012). Future studies should assess whether wider riparian reserves would retain more primary forest-like habitat features, as they do within oil palm and cattle pastures (Luke et al., 2019; Williamson et al., 2020; Zimbres et al., 2017), and thus further enhance their biodiversity conservation value. Despite its limitations, our study represents the first to assess the implications of riparian forest reserves within selectively logged concessions for tropical biodiversity.

4.4 | Management implications

Our results show a clear value of riparian zones for preserving biodiversity in selectively logged forests. This underscores the importance of continuing to provide legal protection for riparian forest reserves, as is the case of legally mandated 'Areas of Permanent Preservation' (APPs) within any landholding in Brazil. Ensuring these areas remain unexploited is key to maintaining their biodiversity and hydrological ecosystem services (Lees & Peres, 2008), especially in seasonally dry areas such as southern Amazonia. Furthermore, the inclusion of riparian reserves as a requirement in sustainable timber harvest certification schemes, such as the Forest Stewardship Council, could promote their safeguarding within logging concessions. Such an approach is key to meeting the growing demand for hardwood timber globally while protecting biodiversity, plus hydrological ecosystem services of riparian zones (Biggs et al., 2019; Luke et al., 2017). Advances in remote-sensing technologies and data analysis provide a cost-effective and accurate way to monitor selective logging in broad regions, which, if implemented correctly, could facilitate legal enforcement of riparian reserves (Hethcoat et al., 2019).

The benefits of riparian buffers for biodiversity in logged areas would likely be enhanced by increasing riparian reserve widths, as shown for birds and insects in oil palm plantations (Mitchell et al., 2018; Williamson et al., 2020). In Brazil, the legally mandated 30-m reserve width on both sides of streams <10 m was insufficient to protect birds and mammals in highly fragmented landscapes dominated by conversion to cattle pastures (Lees & Peres, 2008). However, increasing riparian forest protection could directly compete with setting aside large blocks of primary forest habitat within or in neighbouring concessions,

that is, land-sparing selective logging (Edwards, Gilroy, et al., 2014). Preserving large patches of old-growth forest might be necessary for interior primary forest species that are highly sensitive to disturbance and not found along riparian forests (Betts et al., 2021; Edwards, Gilroy, et al., 2014; Montejo-Kovacevich et al., 2018). Nevertheless, in logging concessions of Borneo, riparian reserves of 50m could have been implemented without changes in timber yields if appropriate spatial planning to exploit less sensitive, but inaccessible, areas had been in place (Griscom et al., 2019).

A key concern for selectively logged forests in the tropics is their potential to recover fully within the designated harvest cycle, which under Brazilian legislation is 30 years if only trees >50 cm in diameter are extracted (Sist & Ferreira, 2007). Riparian reserves can act as reservoirs of primary forest species and biodiversity corridors, by increasing connectivity between protected blocks of old-growth forest, as seen in cattle pastures and plantations for birds (Gillies & Clair, 2008), mammals (Zimbres et al., 2017) and insects (Gray et al., 2019; Luke et al., 2019). In turn, riparian reserves could facilitate re-colonisation and accelerate recovery of biodiversity after logging. Taken together, our study underscores the importance of protecting riparian reserves through legislation and careful spatial planning within selective logging concessions for the conservation of tropical forest arthropods.

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CONFLICT OF INTEREST

None.


AUTHORS' CONTRIBUTIONS

G.M.-K., D.P.E., C.J.M. and C.A.P. conceived the ideas and designed the methodology; C.J.M., G.M.-K. and S.H.S. collected the data; G.M.-K., S.H.S. and D.P.E. analysed the data; G.M.-K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R scripts available via the Zenodo Repository <https://doi.org/10.5281/zenodo.6349414> (Montejo-Kovacevich et al., 2022).

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SUPPORTING INFORMATION

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