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Variable species but similar amphibian community responses across habitats following reduced impact logging

Sami Asad^{a,h,i,*}, Victor Vitalis^b, Roshan Guharajan^{b,c}, Jesse F. Abrams^{d,e}, Peter Lagan^f, Johnny Kissing^f, Julsun Sikui^g, Andreas Wilting^c, Mark-Oliver Rödel^{a,h}

^a Museum für Naturkunde Berlin, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

^b Panthera Malaysia, 46200 Petaling Jaya, Selangor, Malaysia

^c Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

^d Global Systems Institute, University of Exeter, Exeter EX4 4QE, UK

^e Institute for Data Science and Artificial Intelligence, University of Exeter, Exeter EX4 4SB, UK

^f Sabah Forestry Department, Locked Bag 68, 90009 Sandakan, Sabah, Malaysia

^g Forest Research Centre, Sabah Forestry Department, 90009 Sandakan, Sabah, Malaysia

^h Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

ⁱ Institute of Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

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ABSTRACT

Although sustainable forestry methods such as Reduced Impact Logging (RIL) have lower impacts on biodiversity compared to conventional logging, the direct and indirect effects of RIL are poorly understood. Additionally, studies focusing on specific habitats may fail to detect cross-habitat impact variation or the effect on taxa which utilize multiple habitats, i.e. amphibians. We therefore investigated the responses of amphibians in stream and terrestrial habitats to RIL and its direct/indirect impacts. We analysed data from anuran communities sampled before and after RIL within the Deramakot forest reserve in Sabah, Malaysian Borneo. Using multi-species community occupancy models, we determined species and community responses to RIL and covariates representing the direct (leaf depth and canopy closure) and indirect (distance to logging roads and skid trails) effects of logging. Diversity profiles and dissimilarity indices derived from occupancy model results were used to identify shifts in diversity/evenness and community dissimilarity respectively following RIL. Indirect logging impacts (distance to logging roads/skid trails), proved a better predictor of amphibian occupancy in stream habitats compared to direct logging impacts (leaf litter depth shifts), with the opposite trend observed in terrestrial habitats. Anurans in stream and terrestrial sites exhibited greater dissimilarity and community occupancy after logging compared to control sites, with all diversity metrics (species richness, Shannon and Simpson diversity) increasing in logged stream sites. These findings, contrary to our expectations, suggest that whilst amphibian species in different habitats exhibit variable responses to direct and indirect RIL impacts, they exhibit similar community level responses to RIL across habitats.

* Corresponding author at: Museum für Naturkunde Berlin, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany.

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1. Introduction

With global tropical deforestation reaching critical levels (Hansen et al., 2015; Curtis et al., 2018), human-modified forests are increasingly recognized as an integral component of biodiversity conservation management (Corlett, 2015). Logging concessions cover not only the majority of remnant tropical forests (Blaser et al., 2011) but may also maintain high levels of biodiversity (Burivalova et al., 2014; Bicknell et al., 2015; Griscom et al., 2018). However, the impacts of logging are far from uniform and may constitute direct and indirect effects (Laurance et al., 2009; Martin et al., 2015; Walsh et al., 2011), vary between logging types (Chaudhary et al., 2016; Griscom et al., 2018) and across different habitats (Kreutzweiser et al., 2005; Walsh et al., 2011; Hardwick et al., 2015).

The direct impacts of logging on specific ecological factors such as forest structure (Pereira et al., 2002; Martin et al., 2015) and stream dynamics (Iwata et al., 2003; Walsh et al., 2011; Calvão et al., 2016), are often overlooked when seeking to quantify direct logging impacts on biodiversity. Furthermore, indirect impacts following logging infrastructure development (i.e. skid trails and logging roads), can result in additional effects, including greater thermal fluctuations (Laurance et al., 2009), invasions of competitors (Konopik et al., 2014), creation of novel aquatic habitats (Ernst et al., 2016), and ground vegetation clearance (Kleinschroth and Healey, 2017). Determining these direct and indirect logging impacts, is especially important for improving sustainable forestry methods such as Reduced Impact Logging (RIL).

Tropical forests managed under RIL, adopt strict pre/post-harvest planning measures including lower maximum allowable cuts, 30 m wide stream buffers and reduced skid trail construction (among others), resulting in 50% less damage to remnant forests compared to conventional methods (Pinard et al., 1995). This results in comparatively lower biodiversity loss, with forests subject to RIL often able to maintain biodiversity levels comparable with primary forest sites (Burivalova et al., 2014; Bicknell et al., 2015; Chaudhary et al., 2016; Griscom et al., 2018). Disentangling the direct impacts of timber extraction and the indirect impacts of logging road development following RIL, would thus allow us to evaluate the effectiveness of specific logging management protocols (stream buffer widths, skid trail/logging road limitations etc).

Determining direct and indirect RIL impacts is further complicated when extrapolating across habitats, particularly in diverse species communities with life-history dependent usage of aquatic areas (e.g. amphibians). Shifting stream dynamics following logging (Kreutzweiser et al., 2005; Walsh et al., 2011; Asad et al., 2021) may impact tadpole habitat for stream breeding anurans (Gillespie, 2002; Wood and Richardson, 2009), whilst shifts in terrestrial microhabitats (Negrete-Yankelevich et al., 2007; Ewers and Banks-Leite, 2013; Hardwick et al., 2015) may disturb adult amphibian refugia and foraging sites (Gardner et al., 2007). As RIL methods include the maintenance of unlogged stream buffers (Pinard et al., 1995), it is possible that amphibians within stream sites might be less impacted than their terrestrial counterparts. Therefore, determining logging impacts on amphibians across these habitats will serve as an excellent model for assessing cross-habitat variability in RIL responses.

In this study we aimed to determine the effects of RIL on Bornean amphibian communities within terrestrial and stream habitats. The island of Borneo is both an anuran diversity hotspot (Inger, 1966; Inger et al., 2017) and a logging intensive region, with timber concessions covering over 40% of remnant forests (Gaveau et al., 2014; Struebig et al., 2015). Bornean anurans are predominately stream breeding (roughly >75%) with adult stages utilizing both riparian, terrestrial and arboreal habitats, whilst the remaining terrestrial and arboreal species breed in either stagnant water bodies or have direct-developing young (Inger, 1966; Inger et al., 1986; Goutte et al., 2017; Ahmad and Grafe, 2020). The variable life-histories and habitat utilization of species occupying terrestrial and/or stream habitats make them ideal candidates for quantifying disturbance effects across phylogenetically related taxa with variable micro-habitat associations. Within these two habitats, we aimed to determine the direct/indirect impacts of RIL on amphibian species, how species and community-level responses to RIL vary, and how these two communities differ in their responses to all of the above. Specifically, this study aimed to address the following questions: i) How do amphibian species respond to the direct (habitat changes) and indirect (logging infrastructure) effects of RIL? ii) How do amphibian communities shift following RIL? and iii) Are the impacts of RIL consistent across amphibians in terrestrial and stream habitats?

2. Methods

2.1. Study site

We conducted this study within the Deramakot forest reserve (5°14–28'N, 117°19–36'E) in central Sabah, Malaysian Borneo (Fig. 1). The reserve encompasses a 550 km² area predominantly classified as hilly lowland dipterocarp forest (50–350 m a.s.l.) at varying stages of regeneration following Reduced Impact Logging (RIL). In Deramakot, RIL techniques are used in accordance with the Forest Stewardship Council (FSC) guidelines (see introduction and Pinard et al., 1995). The reserve was the first tropical forest certified by the FSC in 1997 and has been credited for its sustainable forest management (Lagan et al., 2007). We established 12 stream and nine terrestrial (total = 21) sites between four logging compartments. Three “control” compartments (a, b and c, see Fig. 1) were previously logged using RIL methods > 10 years ago (stream = 5, terrestrial = 4), whereas one “pre/post-RIL” compartment (stream = 7, terrestrial = 5) was logged following RIL methods in late 2017/early 2018. Although control compartments were previously subject to RIL 10–21 years ago, their amphibian diversity remains high (Asad et al., 2021). Logging within the “pre/post-RIL” compartment involved the extraction of 49.8 m³ of timber per hectare harvested in accordance with the FSC guidelines (see above).

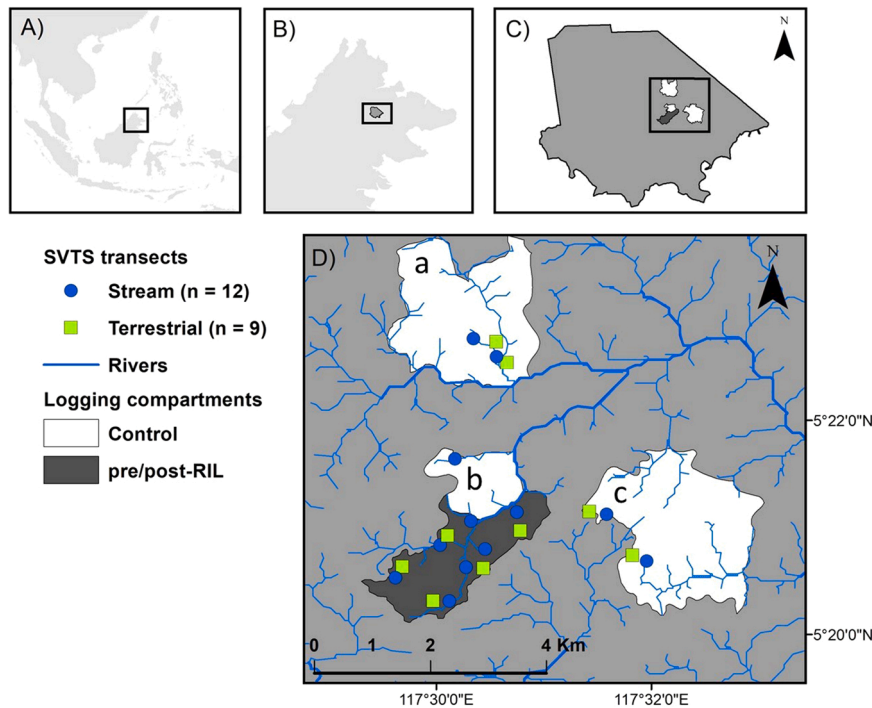


Fig. 1. Map of Sabah, Malaysian Borneo (A) and the location of the Deramakot forest reserve in Sabah (B). Location of the logging compartments sampled within the reserve (C) and the locations of the 21 transects within the sampled logging compartments, including control compartment designations a, b and c (D).

2.2. Amphibian sampling

All 21 sites were surveyed between March and August before (2017) and after (2019) logging. Site surveys occurred on three to seven occasions each year with a minimum of five days between each survey. We conducted Standardized Visual and Acoustic Transect Sampling (SVATS) to detect anurans within sites. This method provides cost effective, repeatable, quantitative data for anurans, whilst maintaining a low impact on the study organisms (Rödel and Ernst, 2004). Stream transect dimensions and survey protocols followed the methods of Asad et al., (2020, 2021). Transects were 100 m long, 5 m wide, and searched from forest floor to a height of two metres. Due to the fine-scale, heterogeneous nature of Bornean stream anuran habitats (Konopik et al., 2015; Goutte et al., 2017; Ahmad and Grafe, 2020), and the comparative structural homogeneity of terrestrial habitats, we nested subplots of different sizes within stream and terrestrial transects. Within stream sites, transects were divided into ten adjacent 10×5 m subplots, whilst terrestrial transects were divided into five adjacent 20×5 m subplots. Two researchers surveyed transects for 30 min (three minutes per plot) between 1830 and 2300 h. All amphibians visually and acoustically detected within the transect bounds were identified to species following Inger et al. (2017). The species complexes *Limnonectes kuhlii* and *Chalcorana raniceps/megaloensa* are herein referred to as *Limnonectes cf. kuhlii* and *Chalcorana cf. raniceps*, respectively.

2.3. Covariate collection and processing

We collected covariates previously linked to amphibian detection probability (Asad et al., 2020), and associated with amphibian activity, calling behaviour and breeding phenology (MacKenzie et al., 2002; Allentoft and O'Brien, 2010; Grant et al., 2013). Time Since Sunset (TSS), moonphase, temperature, humidity and Maximum Daily Rainfall (MDR). Moonphase (0–100% moon presence) and TSS (0–4.11 h): were recorded at the start of each transect survey. Temperature, humidity and MDR were collected from a Sabah Forestry Department (SFD) weather station located 1–13 km from the transects. Although this may not represent subtle climatological variations at each site, we previously identified significant correlation between temperature/humidity at a subset of transects and this weather station. As such, this weather station appears to provide a suitable proxy for local climatological patterns.

To allow comparisons of RIL and control subplots between years, we collected a suite of habitat covariates in both 2017 and 2019. We collected covariates at stream and terrestrial sites associated with amphibian occurrence (Inger, 1966; Goutte et al., 2017; Asad et al., 2020) and the direct impacts of logging (Pereira et al., 2002; Iwata et al., 2003; Walsh et al., 2011; Hölting et al., 2016; Asad et al., 2021). Within terrestrial sites these covariates constituted the following: Aquatic Breeding Sites (ABS), canopy closure, understory density and leaf litter depth. Aquatic breeding sites such as pig wallows, road pools/ditches, seepages and potholes are strongly associated with terrestrial amphibian presence throughout Borneo (Inger, 1966; Inger et al., 2017; Scriven et al., 2018). Therefore, we recorded the number of ABS within each subplot, defined as any body of water > 30 mm (thus including tree holes and

rock depressions) in width and depth. We measured canopy closure using canopy images taken with a Nikon Coolpix S33 on the left, centre and right edge of each subplot. Images were manually converted to black and white with the resulting black pixels divided by total pixels to generate canopy cover estimates. We measured understory density using an image taken with the above camera from the subplot centre, of a 1 m wide 1.5 m tall, red sheet. This sheet was held 2.5 m from the left subplot edge with the bottom touching the forest floor, to highlight the density of vegetation below 1.5 m. Images of these sheets were cropped to show only the extent of the red sheet, converted to black and white manually and divided as above to generate understory density estimates. We collected five leaf litter depth values recorded within two, 1×1 m quadrats on the right/left edge of subplots.

Within stream sites we collected all the above covariates (except ABS) along with the following: Stream volume, stream slope, stream speed, stream siltation and stream width variance. To account for fluctuations in stream volume and speed due to heavy rainfall, we collected these covariates during each transect survey, with the averages per year taken. We multiplied the length (each subplot = 10 m), depth and width of the stream for stream volume. We measured stream speed as metres per second via timing how long a flotation device travelled along a 1 m stream section. All other covariates were collected once. We measured stream width variance as the percent difference between the maximum flooded stream width determined by the high water mark (discernible by previous flood debris) and the average stream width. We measured stream slope as the height difference along the stream between the start and end of each subplot. We visually assessed siltation within a 1×1 m quadrat located at the streambed centre in each subplot in five categories: 0, 0–25, 26–50, 51–75, and 76–100% siltation cover. All habitat covariates were measured at the start and end of each subplot (every 10 m and 20 m in stream and terrestrial transects respectively) and the average per subplot taken.

To determine the indirect effects of logging, we utilized digitized road presence data collected and provided by the SFD. Logging roads have been linked to both positive (Ernst et al., 2016; Hölting et al., 2016) and negative associations with biodiversity (Laurance et al., 2009; Konopik et al., 2014; Edwards et al., 2017). As the effect of different road sizes and types may vary (Kleinschroth and Healey, 2017), we divided logging roads into two categories: skid trails and logging roads. Skid trails are defined as temporary roads built for direct timber extraction whilst logging roads are defined as maintained permanent roads built for the movement of extracted timber. We determined proximity to logging infrastructure (logging roads and skid trails separately) from sampling locations (each subplot) as a function of Euclidean distance (in metres) calculated in ArcGIS 10.3.1.

Habitat and detection covariates were scaled to have a mean of zero and variance of one, and tested for collinearity using Spearman's rank correlation in the package *Hmisc* ver 4.2–0. We excluded all substantially correlated covariates (Coefficient > 0.7) from subsequent analysis (Dormann et al., 2013).

2.4. Analysis

To discern the direct ecological impacts of logging from inter-annual variations, we used Pairwise Wilcoxon tests for habitat covariate comparisons between sampling years. We considered covariates exhibiting significant differences between years to represent inter-annual fluctuations, and covariates exhibiting significant differences between years at logged sites only to represent direct logging impacts. We characterized the optimum inter-annual fluctuation and direct RIL impact covariates as those with the greatest significant differences between treatments (see Fig. 2 for selection process).

All subsequent analysis of species detection probability and responses to RIL were conducted using Bayesian multi-species community occupancy models (Sollmann et al., 2017). These models allow for the estimation of species-specific and community level occupancy probability whilst accounting for imperfect detection as a function of covariates (MacKenzie et al., 2002, 2017). This modelling framework assumes that species-specific parameters are drawn from a common parametric distribution governed by community (or hyper) parameters (Sollmann et al., 2017). Prior to determining RIL impacts however, we first determined the optimum detectability covariates using these community occupancy models. For this, we ran single detection covariate formulations of the multi-species model for terrestrial and stream sites separately, assuming species-specific effects on detection probability for each covariate. We classified the optimum detectability covariates as the two with the most significant (95% CI not overlapping zero) and/or moderate (75% CI not overlapping zero) associations between species in the stream and terrestrial datasets. Following the incorporation of optimum detection covariates, we determined species and community responses to RIL and direct/indirect logging impacts using a final multi-species community occupancy model for each habitat.

Within stream sites, species-specific/community level occupancy probability was modelled using the two best performing occupancy covariates (stream slope and stream volume) as identified by Asad et al. (2020), along with the optimum direct logging impact covariate. We also included the optimum inter-annual fluctuation covariates (one representing stream dynamics and one representing forest structure) to account for non-logging associated yearly fluctuations in occupancy. Within terrestrial sites we modelled species-specific/community level occupancy probability using the ABS covariate which is most frequently associated with terrestrial anuran presence (Inger, 1966; Inger et al., 2017; Scriven et al., 2018), along with the optimum direct logging impact covariate. The optimum inter-annual fluctuation covariate (representing forest structure) was also included in terrestrial sites to account for similar yearly occupancy fluctuations. Additionally, we included distance to skid trail and distance to logging road within both stream and terrestrial models to account for the indirect effects of RIL.

The number of occupancy covariates (seven in stream, five in terrestrial sites) was restricted somewhat to prevent over-parametrization, particularly in the smaller, sparser, terrestrial dataset. To assess species and community level occupancy responses to RIL and simple yearly fluctuations, we modelled occupancy probability with species-specific random intercepts set to RIL- and

control-specific hyperparameters to allow for varying baseline occupancy levels between treatments/years. These intercepts were defined as follows: pre-RIL-2017, post-RIL-2019, control-2017 and control-2019. Due to our nested study design (multiple subplots within transects), we included a random effect for each transect within our analysis (Asad et al., 2020, 2021). The random effect multi-species occupancy model was conducted in a Bayesian framework within JAGS (Plummer, 2003), called via R using the package *rjags* ver. 4.3.0 (Plummer, 2014). We ran three parallel Markov chains with 200,000 iterations, of which we discarded the first 20,000 as burn-in and applied a thin rate of 20. We assessed convergence using the Gelman-Rubin statistic (Gelman, 2004).

To determine dissimilarity from the original amphibian community (sampled in 2017) following RIL, we used a modification of the Bray-Curtis index (Giacomini and Galetti, 2013). Dissimilarity measures determine the degree by which two communities vary across time, space or in this case, following an ‘experimental treatment’ i.e. before/after RIL (De Caceres et al., 2013). The Bray–Curtis index calculates dissimilarity values via comparing the composition of target assemblages to a reference assemblage (Bray & Curtis, 1957). We adapted the index to compare predicted species occupancy probabilities of the target assemblages (post-RIL-2019 and

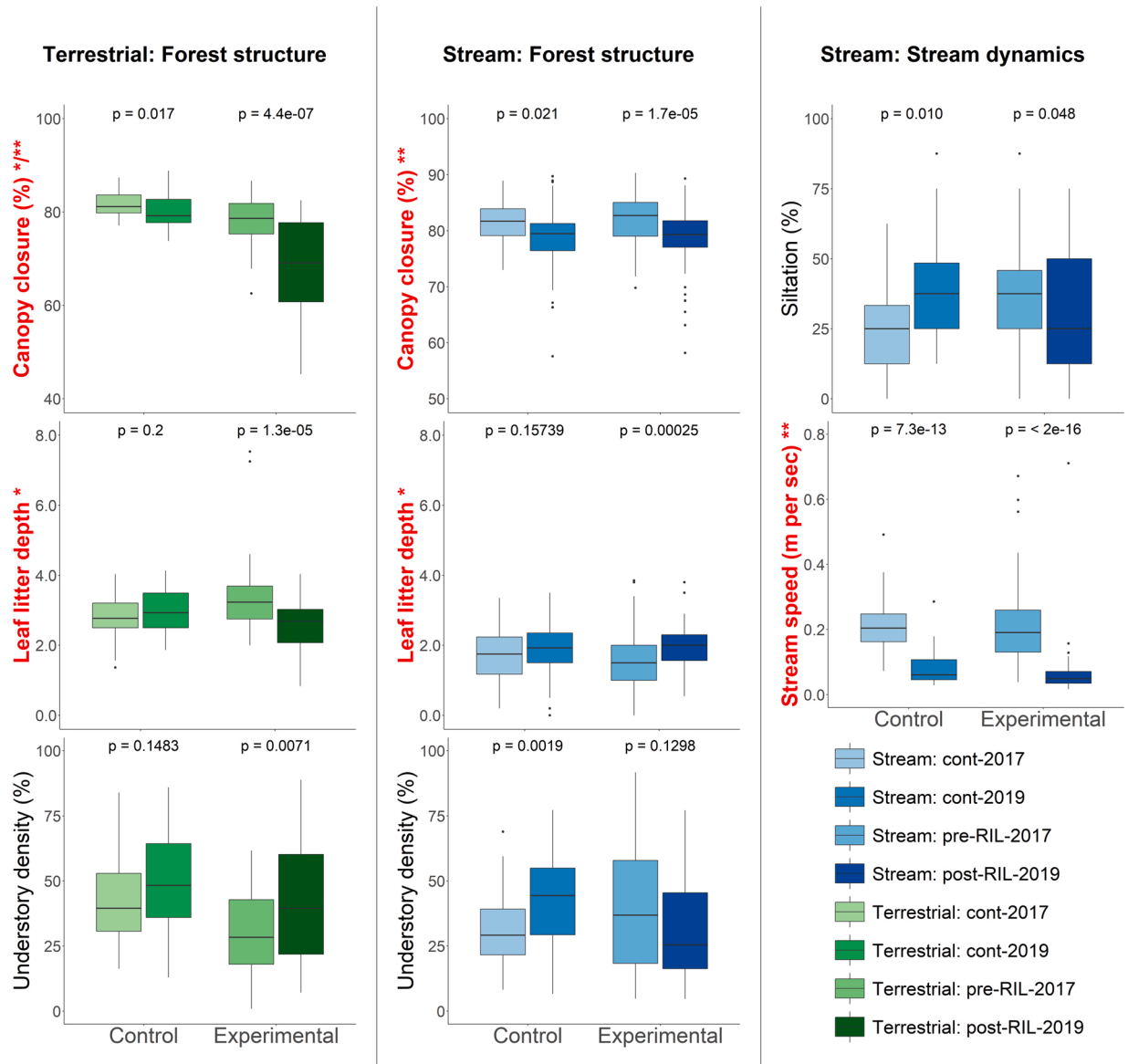


Fig. 2. Stream and terrestrial forest structure and stream dynamic covariate values within each logging treatment (cont = control, pre-RIL = before RIL, post-RIL = after RIL) between years (2017 and 2019). Includes the results of pairwise-Wilcoxon tests between sampling years of each treatment. Inter-annual fluctuation covariates (**) are classified as exhibiting significant variation between sampling years across all treatments, and RIL direct impact covariates (*) are classified as exhibiting significant variation between pre-RIL and post-RIL sites only. Inter-annual fluctuation and RIL covariates marked in red.

control-2019), with the occupancy probabilities of their respective reference assemblages (pre-RIL-2017 and control-2017). To do this, we sampled random values from the posterior distributions of species-specific occupancy probabilities for RIL and control sites in the first (pre-RIL-2017/control-2017) and second (post-RIL-2019/control-2019) sampling year. We repeated this procedure 9000 times using Monte Carlo sampling to generate a distribution of values and took the mean of the posterior distribution. The final values indicate how dissimilar the predicted community-level occupancies are in 2019 (in logged and control sites). Dissimilarity values can range between -1 and 1 . Within our dataset, a value of 0 indicates no differences in occupancy between sites in 2017 and 2019, a value of 1 indicates complete dissimilarity with the 2017 reference sites having lower occupancies than the 2019 sites, and a value of -1 indicates complete dissimilarity with the 2019 sites having lower occupancies than the 2017 reference sites.

To determine the impact of RIL on species diversity, we generated and compared occupancy-based diversity profiles for each of the above treatments (Abrams et al., 2021). Diversity profiles are a plotted series of Hill numbers as a function of the impact of rare species on the measure of diversity (q). Hill numbers (${}^qD'$) allow the estimation of multiple common diversity indices (Species richness, Shannon and Simpson diversity) whilst accounting for the contribution of rare species to site diversity (Jost, 2006). Individual Hill numbers differ by q , where $q = 0$ is species richness, $q = 1$ is Shannon diversity and $q = 2$ is Simpson diversity. The shape of the diversity profile describes the richness and evenness of a community; the more uneven a community is, the faster the curve declines as coefficient q increases. We conducted all analysis in R 3.4.1 (R Core Team, 2019).

3. Results

Over both sampling years the 21 sites were surveyed on 202 separate occasions (4.81 ± 1.42 surveys per site) comprising 115 stream and 87 terrestrial transect surveys. We detected 23 and 21 amphibian species within stream and terrestrial sites respectively (total species = 34), which constituted 1790 detections from six families (Supporting information, Tables 1 and 2). Of these species, 13 and 11 were exclusively detected in stream and terrestrial sites respectively.

3.1. Environmental covariate associations with RIL

Following the removal of correlated covariates (stream width variance only), several habitat covariates exhibited mixed associations with RIL or exhibited inter-annual fluctuations. Within stream sites; siltation, speed and canopy closure, all varied significantly between years (with significantly reduced stream speed and more open canopies in 2019), suggesting inter-annual fluctuations (Fig. 2). As leaf litter depth significantly increased following RIL at stream sites, these covariates (stream speed, canopy closure and leaf litter depth) were included within the subsequent stream community multi-species models. Within terrestrial sites, canopy closure was significantly reduced in 2019 (suggesting inter-annual fluctuation) with an even greater reduction at RIL sites, also suggesting direct logging impacts (Fig. 2). A strong significant decrease in leaf litter depth at terrestrial RIL sites suggests a direct impact of logging on this covariate. As such leaf litter depth and canopy closure were included in the subsequent multi-species models for terrestrial communities.

3.2. Species responses to RIL

Prior to running the complete multi-species occupancy models, we first determined the optimum detectability covariates for the stream and terrestrial communities. These were identified as moonphase and Maximum Daily Rainfall (MDR) for stream species and Time Since Sunset (TSS) and MDR for terrestrial species (Supporting information, Table 3). Within the multi-species occupancy models, amphibian species in stream and terrestrial sites exhibited variable responses to RIL associated covariates. Stream species were generally more associated with indirect RIL impacts (distance from logging roads/skid trails) (Fig. 3A), whereas terrestrial species were more associated with the direct impacts of RIL (reduced leaf litter depth) (Fig. 3B). Stream species exhibited predominately positive moderate associations with increasing distance to skid trails and logging roads (nine and three respectively), whereas terrestrial species exhibited none. Additionally, leaf litter depth was only moderately positively associated with one stream species (Fig. 3A) compared to positive moderate associations with ten terrestrial species (Fig. 3B). The yearly fluctuation covariates stream speed and canopy closure exhibited seven and two moderate positive associations with stream species occupancy respectively. Canopy closure had only one significant and three moderate positive associations with terrestrial species occupancy.

3.3. Amphibian community diversity/dissimilarity following RIL

We identified considerable differences between pre/post-RIL and control amphibian communities. In general, stream and terrestrial community occupancy was higher post-RIL compared to control sites (Fig. 4). Additionally, stream amphibian diversity (species richness, Shannon and Simpson diversity) and evenness increased markedly after RIL but remained relatively stable (with a slight increase in Shannon/Simpson diversity and evenness) in post-RIL terrestrial communities (Fig. 5). Dissimilarity indices showed dissimilarity and considerably higher community occupancy post-RIL compared to pre-RIL states (Fig. 4A), whereas control stream amphibian communities were similar between 2017 and 2019, with slightly higher community occupancy in 2019 (Fig. 4B).

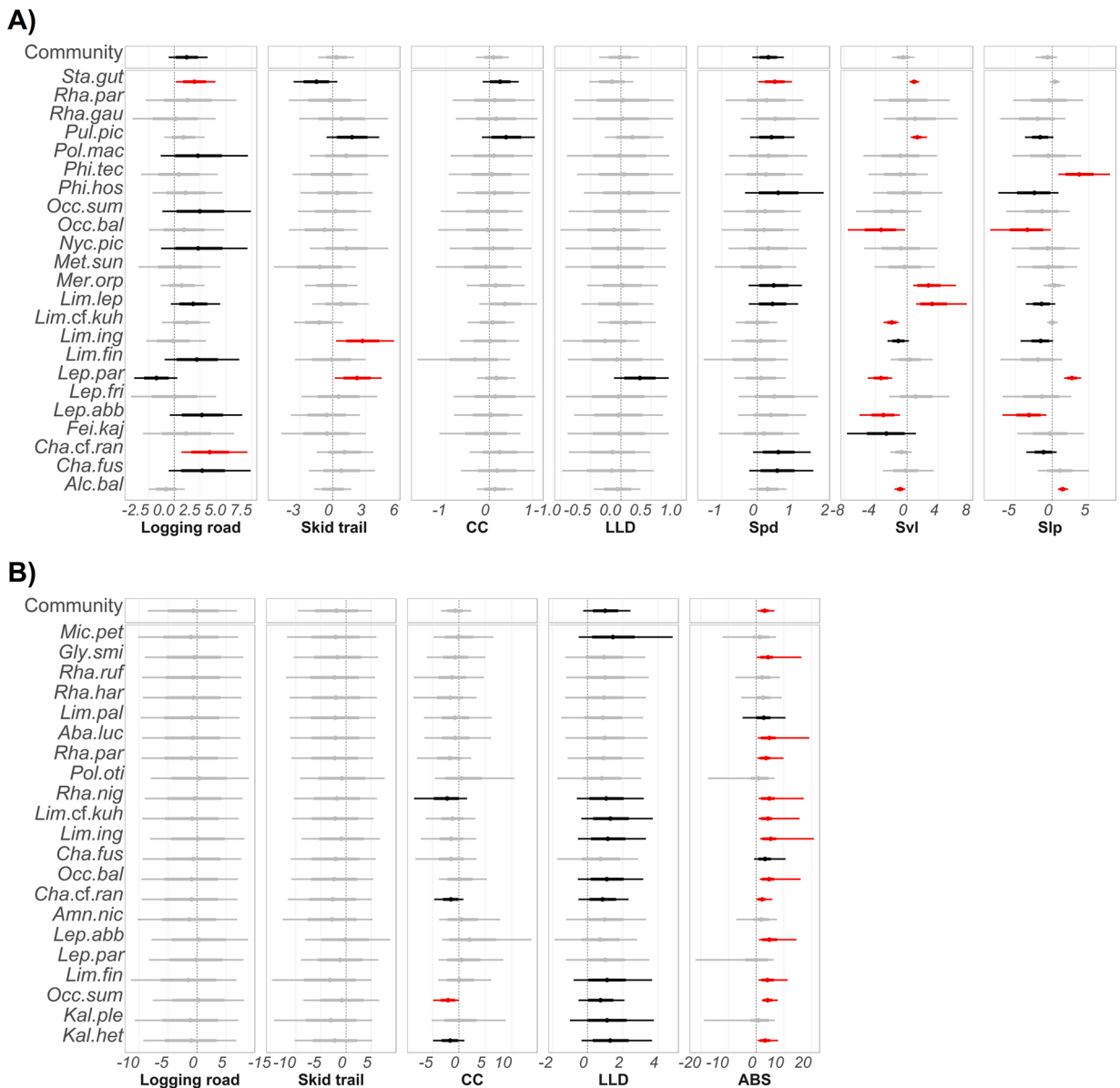


Fig. 3. Habitat covariate effect sizes on the species and community occupancy of amphibians occupying stream (A) and terrestrial (B) habitats respectively. Graph includes the following covariates: Logging road/skid trail = distance to logging road/skid trail, CC = Canopy Closure, LLD = Leaf Litter Depth, Spd = Stream speed, Svl = Stream volume, Slp = Stream slope and ABS = Aquatic Breeding Sites. Confidence intervals not overlapping 95% and 75% are highlighted in red and black respectively. Species names are abbreviated to the first three letters of the genus and species names as per [Supporting information, Table 1](#).

Diversity profile results were consistent with these findings. All diversity metrics increased in the post-RIL stream sites ([Fig. 5A](#)), whereas control stream diversity metrics were almost identical between sampling years ([Fig. 5B](#)). Dissimilarity patterns in terrestrial communities appeared similar to stream sites. Terrestrial site amphibian communities demonstrated marked dissimilarity and higher community occupancy post-RIL ([Fig. 4C](#)), whereas control sites showed dissimilarity with lower community occupancy in 2019 ([Fig. 4D](#)). Terrestrial amphibian diversity patterns varied markedly from those of stream sites, however. Terrestrial site species richness decreased slightly whilst Shannon/Simpson diversity and evenness increased after logging ([Fig. 5C](#)). Conversely, in terrestrial control sites all species diversity metrics decreased markedly in 2019 ([Fig. 5D](#)).

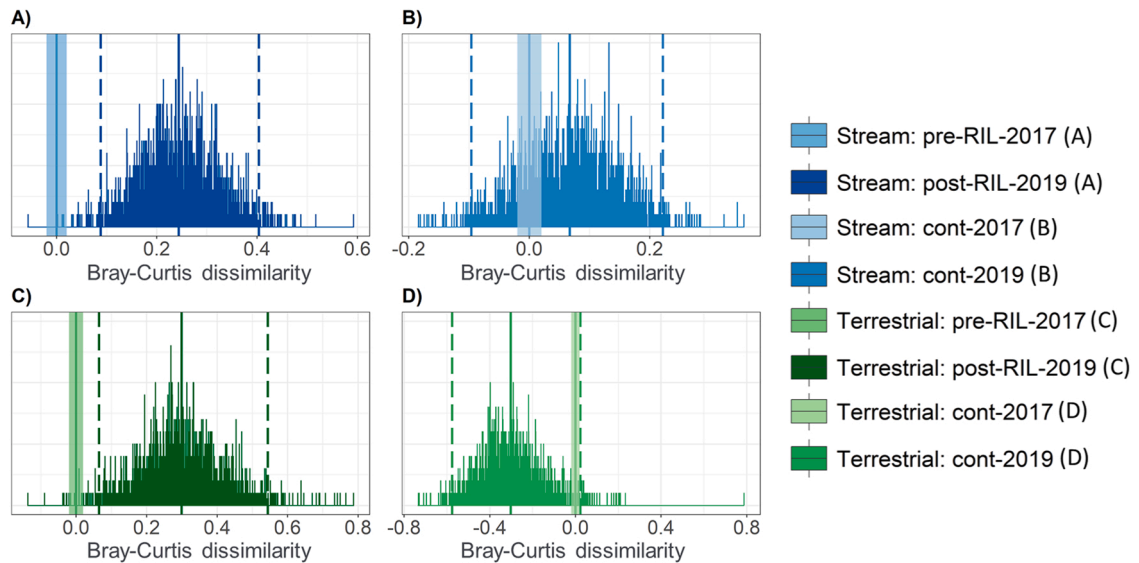


Fig. 4. Dissimilarity indices for stream (A = post-RIL-2019, B = control-2019) and terrestrial (C = post-RIL-2019, D = control-2019) amphibian communities compared to their respective 2017 communities, calculated using multi-species occupancy model predictions. Bray-Curtis dissimilarity values of 0 indicate absolute similarity between years, < 0 indicates community dissimilarity with lower 2019 community occupancy compared to the 2017 reference site, whereas > 0 indicates community dissimilarity with the higher 2019 community occupancy compared to the 2017 reference site. Solid lines represent mean values, dotted lines represent 95% Bayesian credible intervals.

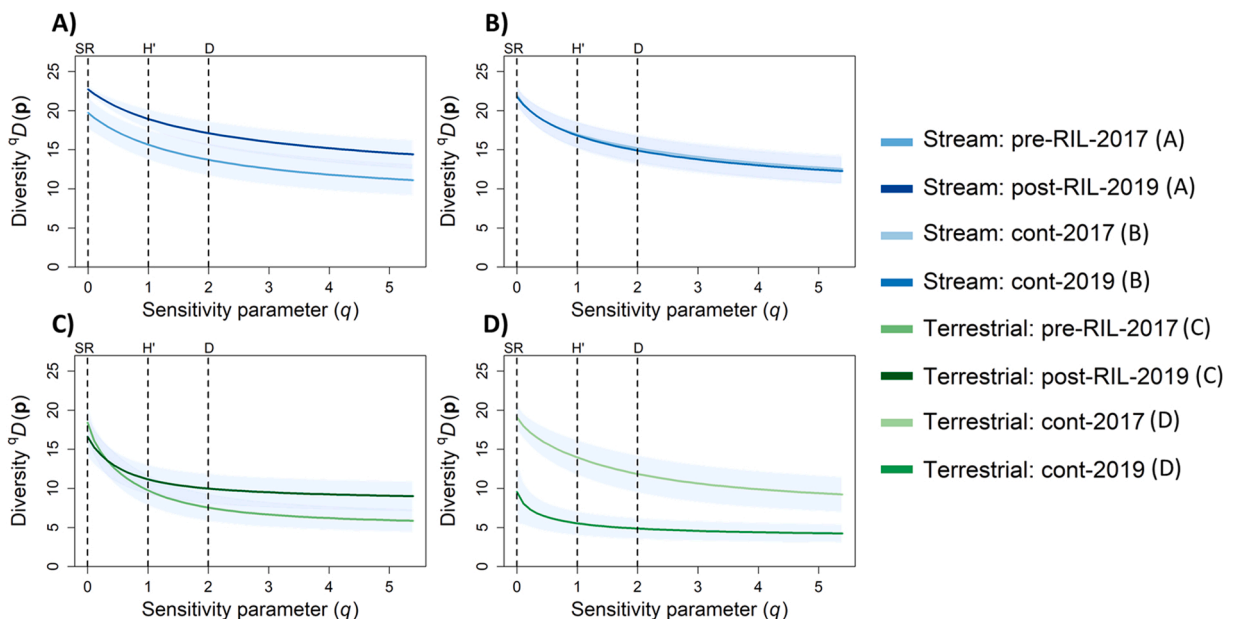


Fig. 5. Diversity profiles for stream (A = pre-RIL-2017/post-RIL-2019, B = control-2017/control-2019) and terrestrial (C = pre-RIL-2017/post-RIL-2019, D = control-2017/control-2019) amphibian communities, calculated using multi-species occupancy model predictions. Includes species richness (SR), Shannon (H') and Simpson (D) diversity indices for each treatment. Standard deviations (lightest blue shading) are provided. The shape of the diversity profile determines the richness and evenness of the community. Curves which decline steeply with increasing “q” coefficients indicate more uneven communities.

4. Discussion

This study aimed to determine the direct and indirect effects of RIL on amphibians within stream and terrestrial sites. We identified variable responses of amphibians within these two habitats. Although half of species occupying stream and terrestrial habitats exhibited negative associations with indirect (logging roads/skid trails) and direct (leaf litter depth shifts) logging impacts

respectively, their community occupancy, diversity and evenness was generally higher following RIL than at control sites.

4.1. Amphibian species responses to direct and indirect RIL impacts

Within our study, stream and terrestrial amphibian communities exhibited variable responses to indirect (skid trail/logging road) and direct RIL impacts (leaf litter depth and canopy closure shifts). Skid trail and logging road construction has been associated with increased siltation (Kreutzweiser et al., 2005), influxes of disturbance tolerant species (Konopik et al., 2014), greater thermal fluctuations (Mollinari et al., 2019) and subsequently negative biodiversity impacts (Laurance et al., 2009; Yamada et al., 2014). In our study over half of all stream site species exhibited at least a moderate positive association with increasing distance from logging roads (nine species) or skid trails (three species). In congruence with similar studies which identified greater disturbance along logging roads compared to skid trails (Malcolm and Ray, 2000; Jackson et al., 2002), our results suggest a greater negative impact of logging roads on stream amphibian communities.

Previous research by the authors identified obligate stream breeding anurans as the most sensitive to RIL (Asad et al., 2021). Species most negatively associated with logging roads in this study however, comprised obligate stream breeding (*Staurois guttatus*, *Limnonectes leporinus*, *Leptobrachella parva*, *Leptobrachium abbotti*, *Limnonectes cf. kuhlii* and *Pulchrana picturata*), stagnant pool breeding (*Polypedates macrotis*, *Nyctixalus pictus* and *Chaperina fusca*), and generalist breeding species (*Chalcorana cf. raniceps*, *Limnonectes ingeri*, *Limnonectes finchi* and *Occidozyga sumatrana*) which utilize a range of stream, terrestrial and arboreal habitats for foraging and refugia (Inger, 1966; Inger et al., 2017; Ahmad and Grafe, 2020). This suggests that logging road development may adversely affect the stream associated habitats of a wide range of species representing various eco-types and life history strategies.

Interestingly, species occupying terrestrial habitats exhibited no associations with logging roads or skid trails, despite the direct impacts of logging infrastructure on their habitats. Furthermore, several terrestrial species encompassing generalist (*Limnonectes ingeri* and *Chalcorana cf. raniceps*) and stagnant pool breeding species (*Microhyla petrigena*, *Rhacophorus nigropalmatus* and *Occidozyga baluensis*) were moderately positively associated with leaf litter depth, which decreased in terrestrial sites following RIL. Generally this should result in reduced species diversity and evenness of the entire terrestrial community following RIL, however, these metrics only slightly decreased (species richness) or increased (Shannon/Simpson diversity and evenness) following logging. A possible explanation is the increase in Aquatic Breeding Sites (ABS) along recently constructed skid trails (S. Asad pers. obs.). Several authors identified similar patterns following logging road/skid trail development, with these ABS often providing novel habitats for amphibian reproduction (Konopik et al., 2014; Ernst et al., 2016; Hölting et al., 2016). As ABS presence proved to be the best predictor of species occupancy in terrestrial sites (12 significant and two moderate associations with ABS), the proliferation of these ABS along skid trails may offset the negative effects of reduced leaf litter depth after RIL.

4.2. Amphibian community responses to RIL

The higher community occupancy and generally higher diversity metrics in stream and terrestrial habitats immediately after logging, suggests that RIL sites can harbour more diverse and even communities than their unlogged neighbours. Whilst appearing counter intuitive this increase could be the result of several co-occurring processes: community flux following RIL, delayed negative impacts of RIL and inter-annual fluctuations. The highly selective timber harvesting practices of RIL results in patchily distributed areas of disturbance (Pinard et al., 1995; Putz et al., 2008). These “pockets” of disturbance may force amphibians into neighbouring less disturbed sections of the same habitats. As RIL practices include unlogged 30 m stream buffers, our buffered stream sites could serve as habitat refugia following logging, particularly for species which utilize both terrestrial and stream habitats. Furthermore, RIL often creates novel habitats within logged areas such as small forest clearings (Schwartz et al., 2012), felled un-salvaged trees (Putz et al., 2008) and small anthropogenically created pools (Hölting et al., 2016). Here, fallen trees can provide amphibian micro-habitats (Earl and Semlitsch, 2015) and thermal refugia (Otto et al., 2013), whilst novel aquatic breeding sites are utilized by both forest specialist tree frogs (Konopik et al., 2014) and disturbance tolerant pool breeding species (Ernst et al., 2016; Hölting et al., 2016). These factors may combine to create a temporary “state of flux”, whereby species emigrate either from now unsuitable into adjacent suitable habitats such as un-logged stream buffers (Surasinghe and Baldwin, 2015; Calvão et al., 2016; Dala-Corte et al., 2020) or to the novel habitats created via logging (Hamer et al., 2003; Berry et al., 2010; Edwards et al., 2014).

Regardless, this increase immediately following RIL should be assessed with caution, as logging activities ceased only within one year previously. In a former study within Deramakot, stream amphibian diversity metrics were lowest 4–5 years after RIL, and exhibited a steady increase with increasing time since RIL (Asad et al., 2021). These contradicting results could be due to delayed negative effects of RIL on amphibian communities, potentially resulting in reduced juvenile recruitment. Low juvenile recruitment, rather than adult survival, has been cited as the major factor contributing to amphibian population fluctuations in other areas (Alford and Richards, 1999; Muths et al., 2011). Reduced recruitment within one year of RIL is unlikely to be apparent within the population. Furthermore, habitat disturbance following RIL, may take several years to accrue. In a Canadian site stream sedimentation gradually increased in the three years following logging road development (Kreutzweiser et al., 2005). Furthermore, lower rainfall in early 2019 due to a dry El Niño event likely reduced sediment run off prior to this study (Payus et al., 2020), as has been observed during other El Niño events (Hestir et al., 2013). In our previous study, stream siltation, which was highest in sites subject to RIL 4–5 years ago was negatively associated with the occupancy of two obligate stream breeders (*Alcalus baluensis* and *Leptobrachella parva*) (Asad et al., 2021). As such, it is possible that the negative effects of RIL on sedimentation, and potentially other environmental factors (leaf litter depth, canopy closure etc.), may increase for several years following RIL, negatively impacting amphibians before they both begin their recovery.

4.3. Caveats

The RIL impacts on amphibian species and communities outlined in this study provide valuable insights into this taxa's responses to logging. However, potential inter-annual fluctuations, specifically the climatic extremes resulting from the 2019 El Niño southern oscillation event, may have confounded some of our results. Although we lacked sufficient yearly measurements to quantify inter-annual fluctuations as El Niño impacts, the decreases in stream speed and canopy closure could be linked to El Niño. This event was characterized by a severe decline in rainfall across Sabah, Malaysian Borneo (Payus et al., 2020). Within our study site this resulted in major shifts in stream composition and the shrinking or drying of small aquatic breeding sites (Asad et al., 2022). Whilst this may have impacted our results, we believe the stability of control stream diversity metrics between years suggest a robustness of stream communities to severe droughts. However, amphibians occupying terrestrial habitats are generally more susceptible to water scarcity, desiccation and decreased humidity (Kiesecker et al., 2001; Corn, 2005). This may explain the decline in diversity metrics at terrestrial control sites. Amphibians in logged terrestrial sites may have been buffered from these negative effects due to the creation of novel aquatic habitats following RIL as has been observed in other areas (Laurance et al., 2009; Ernst et al., 2016; Hölting et al., 2016). As such, sites recently subject to RIL may provide a short-term buffer against desiccation and breeding site loss due to the availability of novel aquatic habitats. However, considering our sample size of two years we cannot determine whether habitat/amphibian diversity shifts are the result of El Niño or inter-annual fluctuations, and thus cannot confirm this observation.

An additional concern regarding our sampling is the underrepresentation of tree frogs, which represent a significant portion of Borneo's amphibian diversity (Hertwig et al., 2013). These species are particularly difficult to sample due to their arboreality, with the majority of our detections (38 detections across 11 species) occurring when species utilized terrestrial ABS and streams for breeding/egg laying. Furthermore, previous research identified greater disturbance impacts on butterfly and mammalian diversity within the forest canopy compared to understory and terrestrial habitats (Whitworth et al., 2016, 2019). It is therefore possible that arboreal amphibians are either more negatively impacted by RIL compared to other species, or that tree frogs exhibit a similar trend to stream and terrestrial communities, with variable species but similar community responses to RIL. Regardless, direct sampling of arboreal tree frogs will be required to determine this elusive group's responses to disturbance.

5. Conclusions

Despite negative associations between species occupancy and the direct and indirect impacts of RIL (particularly responses to logging roads in stream species), we found that stream and to a lesser extent terrestrial amphibian community occupancy, species diversity and evenness, appears predominately unaffected and even increases immediately following RIL. While these results are promising, we believe these increases are likely the result of a temporary flux state following disturbance and/or the delayed negative impacts of logging. Viewed in the context of our previous study (Asad et al., 2021), it appears that stream amphibians exhibit a brief increase in biodiversity metrics immediately following RIL (< 1 year), exhibit a decline 1–5 years post logging, then subsequently begin a swift recovery toward pre-logging states. These findings suggest that future studies using pre/post disturbance treatments over short timeframes should consider potential temporal community flux and delayed negative effects when making conclusions on disturbance impacts. Furthermore, this study highlights that while discrepancy between the direct and indirect impacts of logging may vary between species in different habitats, that cross-habitat community responses to RIL may be similar.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02061](https://doi.org/10.1016/j.gecco.2022.e02061).

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