

Amphibian community responses to different logging techniques in Bornean production forests

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The scientific work presented in this thesis was conducted from November 2018 to June 2022 at the Deramakot forest reserve in Sabah, Malaysian Borneo, the Museum für Naturkunde Berlin (MfN), the Leibniz Institute for Zoo and Wildlife Research (IZW), and Freie Universität Berlin. This work was supervised by Prof. Dr. Jonathan M. Jeschke, head of the Ecological Novelty group at FU, and PD Dr. Mark-Oliver Rödel, head of the Diversity Dynamics department at the MfN, and was co-supervised by Dr. Andreas Wilting, senior scientist at the Department of Ecological Dynamics of the IZW.

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I hereby declare that this dissertation was written and prepared by me independently. Furthermore, no sources and aids other than those indicated have been used. Intellectual property of other authors has been indicated accordingly. I also declare that I have not applied for an examination procedure at any other institution and that I have not submitted the dissertation in this or any other form to any other faculty as a dissertation

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SUMMARY

Whilst tropical forests contain the majority of earth's biodiversity, they are subject to extreme anthropogenic pressure, primarily via conversion to plantations, clearance for livestock and commercial timber harvesting. Previous, unsustainable management of tropical timber reserves, primarily via Conventional selective Logging (CL) has resulted in severe habitat degradation and biodiversity declines. This is particularly troubling within Southeast Asia, where high deforestation rates are coupled with high biodiversity. Given the economic value of tropical forests for providing local ecosystem services and mitigating global climate change, ensuring the sustainable management of timber reserves in Southeast Asia and globally is paramount for meeting current sustainability targets. Previous research suggests that timber reserves managed utilizing sustainable methods such as Reduced Impact Logging (RIL), can maintain forest structures and biodiversity comparable to unlogged primary forests. However, whilst several studies have determined the landscape level effects of RIL and CL on vertebrate biodiversity, comparatively few have compared the two logging methods within the same region, species recoveries during post-logging forest regeneration, or compared the direct and indirect effects of logging on biodiversity. Additionally, the vertebrate communities of Southeast Asia, particularly amphibians are severely understudied making conclusions regarding their responses to disturbance highly problematic. The complex, water dependent life histories and physiological restrictions of amphibians, make them highly sensitive to the environmental shifts caused by anthropogenic disturbances including logging. As such, amphibians provide an excellent model system, for determining the impacts of different logging types.

The aim of this study was to determine the effects of CL and RIL and their direct/indirect impacts over a period of regeneration on an understudied amphibian community and their habitats in Borneo, Southeast Asia. In particular, I aimed to highlight the detectability and habitat associations of an understudied Bornean stream amphibian community. Using this information, I then aimed to determine how this community and their associated habitats responded at the landscape level to RIL and CL within sites over a 21 year recovery period. This was supplemented by determining the direct and indirect impacts of RIL (within 1 year of logging) on stream and terrestrial amphibians and their habitats.

Within the most frequently detected stream amphibians of this study, species detectability exhibited highly variable associations with climatological and temporal covariates, with moon phase (six species), time since sunset (five species) and humidity (five species) proving the best predictors of detection probability (Chapter 2). Species occupancy was significantly associated with stream slope and stream volume (six species each), suggesting that these covariates provide the best predictors of stream amphibian occurrence. The species habitat relationships identified within our RIL sites most closely resemble those found in primary forests, compared to conventionally logged streams. The high level of variability in detectability associations, suggests highly variable activity patterns in stream anurans, namely those utilizing aquatic habitats for breeding, potentially resulting in temporal separation in breeding phenology.

Utilizing the habitat and detectability associations within the first section, I compared stream communities between CL and RIL sites at varying stages of regeneration (Chapter 2). Our results suggested that several stream amphibians respond negatively to the environmental covariates linked to direct logging impacts (higher siltation and lower aboveground carbon). I identified lower stream breeding species occupancy probability in CL sites compared to RIL sites of the same age, with the opposite trend observed in generalist breeding species. Diversity profiles, which capture representative diversity indices while accounting for community evenness, showed lower species diversity and evenness in CL sites logged 18-21 years ago compared to RIL sites logged recently (4-5 years ago). Additionally, amphibian species diversity and evenness exhibited a distinct recovery in RIL sites from 4 to 21 years since logging.

Lastly, via conducting a quasi-experimental treatment involved pre and post RIL amphibian sampling within the same subset of sites, I was able to determine the responses of amphibians and their associated habitats to direct and indirect RIL impacts (Chapter 3). I found that the almost half of stream amphibian species sampled exhibited a negative association with indirect logging impacts, namely logging associated infrastructure (logging roads and skid trails). Conversely, terrestrial amphibian communities appeared comparatively unaffected by logging road networks and were mostly negatively associated with direct logging impacts (reduced terrestrial leaf litter depth following RIL). Interestingly, stream and terrestrial amphibians exhibited higher community occupancy and greater dissimilarity following RIL compared to unlogged control sites, with logged stream sites exhibiting a marked increase in species diversity and evenness. Within terrestrial sites, species diversity and

evenness declined dramatically in unlogged control areas, whilst these metrics remained stable in terrestrial amphibian communities following RIL. This decline in unlogged terrestrial sites is likely due to an el Niño event which occurred the same year. The negative effects of which, may have been mitigated in the logged sites due to the creation of novel aquatic habitats following RIL. Regardless, I demonstrate that despite negative associations between species occupancy and indirect (stream communities) and direct (terrestrial communities) logging impacts, that stream and to a lesser extent terrestrial amphibian community occupancy, species diversity and evenness, appears predominately unaffected, and even increases immediately following RIL. These increases however, may be the result of delayed native effects of RIL and/or a temporary state of flux. Considering the landscape level impacts of RIL, where I found the lowest diversity and evenness in RIL sites logged 4-5 years, followed by a steady recovery (Chapter 2). As such, the higher diversity and evenness immediately following RIL (within 1 year) may be due to an influx of species resulting from the creation/maintenance of suitable habitats locally, and the destruction of habitats adjacent to sampling locations. This may then be followed by an accrument of negative environmental effects in the coming years (2-5), such as increased siltation which was negatively association with the occupancy of several stream species at the landscape level (Chapter 2). Regardless, this study highlights that although amphibian species throughout different habitats exhibit varied responses to direct (terrestrial) and indirect (stream) RIL impacts, they may exhibit similar community level responses to RIL across habitats.

I have acknowledged the methodological constraints within our data collection and modelling process, and highlighted how this may have affected our conclusions. I hope that the results of this dissertation not only increases our understanding of little known Bornean amphibians, but provides guidance for the improvement and value of reduced impact logging for maintaining amphibian biodiversity in tropical timber reserves.

Keywords

Borneo; anurans; occupancy modelling; anthropogenic disturbance responses; streams; sustainable forestry

ZUSAMMENFASSUNG

Obwohl Tropenwälder den Großteil der Biodiversität der Erde beherbergen, sind sie einem extremen anthropogenen Druck ausgesetzt, hauptsächlich durch ihre Umwandlung in Plantagen, Rodung für Viehzucht und kommerzielle Holznutzung. Frühere, nicht nachhaltige Bewirtschaftung von Tropenholzreserven, hauptsächlich durch konventionellen, selektiven Holzeinschlag (CL), hat zu einer schwerwiegenden Verschlechterung des Lebensraums und einem Rückgang der Artenvielfalt geführt. Dies ist besonders in Südostasien besorgniserregend, wo hohe Entwaldungsraten auf eine hohe Biodiversität treffen. Angesichts des wirtschaftlichen Werts tropischer Wälder, durch die Bereitstellung lokaler Ökosystemleistungen und die Eindämmung des globalen Klimawandels, ist die Gewährleistung einer nachhaltigen Bewirtschaftung der Holzreserven in Südostasien und weltweit von größter Bedeutung, um die aktuellen Nachhaltigkeitsziele zu erreichen. Frühere Untersuchungen deuten darauf hin, dass Nutzwälder, die mit nachhaltigen Methoden wie Reduced Impact Logging (RIL) bewirtschaftet werden, Waldstrukturen und Biodiversität erhalten können, die mit nicht abgeholzten Primärwäldern vergleichbar sind. Während jedoch mehrere Studien die Auswirkungen auf der Landschaftsebene von RIL und CL auf die Biodiversität von Wirbeltieren ermittelt haben, haben vergleichsweise wenige die beiden Holzeinschlagsmethoden innerhalb derselben Region verglichen oder die zeitlichen und räumlichen Unterschiede in den Auswirkungen des Holzeinschlags auf die Biodiversität untersucht. Darüber hinaus sind die Wirbeltiergemeinschaften Südostasiens, insbesondere die Amphibien, unzureichend untersucht, was Schlussfolgerungen hinsichtlich ihrer Reaktionen auf Störungen sehr schwierig macht. Die komplexen, wasserabhängige Lebensgeschichten und physiologischen Einschränkungen von Amphibien, machen sie sehr empfindlich gegenüber Umweltveränderungen, die durch anthropogene Störungen, einschließlich Holzeinschlag, verursacht werden. Deshalb sind Amphibien ein hervorragendes Modellsystemum die Auswirkungen verschiedener Abholzungsarten auf unterschiedlichen räumlich-zeitlichen Skalen zu analysieren.

Das Ziel meiner Doktorarbeit war es, die Auswirkungen von CL und RIL auf unterschiedlichen räumlich-zeitlichen Skalen auf eine wenig untersuchte Amphibiengemeinschaft in Borneo, Südostasien, zu bestimmen. Insbesondere wollte ich u.a. die die Habitatabindungen innerhalb der Amphibiengemeinschaften von Bächen verstehen. Anhand dieser Daten wollte ich dann bestimmen, wie diese Gemeinschaften und ihr Lebensraum auf der Landschaftsebene nach Anwendung von RIL und CL reagieren und regenerieren. Ergänzt wurde diese Analysen durch die vergleichende Bestimmung der direkten, lokalen Auswirkungen von RIL auf Fluss- und Landamphibien (und deren Lebensräume), inkl. der Wechselwirkungen zwischen den Effekten durch Abholzung und einem El-Niño Ereignis. Bei den am häufigsten in dieser Studie nachgewiesenen Flussamphibien zeigten die

Arten sehr unterschiedliche Assoziationen mit klimatologischen und zeitlichen Kovariaten, wobei sich die Mondphase (sechs Arten), die Zeit seit Sonnenuntergang (fünf Arten) und die Feuchtigkeit (fünf Arten) als die besten Prädiktoren für die Nachweiswahrscheinlichkeit erwiesen (Kapitel 2). Die Artenzusammensetzung war signifikant mit dem Gefälle und dem Volumen der Flüsse (jeweils sechs Arten) verbunden, was darauf hindeutet, dass diese Kovariaten die besten Prädiktoren für das Vorkommen von Flussamphibien sind. Die innerhalb unserer RIL-Standorte identifizierten Arten-Lebensraum-Beziehungen ähneln, verglichen mit konventionell abgeholzten Bächen, am ehesten denen in Primärwäldern. Das hohe Maß in der Variabilität in den Habitat- und Umweltfaktoren bei der Nachweisbarkeit der verschiedenen Arten, deutet auf sehr variable Aktivitätsmuster der Bachanuran hin, insbesondere zwischen denen die die Flüsse als Laichgewässer nutzen, was möglicherweise zu einer zeitlichen Trennung in der Reproduktionsbiologie zwischen diesen Arten führt.

Unter Verwendung der Habitatsassoziationen und Vorhersagbarkeitsfaktoren im ersten Kapitel zielten wir dann darauf ab, Flussgemeinschaften zwischen CL- und RIL-Standorten in verschiedenen Regenerationsstadien zu vergleichen (Kapitel 3). Unsere Ergebnisse deuten darauf hin, dass mehrere Flussamphibien negativ auf Umweltkovariaten reagieren die mit dem Holzeinschlag verbunden sind (höhere Verschlammung und niedrigerer oberirdischer Kohlenstoff). Wir identifizierten eine niedrigere Vorkommenswahrscheinlichkeit für Flusslaicher an CL-Standorten im Vergleich zu gleichaltrigen RIL-Standorten, wobei der gegenteilige Trend bei generalistischen (nicht spezialisierten) Arten beobachtet wurde. Diversitätsprofile, die repräsentative Diversitätsindizes erfassen und gleichzeitig die Eveness der Gemeinschaft berücksichtigen, zeigten eine geringere Artenvielfalt und Eveness in CL-Standorten, die vor 18 bis 21 Jahren eingeschlagen wurden, im Vergleich zu RIL-Standorten, die vor kurzem (vor 4 bis 5 Jahren) abgeholzt wurden. Darüber hinaus zeigten die Diversität und Eveness der Amphibienarten eine deutliche Erholung an RIL-Standorten nach 4 bis 21 Jahren seit der Abholzung.

Schließlich konnten wir durch den quasi-experimentellen Vergleich von Amphibiendaten an identischen Standorten vor und nach RIL die Reaktionen der Arten auf RIL auf der lokalen Ebene bestimmen. Darüber hinaus konnten wir aufgrund eines unerwarteten El-Niño-Ereignisses während des letzten Untersuchungsjahres auch die Auswirkungen dieses Extremwetterereignisses und seine Wechselwirkungen auf Amphibien untersuchen. Ich fand heraus, dass fast die Hälfte der beprobten Flussamphibienarten einen negativen Zusammenhang mit der mit dem Holzeinschlag verbundenen

Infrastruktur aufwies, nämlich Holzeinschlagsstraßen und Rückepfade. Umgekehrt schienen terrestrische Amphibiengemeinschaften vergleichsweise unbeeinflusst vom Abholzungsstraßennetzwerk zu sein. Sie reagierten hingegen meist negativ auf eine nach RIL reduzierten Laubstrettiefe. Interessanterweise zeigten Fluss- und terrestrische Amphibien nach RIL eine höhere Gemeinschaftsbelegung und größere Unähnlichkeit im Vergleich zu den Kontrollstandorten, wobei Flussstandorte eine deutliche Zunahme der Artenvielfalt und Eveness aufwiesen. In den terrestrischen Standorten nahmen die Artenvielfalt und Eveness an den Kontrollstandorten dramatisch ab, sie in terrestrischen Amphibiengemeinschaften nach RIL stabil blieben. Der Rückgang an nicht abgeholzten terrestrischen Standorten ist wahrscheinlich das Ergebnis des El-Niño-Ereignisses, das an den abgeholzten Standorten möglicherweise durch die Schaffung neuer aquatischer Lebensräume nach RIL gemildert wurde. Ungeachtet dessen zeige ich, dass trotz negativer Assoziationen zwischen Artenzusammensetzung und Abholzungskovariaten (insbesondere Reaktionen auf Abholzungsstraßen bei Flussarten) die Besiedlung von Flüssen und in geringerem Maße von terrestrischen Lebensräumen, Artenvielfalt und Gleichmäßigkeit überwiegend unbeeinflusst erscheint und sogar unmittelbar nach RIL zunimmt. Diese Zunahmen können jedoch das Ergebnis verzögerter nativer Wirkungen von RIL und/oder eines vorübergehenden Zustands des Flusses sein. Bei den Auswirkungen von RIL auf Amphibien auf der Landschaftsebene fanden wir die niedrigste Diversität und Eveness in RIL-Standorten, die 4-5 Jahre abgeholzt wurden, gefolgt von einer stetigen Erholung. Die höhere Diversität und Eveness unmittelbar nach der RIL (innerhalb eines Jahres) kann daher auf einen Zustrom von Arten zurückzuführen sein, der sich aus der Schaffung und/oder Erhaltung geeigneter Lebensräume und der Zerstörung von Lebensräumen in der Nähe des Holeinschlages ergibt. In den kommenden Jahren kann es dann zu einem Anstieg der negativer Umweltauswirkungen kommen, wie eine zunehmende Verschlammung, die negativ mit dem Vorkommen mehrerer Bacharten auf Landschaftsebene in Verbindung gebracht wurde. Unabhängig davon hebt meine Studie hervor, dass, während die Diskrepanz zwischen den Auswirkungen von RIL auf lokaler Ebene (Holzfällerstraßen und Laubstrettiefe) zwischen den Gemeindemitgliedern variieren kann, die großräumigen (RIL und El-Niño) Auswirkungen in allen Amphibiengemeinschaften ähnlich sein können.

Die möglichen methodischen Einschränkungen meines Datenerfassungs- und Modellierungsansatzes habe ich in allen Kapiteln diskutiert. Ich hoffe, dass die Ergebnisse meiner Dissertation nicht nur unser Verständnis über wenig bekannte Amphibienarten in Borneo und ihre Ansprüche erweitert, sondern insbesondere eine Anleitung für die Verbesserung und das Management

von Forstmethoden wie dem Reduced Impact Logging für die Erhaltung der Biodiversität in tropischen Holzreservaten sein wird.

Schlüsselwörter

Borneo; Anuren; Belegungsmodellierung; anthropogene Störungsreaktionen; Ströme; nachhaltige Forstwirtschaft

THESIS OUTLINE

This dissertation consists of a General Introduction, three separate chapters and a General Discussion. The General Introduction describes the background research and rationale for the study and defines the project objectives. Chapters one, two and three each represent independent research papers and follow the conventional structure of scientific manuscripts (introduction, methods, results, discussion). In the General Discussion section, the findings of the thesis are evaluated and discussed with reference to previous research in this area. In particular, recommendations for improved sustainability practices are outlined as well as recommendations for further research.

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General Introduction

Global biodiversity is currently under sustained pressure due to anthropogenic activities. While this pressure is globally distributed, it is most concentrated in the world's tropical forests. Although tropical forests represent only 7% of Earth's land surface, they contain over 60% of all known species (Bradshaw et al. 2009). Despite this, they are amongst the most threatened ecosystems globally (Betts et al. 2017), with roughly 1.2% (>15 million hectares) of tropical forest cover lost each year. These losses are linked to estimated extinction rates of 14,000-40,000 tropical forest species annually (Hughes et al. 2007). In areas of high tropical forest density, biodiversity and rapid development such as central Africa, Amazonia and Southeast Asia, these tropical deforestation rates are typically higher (Wright 2005). Considering the correlation between human population density and increasing deforestation (Bradshaw et al. 2009), the economic demands of these region's growing populations, will no doubt accelerate the exploitation of tropical forests and subsequent biodiversity loss. This is particularly troubling given the economic value of tropical biodiversity for providing local ecosystem services and mitigating global climate change (Mace et al. 2012). Current protected area networks, whilst essential for mitigating land-use change, are unlikely to be effective biodiversity conservation tools at a landscape scale, particularly in developing nations with high natural resource use (Laurance et al. 2012). Consequently, maintaining biodiversity within human altered landscapes, is increasingly being recognised as an essential component for practical and effective conservation (Corlett 2015). Biodiversity responses to anthropogenically altered tropical forests are multifaceted, and dependent on the intensity and type of land-use. The impacts of human use on tropical forests can vary from complete deforestation following urbanisation and commodity production (e.g. beef, soy, palm oil and wood plantations) to partial damage following commercial logging (Curtis et al. 2018). Of these industrial land-uses, forests managed for commercial timber extraction, provide the most promising option for biodiversity conservation and the sustainable management of tropical forests.

Logging and sustainable forestry

Over 53% (400 million hectares) of the world's tropical forests are currently designated as timber concessions (Blaser et al. 2011). Previous, unsustainable management of these logged forests however, has resulted in severe habitat degradation and declining biodiversity (Asner 2009, Curtis et al. 2018). The predominant method of timber extraction, Conventional selective Logging (CL), typically involves the extraction of the maximum quantity of valuable timber, with no best-management practices and damage mitigation measures (Picard et al. 2012). As

such, CL usually involves considerable damage to remnant forest structure (Pereira et al. 2002), and is often associated with depauperate biodiversity compared to unlogged forests (Fisher et al. 2011, Wilcove et al. 2013). Previous research however, indicates that biodiversity may be retained within sustainably managed tropical timber concessions. Several global meta-analysis of logging intensity effects on biodiversity, identified higher species richness in reserves utilising reduced harvesting rates (<30m³ timber per hectare) and best practice harvesting techniques compared to conventionally logged sites (Bicknell et al. 2014, 2015, Burivalova et al. 2014, Chaudhary et al. 2016). One such method, Reduced Impact Logging (RIL), implements strict guidelines for sustainable timber harvesting, including maximum allowable cuts (three trees per hectare), liana cutting, 30 m wide stream buffers, directional felling, reduced skid trail construction and pre/post-harvest planning which are designed to minimize the negative effects on remnant forest structure (Putz et al. 2008). These RIL methods have resulted in 50% less damage to remnant forest structure (Pinard et al. 1995), and lower net loss of species richness compared to conventional selective logging methods (Bicknell et al. 2014, 2015, Burivalova et al. 2014, Chaudhary et al. 2016). These studies, collectively indicate the potential value of RIL managed timber reserves for mitigating tropical biodiversity loss in the face of increasing anthropogenic pressure. Although previous research suggests that RIL management mitigates biodiversity loss greater than reduced harvesting rates alone (Bicknell et al. 2014), the impacts of specific RIL practices (reduced skid trail construction, 30 m stream buffers etc) have rarely been quantified. Additionally, the delineation of both the direct (via timber extraction) and indirect (logging infrastructure) impacts of RIL and the utility of damage mitigation measures for limiting this impact is poorly understood. While the establishment of stream buffers may decrease stream siltation (Pinard et al. 1995, Ellis et al. 2019), the contribution of these buffers for preserving stream biodiversity is unclear. Additionally, the impact of RIL logging infrastructure (such as logging roads and skid trails) compared to the impacts of conventional logging infrastructure is unknown. Disentangling these direct and indirect impacts of RIL will allow us to evaluate the effectiveness of certain damage mitigation measures, such as minimum stream buffer widths and skid trail/logging road limitations, for preserving tropical biodiversity.

Regardless, whilst numerous studies have delineated the general impacts of logging on mammal and bird communities (Berry et al. 2010, Edwards et al. 2014), the effects of logging, particularly RIL, are comparatively understudied in tropical amphibians. This is particularly troubling considering the global decline of this taxon (Stuart et al. 2004). Furthermore, the high

diversity of understudied amphibian communities in deforestation hotspots with high timber reserve density such as Southeast Asia is cause for concern (Rowley et al. 2010, Fisher et al. 2011, Wilcove et al. 2013).

Amphibian responses to logging

The physiological limits (narrow temperature and humidity ranges) and complex life-histories of amphibians (Wells 2010) make them highly sensitive to the environmental changes caused by logging (Gardner et al. 2007). Conventional selective logging typically results in reduced forest structural complexity (Pereira et al. 2002, Putz et al. 2008), increased sedimentation of water courses (Kreutzweiser et al. 2005, Walsh et al. 2011), increased temperatures and reduced humidity (Hardwick et al. 2015). This leads to increased desiccation risk, a lack of microhabitat heterogeneity and a deterioration in amphibian breeding site quality (Gardner et al. 2007). Although variation in amphibian responses to logging is dependent on the geographic, phylogenetic and disturbance history of sites, CL generally results in the replacement of expatriated forest specialist amphibians by a community of disturbance tolerant species, resulting in reduced species richness and/or functional diversity (Ernst et al. 2006, Gardner et al. 2007, Burivalova et al. 2014). This decline in amphibian species richness (due to forest specialist expatriation/generalist immigration) following CL has been recorded in Malaysian (Faruk et al. 2013), Bornean (Gillespie et al. 2012, Konopik et al. 2015) and Ugandan amphibian communities (Lukwago et al. 2020). However, in some cases species richness may remain the same (Fredericksen and Fredericksen 2004, Vallan et al. 2004, Ernst and Rödel 2005) or even increase after logging (Ernst et al. 2006, Ofori-Boateng et al. 2013), due to the immigration of generalist species offsetting the loss of forest specialists. Regardless, sites subject to CL typically contain different community members compared to unlogged forests and may not return to unlogged community states 45 years after logging (Kpan et al. 2021). The cause for this considerable delay in community recovery, is likely linked to the severe structural damage to forests inflicted via CL methods (Pereira et al. 2002, Putz et al. 2008). Several authors identified an association between amphibian recovery following CL and recovery of important habitat features (Ernst et al. 2006, Kpan et al. 2021). As such, identifying the environmental features linked to amphibian habitat associations and how these are affected by CL is paramount for quantifying the effects of this practice on tropical amphibians. Furthermore, comparisons of the direct impacts on amphibians and their environment between CL and RIL will allow researchers and foresters to verify the sustainability of RIL for amphibian conservation.

Currently, few studies exist on amphibian responses to RIL, with these suggesting that the effects of RIL appear considerably lower compared to CL (Bicknell et al. 2014, Burivalova et al. 2014). Amphibian beta diversity remained similar in Guyanan forests post-RIL harvesting, despite significant reductions in the abundance of several species (Hölting et al. 2016). Conversely, within a Ghanaian forest logged using modified RIL methods, amphibian species richness increased immediately following logging (due to an influx of generalist species), with this community returning to pre-harvest states within 20 years (Adum et al. 2013). Although these studies show slight variations in amphibian responses to RIL and CL, direct comparisons between the two logging types in the same geographical area are currently unavailable. Furthermore, the majority of these studies are heavily reliant on species richness as a metric of amphibian biodiversity decline. Although loss of species richness and diversity should be classified as a negative effect, it fails to account for shifts in individual species abundance/occurrence (Aggemyr et al. 2018), or the species-level responses to specific logging impacts (Matthews et al. 2014). The determination of amphibian responses to CL and RIL at the species and community level is further undermined by an often overlooked parameter in ecological field studies: detection probability.

Detection probability and occupancy modelling

Determining a species responses to disturbance such as logging, is highly dependent on ones ability to detect the species. Amphibians, and most mobile species are rarely detected perfectly and thus several surveys are conducted to confirm their presence or absence (MacKenzie et al. 2002). However, even count data based on multiple surveys fails to discern between true absences and false absences, i.e. recording a species as absent when it is present but undetected (Mackenzie and Royle 2005). These studies risk considerable error when omitting detectability, as underestimated non-detection can increase positive and negative bias when discerning habitat covariate associations (Gu and Swihart 2004). When determining species responses to disturbances, these biases can significantly affect the assumed impact of the disturbance type, and potentially undermine subsequent conservation strategies (Olea and Mateo-Tomás 2011). Accounting for detectability, is further complicated in elusive, cryptic species with highly fluctuating activity, such as amphibians (Wells 2010). Difficulties in detection have been identified in previous studies which determined that amphibian detection probability is strongly associated with a multitude of factors (MacKenzie et al. 2002, Homyack et al. 2016, Barata et al. 2017, Ribeiro Jr et al. 2018, Guzy et al. 2019). Furthermore, amphibians present additional

concerns as previous studies have identified both variable detection probabilities for species within the same community (Ribeiro Jr et al. 2018), and varying detectability associations with climatological and temporal factors (MacKenzie et al. 2002). These associations are linked to the variable ecology, breeding behaviour and activity of co-occurring amphibians (Wells 2010). In many cases, climatological and temporal factors serve as phenological cues, triggering breeding events (either episodic or explosive) in anurans (MacKenzie et al. 2002, Allentoft and O'Brien 2010, Grant et al. 2013, Homyack et al. 2016). These breeding events include highly conspicuous behaviours such as calling, finding mates and egg deposition, and as such increase the likelihood of detection. Understanding these detectability associations in an understudied tropical amphibian community, will improve our understanding of amphibian breeding phenology. Furthermore, reliable estimates of detection probability will allow for more robust estimation of amphibian responses to anthropogenic disturbances such as logging.

To this end, methods such as occupancy modelling, which account for non-perfect detection resulting from covariates, allow for more accurate estimations of species occurrence (MacKenzie et al. 2002). These methods, can be applied to entire communities, allowing the estimation of species-specific and community level occupancy probability as a function of covariates, whilst accounting for species detection probability (MacKenzie et al. 2017, Sollmann et al. 2017). Furthermore, occupancy probabilities generated within these models, can be used in place of raw-count derived relative abundance values. Although raw-count data are regularly used within diversity indices they are often prone to detection bias due to their failure to account for species detection probability (Abrams et al. 2021). Estimating diversity metrics utilizing occupancy probabilities, therefore allows for a more robust modelling framework for determining diversity responses to disturbance whilst accounting for imperfect detectability.

Thesis objectives

Responses of amphibians to logging is often dependent on several co-occurring factors: the composition of the amphibian community, the intensity/type of logging conducted, time since disturbance and spatial processes. As such, using a Bornean amphibian community in a logged area of central Sabah, Malaysian Borneo, I addressed the following questions utilizing an occupancy modelling framework: (1) What are the detectability and habitat associations for a

community of Bornean stream anurans, and are habitat associations more similar to primary (unlogged) or heavily disturbed (conventionally selectively logged and oil palm plantation) forest streams, (2) How do Bornean stream amphibian communities vary between two logging types (Reduced Impact and Conventional selective) over a temporal recovery gradient of time since logging (4 – 21 years), and (3) How do species and community level responses to the direct/indirect impacts of RIL vary between two amphibian communities (stream and terrestrial)?

Due to their physiological constraints/variable reproductive strategies, amphibian species occurrence is closely linked to local environmental factors. These variations additionally lead to highly variable activity patterns, and subsequently detectability. As such, in chapter 1 I aimed to determine the detectability and habitat relationships for a community of stream amphibians within a reserve subject to RIL. I sampled a network of heterogeneous streams within an RIL managed reserve to not only delineate potential stream amphibian climatological breeding cues and species-habitat relationships, but to compare amphibian habitat associations between RIL streams, and those in primary (unlogged) and heavily disturbed (conventionally selectively logged and palm oil plantation streams) streams in neighbouring sites. Additionally, these results (identification of important detectability and occupancy covariates) will be used to improve subsequent occupancy models of amphibian responses to logging.

Although Reduced Impact Logging (RIL) is touted as a sustainable alternative to Conventional selective Logging (CL), the effects of this harvesting type on amphibians are not fully understood. In chapter 2, I compare the effects of Conventional selective (CL) and Reduced Impact Logging (RIL) on stream amphibian communities and their habitats at varying stages of regeneration following logging (4-21 years). I used multi-species occupancy modelling in combination with diversity profiles to elucidate the responses of individual species to these logging types/their direct impacts on stream habitats, and how these compare to community level responses (diversity). Furthermore, I aimed to determine the variations in amphibian species/community recovery following logging over time (4-21 years) to assess the recovery potential following logging, and the purported sustainability of RIL practices.

Chapter 3, investigates whether variations between immediate direct/indirect RIL impacts (<1 year of logging) exist between amphibian communities in different habitats (stream and terrestrial). Using a quasi-experimental treatment of pre/post RIL sampling with adjacent control sites, I assessed how species/communities changed after RIL between habitats.

Furthermore, I aimed to discern how direct (logging associated habitat shifts following timber extraction) and indirect (logging infrastructure development) RIL impacts affected amphibians in both habitats.

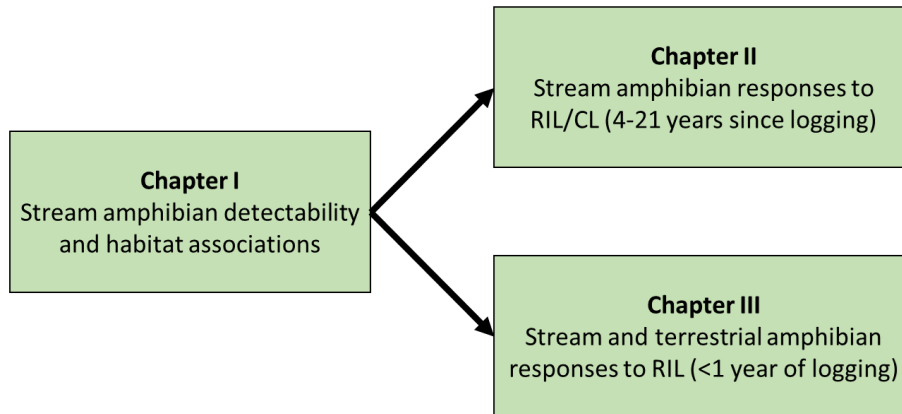


Figure 1 – Flow chart of thesis chapters, with arrows indicating chronological order.

In the last section of this thesis, I summarize the chapters and discuss the implications of this research in regards to amphibian conservation in commercial timber reserves and potential improvements to sustainable logging practices. The limited negative direct/indirect impacts of RIL, swift recovery of amphibian communities/habitats and similarity between RIL and primary forest amphibian habitat associations, suggests that RIL holds true to its promise of a sustainable logging alternative. I therefore suggest that RIL should become the standard practice for tropical timber management, especially considering the higher amphibian diversity/habitat quality compared to CL sites. Furthermore, I highlight the applicability and utility of multi-species occupancy modelling, and occupancy derived biodiversity metrics with reference to amphibian research and studies seeking to elucidate species responses to disturbance.

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Chapter 1: Stream amphibian detectability and habitat associations in a reduced impact logging concession in Malaysian Borneo

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Chapter 3: Variable species but similar amphibian community responses to reduced impact logging across habitats

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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.

Keywords: Anurans, Malaysia, Community occupancy, Logging roads, Sustainable forestry

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 impact of logging road development following RIL, would thus allow us to evaluate the effectiveness of specific 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 affect 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.

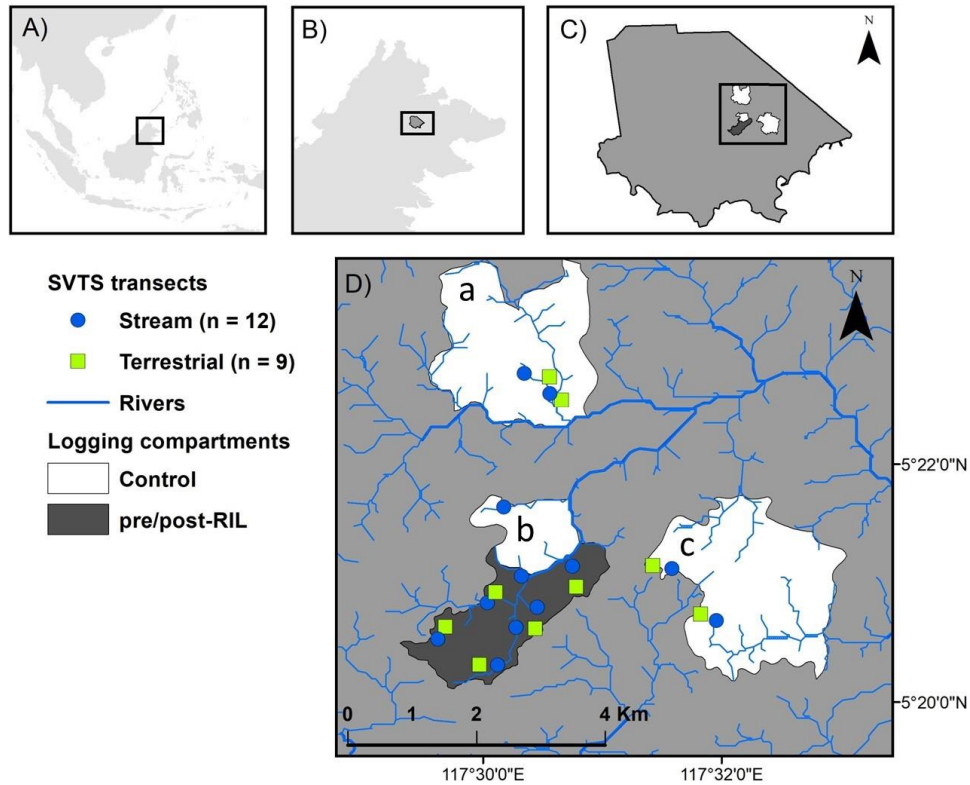
In this study we aimed to determine the effects of RIL on Bornean amphibian communities within terrestrial and stream habitats. The island of Borneo is both an anuran diversity hotspot (Inger, 1966; Inger et al., 2017) and a logging intensive region, with timber concessions covering over 40% of remnant 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?

Methods

Study site

We conducted this study within the Deramakot forest reserve (5°14-28'N, 117°19-36'E) in central Sabah, Malaysian Borneo (Figure 4.1). 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 Figure 4.1) 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).

Figure 4.1 – 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).

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 protocol 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 meters. 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 x 5 m subplots, whilst terrestrial transects were divided into five adjacent 20 x 5 m subplots. Two researchers surveyed transects for 30 minutes (three minutes per plot) between 1830–2300 hrs. 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.

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 hrs): 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 x 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 meters 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 x 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 meters) 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).

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 Figure 4.2 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; Asad et al., 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 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 (${}^qD^Z$) 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).

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 3.1 and 3.2). Of these species, 13 and 11 were exclusively detected in stream and terrestrial sites respectively.

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 (Figure 4.2). 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 (Figure 4.2). 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.

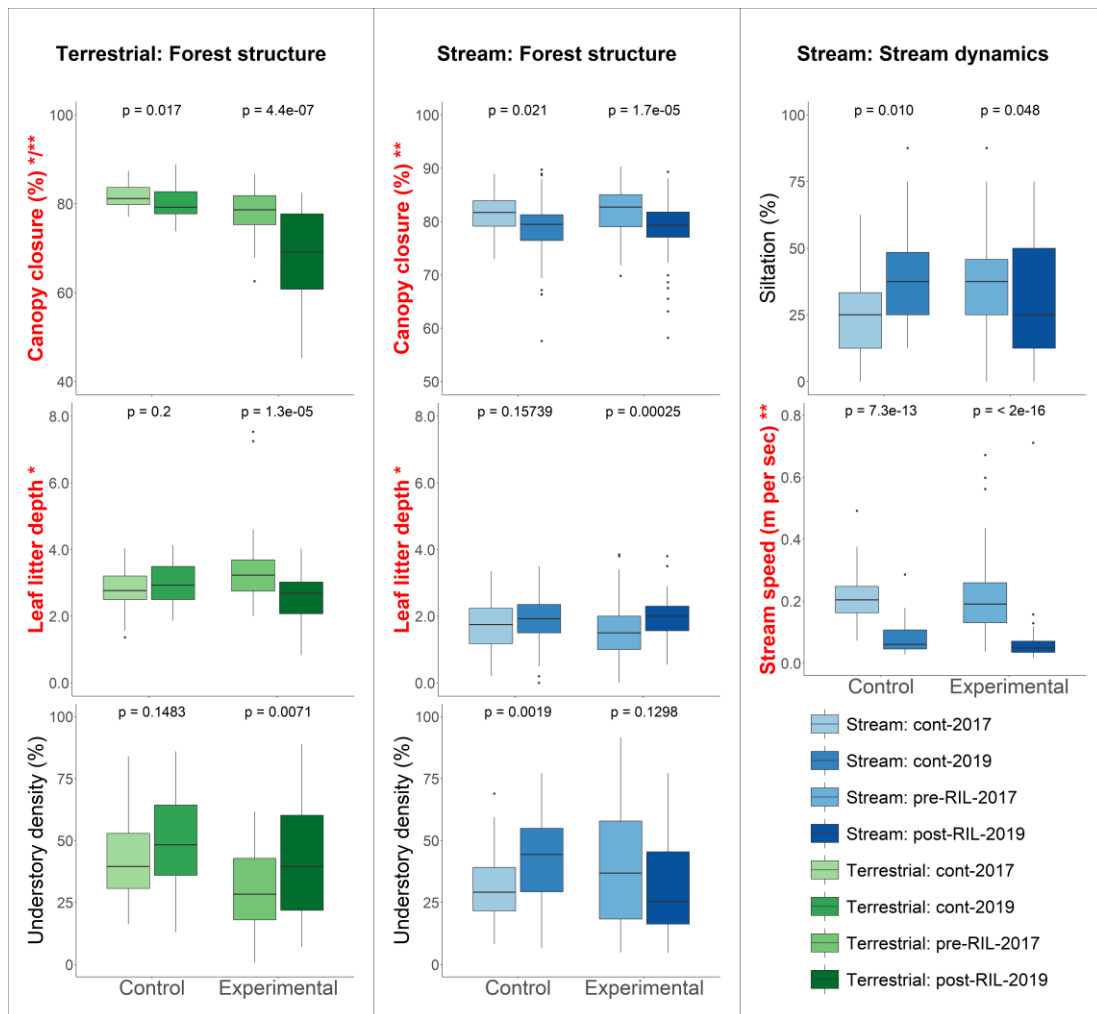


Figure 4.2 – Stream and terrestrial forest structure and stream dynamic covariate values within each logging treatment (cont = control, pre-RIL = before RIL, post-RIL = after RIL) between years (2017 and 2019). Includes the results of pairwise-Wilcoxon tests between sampling years of each treatment. 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.

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 3.3). 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) (Figure 4.3A), whereas terrestrial species were more associated with the direct impacts of RIL (reduced leaf litter depth) (Figure 4.3B). 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 (Figure 4.3A) compared to positive moderate associations with ten terrestrial species (Figure 4.3B). 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.

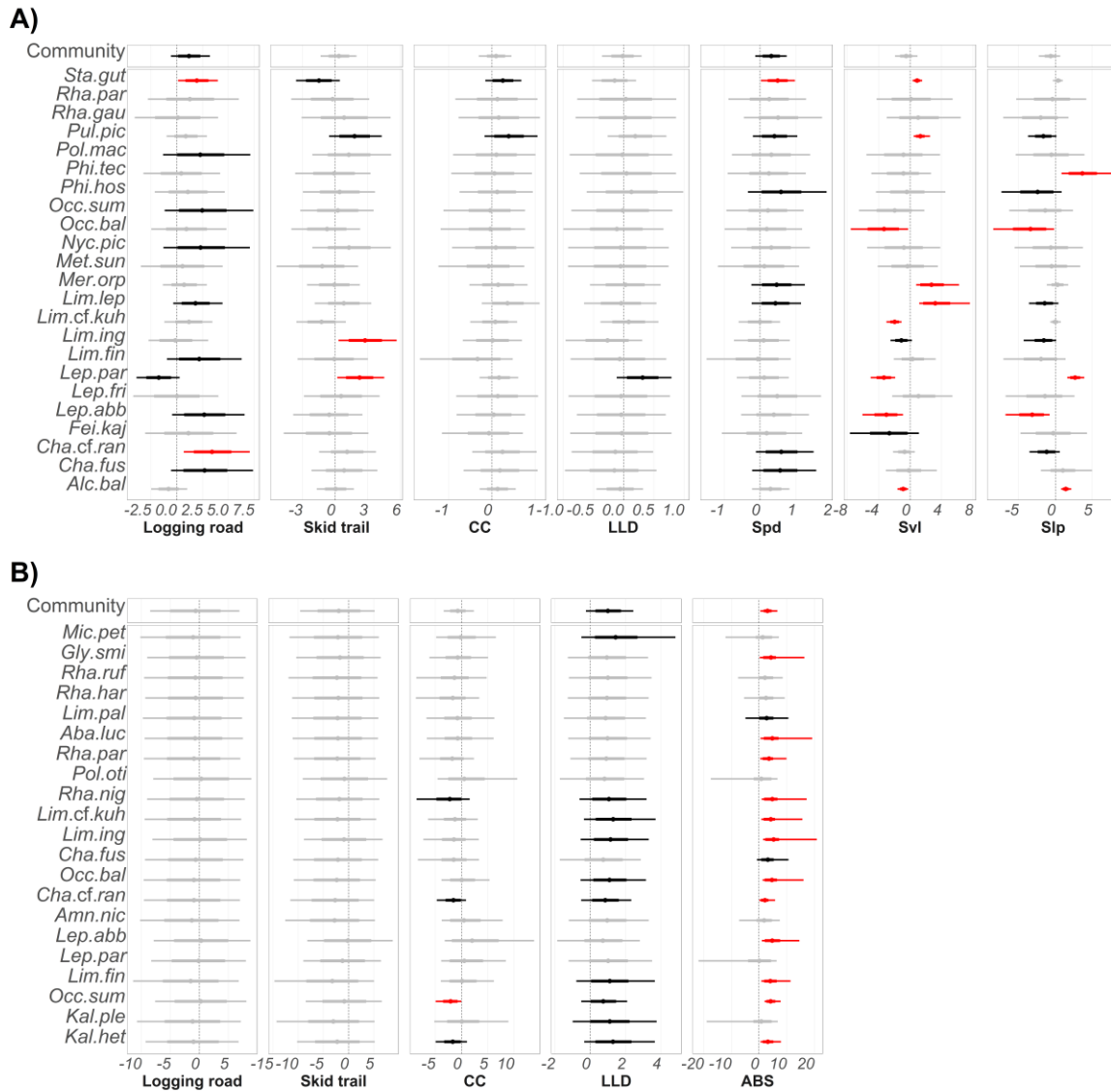


Figure 4.3 – Habitat covariate effect sizes on the species and community occupancy of amphibians occupying stream (A) and terrestrial (B) habitats respectively. Graph includes the following covariates: Logging road/skid trail = distance to logging road/skid trail, CC = Canopy Closure, LLD = Leaf Litter 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 3.1.

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 (Figure 4.4). 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 (Figure 4.5). Dissimilarity indices showed dissimilarity and considerably higher community occupancy post-RIL compared to pre-RIL states (Figure 4.4A), whereas control stream amphibian communities were similar between 2017 and 2019, with slightly higher community occupancy in 2019 (Figure 4.4B).

Diversity profile results were consistent with these findings. All diversity metrics increased in the post-RIL stream sites (Figure 4.5A), whereas control stream diversity metrics were almost identical between sampling years (Figure 4.5B). Dissimilarity patterns in terrestrial communities appeared similar to stream sites. Terrestrial site amphibian communities demonstrated marked dissimilarity and higher community occupancy post-RIL (Figure 4.4C), whereas control sites showed dissimilarity with lower community occupancy in 2019 (Figure 4.4D). 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 (Figure 4.5C). Conversely, in terrestrial control sites all species diversity metrics decreased markedly in 2019 (Figure 4.5D).

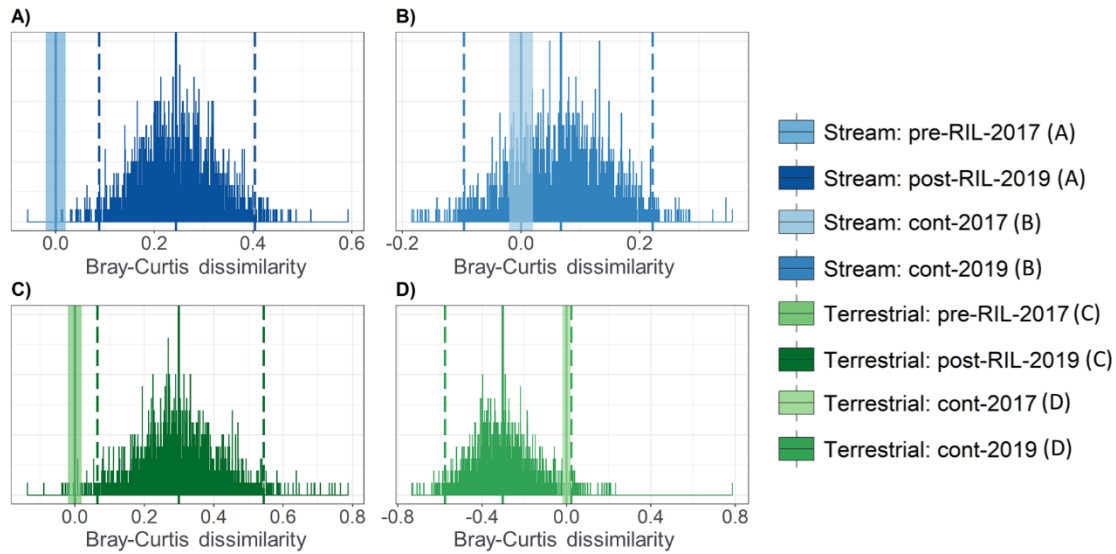


Figure 4.4 – Dissimilarity indices for stream (A = post-RIL-2019, B = control-2019) and terrestrial (C = post-RIL-2019, D = control-2019) amphibian communities compared to their respective 2017 communities, calculated using multi-species occupancy model predictions. Values of 0 indicate absolute similarity 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.

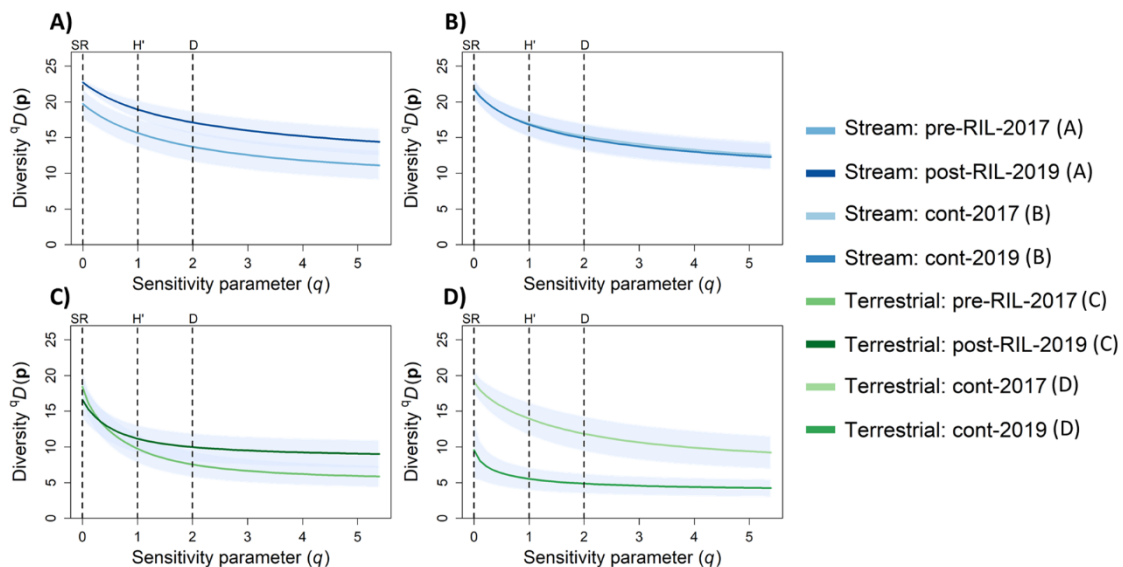


Figure 4.5 – Diversity profiles for stream (A = pre-RIL-2017/post-RIL-2019, B = control-2017/control-2019) and terrestrial (C = pre-RIL-2017/post-RIL-2019, D = control-2017/control-2019) amphibian communities, calculated using multi-species occupancy model predictions. Includes species richness (SR), 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.

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.

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*, *Leptobranchella parva*, *Leptobranchium 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*, *Limnonecte 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.

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 utilised 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, 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.

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; Whitworth et al., 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.

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.

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Supporting information

Table 3.1 –Data for the 34 amphibians recorded throughout all sites during the study. Including the transect types where species were detected (S = Stream, T = Terrestrial), the number of occupied plots/detections within each logging treatment, and the number of transects per treatment (n). Species names abbreviated to the first three letters of the genus and species name.

Family	Species	Stream/ Terrestrial	Experimental (n = 12)		Control (n = 9)		Total (n = 21)	
			2017	2019	2017	2019		
Ceratobatrachidae	<i>Alcalus baluensis</i> - <i>Alc.bal</i>	S	39 / 92	36 / 75	9 / 28	13 / 31	97 / 226	
Dicroglossidae	<i>Limnonectes finchi</i> - <i>Lim.fin</i>	S - T	4 / 4	4 / 4	1 / 1	1 / 1	10 / 10	
	<i>Limnonectes ingeri</i> - <i>Lim.ing</i>	S - T	11 / 17	5 / 5	9 / 15	5 / 9	30 / 46	
	<i>Limnonectes cf. kuhlii</i> - <i>Lim.cf.kuh</i>	S - T	32 / 54	27 / 36	21 / 62	20 / 27	100 / 179	
	<i>Limnonectes leporinus</i> - <i>Lim.lep</i>	S	15 / 31	9 / 10	7 / 12	7 / 17	38 / 70	
	<i>Limnonectes palavanensis</i> - <i>Lim.pal</i>	T	-	-	-	1 / 1	1 / 1	
	<i>Occidozyga baluensis</i> - <i>Occ.bal</i>	S - T	1 / 32	4 / 5	5 / 5	1 / 1	11 / 43	
	<i>Occidozyga sumatrana</i> - <i>Occ.sum</i>	S - T	2 / 34	3 / 14	4 / 66	2 / 9	11 / 123	
Megophryidae	<i>Leptobranchella parva</i> - <i>Lep-par</i>	S - T	35 / 121	28 / 95	20 / 142	19 / 63	102 / 421	
	<i>Leptobranchium abbotti</i> - <i>Lep.abb</i>	S - T	4 / 5	6 / 8	5 / 5	11 / 15	26 / 33	
	<i>Leptotalax fritinniensi</i> - <i>Lep.fri</i>	S	1 / 1	1 / 1	-	-	2 / 2	
Microhylidae	<i>Glyphoglossus smithi</i> - <i>Gly.smi</i>	T	-	1 / 1	-	-	1 / 1	
	<i>Chaperina fusca</i> - <i>Cha.fus</i>	S - T	2 / 3	5 / 6	2 / 6	-	9 / 15	
	<i>Kalophrynus heterochirus</i> - <i>Kal.het</i>	T	6 / 6	12 / 15	2 / 2	9 / 9	29 / 32	
	<i>Kalophrynus pleurostigma</i> - <i>Kal.ple</i>	T	2 / 2	1 / 1	-	-	3 / 3	
	<i>Metaphrynella sundana</i> - <i>Met.sun</i>	S - T	-	2 / 2	-	-	2 / 2	
	<i>Microhyla petrigena</i> - <i>Mic.pet</i>	T	1 / 1	1 / 1	-	-	2 / 2	
Ranidae	<i>Abavorana luctuosa</i> - <i>Aba.luc</i>	T	-	-	1 / 1	-	1 / 1	
	<i>Amnirana nicobariensis</i> - <i>Amn.nic</i>	T	-	-	1 / 1	2 / 2	3 / 3	
	<i>Chalcorana cf. raniceps</i> - <i>Cha.cf.ran</i>	S - T	6 / 17	4 / 5	8 / 9	5 / 5	23 / 36	
	<i>Meristogenys orphnocnemis</i> - <i>Mer.orp</i>	S	6 / 7	10 / 20	3 / 4	3 / 12	22 / 43	
	<i>Pulchrana picturata</i> - <i>Pul.pic</i>	S	7 / 24	6 / 10	9 / 34	3 / 3	25 / 71	
	<i>Staurois guttatus</i> - <i>Sta.gut</i>	S	18 / 80	22 / 271	1 / 1	2 / 2	43 / 354	
Rhacophoridae	<i>Feihyla kajau</i> - <i>Fei.kaj</i>	S	-	1 / 1	-	1 / 1	2 / 2	
	<i>Nyctixalus pictus</i> - <i>Nyc.pic</i>	S	-	-	1 / 1	-	1 / 1	
	<i>Philautus hosii</i> - <i>Phi.hos</i>	S	1 / 1	2 / 2	-	1 / 1	4 / 4	
	<i>Philautus tectus</i> - <i>Phi.tec</i>	S	-	1 / 1	1 / 1	2 / 4	4 / 6	
	<i>Polypedates macrotis</i> - <i>Pol.mac</i>	S	-	-	1 / 1	-	1 / 1	
	<i>Polypedates otlophus</i> - <i>Pol.oti</i>	T	-	1 / 1	1 / 1	-	2 / 2	
	<i>Rhacophorus gauni</i> - <i>Rha.gau</i>	S	2 / 3	-	-	-	2 / 3	
	<i>Rhacophorus harrissoni</i> - <i>Rha.har</i>	T	-	1 / 1	-	-	1 / 1	
	<i>Rhacophorus nigropalmatus</i> - <i>Rha.nig</i>	T	2 / 4	-	-	-	2 / 4	
	<i>Rhacophorus pardalis</i> - <i>Rha.par</i>	S - T	-	1 / 7	1 / 7	-	2 / 14	
	<i>Rhacophorus rufipes</i> - <i>Rha.ruf</i>	T	-	1 / 1	-	-	1 / 1	
	Total species			21	27	22	19	34

Table 3.2 – Total number of amphibian detections within each study transect each year. Transects are divided by their treatment type/year (pre-RIL-2017, post-RIL 2019, control 2017 and control 2019) with control compartments additionally divided by designation (a, b and c, see Figure 1). Stream and terrestrial transects indicated by S and T respectively.

Species	pre-RIL 2017												post-RIL 2019												Control (b) 2017/Control (b) 2019			Control (c) 2017			Control (c) 2019				
	S1	S2	S3	S4	S5	S6	S7	T1	T2	T3	T4	T5	S1	S2	S3	S4	S5	S6	S7	T1	T2	T3	T4	T5	S1	S2	S1	S1	S2	T1	T2	T1	T2	T1	T2
Ceratobatrachidae	18	16	0	6	11	2	11	0	0	0	0	0	26	11	9	3	8	4	4	0	0	0	0	0	28		10	15	8	0	0	17	13	0	0
<i>Alcalus baliuensis</i>	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Limnonectes finchi</i>	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnonectes ingeri</i>	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limnonectes cf. kuhlii</i>	15	6	0	2	13	1	8	0	0	0	4	2	6	3	4	3	0	8	0	0	0	0	0	0	9	4	0	11	36	0	2	5	8	0	0
<i>Limnonectes teponius</i>	0	0	15	14	0	2	0	0	0	0	0	0	0	0	2	6	0	2	0	0	0	0	0	0	5	10	0	0	0	0	0	0	0	0	0
<i>Limnonectes palawanensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oxidizya baliuensis</i>	0	0	0	0	0	0	0	0	0	0	32	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oxidizya sumatrana</i>	0	0	0	0	0	0	0	0	0	0	31	0	0	0	0	0	0	2	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0
Megophryidae	17	1	0	0	15	0	28	1	1	0	0	1	23	1	0	0	35	0	3	0	0	0	0	0	57	33	0	78	32	1	1	19	11	0	0
<i>Leptobrachella parva</i>	0	3	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	
<i>Leptobrachium abhatti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Leptotriton fritziensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
Microhylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Calluella smithi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Chaperina fusca</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Kalophrynus heterochinus</i>	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Kalophrynus pleurostigma</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Metaphrynella sundana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Microhyla pestrigena</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ranidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Abavorana luctuosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Amirana nicobarensis</i>	0	2	1	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Chalcophaps cf. raniceps</i>	0	1	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Meristogenys orphnaceensis</i>	0	1	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pulchriana picturata</i>	0	20	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Staurosis guttata</i>	0	2	0	12	3	62	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Rhacophoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Feihyla kajau</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Nyctaxalus pictus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Phyllautus hosii</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Phyllautus tectus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Polypedates macratis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Polypedates atelopagus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhacophorus gauhi</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhacophorus harrisseni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhacophorus nigropalmatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhacophorus parvialis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhacophorus rufipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total species	3	7	7	9	8	5	6	3	6	1	2	9	4	9	9	11	5	4	9	2	2	2	2	6	6	7	0	4	5	5	9	4	7	3	2

Table 3.3 – Results of the multi-species occupancy models for the stream (above) and terrestrial (below) communities, obtained from single detection covariate models. The estimates, \pm standard errors, moderate ($< 75\%$ CI = $^*^1$) and significant ($< 95\%$ CI = $^*^1*$) associations between all species and each detection covariate are included. MDR represents maximum daily rainfall whilst TSS represents time since sunset. The two covariates with the most moderate ($< 75\%$ CI) and significant ($< 95\%$) associations with each community (Stream = MDR and moonphase, terrestrial = TSS and MDR) were included in the final, multi-covariate, multi-species occupancy models. Species names abbreviated to the first three letters of the genus and species name.

Species	Stream community (n = 23)				
	Humidity	MDR	Moon	Temperature	TSS
<i>Alc.bal</i>	0.09 \pm 0.09	-0.04 \pm 0.08	0.14 \pm 0.09 $^*^1$	-0.07 \pm 0.09	0.16 \pm 0.09 $^*^1$
<i>Cha.cf.ran</i>	-0.22 \pm 0.23	-0.33 \pm 0.22 $^*^1$	-0.13 \pm 0.21	0.16 \pm 0.21	0.23 \pm 0.22
<i>Cha.fus</i>	-0.19 \pm 0.29	-0.07 \pm 0.22	0.29 \pm 0.27	0.29 \pm 0.3	-0.02 \pm 0.33
<i>Fei.kaj</i>	-0.3 \pm 0.34	-0.2 \pm 0.26	0.31 \pm 0.3	0.28 \pm 0.32	-0.01 \pm 0.39
<i>Lep.abb</i>	-0.23 \pm 0.21	-0.36 \pm 0.22 $^*^1$	0.46 \pm 0.2 $^*^1*$	0.22 \pm 0.18 $^*^1$	0.1 \pm 0.2
<i>Lep.fri</i>	-0.3 \pm 0.32	-0.22 \pm 0.27	0.2 \pm 0.3	0.2 \pm 0.31	0.1 \pm 0.39
<i>Lep.par</i>	0.1 \pm 0.09 $^*^1$	-0.08 \pm 0.08	0.57 \pm 0.1 $^*^1*$	-0.37 \pm 0.09 $^*^1*$	-0.02 \pm 0.1
<i>Lim.cf.kuh</i>	-0.07 \pm 0.1	-0.02 \pm 0.08	-0.04 \pm 0.09	0.06 \pm 0.09	0.01 \pm 0.1
<i>Lim.fin</i>	-0.01 \pm 0.29	-0.17 \pm 0.25	0.17 \pm 0.26	0.21 \pm 0.28	-0.19 \pm 0.33
<i>Lim.ing</i>	-0.17 \pm 0.18	-0.03 \pm 0.14	0.26 \pm 0.19 $^*^1$	-0.16 \pm 0.17	-0.07 \pm 0.19
<i>Lim.lep</i>	-0.12 \pm 0.18	-0.11 \pm 0.15	-0.03 \pm 0.15	-0.09 \pm 0.16	-0.24 \pm 0.16 $^*^1$
<i>Mer.orp</i>	0.07 \pm 0.2	-0.25 \pm 0.2 $^*^1$	0.27 \pm 0.18 $^*^1$	-0.01 \pm 0.17	0.05 \pm 0.19
<i>Met.sun</i>	-0.13 \pm 0.31	-0.16 \pm 0.26	0.26 \pm 0.29	0.3 \pm 0.33	0.23 \pm 0.39
<i>Nyc.pic</i>	-0.1 \pm 0.33	-0.19 \pm 0.26	0.24 \pm 0.31	0.09 \pm 0.31	0.12 \pm 0.42
<i>Occ.bal</i>	0.17 \pm 0.26	-0.15 \pm 0.22	0.17 \pm 0.24	0.02 \pm 0.24	-0.07 \pm 0.29
<i>Occ.sum</i>	-0.03 \pm 0.32	-0.03 \pm 0.25	0.33 \pm 0.3	0.13 \pm 0.3	0.3 \pm 0.4
<i>Phi.hos</i>	-0.42 \pm 0.34 $^*^1$	-0.26 \pm 0.27	0.39 \pm 0.29 $^*^1$	0.37 \pm 0.32 $^*^1$	-0.07 \pm 0.33
<i>Phi.tec</i>	-0.01 \pm 0.27	-0.07 \pm 0.23	0.18 \pm 0.27	0.18 \pm 0.27	0.03 \pm 0.33
<i>Pol.mac</i>	-0.14 \pm 0.33	-0.19 \pm 0.27	0.18 \pm 0.3	0.08 \pm 0.32	0.13 \pm 0.4
<i>Pul.pic</i>	-0.58 \pm 0.25 $^*^1*$	0.02 \pm 0.17	0.1 \pm 0.18	-0.08 \pm 0.18	0.04 \pm 0.18
<i>Rha.gau</i>	-0.14 \pm 0.32	-0.16 \pm 0.25	0.14 \pm 0.29	-0.02 \pm 0.3	0.39 \pm 0.38
<i>Rha.par</i>	-0.03 \pm 0.32	-0.12 \pm 0.26	0.23 \pm 0.31	0.15 \pm 0.32	-0.18 \pm 0.42
<i>Sta.gut</i>	0.09 \pm 0.14	-0.31 \pm 0.15 $^*^1*$	0.06 \pm 0.12	0.22 \pm 0.12 $^*^1$	-1.19 \pm 0.2 $^*^1*$
Community	-0.12 \pm 0.11	-0.15 \pm 0.09 $^*^1$	0.21 \pm 0.1 $^*^1*$	0.1 \pm 0.11	-0.01 \pm 0.13

Species	Terrestrial community (n = 21)				
	Humidity	MDR	Moon	Temperature	TSS
<i>Aba.luc</i>	-0.49 \pm 0.56	0.12 \pm 0.42	-0.08 \pm 0.39	0.1 \pm 0.4	-0.27 \pm 0.77
<i>Amn.nic</i>	-0.08 \pm 0.39	0.05 \pm 0.35	-0.18 \pm 0.35	-0.09 \pm 0.31	0.3 \pm 0.64
<i>Cha.cf.ran</i>	-0.39 \pm 0.4	0.22 \pm 0.3	-0.24 \pm 0.3	0 \pm 0.29	-1.17 \pm 0.5 $^*^1*$
<i>Cha.fus</i>	-0.45 \pm 0.47	0.28 \pm 0.34	0.27 \pm 0.33	0.3 \pm 0.37	0.22 \pm 0.72
<i>Gly.smi</i>	-0.19 \pm 0.5	0.43 \pm 0.38 $^*^1$	0.23 \pm 0.37	0.1 \pm 0.38	0.1 \pm 0.8
<i>Kal.het</i>	0.19 \pm 0.19	0.31 \pm 0.17 $^*^1$	0.46 \pm 0.21 $^*^1*$	0.04 \pm 0.16	0.49 \pm 0.23 $^*^1*$
<i>Kal.ple</i>	-0.23 \pm 0.41	0.39 \pm 0.31 $^*^1$	-0.08 \pm 0.33	0.09 \pm 0.33	-0.72 \pm 0.74
<i>Lep.abb</i>	-0.34 \pm 0.41	-0.05 \pm 0.39	0.13 \pm 0.32	-0.01 \pm 0.32	0.74 \pm 0.59 $^*^1$
<i>Lep.par</i>	-0.32 \pm 0.41	0.2 \pm 0.29	0.24 \pm 0.3	-0.28 \pm 0.37	-0.66 \pm 0.45 $^*^1$
<i>Lim.cf.kuh</i>	-0.95 \pm 0.65 $^*^1$	0.2 \pm 0.43	-0.04 \pm 0.33	0.02 \pm 0.35	-1.24 \pm 0.73 $^*^1$
<i>Lim.fin</i>	-0.19 \pm 0.38	0.24 \pm 0.3	-0.16 \pm 0.31	0.15 \pm 0.34	-0.78 \pm 0.47 $^*^1$
<i>Lim.ing</i>	-0.49 \pm 0.46 $^*^1$	0.08 \pm 0.43	-0.04 \pm 0.32	0.16 \pm 0.36	-1.68 \pm 0.7 $^*^1*$
<i>Lim.pal</i>	-0.16 \pm 0.46	0.08 \pm 0.4	0.02 \pm 0.37	0 \pm 0.35	0.03 \pm 0.75
<i>Mic.pet</i>	-0.34 \pm 0.45	0.08 \pm 0.37	0.09 \pm 0.34	0.04 \pm 0.34	-0.71 \pm 0.79
<i>Occ.bal</i>	0.14 \pm 0.43	0.1 \pm 0.43	0.18 \pm 0.3	-0.2 \pm 0.35	-1.7 \pm 0.74 $^*^1*$
<i>Occ.sum</i>	0.13 \pm 0.34	0.28 \pm 0.31	0.27 \pm 0.26	-0.01 \pm 0.26	-0.9 \pm 0.36 $^*^1*$
<i>Pol.oti</i>	-0.07 \pm 0.48	0.54 \pm 0.34 $^*^1$	0.06 \pm 0.35	-0.05 \pm 0.34	-0.15 \pm 0.72
<i>Rha.har</i>	-0.51 \pm 0.54	0.11 \pm 0.4	0.22 \pm 0.38	0.14 \pm 0.38	-0.29 \pm 0.82
<i>Rha.nig</i>	-0.6 \pm 0.49 $^*^1$	0.09 \pm 0.39	0.04 \pm 0.33	0 \pm 0.35	-0.82 \pm 0.56 $^*^1$
<i>Rha.par</i>	-0.34 \pm 0.56	0.18 \pm 0.45	0 \pm 0.38	0.09 \pm 0.41	-1.27 \pm 0.87 $^*^1$
<i>Rha.ruf</i>	0.13 \pm 0.5	0.32 \pm 0.37	0.1 \pm 0.37	-0.27 \pm 0.38	-0.03 \pm 0.76
Community	-0.26 \pm 0.21 $^*^1$	0.2 \pm 0.17 $^*^1$	0.07 \pm 0.15	0.01 \pm 0.16	-0.51 \pm 0.3 $^*^1$

General Discussion

In this thesis, I aimed to determine the responses of amphibians to different logging types and their direct/indirect effects. I began, by determining the detectability and habitat associations for a community of stream anurans in a reduced impact logged area (chapter 1). This provided invaluable insights into the ecology/potential breeding phenology of these species and allowed comparisons of habitat associations between amphibians in RIL sites and those in more (palm-oil and conventionally logged) or less disturbed (unlogged primary) forests. Furthermore, these results provided invaluable information (detection/occupancy covariates) for improving model performance in subsequent chapters. With this information, I was able to determine the responses of individual stream amphibian species and community diversity metrics to different logging types (RIL/CL) and the direct environmental impacts of logging. Additionally, I was able to determine how amphibian species/communities recovered over a regeneration gradient of time since logging (Chapter 2). Finally, by using pre- and post-RIL sampling, I assessed the responses of both stream and terrestrial amphibian species to the immediate (within 1 year) direct and indirect impacts of RIL. This also permitted the assessment of stream/terrestrial amphibian community shifts immediately following RIL (Chapter 3). Throughout this thesis, I used comparisons between RIL and conventional logging methods over recovery gradients, assessments of direct and indirect logging impacts on species and their habitats, compared logging impacts across habitats, all whilst accounting for variable species detectability. As such, I believe this thesis provides the most complete and in-depth assessment of amphibian responses to RIL. These results, can be summarized as follows:

Chapter 1 identified variable species-specific associations between detection covariates in the stream amphibians of this study. This suggests a high level of separation in the activity and breeding phenology of these co-occurring species. Furthermore, the two best predictors of stream anuran occurrence (stream slope and stream width) within this RIL site, were more similar to these species' habitat associations in undisturbed primary forests compared to highly disturbed conventionally logged/palm oil plantation streams from other areas.

Chapter 2 showed that amphibian communities were far more diverse in RIL sites compared to CL sites of the same age and exhibited a swift recovery over a 21 year period following RIL. I found that the direct logging impacts: decreased aboveground carbon density and increased stream siltation, were negatively associated with the occupancy of several obligate stream

breeding species. Obligate stream breeding species occupancy was also generally lower in CL compared to RIL streams, with the opposite association in generalist breeding species.

Chapter 3 identified variable responses of amphibian species to RIL in stream and terrestrial habitats, but similar community responses across these habitats. Most notably, amphibians in stream habitats generally exhibited negative associations with indirect (proximity to logging roads/skid trails) logging impacts whilst those in terrestrial habitats were most associated with direct logging impacts (terrestrial decrease in leaf litter depth). Despite this, amphibian community occupancy and diversity metrics were generally higher following RIL. I believe this logging associated increase in amphibian diversity immediately after RIL is the result of a community flux following logging and the delayed negative impact of RIL on amphibian habitats.

Amphibian conservation in tropical timber concessions

For effective biodiversity conservation within tropical forests, governments, NGOs and conservation practitioners, must turn to human-modified landscapes (Corlett 2015). While 27% of global forest loss between 2001 and 2015 can be attributed to permanent, commodity driven (agriculture, live-stock, tree plantations etc) land conversion, the remaining forested areas subject to wildfires, shifting agriculture and forestry provide considerable opportunities for forest recovery and conservation of biodiversity (Curtis et al. 2018). As commercial timber concessions, cover 53% of these remaining tropical forests (Blaser et al. 2011), the utilization and improvement of sustainable forestry practices such as Reduced Impact Logging (RIL), should thus become a priority for biodiversity conservation, including amphibians (Fisher et al. 2011). Previous research, has identified minimal impacts of RIL on mammalian, bird, arthropod and amphibian communities compared to Conventional selective Logging (CL) methods (Azevedo-Ramos et al. 2006, Wunderle Jr et al. 2006, Bicknell et al. 2014, 2015, Burivalova et al. 2014, Hasegawa et al. 2014, Sollmann et al. 2017, Tobler et al. 2018). Furthermore, the majority of these studies identified minimal shifts in species richness across taxa immediately following RIL compared to unlogged states (Azevedo-Ramos et al. 2006, Bicknell et al. 2015). However, variability within these impacts exists geographically and within/between taxonomic groups. Neo-tropical mammals for example, varied across sites in their responses to RIL, from minor decreases in species richness (Brazil: Azevedo-Ramos et al. 2006, Carvalho Jr et al. 2021), no shifts in species richness (Guatemala and Peru: Tobler et al. 2018) to increases in richness with higher logging road density (Brazil, Guatemala and Peru: Carvalho Jr et al. 2021,

Tobler et al. 2018). Additionally, multi-taxa studies typically fail to identify consistently positive or negative associations between species richness and RIL (Azevedo-Ramos et al. 2006, Bicknell et al. 2014, 2015, Burivalova et al. 2014). However, one consistently universal trend exists across taxa, geographic locations and studies: shifts in species richness (either positive or negative) are low following RIL, particularly in comparison to conventionally logged sites.

Within this thesis, the similarity in amphibian habitat associations between RIL and primary forests (chapter 1), high obligate stream breeding species occupancy/diversity (chapter 2) and increases in amphibian diversity throughout terrestrial and stream habitats following RIL (chapter 3), suggests that RIL also has limited negative impacts on amphibians.

Furthermore, previous research conducted within the same timber reserves, identified higher mammalian species richness (Sollmann et al. 2017) and less degraded soil macro-fauna communities (Hasegawa et al. 2014) in RIL managed areas compared to neighbouring CL sites. As such, the results of this thesis (and previous studies from the area) support the large body of research (Berry et al. 2010, Bicknell et al. 2014, 2015, Burivalova et al. 2014, Chaudhary et al. 2016) which indicates that reduced impact logging maintains relatively high diversity and has minimal impacts across a range of taxonomic groups, especially compared to conventional selective logging (chapter 2).

Whilst our results generally conform to previous findings regarding biodiversity responses to logging, our results do exhibit some differences compared to other amphibian research conducted within previously logged forests.

One important distinction, is the lack of a uniform “recovery period” for amphibian communities following both CL and RIL. Within Chapter 2, I identified a swift recovery of amphibians and their habitats over a 21 year period following RIL. Unfortunately, due to a lack of pre-logging sampling, I was unable to quantify whether this recovery returned to pre-logging levels. Within other areas, landscape level amphibian diversity either remained similar (Hölting et al. 2016) or exhibited a minor increase after a modified version of RIL (Adum et al. 2013). This was underscored by an influx of disturbance tolerant species/decline in forest specialists, with these shifts reversing and returning to pre-logging levels over a 20 year period (Adum et al. 2013). While our chapter 2 results somewhat mirror this (recovery of amphibian diversity 4-21 years post-RIL), our chapter 3 results show an influx of both disturbance tolerant species and forest specialists immediately following RIL (<1 years). The possible cause of this

discrepancy, is the modification of RIL methods used within the Southwest Ghanaian site, surveyed by Adum et al. (2013). While these methods include limited allowable cuts (3 trees per ha) and a 40 year felling cycles, they do not specifically mention other important RIL management procedures (liana cutting, directional felling, reduced skid trail construction, pre/post-harvest planning etc). A global meta-analysis of CL and RIL sites logged at the same intensity (three trees per hectare) found considerably higher biodiversity in RIL forests, suggesting that best practice forestry techniques prevent greater biodiversity loss than lower harvesting rates alone (Bicknell et al. 2014). Therefore, whilst the results of Adum et al. (2013) provide invaluable insight into amphibian responses to a modified version of RIL, they can not be strictly compared to the results of this study.

Regardless, one overwhelming dissimilarity between our results and previous research, is the lack of a uniform amphibian recovery following CL. Studies of amphibian responses to CL in other areas identified no changes (Bolivia: Fredericksen and Fredericksen 2004, Madagascar: Vallan et al. 2004), increases (West Africa: Ofori-Boateng et al. 2013, Guyana: Ernst et al. 2006) and decreases in species richness (Malaysia: Gillespie et al. 2012; Konopik et al. 2015, Ivory Coast: Kpan et al. 2021) following conventional logging. Despite this variance, one consistent finding is the shift in amphibian community composition, with a decrease in forests specialists and an increase in disturbance tolerant species following disturbance (as recorded in chapter 2). The return of amphibian diversity and community composition to pre-logging states varies tremendously throughout these studies. Many identified a reduction in generalist species occurrence and diversity 10-20 years following logging (Ernst et al. 2006, Konopik et al. 2015), whereas some amphibian communities still exhibited dissimilarity from their primary forest states 45 years after CL (Kpan et al. 2021). The causes for this high disparity between these results (and those of our study), could be the contribution of the local species pool, the surrounding habitat mosaic and the site's disturbance history. Whilst the species composition and surrounding habitat mosaics for these studies can be easily quantified, assessing the level of disturbance following CL is relatively difficult. As there are no universal best management practice guidelines for CL, the maximum quantity of marketable timber is typically extracted with little regard for sustainability measures (Picard et al. 2012). This results in remnant forest structural damage varying between areas based on the density of valuable timber, topography, available infrastructure and the specific management strategies of individual timber concession managers. As such, biodiversity responses to CL can be difficult to quantify, due to the highly variable, un-quantifiable scale of forest damage resulting from this logging practice (Pinard et al. 1995, Pereira et al. 2002). This inconsistent management, coupled with the greater

biodiversity loss and higher habitat degradation compared to RIL (Bicknell et al. 2014, Burivalova et al. 2014, Chaudhary et al. 2016), provides further support for the universal adoption of RIL practises throughout tropical concessions worldwide. The specific management practices associated with RIL, not only reduce biodiversity loss/habitat disturbance, but also allow for comparisons between RIL managed forests in different areas. Comparability between studies, will allow the determination of particularly sensitive amphibian communities (and biodiversity in general) to RIL, due to the similarity in timber extraction techniques.

Furthermore, the application of RIL methods may not only mitigate biodiversity loss, but also potentially increases habitat quality for many tropical amphibians thus increasing diversity (as reported in chapter 3). The specific management interventions of RIL such as directional felling, liana cutting and careful skid trail construction facilitate the maintenance of remnant forest structures, whilst also creating highly localised areas of disturbance (Pinard et al. 1995, Putz et al. 2008). These restricted disturbances create novel habitats in the form of small clearings in the forest canopy, increased density of fallen trees and most importantly, increased small pond density (Ernst et al. 2016, Hölting et al. 2016). These novel habitats may provide thermal refugia and micro-habitats (Otto et al. 2013, Earl and Semlitsch 2015) and potential aquatic breeding sites (Hölting et al. 2016). The creation of Aquatic Breeding Sites (ABS) following logging, particularly along skid trails has previously been documented in other areas, and has been linked to an increase in both forest specialist and generalist pool breeding species (Chambers 2008, Konopik et al. 2014, Ernst et al. 2016, Hölting et al. 2016). Furthermore, the proliferation of these ABS following logging provides a potential buffer from desiccation and breeding site loss as a result of climatic extremes (Hölting et al. 2016). Within chapter 3 I identified a similar pattern, as unlogged terrestrial amphibian diversity declined during a dry el niño year, whereas terrestrial amphibian diversity in sites recently subject to RIL exhibited a slight increase during this period. While the micro-habitats and potential benefits generated following RIL are also typical during CL, the associated high level of disturbance in the surrounding forests following CL (Pereira et al. 2002, Picard et al. 2012) likely offsets the suitability of these habitats for forest specialists. This results in their swift colonisation by a predominantly disturbance tolerant community (Gillespie 2002, Ofori-Boateng et al. 2013, Konopik et al. 2015, Kpan et al. 2021). Within RIL forests however, these novel habitats are surrounded by structurally complex, relatively undisturbed forests (Pinard et al. 1995, Putz et

al. 2008), permitting their utilization by disturbance sensitive forest specialists and generalist species.

The utilization of logging associated micro-habitats and the responses of amphibians to RIL and CL listed here are exclusively based on studies of adult amphibians. The results of this thesis and majority of previous research, fails to account for the responses of amphibian larval stages/breeding success to logging. As juvenile recruitment, not adult survival typically shapes amphibian population fluctuations (Alford and Richards 1999, Muths et al. 2011), the utility of novel ABS created along logging roads, and potential damage to suitable tadpole habitat following logging could potentially undermine the long-term suitability of logged sites for amphibian conservation.

Amphibian recruitment is typically associated with human disturbance in areas subject to such pressure (Hayes et al. 2010). Juvenile amphibian recruitment may decrease with increasing forest disturbance (Jachowski and Hopkins 2018), degradation and isolation of breeding habitat (Harper et al. 2008) and with increasing logging intensity (Todd et al. 2009). Although I detected limited, predominantly short-term impacts of RIL on the amphibians of this study, I was unable to quantify the impacts of logging on amphibian aquatic larvae. Within chapter 2, I identified an increase in stream siltation within CL and recently RIL sites. Although these increases were only linked to the occupancy of several stream species, the impacts of increased, logging associated siltation on larval habitats could differ markedly. Logging associated sedimentation, has previously been linked to the suitability of tadpole habitats (Gillespie 2002, Wood and Richardson 2009). As such, potential deterioration in tadpole habitat, and juvenile recruitment cannot be ruled out within the scope of this study. The amphibian diversity increase immediately following RIL (chapter 3), subsequent decreases 4-5 years after RIL followed by a steady increase over a 20 year period (Chapter 2) is potentially explained by this phenomenon. This could be due to the delayed negative effects of RIL on tadpole habitats, and subsequently juvenile recruitment. Previous research identified increasing sedimentation with time following forest disturbance (Kreutzweiser et al. 2005, Betts et al. 2021), suggesting that the negative impacts of logging on streams and tadpole habitats may take several years to accrue. However, given the swift recovery of stream dynamics throughout RIL sites in chapter 2, it is likely that such negative impacts on tadpole habitats would be short-term, and their contribution to amphibian recruitment limited.

While this appears the case for stream sites, novel aquatic breeding sites within terrestrially logged sites, may not recover as quickly. Given the exposed and thermally dynamic nature of logging roads/tree felling areas (Laurance et al. 2009, Hardwick et al. 2015, Mollinari et al. 2019), ABS within these areas may contain suboptimal conditions for amphibian larval growth. Conditions within more disturbed ABS typically favour generalist species with adaptable tadpole stages, whereas these conditions may be unsuitable for the survival and growth of forest specialist tadpoles (Chambers 2008). Furthermore, forest specialist tadpoles in these environments are likely subject to greater competition pressure from both congeners, and better adapted generalists (Paull et al. 2012). As such, the increase in ABS resulting from RIL, may only appear to increase forest specialist occurrence at breeding sites. If forest specialist tadpole survivability is reduced in these pools, the subsequent decline in recruitment may ultimately lead to a decline in these species and ultimately amphibian diversity.

To determine the effects of logging on amphibian recruitment, and the suitability of logged habitats for amphibian's aquatic larvae, further research is required. However, given the relatively robust results of this thesis, and the apparent increase in amphibian diversity in RIL sites over a 21 year period, it is likely that any declines in amphibian recruitment/tadpole survivability are temporally limited, and do not impact these populations on a long-term scale. Regardless, there are several short-term negative impacts of RIL in particular, which should be discussed in relation to this practise's sustainability.

Improving RIL: possible damage mitigation measures

Although amphibian responses to RIL were generally low, there were several negative impacts of this practice on amphibians and their habitats over different time frames. Immediately after RIL (<1 year) logging roads/skid trails and reduced leaf litter depth negatively impacted stream and terrestrial species respectively (chapter 3), whilst increased siltation/lower Aboveground Carbon Density (ACD) was negatively associated with a handful of stream species 4-21 years after RIL (chapter 2). Here, I provide potential improvements to RIL management practices which could mitigate these negative effects. These are discussed within the context of our results, current RIL practices, infrastructure of the Deramakot forest reserve (the RIL managed timber reserve of this study) and the potential logistical issues/associated costs of further mitigation methods.

The establishment of logging roads, an often overlooked aspect of logging impacts, has resulted in increased stream siltation, influxes of disturbance tolerant species and greater thermal

fluctuations in other areas (Kreutzweiser et al. 2005, Konopik et al. 2014, Mollinari et al. 2019). Within chapter 3, I found negative associations between logging infrastructure and the occupancy of half of all stream species. As such the further reduction of skid trail and logging road construction within RIL reserves could minimize the negative impacts on stream amphibians. However, guidelines for the establishment of logging roads/skid trails in accordance with RIL principles already exist (avoiding high slope areas, the establishment of cross drains etc) and are typically limited by the topography of the logging reserve and density of harvestable timber (Pinard et al. 1995, Putz et al. 2008). Furthermore, the effects of different logging infrastructures may vary. Our findings (chapter 3) are in accordance with previous research which identified greater disturbance along maintained logging roads compared to skid trails (Malcolm and Ray 2000, Jackson et al. 2002). Within our RIL study site (Deramakot), only one consistently maintained logging road exists, bisecting the center of the reserve from west to east. Skid trails and unmaintained secondary roads are then periodically established adjacent to this road for the harvesting of timber. Following harvesting, these roads are typically blocked to prevent further erosion and access. Forest structure quickly recovers along these skid trails, as evidenced by our data and personal observations of renewed tree growth on skid trails within 1 year of logging. As such, to mitigate the negative impacts of logging infrastructure on amphibians, RIL practitioners should primarily rely on temporary skid trails/unmaintained access roads for access to harvesting blocks, which feed to a central maintained network road, as is the case within Deramakot forest reserve.

The direct RIL impacts on important amphibian forest habitats: leaf litter depth and Aboveground Carbon Density (ACD), while potentially possible to mitigate, would come so at considerable cost and would likely be of limited effect in preventing negative impacts on amphibians. Lower ACD was not only associated with lower occupancy for several stream amphibians (chapter 2), but has also been associated with poorer ecosystem functioning, net ecosystem productivity and lower biodiversity (Catovsky et al. 2002, Standish and Prober 2020). Unfortunately, aside from adhering to RIL felling practices such as liana cutting to reduce residual tree damage, directional felling and reduced skid trail construction, the reduction of ACD is unavoidable during RIL due to the direct extraction of timber. The application of RIL-C measures, which aim to further limit remnant forest structural damage and emissions, could potentially be applied, although the reductions in biomass removal with this method would likely be negligible compared to standard RIL practices (Ellis et al. 2019, Griscom et al. 2019). I did however, detect a swift increase in ACD with increasing time since RIL (10-21 years), suggesting that this covariate may recover to pre-harvesting levels over

relatively short time frames. Therefore, any attempts to further reduce ACD loss during RIL could come at considerable operational costs and likely be of limited benefit to amphibians and their habitats, due to the temporally constrained reduction in ACD following RIL.

Although the associations between ACD and amphibian occupancy were limited, roughly half of all terrestrial species were positively associated with greater leaf litter depths (chapter 3). Terrestrial leaf litter depth decreased immediately following RIL, suggesting a direct RIL impact on these amphibians. High leaf litter depths have been associated with greater microhabitats, increased humidity (Oliveira et al. 2013), and higher invertebrate density (Roeder et al. 2022), and are thus important habitats for terrestrial amphibians (Cortés-Gómez et al. 2013, Oliveira et al. 2013). Whilst reductions in leaf litter invertebrates have been recorded in forests subject to conventional logging (Burghouts et al. 1992), this habitat still supports juvenile amphibian survival following disturbance (Earl and Semlitsch 2015). As such, leaf litter appears to form a key habitat for terrestrial amphibians, as identified within chapter 3. Attempting to mitigate disturbance to leaf litter communities following RIL could be achieved through targeted restoration of particularly disturbed areas such as log landing sites and skid trails. Here, the use of applied nucleation (cluster planting of native tree saplings) could increase the rate of leaf litter recovery (Celentano et al. 2011), and has previously resulted in increased leaf litter arthropod abundance and diversity (Cole et al. 2016). However, the potential costs and logistical challenges of this intervention should be considered within the context of our findings. Although leaf litter depth reductions following RIL impacted several terrestrial species, these impacts were recorded within 1 year of logging. Older RIL sites (4-21 years post-logging) did not exhibit significant differences in leaf litter depth, suggesting that leaf litter depths quickly recover in the years following RIL. As such, maintenance of current RIL protocols, particularly those regarding skid trail construction, directional felling and pre/post harvest management, I believe are sufficient for limiting the negative impacts of RIL on amphibian's terrestrial leaf litter habitat.

The direct RIL impacts on stream siltation detected in chapter 2, provide the most feasible option for management interventions, however the logistical challenges of implementation must be considered. Increased stream siltation was recorded 4-5 years after (chapter 2), but not immediately following (<1 year) RIL (chapter 3). This is likely due to a delay in sediment build up as has been detected in other stream networks following disturbance (Kreutzweiser et al. 2005, Betts et al. 2021). Several obligate stream breeding amphibians exhibited negative associations with increased siltation (chapter 2), suggesting a negative association between

these amphibians and greater siltation rates in the years recently following RIL. Although RIL guidelines include the maintenance of unlogged, 30 m stream buffers, these are typically only applied to larger, perennial rivers (Pinard et al. 1995, Putz et al. 2008, Ellis et al. 2019, Griscom et al. 2019). In hilly dipterocarp forests (such as Deramakot) the undulating topography often results in a network of perennial and seasonal small stream networks. Due to logistical constraints within Deramakot (difficult topography and avoiding larger river networks), skid trails were occasionally built in close proximity to these streams (<2m in width). This, combined with spill-over damage typical of RIL (Jacob et al. 2021), resulted in some stream disturbance, with occasional fallen trees and sediment build up in streams directly adjacent to skid trail and felling areas. A potential mitigation measure, could be either increasing stream buffer width (50-60 m) around perennial rivers (to increase habitat quality) or the application of stream buffers around both perennial and small seasonal stream networks. Additionally, the application of RIL methods for climate mitigation (RIL-C), may provide potential stream and forest structural damage mitigation measures (Ellis et al. 2019, Griscom et al. 2019). This method, further reduces forest structural damage via increased long-line cable timber winching, and relocating harvesting sites from riparian areas to less-sensitive sites (Ellis et al. 2019, Griscom et al. 2019). Although adjustments to stream buffer widths/density could be complicated by logistical constraints (increased skid trail length due to small stream avoidance and a reduction in potentially harvestable timber), the implementation of RIL-C methods should be encouraged. However, as the negative impacts of RIL on stream siltation have only been observed in a handful of stream species, it possible such mitigation measures would have little impact on stream amphibian communities. Furthermore, stream siltation and stream amphibian diversity exhibited a swift recovery in the years following RIL (10-21 years). As such, while negative impacts of RIL on stream siltation and amphibians do occur, these effects appear to be temporally constrained (within the first 5 years of RIL), and offset by the swift recovery of streams/amphibian communities. Therefore, while the above mitigation measures could be applied, I do not believe these would provide considerable benefit to stream amphibians following RIL, due to the limited associations with this covariate, the swift recovery of streams/amphibians following RIL, and the logistical difficulties in implementing such practices.

In conclusion, considering the temporary impacts of RIL (within 5 years) and current sustainable management practices, I believe that any further damage mitigation measures would have limited utility. While some minimization in amphibian and habitat disturbance could be achieved, this would likely come at considerable logistical cost. Increases in RIL operational

costs may undermine the economic practicality of this method and dis-incentivize practitioners who may then resort to more profitable, less-sustainable harvesting methods. Furthermore, it appears that the forestry practices of RIL are sufficient for facilitating a recovery of amphibians and their habitats over a 21 year period. While conversion to RIL-C methods could reduce forest structural damage (Ellis et al. 2019, Griscom et al. 2019), determining whether this would reduce short-term habitat disturbance and subsequently amphibian occupancy/diversity declines immediately following RIL requires further investigation. As such, an adherence to all RIL management guidelines (namely limitations on road/skid trail construction and 30m stream buffers), appears to be sufficient for ensuring amphibian conservation within RIL reserves.

Multi-species occupancy modelling: Utility and application

While much research exists on amphibian responses to human-disturbance, the application of occupancy models which account for amphibian detectability within tropical human-modified landscapes is relatively novel. The application of single species (chapter 1) and multi-species (chapters 2 and 3) occupancy models within this research not only determined species responses to logging whilst accounting for detectability, but also provided invaluable insights into amphibian breeding phenology and activity.

Within chapter 1, I found significant positive and negative associations between species detection probability and humidity, temperature, rainfall, moon phase and time since sunset. Increases and decreases in amphibian activity with these covariates is assumed to be driven by amphibian's restricted physiological requirements, predator avoidance, foraging activity and breeding/calling behaviour (MacKenzie et al. 2002, Allentoft and O'Brien 2010, Grant et al. 2013, Ribeiro Jr et al. 2018). Amphibian breeding behaviour, is by far the most conspicuous of these activities, often involving calling, movement to breeding sites, mate competition, nest building/guarding, amplexus and egg deposition (Wells 2010). Given their conspicuous breeding behaviour, many amphibian occupancy studies rely on amphibian calling behaviour to confirm species presence (Carter et al. 2021, Estes-Zumpf et al. 2022). Additionally, all species recorded during chapter 1 exhibited breeding behaviours during the course of the study including: calling, amplexus, egg deposition and nest guarding. As such, the covariates identified within this study, likely either confer more suitable conditions for amphibian breeding i.e. decreased rainfall for greater amphibian acoustic potential (Lengagne and Slater 2002), or provide phenological cues for breeding events (While and Uller 2014, Ficetola and Maiorano 2016, Canavero et al. 2019, Chmura et al. 2019). Furthermore, variation in associations with these climatological (humidity, temperature and rainfall) and temporal factors

(moon phase and time since sunset) potentially provides temporal separation in breeding and activity between species in the stream communities of our study. The habitat associations outlined in chapter 1 (stream slope and stream volume), supports previous research suggesting that these stream species are roughly divided into small sloped and large flat stream communities (Inger 1966, Inger et al. 1986, Goutte et al. 2017, Ahmad and Grafe 2020). This subsequently results in some degree of overlap in habitat associations and spatial co-occurrence. Similar species occupying the same habitat are likely to compete for resources (Tilman 2020). However, whilst the stream species of this study vary morphologically (adults and tadpoles) and by tadpole micro-habitat use, they all occupy the same acoustic landscape (Inger 1966, Konopik et al. 2015, Goutte et al. 2017, Ahmad and Grafe 2020). The acoustic niche hypothesis suggests that partitioning in calling behaviour must occur, either spatially, temporally or with call dynamics, for species to occupy the same habitat (Krause 1993). The detectability associations identified within the chapter 1 analysis support this theory, as these species exhibit variable positive and negative detectability associations with climatological and temporal covariates. This suggests that a high degree of separation in optimal activity and breeding conditions exists for these stream species, permitting diverse, co-occurring amphibian communities. As such I believe that occupancy modelling should become the norm for amphibian sampling, as not only are detectability associations outlined here invaluable for elucidating the activity and breeding behaviour of amphibians, but they also provide invaluable information for further amphibian studies which seek to account for imperfect detection.

The detection of a species is rarely perfect, and is often associated with a multitude of factors as outlined above. Imperfect detection, i.e a species reported as absent when it is in fact present, may lead to serious bias when modelling habitat associations or responses to disturbance (MacKenzie et al. 2002, Mackenzie and Royle 2005). Increases in positive and negative bias in habitat associations have been reported within models which failed to account for underestimated non-detection (Gu and Swihart 2004). Therefore, determining amphibian (or any) species responses to disturbance, should incorporate detectability estimations as presented here, to prevent erroneous conclusions, particularly when delineating the absence of a species due to disturbance or simple non-detection (Olea and Mateo-Tomás 2011).

An additional benefit of the occupancy modelling framework utilized in chapters 2 and 3, was the application of species occupancy probabilities for the calculation of diversity profiles. The measurement of a site's community diversity, is often used by researchers and conservationists, when aiming to determine the perceived "conservation value" of a site (Morris et al. 2014).

Diversity indices (such as species richness, Shannon and Simpson diversity) are thus often applied to studies attempting to delineate species responses to disturbance (Patil and Taillie 1982, Morris et al. 2014). The majority of previously cited research describing amphibian responses to logging, are reliant upon these metrics. However, not only can different diversity indices produce different values (Patil and Taillie 1982), all are undermined by a reliance on relative abundance obtained from raw count data. Raw count data often fails to account for species detectability, and thus inferences derived from diversity indices obtained from this data may be considerably biased (MacKenzie and Kendall 2002, Sollmann et al. 2013). The utilization of occupancy probabilities within diversity indices as outlined in this study, helps to circumvent this issue via using a probability of species occurrence accounting for variable species detectability. Additionally, the diversity profiles presented here (chapters 2 and 3) include multiple diversity indices (species richness, Shannon and Simpson diversity) whilst accounting for the contribution of rare species (evenness) (Abrams et al. 2021). As such I believe our conclusions regarding amphibian species/community responses to logging provide a greater resolution for determining species responses to disturbance than methods which do not account for detectability, or which do not involve the results of multiple diversity metrics.

Conclusions

Our findings suggest that not only are amphibian habitat associations within an RIL managed timber concession (Deramakot forest reserve) most similar to unlogged sites, but that amphibian occupancy, diversity and evenness are considerably higher in RIL sites compared to Conventionally selectively Logged (CL) areas. Although I found some evidence of negative associations between species occupancy and the direct and indirect impacts of RIL (responses to logging roads and reduced leaf litter depth in stream and terrestrial species respectively), I found that amphibian community occupancy, diversity and evenness, appears to generally increase across habitats immediately after RIL (within 1 year). Furthermore, while stream amphibian diversity, evenness and habitat quality decrease after this period (between 1-5 years after RIL), these metrics all swiftly recover over 21 years (far quicker than CL sites). The combination of these results, suggests that RIL has a limited negative impacts on amphibians and their habitats, especially when compared to conventional logging methods. Negative impacts of this practice, appear to be both short-lived (within 5 years of RIL) and locally restricted (directly adjacent to logging activities), as evidenced by our findings. As such, I recommend that reduced impact logging protocols should become the standard practice within

tropical timber concessions worldwide, for ensuring sustainable forest management and amphibian conservation.

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