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# **Understanding the impacts of tropical selective logging on ecological mechanisms**

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# Abstract

Selectively logged tropical forests have been recommended for forest protection and restoration initiatives as these forests maintain a substantial amount of biodiversity and ecosystem functions compared to other tropical land-uses. Most work on selective logging impacts on biodiversity examines species richness, abundance and community composition, yet these metrics can conceal underlying impacts. It is important that we examine the impacts of logging on processes that underpin biodiversity changes, including species' vital rates (i.e. survival, reproductive success and movement) and community function (i.e. mass-abundance scaling). In Chapter 2, I conducted a literature review to examine the state of our current knowledge on how tropical land-use change impacts species' vital rates. I found that empirical research on species' vital rates across taxa and regions were greatly lacking and had considerable variation, with some taxa and land-use biases. In Chapter 3, I focused explicitly on tropical selective logging and investigated its impacts on the mass-abundance scaling of avian communities, an underlying response describing the flow of energy through communities, by conducting a meta-analysis to examine pantropical trends. Only the omnivore guild from mist-netting studies and the frugivore guild from point-count studies had mass-abundance relationships affected by selective logging. I then used field data from a capture-mark-recapture mist-netting study of Bornean understory birds to assess species' vital rate responses (i.e. local movements and survival) to selective logging at the community- and species-level. In Chapter 4, I developed hierarchical Bayesian models, adapting developments from joint-species modelling, to assess local avian movement and found a higher probability of moving shorter distances (below 200 m) in logged forests and higher movement probability at longer distances (above 200 m) in unlogged forests across 71 species. Finally, in Chapter 5, I developed a multi-species hierarchical Cormack-Jolly-Seber model in a Bayesian framework to determine avian survival rates, revealing similar apparent survival probabilities across 71 species in both unlogged and logged forests. Together, these results suggest limited impacts on avian species and communities. This highlights the potential high ecological value of selectively logged forests, lending further support for the protection of these forests for biodiversity conservation. Integrating post-logging management interventions with various restoration funds, long-term commercial investments, and effective governance will drive transformative change for the long-term environmentally sustainable management of logging concessions.

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# Chapter 1

## General Introduction



Sunrise over Danum Valley.

## 1.1 Biodiversity crisis

The global biodiversity crisis is one of the most pressing concerns in the Anthropocene (Zalasiewicz *et al.* 2011). We are entering into the sixth mass extinction with around 25% of species worldwide already facing extirpation (Barnosky *et al.* 2011; Díaz *et al.* 2020). These extinction rates are hundreds or thousands of times faster than background extinction rates (Barnosky *et al.* 2011; Ceballos *et al.* 2020), leading to the collapse of ecosystems globally. Ecosystems on which we highly depend for our food security, clean water, climate regulation, pharmaceuticals, pest and disease control, and other essential services for our survival and quality of life (Balmford *et al.* 2002; Mace *et al.* 2012; Chaplin-Kramer *et al.* 2019).

Humanity has become a geophysical force, altering planet Earth faster and more dramatically than any other species, on par with Earth's own geological forces in the 4.5 billion years of its existence (Zalasiewicz *et al.* 2011). We determine the fates of ecosystems, species and even the Earth's climate. The accelerated growth in human population, which has now reached 7.8 billion people, is requiring increasingly more resources to sustain it. We are also consuming resources unsustainably, expanding the extent of land-use change to keep up with our needs at the expense of ecosystems and biodiversity (Sala *et al.* 2000; Ehrlich & Ehrlich 2013). This increase in land-use change is the key driver of biodiversity loss, destroying and degrading ecological habitats, while producing emissions that lead to climate change (Sala *et al.* 2000). Interactions between land-use change and climate change further exacerbate the detrimental impacts on biodiversity (Mantyka-Pringle *et al.* 2012; Sirami *et al.* 2017).

There is currently not enough habitat to sustain all biodiversity due to the rising magnitude of disturbed habitats and declines in the amounts of undisturbed habitats (Díaz *et al.* 2020). Therefore, there is an urgent need to reconcile land-use change and biodiversity conservation. Funding for conservation and habitat protection is a crucial part of restoring

this balance, yet these funds are limited (McCarthy *et al.* 2012; Waldron *et al.* 2013). A vital question is thus where do we prioritize nature conservation and habitat protection initiatives?

## **1.2 Deforestation and forest degradation in the tropics**

The tropics is the most biodiverse place on Earth, sustaining more than 75% of the world's species and containing a high proportion of rare and endemic species (Barlow *et al.* 2018). Besides most of Earth's biodiversity, the tropics are also incredibly socially diverse; home to almost half of the global human population, including most of the world's impoverished people, and where over 80% of languages globally are spoken (Barlow *et al.* 2018; State of the Tropics 2020). Tropical forests provide vital ecosystem services both locally and at the global scale. They are responsible for producing over 30% of global net primary productivity, storing one-quarter of global carbon in the terrestrial biosphere and driving atmospheric circulation (Bonan 2008; Barlow *et al.* 2018; State of the Tropics 2020). Additionally, the tropics are experiencing high levels of anthropogenic disturbances, threatening many of its unique and diverse species (Sala *et al.* 2000; State of the Tropics 2020).

Deforestation and forest degradation in the tropics have significantly contributed to the destruction of ecosystems, biodiversity losses and the release of greenhouse gas emissions globally (Gibson *et al.* 2011; Armenteras *et al.* 2017; Baccini *et al.* 2017). Deforestation refers to the wholesale removal of a forest, which is usually then converted into a farmed land use, while forest degradation is the diminished ecological value of a forest caused by anthropogenic disturbances. Forest degradation is significantly more widespread than deforestation in the tropics, for example, 1.4% of the tropics were deforested and at least 20 times more degraded between the years 2000 to 2005 (Hansen *et al.* 2008; Asner *et al.* 2009). Nevertheless, degraded forests retain significantly more biodiversity compared to land-use

change by deforestation, including species of conservation concern, making degraded forests important for biodiversity conservation (Gibson *et al.* 2011; Edwards & Laurance 2013).

Across the tropics, forest degradation is primarily driven by selective logging activities (Kissinger *et al.* 2012; Edwards *et al.* 2014b), which, in turn, is a catalyst for deforestation (Shearman *et al.* 2012). Selective logging is the targeted removal of specific timber tree species above a certain minimum trunk diameter (Edwards *et al.* 2014b). It is a disturbance which is more diffused. Selectively logged forests lie on a continuum between deforestation and old-growth forests, commonly characterised by having overall canopy cover with gaps in the canopy from treefall or logging roads (Ghazoul *et al.* 2015). These forests vary in the amount of degradation depending on the logging intensity, which is determined by either the extent of reduced-impact logging techniques used or the volume of wood extracted (Pinard & Putz 1996; Burivalova *et al.* 2014).

Selective logging alters the forest structure by fragmenting the canopy, reducing canopy height and density (Okuda *et al.* 2003). The action of felling and removing trees creates canopy gaps and subjects neighbouring vegetation to damages, as removing small pieces of bark from the trees exposes the xylem to infection by pathogens (Putz *et al.* 2008). Furthermore, soil damage and the persistent growth of early successional vines and non-tree plant species, that require lots of light, impedes forest regeneration for decades (Putz *et al.* 2008; Hawthorne *et al.* 2012; Osazuwa-Peters *et al.* 2015). Its economic importance to many tropical countries in the global south (Putz *et al.* 2012) has imposed selective logging activities on over 400 million hectares of tropical forests worldwide (Asner *et al.* 2009). Selective logging activities are expected to increase as timber demands, predominantly for fuelwood, are predicted to double by 2030 and increase six-fold by 2060 (FAO 2009; Raunika *et al.* 2010).

## 1.2.1 Ecological value of selectively logged forests

Despite alterations in forest structure, selectively logged forests harbour a substantial amount of biodiversity compared to other tropical land-uses (Gibson *et al.* 2011; Putz *et al.* 2012). Putz *et al.* (2012) conducted a meta-analysis, containing more than 100 studies, finding that 85% to 100% of bird, mammal, plant and invertebrate species richness was retained in logged forests after one logging rotation. Even after two logging rotations, over 75% of Bornean dung beetle and bird species were maintained (Edwards *et al.* 2011). This retention in species depends on the intensity of logging, where species richness of trees, amphibians, mammals and invertebrates decline with increased logging intensity (Burivalova *et al.* 2014; Martin *et al.* 2015). Increased logging intensity also changes the community composition of plants, mammals, birds and invertebrates in selectively logged forest (Edwards *et al.* 2011; Schleuning *et al.* 2011; Burivalova *et al.* 2014; Osazuwa-Peters *et al.* 2015).

Selectively logged forests also maintain much functional diversity and ecosystem services (Edwards *et al.* 2014b; Costantini *et al.* 2016). Functional diversity is linked to ecosystem function (Loreau *et al.* 2001) as the presence of species with certain functional traits determine the processes that occur in the ecosystem. Selective logging impacts functional diversity variably and this is dependent on the sensitivity of the taxa to habitat degradation. Tree, bird and dung beetle communities have similar functional diversity in logged forests compared to old-growth unlogged forests (Baraloto *et al.* 2012; Carreno-Rocabado *et al.* 2012; Edwards *et al.* 2014b; Osazuwa-Peters *et al.* 2015), while some amphibian communities had the opposite pattern (Ernst *et al.* 2006). This preservation in substantial biodiversity allows selectively logged forests to retain many ecosystem services, such as providing watershed services, carbon storage, temperature regulation and maintaining habitat connectivity between intact forests to sustain meta-community processes (Putz *et al.* 2012;

Edwards *et al.* 2014b); highlighting the high ecological value of selectively logged forests, at least in the short-term.

## **1.2.2 Global programs and policies for degraded forest protection and restoration**

With degraded forests increasingly dominating the tropical forest landscape, a global restoration agenda is emerging. Motivated by international initiatives and potentially lucrative carbon markets, this agenda has led to a policy focus on the restoration and protection of degraded tropical forests for biodiversity and ecosystem recovery (Blaser *et al.* 2011; Ciccarese *et al.* 2012). Increasing attention is being placed on the restoration and protection of degraded forests due to multiple factors such as, the rising demands in biofuels and forest goods and the capacity to improve food security, increase carbon storage, and create socio-economic benefits (Ciccarese *et al.* 2012; Stanturf *et al.* 2014; Adams *et al.* 2016; Stanturf *et al.* 2019). International initiatives such as the Bonn Challenge, launched in 2011 by the Government of Germany and the IUCN, aims to commit restoration of 350 million hectares of degraded and deforested landscapes worldwide by 2030, reaching Sustainable Development Goals by improving food and water security whilst contributing to mitigating global climate change, biodiversity loss and land degradation (Bonn Challenge 2020). The forest and landscape restoration (FLR) approach underlies the Bonn Challenge where both biodiversity conservation and people's livelihoods are given the same importance (Stanturf *et al.* 2014). Recent estimates suggest that the Bonn Challenge's restoration target would produce between U.S.\$0.7 and 9 trillion in net benefit (Verdone & Seidl 2017). Currently, 210 million hectares globally have been pledged for forest landscape restoration activities, already surpassing the 2020 goal of 150 million hectares (Bonn Challenge 2020). Other initiatives such as payment for ecosystem services (PES) provide financial incentives

for the restoration of degraded forests for ecosystem services (Ferraro & Simpson 2002). Programs like the United Nations Reducing Emissions from Deforestation and Forest Degradation (REDD+) program facilitate PES mechanisms, which fosters the sustainable management of forests and places value in forest carbon stocks (Pagiola & Bosquet 2009).

In the context of selectively logged forests, restoration can be both passive and active. Passive restoration is the natural regeneration after logging has ceased, while active restoration requires interventions to accelerate regeneration, for example, planting trees. The types of active restoration which are frequently applied individually or together are (1) enrichment planting of trees and (2) liberation cutting of competing early successional trees, vines, herbaceous plants and bamboos (Kobayashi 2007). The type of restoration intervention depends on the post-logging management goal (Cerullo & Edwards 2019). Ecosystem restoration aims to recover biodiversity, ecosystem services and the complexity of forest structure towards old-growth forest levels; timber enhancement focuses on maintaining sustainable timber yields by recovering timber stocks; carbon enhancement targets the recovery of carbon stocks to improve carbon sequestration; and ecosystem service enhancement aims to recover ecosystem services that are important for people's livelihoods (Cerullo & Edwards 2019). An example of the types of restoration activities for ecosystem restoration are protecting forests from conversion, restoring key habitat features damaged during logging, performing liberation cutting of competing vegetation and enrichment planting of native trees which are important to wildlife.

Restoring logged forests has been shown to have multiple benefits for carbon sequestration, biodiversity, ecosystem services and timber harvests (Kobayashi 2007; Gourlet-Fleury *et al.* 2013; Philipson *et al.* 2020). Restoration techniques like liberation cutting of vines and pioneer tree removal by thinning has been shown to significantly increase carbon sequestration by accelerating the growth of large trees, which store a lot of

carbon (Villegas *et al.* 2009; Philipson *et al.* 2020). However, if the main restoration goals are for carbon or timber recovery, restoration may have some adverse impacts on biodiversity. Planting a few species of fast-growing timber trees result in an even-aged stand with little diversity, leading to lower resilience to climate change effects and high ecological damage from bulk timber extraction (Putz & Romero 2015; O'Brien *et al.* 2017). Furthermore, removing too many vines and understory plants by liberation cutting could negatively impact species that rely on these vines and plants for food and nesting material (Edwards *et al.* 2009; Cosset & Edwards 2017). It is thus important to consider the trade-offs associated with each restoration intervention.

### **1.2.3 Protecting selectively logged forests**

Selectively logged forests have been proposed as a good candidate for forest protection and restoration efforts in the tropics (Meijaard & Sheil 2007; Edwards *et al.* 2014b). This potential solution could help tropical countries achieve the Sustainable Development Goals for multiple biodiversity and human benefits. Reasons for selectively logged forests being the ideal candidate include: (1) the potential to sustain substantial biodiversity in the short-term, depending on the logging regime and intensity (Edwards *et al.* 2011; Burivalova *et al.* 2014); (2) it is cheaper to protect selectively logged forests than old-growth pristine forests, due to its reduced opportunity costs from absent timber revenues (Fisher *et al.* 2011b); and (3) protected logged forests can expand and connect existing protected areas as they can encourage dispersal between areas of intact forests (Gillies & Clair 2008; Edwards *et al.* 2014b). However, for this to be an effective conservation strategy, there needs to be a comprehensive understanding of its effectiveness for biodiversity conservation in the long-term.

### 1.3 Underlying biodiversity responses

Despite the vast amount of research conducted on the effects of selective logging on biodiversity, there is still a lot we do not know about selective logging impacts. Most existing work examines short-term species richness, abundance and community composition (Gibson *et al.* 2011; Putz *et al.* 2012; Burivalova *et al.* 2014), which can conceal underlying impacts. Furthermore, presence-absence and abundance, especially for long-lived species, can be slow to respond to habitat changes and are difficult to detect initially. It is thus crucial that we fully understand logging impacts before proceeding with protecting logged forests for biodiversity conservation. Underlying impacts can be masked in situations where dominant individuals occupy higher quality habitats and force others in higher abundances into habitats of poorer quality (Holt 1985); when degraded habitats become ‘ecological traps’ where habitat attractiveness does not decline with habitat quality (Bock & Jones 2004; Gilroy & Sutherland 2007); or where immigration from surrounding habitats helps sustain populations in degraded habitats (Prugh *et al.* 2008; Gilroy & Edwards 2017).

To have a better understanding of the long-term effects of selective logging on biodiversity, it is important that we examine the impacts of logging on underlying vital rate responses (i.e. survival, reproductive success and movement) and community function (i.e. mass-abundance scaling). Vital rates can better inform us about population density, stability and viability (Saether & Bakke 2000; Haridas *et al.* 2013), while underlying community function such as the mass-abundance scaling of communities can inform us about energy flow in the system as well as ecosystem functioning (White *et al.* 2007). However, to date, there is very limited research tackling species’ vital rate and underlying community function responses within selectively logged forest. In terms of underlying community function, the impacts of selective logging on the mass-abundance scaling of ecological communities is contentious. The mass-abundance scaling is the negative relationship between a species' body

mass and population abundance, where changes in this relationship from anthropogenic pressures may have implications on ecosystem processes and function (Damuth 1981). In the Himalayas, Srinivasan (2013) found that the mass-abundance relationship of subtropical montane understory insectivorous bird communities became more negative as logging intensity increased, while in Sri Lanka, Sreekar *et al.* (2015) found no changes in avian mass-abundance scaling in degraded forests.

For vital rates, studies on species movement responses to selective logging have mainly focused on a single species of mammal (Colón *et al.* 2002; Wong *et al.* 2004; Wells *et al.* 2008; but see Wells *et al.* 2006) or bird (Dale & Slembe 2005), with almost no community wide studies of selective logging impacts on species movements. There was some effect of selective logging on all mammal studies, especially on species' movement strategies. However, the understory passerine red-tailed bristlebill (*Bleda syndactyla*) in Uganda had higher movement rates and larger home-ranges in unlogged forests as their preferred dense understory habitat was scattered, compared to in selectively logged forests. Furthermore, assessments of selective logging impacts on species survival are severely lacking in lowland tropical forests. Survival rates have generally been shown to be a better indicator of fitness compared to reproductive rates (Crone 2001; but see Manlik *et al.* 2016). The only studies are in tropical montane forests where Hawaiian Elepaio flycatcher bird populations (*Chasiempis sandwichensis*) survival rates were not affected by selective logging (VanderWerf 2004) and the survival rates of understory birds in the eastern Himalayas were trait dependent in selectively logged forests (Srinivasan 2019).

Therefore, my thesis aims to fill these research needs of (1) determining the global trend of the mass-abundance scaling after selective logging, (2) understanding the community-wide selective logging impacts on species' movement, and (3) assessing how selective logging impacts species survival rates in lowland tropical forests.

## 1.4 Thesis overview

The over-arching aim of this thesis was to determine the long-term ecological value of selectively logged tropical forests, by assessing how selective logging affects underlying community and vital rate responses such as (1) the mass-abundance scaling of avian communities, (2) the local movements of avian species, and (3) the survival rates of avian species. I focus my research on birds and use them as a proxy for biodiversity. This is because birds are well known taxonomically and phylogenetically (Jetz *et al.* 2012), they are good indicators of overall biodiversity trends and forest health (Edwards *et al.* 2014a), and are important for many ecosystem functions (Sekercioglu 2006). First, I conducted a literature review to examine the state of our current knowledge on how tropical land-use change impacts species' vital rates across the tropics. I then focus explicitly on tropical selective logging, which I found was one of the land-uses that severely lacked information about the underlying responses of biodiversity. I collated avian mass and abundance data from the literature to compare an underlying community level response, the mass-abundance relationship, in selectively logged and unlogged old-growth forests across the tropics globally. Next, I used field data from a capture-mark-recapture mist-netting methodology of understory birds from Borneo to assess underlying species' vital rate responses to selective logging at the community and species level. In combination with this field data, I developed hierarchical Bayesian models, adapting recent developments in joint species occupancy modelling, to compare local movement patterns in selectively logged and unlogged old-growth forests. Finally, using the aforementioned field data, I developed a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework, adapting recent works, to compare habitat-specific survival at the community and species levels in selectively logged and unlogged old-growth forests. All results are synthesized in the General Discussion to illustrate the overall ecological value of selectively logged forests, provide post-logging

management and policy recommendations for integrating sustainable management of timber concessions with biodiversity conservation, and directions for future research. The objectives of the main chapters are as follows:

## **Chapter 2: Impacts of tropical forest disturbance on species' vital rates**

The majority of our knowledge on the impacts of anthropogenic disturbances on tropical species comes from studies examining patterns of species richness and abundance. Anthropogenic disturbances impact species' vital rates (i.e. survival, reproduction, and movement) by increasing species vulnerability to extirpation, but in many cases these impacts may not be manifested in short-term abundance or species richness changes. The objectives of this chapter were to assess the state of our current knowledge on the impacts of anthropogenic disturbance on tropical forest vertebrate species' vital rates such as (1) survival, (2) reproductive success and (3) movement.

## **Chapter 3: Mass–abundance scaling in avian communities is maintained after tropical selective logging**

Selective logging is the dominant anthropogenic disturbance across the tropics. Most studies examining selective logging impacts on biodiversity consider conventional metrics, like species richness, but these can conceal hidden biodiversity impacts. The mass–abundance relationship is a fundamental feature of ecological communities, describing the negative relationship between body mass and population abundance, where, in a system without anthropogenic influence, larger species are less abundant due to higher energy requirements. Changes in this relationship can indicate community structure and function changes. The objective was to investigate the impacts of selective logging on the mass–

abundance scaling of avian communities by conducting a meta-analysis to examine its pantropical trend.

## **Chapter 4: Selective logging drives local movement in tropical understory avian communities**

Despite the structural damage incurred by selective logging, these forests can still retain a substantial amount of biodiversity. However, our understanding of how selective logging impacts the mechanistic processes underpinning biodiversity change is scant. Movement is a vital mechanistic process, determining an organism's survival, growth, and breeding, and underpinning demographic changes and many integral ecological and evolutionary mechanisms. Movement varies depending on food resource and availability, the degree of species' dietary flexibility, and thus a species' trophic position, which is often higher in logged versus old-growth forest. Using a capture-mark-recapture methodology and a hierarchical Bayesian analytical framework to model maximum observed local movement distances, this chapter's objectives were to (1) assess how tropical selective logging impacts the local movements of understory avian species at the community and species level in Sabah, Malaysian Borneo, (2) determine whether species traits or conservation status are important determinants of local movement patterns, (3) determine if differences in movement patterns are related to species' sensitivity to selective logging, and (4) determine whether local movement patterns relate to changes in avian species' trophic positions.

## **Chapter 5: Apparent survival of tropical understory birds after selective logging**

In the short term, selective logging maintains species richness, underpinned by changes in species' abundance from more to less common. A key issue is that species retention does

not guarantee long-term population viability. Assessments of species survival rates, which determine population size and long-term population viability, are severely lacking in selectively logged forest. Using a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework to estimate habitat-specific survival at the community and species levels, the objectives of this chapter were to (1) assess the survival rates of tropical understory birds in lowland selective logged and unlogged old-growth forests of Sabah, Malaysian Borneo, a global biodiversity hotspot, and (2) determine how the 2015-16 El Niño event affected species survival in these logged and unlogged forests.

## Chapter 2

# Impacts of tropical forest disturbance on species' vital rates



Selectively logged forests in the morning mist at Yayasan Sabah logging concession.

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## 2.1 Abstract

Tropical forests are experiencing enormous threats from deforestation and habitat degradation. Much knowledge of the impacts of these land-use changes on tropical species comes from studies examining patterns of richness and abundance. Demographic vital rates (survival, reproduction, and movement) can also be affected by land-use change in a way that increases species vulnerability to extirpation, but in many cases these impacts may not be manifested in short-term changes in abundance or species richness. We conducted a literature review to assess current knowledge and research effort concerning how land-use change affects species vital rates in tropical forest vertebrates. We found a general paucity of empirical research on demography across taxa and regions, with some biases toward mammals and birds and land-use transitions, including fragmentation and agriculture. There is also considerable between-species variation in demographic responses to land-use change, which could reflect trait-based differences in species sensitivity, complex context dependencies (e.g., between-region variation), or inconsistency in methods used in studies. Efforts to improve understanding of anthropogenic impacts on species demography are underway, but there is a need for increased research effort to fill knowledge gaps in understudied tropical regions and taxa. The lack of information on demographic impacts of anthropogenic disturbance makes it difficult to draw definite conclusions about the magnitude of threats to tropical ecosystems under anthropogenic pressures. Thus, determining conservation priorities and improving conservation effectiveness remains a challenge.

## 2.2 Tropical deforestation and degradation

Despite a wealth of research identifying tropical deforestation and degradation as primary drivers of global biodiversity loss (Gibson *et al.* 2011; Barlow *et al.* 2016), most empirical work examines patterns of species richness and abundance across spatial or temporal gradients of anthropogenic impact (Gibson *et al.* 2011; Burivalova *et al.* 2014). Such patterns can mask underlying impacts on species that persist following land-use change. For example, forest degradation following selective logging may not affect a species' abundance in the short-term, but long-term population viability could be reduced via declines in survival or reproductive success (Srinivasan *et al.* 2015). Core drivers of overlooked impacts include when populations in degraded habitats are buffered by immigration from surrounding areas (Gilroy & Edwards 2017), when high-quality habitats are occupied by dominant individuals that force others to occur in higher abundance in marginal habitats (Holt 1985), or when degradation causes declines in habitat quality without influencing the relative attractiveness of the habitat ("ecological traps" [Gilroy & Sutherland 2007]).

To generate a robust understanding of the true long-term impacts of anthropogenic-induced land-use change on ecological communities requires understanding how underlying demographic vital rates, such as survival, reproductive success, and movement (dispersal) change. Dispersal rate, for instance, can determine the ability of populations to persist in degraded and fragmented habitats (Fahrig 2007) and to traverse inhospitable barriers (Lees & Peres 2009). Vital rates can thus better indicate the state of a population because both population stability and viability are driven by demography (Saether & Bakke 2000; Haridas *et al.* 2013).

We examined the state of current understanding of the impacts of tropical land-use change on species' vital rates to identify knowledge gaps and assess general trends in responses. Such understanding can give us a better picture of the long-term resilience of species

in degraded habitats. We assessed demographic vital rates of terrestrial vertebrates (birds, mammals, reptiles, and amphibians) in the tropics, exploring patterns of research effort across regions and taxonomic groups for four key land-use changes: forest conversion to agriculture, forest fragmentation, selective logging, and fire.

## 2.3 Literature review

We reviewed studies that assessed the impacts of anthropogenic disturbance on survival, reproductive success, and movement in tropical forest vertebrate species (birds, mammals, reptiles, and amphibians). For survival, we included only studies that calculated empirical estimates of survival rates from observed data (e.g., mark-recapture, telemetry studies). For simplicity, we defined measures of reproductive success as any assessment of fecundity, breeding success, or recruitment rate (including population growth rate). We defined movement studies as those considering dispersal rates (i.e., movements resulting in successful or unsuccessful gene flow) or temporary movement (e.g., foraging movements) because foraging is important for survival.

Using the online Web of Science database, we searched for studies with the keywords [degradation or deforestation or “habitat change” or “land use” or “habitat conversion”] and [survival or dispersal or movement or “population growth” or “birth rate” or “death rate” or fecundity or “breeding success” or “clutch size” or “reproductive success” or “brood size” or productivity or lambda or demography]. The search was refined by [tropic\*] and either [logging], [agriculture], [fragmentation], or [fire]. This search was conducted from 6 October 2016 to 20 November 2016. We found 3076 studies with this keyword search. Of these, we selected studies for inclusion only if they were conducted in the tropical region (between 23.43706°N and 23.43706°S); conducted in closed-canopy tropical forests, excluding studies in open, grassland-dominated systems such as Cerrado; studied only terrestrial tropical

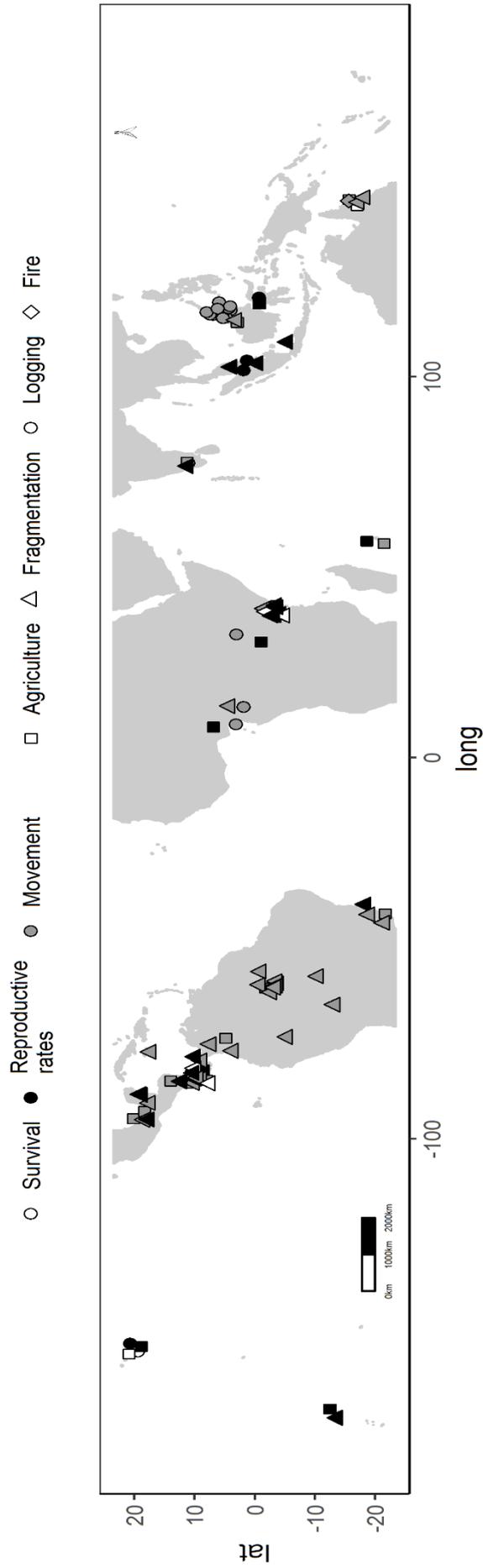


Figure 2.1. Distribution of studies of vital rates across regions by land-use type (agriculture, fragmentation, selective logging, and fire) and vital rate category (survival, white; reproductive rate, black; movement, grey).

vertebrates; and assessed the impacts of anthropogenic disturbances based on any measure of survival, demography, and movement in the analyses. The COMADRE database (Salguero-Gomez *et al.* 2016) was used to supplement the search. 62 studies out of 3076 studies from the Web of Science database search were based in the tropics, while the COMADRE database produced an additional 9 studies based in the tropics. In the combined 71 studies found on the tropics, 64 studies met our criteria (Figure 2.1; see Appendix A.1 for full list of studies). The remaining 7 were conducted in open, grassland dominated systems. These 64 studies were separated into the different vital rates (survival, reproductive success, movement) and then classified by land-use disturbance (selective logging, agriculture, fragmentation, fire), tropical region (Neotropics, Afrotropics, Indomalayan tropics, Australasian tropics or Oceania), and study area elevation (lowland, submontane, montane). Studies that reported results for multiple rates, regions, or land-use classes were counted for each class separately.

## **2.4 Impacts of anthropogenic disturbances on vital rates**

Seven studies across the tropics reported impacts of anthropogenic disturbances on forest vertebrates based on measures of survival, 22 based on reproductive success, and 40 based on movement (Table 2.1 & Figure 2.1). Overall, these totals highlight a paucity of information on how anthropogenic changes affect the vital rates of vertebrate biodiversity across the tropics. Studies were largely restricted to birds and mammals; only 3% concerned amphibians and none on reptiles (Figure 2.1d). For all 3 vital rate classes, deforestation for agriculture and forest fragmentation were the predominant anthropogenic impacts addressed by research. Far fewer studies considered selective logging or fire (Figure 2.2).

Table 2.1. Number of studies that showed positive, negative, and varying effects of land-use change on species by land use, region, and taxa.

	Survival	Reproductive success	Movement	Response
<b>Land use</b>				
	1	3	7	positive
Agriculture	1	4	7	negative
	1	1	5	varies
<hr/>				
	1	6	8	positive
Fragmentation	2	7	9	negative
	1	2	11	varies
<hr/>				
	1	2	3	positive
Logging	0	2	3	negative
	0	0	1	varies
<hr/>				
	0	0	0	positive
Fire	0	0	1	negative
	0	0	0	varies
<hr/>				
<b>Region</b>				
	0	2	9	positive
Neotropics	1	3	7	negative
	2	2	9	varies
<hr/>				
	1	4	2	positive
Afrotropics	1	4	3	negative
	0	0	1	varies
<hr/>				
	0	2	3	positive
Indomalayan tropics	0	2	2	negative
	0	1	0	varies
<hr/>				
	1	1	1	positive
Australasian tropics, Oceania	1	1	2	negative
	0	0	1	varies
<hr/>				
<b>Taxa</b>				
	2	8	3	positive
Birds	2	9	7	negative
	1	2	9	varies
<hr/>				
	0	1	11	positive
Mammals	1	1	6	negative
	1	1	2	varies
<hr/>				
	0	0	0	positive
Reptiles	0	0	0	negative
	0	0	0	varies
<hr/>				
	0	0	1	positive
Amphibians	0	0	1	negative
	0	0	0	varies

### 2.4.1 Forest conversion to agriculture

The rate of forest conversion to farmland in the tropics was around 7 million ha annually from 2000 to 2010 (FAO 2016) and it is well established that this conversion produces strong negative impacts on tropical biodiversity (Gibson *et al.* 2011; Edwards *et al.* 2014a). Agricultural conversion typically removes important food sources, breeding habitats, and refugia from inhospitable climates (Fitzherbert *et al.* 2008). Nevertheless, low-intensity farmland and polyculture landscapes can support a surprising amount of wildlife (Karp *et al.* 2011), particularly if crop plants themselves provide diverse food sources (Wickramasinghe *et al.* 2004).

Only 3 studies assessed the impact of forest conversion to agriculture on survival rates (Newell 1999; VanderWerf 2004; Peery & Pauli 2014). In 2 cases, conversion did not significantly affect survival (Hawaii Elepaio [*Chasiempis sandwichensis*] [VanderWerf 2004] and Hoffmann's two-toed sloths [*Choloepus hoffmanni*] [Peery & Pauli 2014]) because the agricultural lands in question apparently provided sufficient resources to fulfill niche requirements, and the species exhibited plasticity in their foraging behaviours (Vaughan *et al.* 2007). However, studies showed that deforestation reduced the survival of 2 other mammal species, due to increased predation and poor habitat quality in the agricultural systems.

Eight studies evaluated the impacts of deforestation on reproductive rates, again concerning bird and mammal species. The effects of deforestation on reproductive rates were species-dependent where 4 studies showed declines in breeding success of birds and mammals, 3 did not detect any impacts on avian nest survival and one study on Hoffmann's two-toed sloths and brown-throated three-toed sloths *Bradypus variegatus* found variations in population growth rates. Conversion to agriculture can have little impact on reproductive rates if species are able to utilize resources within the novel habitat (Sekercioglu *et al.* 2015) or if other limiting factors such as predator populations are controlled by human activities (Bobo & Waltert 2011).

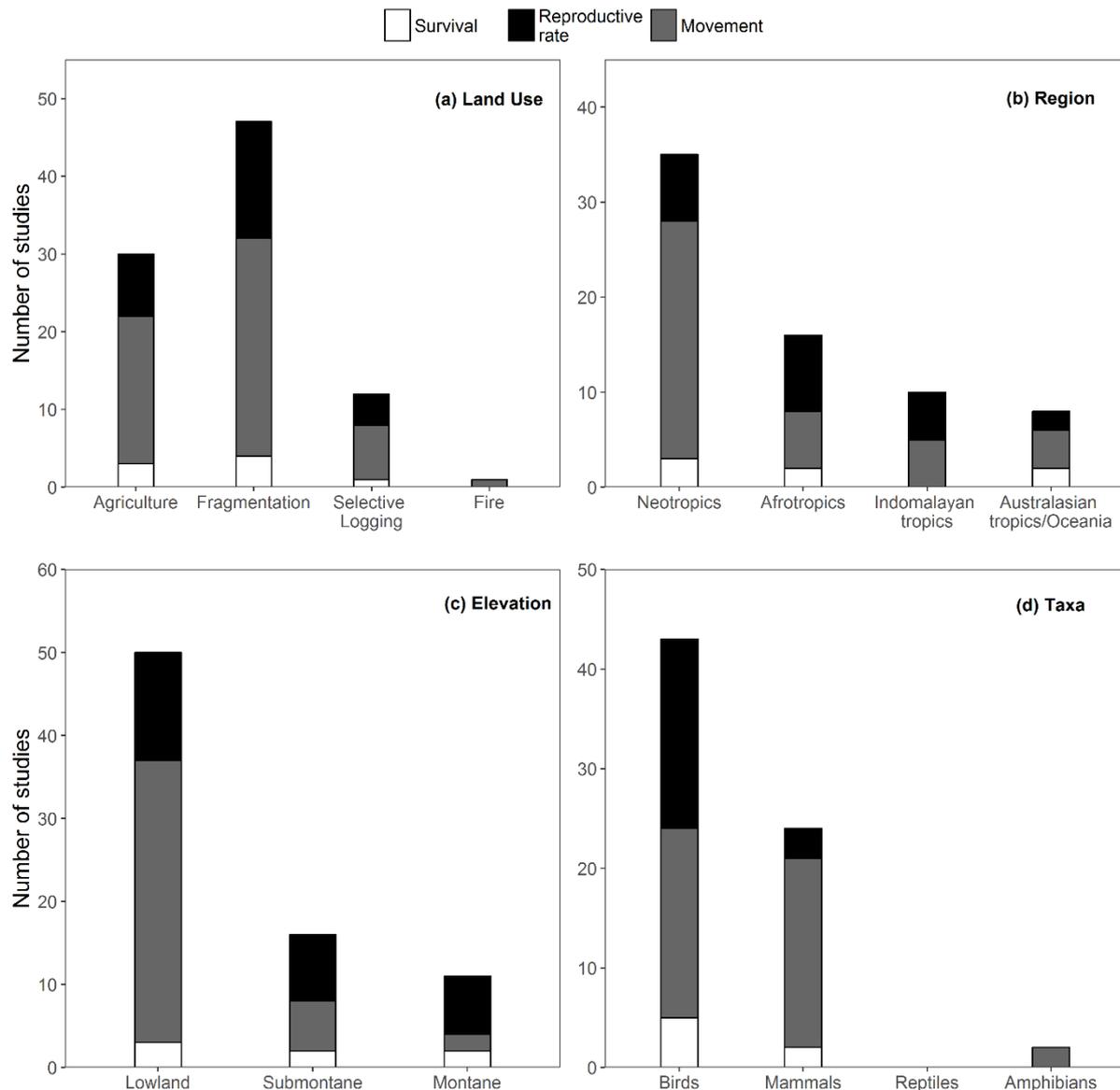


Figure 2.2. Number of studies in which animal vital rates were assessed grouped by (a) land-use type, (b) region, (c) elevation, and (d) taxa. In each grouping, studies are classified into vital-rate category: survival, reproductive rate, or movement.

We found 19 studies examining the impacts of animal movements in agricultural lands after deforestation: 2 on amphibians and the rest on birds and mammals. Again, these studies found a varied range of effects of conversion on movement, from less (Ibarra-Macias *et al.* 2011) to no effect (Medina *et al.* 2007) to more movement (Powell *et al.* 2016). Factors that can cause changes in movement behaviour include increased competition, increased predation (Lees & Peres 2009; Shadbolt & Ragai 2010), and higher mortality risks from inhospitable

microclimates (Lees & Peres 2008). Alternatively, species movement can be unaffected by agriculture if farmlands provide adequate resources (Luck & Daily 2003) or if species are already highly vagile (Estrada *et al.* 1993).

## 2.4.2 Forest fragmentation

Deforestation fragments the remaining forest, creating abundant edges impacted by hotter, windier, and drier climates (Laurance *et al.* 2002). Detailed autoecological studies have shown that many forest-dependent species are unable to persist within forest patches and/or cross gaps (Ferraz *et al.* 2003; Lees & Peres 2009), such that smaller and more isolated fragments have strong negative impacts on species diversity and abundance (Ferraz *et al.* 2003; Russildi *et al.* 2016). Furthermore, increased edge effects mean fragmentation can alter the community composition of landscapes, causing shifts from interior specialists to edge specialists and generalists (Laurance *et al.* 2002; Magnago *et al.* 2014; Pfeifer *et al.* 2017).

Four studies assessed species survival on birds in fragmented forest landscapes. Fragmentation resulted in reduced survival in 24 species, relative to contiguous forest, likely caused by increased predation, reduced resources, and higher mortality risks when vagile species traverse the matrix (Lees & Peres 2008; Shadbolt & Ragai 2010). Conversely, eight bird species exhibited no negative effects from fragmentation. The survival of White-starred Robins (*Pogonocichla stellata*) in Southeast Kenya, for example, was similar in all fragment sizes (Githiru & Lens 2006). However, the major causes of mortality varied with fragment size: mortality associated with dispersal was more prominent in larger fragments, whereas mortality from nest predation was more important in smaller fragments.

Fifteen studies assessed the impacts of forest fragmentation on reproductive rates, 14 of birds and 1 of mammals (Umapathy *et al.* 2011). The majority of these studies examined reproductive success using nest predation experiments. Common detrimental effects of

fragmentation on reproductive rates include increased nest predation (Stirnemann *et al.* 2015) and negative population growth rates (Korfanta *et al.* 2012). Conversely, fragmentation had little effect on breeding rates in a few cases. Reproductive rates can be robust to fragmentation if key resources remain intact inside fragments or if vagile species can use the matrix to meet their foraging needs (Lees & Peres 2009).

Forest fragmentation impacts on movement were examined in 28 studies, considering birds and mammals with only one study on frogs (Robinson *et al.* 2013). Some species exhibited changes in their movement patterns in fragmented landscapes relative to contiguous forests. For instance, understory birds in Central Amazonian Brazil have their movement restricted by open narrow roads and these roads act as territorial boundaries (Develey & Stouffer 2001). This could be due to intolerance of crossing fragment edges (Laurance *et al.* 2004), higher predation risks or increased competition from matrix-tolerant species that invade forest edges (Lees & Peres 2009; Shadbolt & Ragai 2010). However, other studies showed limited effects of fragmentation on movement. This could reflect species using the matrix for refuge (Robinson *et al.* 2013) or food (Estrada & Coates-Estrada 2002; Luck & Daily 2003), allowing species to traverse the matrix (Manning *et al.* 2006; Lees & Peres 2009).

### **2.4.3 Selective logging**

Over 20% of tropical forests were degraded by selective logging from 2000 to 2005 (Asner *et al.* 2009), yet selective logging has minimal negative impacts on biodiversity, often allowing the retention of similar species richness to primary forest (Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014a), including species of conservation concern (Edwards *et al.* 2011). However, selective logging changes community composition (Chapman *et al.* 2000; Edwards *et al.* 2011, 2014) and can have more adverse effects on biodiversity at higher logging

intensities (Burivalova *et al.* 2014; Martin *et al.* 2015) or when using poor logging techniques (Bicknell *et al.* 2014).

One study evaluated the impacts of selective logging on avian survival (VanderWerf 2004). No impact of selective logging was found on the survival of Hawaiian “Elepaio” bird populations (VanderWerf 2004) despite logged sites having a lower estimated carrying capacity. In this case, populations appeared to buffer disturbance impacts by increasing their territory sizes.

Four studies examined the impacts of selective logging on reproductive rates, again all on birds. These showed varying responses to logging, including increased nest predation rates (Cooper & Francis 1998; Pangau-Adam *et al.* 2006) due to increased forest access for predators (Andren & Angelstam 1988) and mesopredator release after logging (Crooks & Soule 1999). Positive or neutral responses were also found in some cases, including no change in breeding success in logged areas relative to unlogged (VanderWerf 2004; Yap *et al.* 2007).

Seven studies examined the effects of selective logging on mammal and bird movements. Again, these studies showed varying responses; some species exhibited no change and others showed inhibitions or movement changes. Species movement can be affected by selective logging if the exposed forest gaps and logging roads have harsher microclimates that deter species or if changes in forest structure alter movement strategies (Cunha & Vieira 2002). Alternatively, movement can remain unaffected if logged forests provide habitat or if there is plasticity in species behaviours (Wells *et al.* 2008).

#### **2.4.4 Forest fire**

Forest degradation increases fire risk by increasing fuel load and exposing the forest to more wind and sun, which increases desiccation (Peres *et al.* 2006, Nepstad *et al.* 2008). El Niño drought-induced fires severely degraded 20 million ha of tropical forests in 1997–1998

(Cochrane 2003) and millions of hectares in 2015–2016. Burning can result in severe tree mortality, leading to the replacement of forest interior animals and hardwood emergent trees with generalist wildlife and pioneer plants (Barlow & Peres 2004; Brando *et al.* 2014). Fire typically reduces bird species abundance and richness, changing community composition (Barlow & Peres 2004, 2008; Slik & Van Balen 2006).

No studies assessed survival and reproductive rates in fire-prone tropical forest landscapes. One study showed significant changes in movement behaviour of northern bettongs after fire (Vernes & Haydon 2001), indicating behavioural plasticity in movement in response to habitat alteration, though the potential consequences for demography were unclear. It is crucial that we better understand the implications of fire on species vital rates, given the drastic effects of fire on tropical forest structure, resources, and biodiversity.

### **2.4.5 Research effort by region and elevation**

We found many regional and elevational biases in research (Figure 2.1). Survival, reproductive rate, and movement studies spanned all tropical regions, but there was a preponderance of studies from the Neotropics (35, total; 3, survival; 7, reproductive rate; 25, movement). Less than one-half the number of studies were in the Afrotropics (total = 16; survival = 2; reproductive rate = 8; movement = 6), less than one-third in the Indomalayan tropics (total = 10; survival = 0; reproductive rate = 5; movement = 5), and less than one-quarter in the Australasian or Oceanic tropics (total, 8; survival, 2; reproductive rate, 2; movement, 4) (Figure 2.1; Table 2.1). All 3 vital rates were studied at all elevational classes, although more studies were conducted in the lowlands (50) compared with sub-montane (16) or montane elevations (11), despite uplands harbouring high endemism and extinction risk (Table A.1). This trend is expected, however, being broadly in line with the total area covered by each elevational class across the tropics.

## 2.5 Discussion

Deforestation and forest degradation are key drivers of the current extinction crisis (Gibson *et al.* 2011; Barlow *et al.* 2016), but most knowledge of their impacts on biodiversity comes from one-off censuses conducted across a short time frame used to generate estimates of species richness and abundance patterns (Gibson *et al.* 2011; Burivalova *et al.* 2014; Edwards *et al.* 2014a; Barlow *et al.* 2016). However, species richness and abundance may change over time if the degraded habitat is in extinction debt or if it recovers. These abundance-based metrics can sometimes mask more severe underlying longer-term impacts on species persistence (Srinivasan *et al.* 2015; Gilroy & Edwards 2017). That so few studies have been carried out in the tropics suggests that anthropogenic impacts may be underestimated. This may mean that the true biodiversity impact of anthropogenic disturbances such as selective logging and low-intensity agriculture are much more significant than currently recognized and thus that greater efforts are needed to assess impacts on demographic vital rates.

We found wide variation in observed vital-rate responses to anthropogenic change across tropical vertebrates. This may reflect the variation in species-specific responses to disturbance; many species possess traits that allow them to persist in novel environments, whereas others are more vulnerable (Isaac & Cowlishaw 2004). However, we caution against making definite conclusions regarding these trends due to the different natures of these studies and varied methodologies, which makes direct comparison impossible. Furthermore, vital rate responses can vary regionally among populations of the same species (Frederiksen *et al.* 2005). Changes in species' vital rates have been linked to abiotic (soil nutrients, light availability, etc.) and biotic (competition, predation, etc.) processes at local scales, which adds further complexity to efforts to understand and predict land-use impacts (Ehrlén & Morris 2015). Many studies had small sample sizes (e.g., Suarez-Rubio *et al.* 2015) because rare or more elusive species were targeted or study species inhabited inaccessible areas.

It is common practice to extrapolate a species' vital rate responses from a few locations to a wider area (Sæther *et al.* 2005) because it is not possible to sample every species in every location. However, the robustness of these extrapolation approaches has seldom been tested, and it is unclear which metrics are best used for extrapolating across populations. Coutts *et al.* (2016) showed that extrapolation is possible but at limited spatial scales, finding that demographic rates cannot be robustly extrapolated further than 20 km geographically. Extrapolation between species is further limited; robust extrapolation is unlikely for species pairs where phylogenetic distance exceeds 10 million years since the last common ancestor (Coutts *et al.* 2016). Although this does not mean that it is impossible to apply the responses of one population over a larger range or to use rules of thumb derived from one species to make predictions about others, it suggests that more studies are required, sampling over larger areas and across more taxa, if we are to properly understand how underlying vital rates respond to land-use change.

We focused only on terrestrial vertebrates, though the research paucity identified will likely extend to other taxa. Land-use change impacts on tropical plant demography, in particular, may be critically important in determining long-term ecological resilience following anthropogenic impact. Terrestrial vertebrates are important pollinators and dispersers for plants and are likely to drive the vital rates of plants (Kremen *et al.* 2007; Peres *et al.* 2016). For example, fragmentation can be detrimental to plant vital rates (Laurance *et al.* 1998; Bruna 2002) if their pollinators and seed dispersers are negatively affected (Regan *et al.* 2015; Peres *et al.* 2016) or seed predation increases (Curran & Webb 2000; Scariot 2000).

It is difficult to reliably compare demographic studies because of a lack of consistency in the methods and metrics used. This lack of consistency combined with the paucity of vital-rate data make it difficult to understand or predict patterns in species' demographic responses to environmental change (Sutherland *et al.* 2013). Two examples of efforts to promote the

standardization of data are the COMPADRE Plant Matrix (Salguero-Gomez *et al.* 2015) and COMADRE Animal Matrix (Salguero-Gomez *et al.* 2016) databases. These open-data repositories contain matrix population models for both plant and animal species that aim to encourage more comparative studies. So far, COMPADRE has facilitated more than 35 comparative studies since its establishment in 1990 (e.g. Stott *et al.* 2011). By compiling and standardizing vital rate data, ecologists will be better able to identify gaps in knowledge and thus broaden the coverage of data across species and geographical locations.

### 2.5.1 Role of Indirect Evidence

As direct measurement of species vital rates to determine the long-term risk posed by tropical forest disturbance are relatively rare, a key question is the degree to which it is possible to use indirect evidence to infer impacts. One method is to use count-based abundance and density trends to infer demographic change (Durant *et al.* 2011), especially when data are collected over a long-time series (Durant *et al.* 2011; Keith *et al.* 2015). However, long-term trends in abundance and density may still mask negative demographic impacts in situations that involve source–sink dynamics (Gilroy & Edwards 2017), where population density can be maintained despite reductions in population growth rate by immigration of individuals from surrounding habitat (Pulliam 1988). Furthermore, density can be higher in disturbed habitats, despite declining demographics, from processes such as competitive exclusion (dominance hierarchies [Holt 1985]), the crowding effect (Debinski & Holt 2000) or individuals mistaking poorer quality habitats as being more attractive (ecological traps).

Another potential method is to use observed contractions in species ranges due to land-use change as a predictor for increased species' extinction risk (Harris & Pimm 2008). For instance, incorporating geospatial data by refining species geographical ranges using elevation maps and the extent of remaining habitat cover could improve the accuracy of predictions in

species extinction risk analyses (Ocampo-Penuela *et al.* 2016). Evaluating change in habitat quality and area can also allow inferences of changes in species abundance and ranges to be drawn, providing insights into resilience under changing habitat conditions (Jennings 2000; Harris & Pimm 2008). Such regular assessments are especially important for tropical species, where land-use change occurs rapidly (Barlow *et al.* 2016). Although Negret *et al.* (2015) conducted a one-off assessment of the range size of Black Tinamou (*Tinamus osgoodi hershkovitzii*), it revealed that their habitats are increasingly degraded by logging, hunting and agricultural activities, thus threatening the species with extinction despite populations currently occurring at high densities. Such data are important for providing a better understanding of the future resilience of species.

The current paucity of data makes it difficult to draw definite conclusions about the state of many tropical forest ecosystems, potentially influencing the robustness of conservation prioritization and management efficacy. We call for significant increases in long-term research efforts to measure demographic responses in a far wider variety of taxa, regions, and land-cover types across the tropics. Such data are also critical to assessing the reliability of predictions made from indirect evidence and may ultimately permit greater confidence, under certain circumstances at least, in the use of those forms of data to infer demographic change. Both would greatly aid the development of conservation approaches to reduce the impacts of land use change through more sustainable natural resource use and improved protected-area design throughout the tropics.

## **2.6 Acknowledgements**

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## Chapter 3

# Mass-abundance scaling in avian communities is maintained after tropical selective logging



Banded broadbill (*Eurylaimus javanicus*).

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### 3.1 Abstract

Selective logging dominates forested landscapes across the tropics. Despite the structural damage incurred, selectively logged forests typically retain more biodiversity than other forest disturbances. Most logging impact studies consider conventional metrics, like species richness, but these can conceal subtle biodiversity impacts. The mass-abundance relationship is an integral feature of ecological communities, describing the negative relationship between body mass and population abundance, where, in a system without anthropogenic influence, larger species are less abundant due to higher energy requirements. Changes in this relationship can indicate community structure and function changes. We investigated the impacts of selective logging on the mass-abundance scaling of avian communities by conducting a meta-analysis to examine its pan-tropical trend. We divide our analysis between studies using mist netting, sampling the understorey avian community, and point counts, sampling the entire community. Across 19 mist-netting studies, we found no consistent effects of selective logging on mass-abundance scaling relative to primary forests, except for the *Omnivore* guild where there were fewer larger-bodied species after logging. In eleven point-count studies, we found a more negative relationship in the whole community after logging, likely driven by the *Frugivore* guild, showing a similar pattern. Limited effects of logging on mass-abundance scaling may suggest high species turnover in logged communities, with like-for-like replacement of lost species with similar sized species. The more negative mass-abundance relationship found in some logged communities could result from resource depletion, density compensation or increased hunting; potentially indicating downstream impacts on ecosystem functions. Our results suggest that size distributions of avian communities in logged forests are relatively robust to disturbance, potentially maintaining ecosystem processes in these forests. This underscores the high conservation value of logged tropical forests, indicating an urgent need to focus on their protection from further degradation and deforestation.

## 3.2 Introduction

Selective logging is the dominant anthropogenic activity in the tropics (Edwards *et al.* 2014b), affecting the largest area of tropical forests. It is responsible for degrading over 390 million hectares of tropical forests globally (Asner *et al.* 2009; Blaser *et al.* 2011), with extensive additional illegal logging that go undetected (Lawson & MacFaul 2010). Despite the structural damage to forests caused by logging (Putz *et al.* 2008; Hawthorne *et al.* 2012; Osazuwa-Peters *et al.* 2015), selectively logged forests retain more biodiversity than other forest disturbances (Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014a), although community composition is altered compared to primary forests and impacts on biodiversity are more adverse at higher logging intensities (Edwards *et al.* 2011; Burivalova *et al.* 2014; Edwards *et al.* 2014a; Martin *et al.* 2015). However, studies using conventional metrics (i.e. species richness, community composition; Burivalova *et al.* 2014; Costantini *et al.* 2016) can conceal hidden impacts on ecosystem functioning. For instance, in Borneo, high intensity logging (twice-logged) resulted in a half-trophic level increase in the trophic position of nine of ten understory bird species (Edwards *et al.* 2013), indicating that these species were feeding from higher up the food chain, via a switch to a more invertebrate-rich diet. There is thus a need to investigate the impacts of selective logging on ecosystem properties that represent community function to better understand the future of biodiversity in selectively logged forests.

Mass-abundance scaling describes the negative relationship between a species' body mass and population abundance (Damuth 1981), where, in a system without anthropogenic pressures, larger species typically occur at lower abundances due to their higher energy and resource requirements compared to smaller species. Because body mass determines metabolic rate, and thus resource use, the mass-abundance relationship describes resource partitioning within an ecosystem (White *et al.* 2007) and underpins food-web stability in ecological systems (Otto *et al.* 2007; O'Gorman & Emmerson 2011; Riede *et al.* 2011). Shifts in the mass-

abundance relationship after land-use changes can indicate alterations in the structure and function of ecological communities. For example, selective logging can impose primary and secondary impacts on ecosystems. Its primary impacts are that larger species tend to be more vulnerable to selective logging (Burivalova *et al.* 2015), which could lead to losses in large-seed dispersers. The secondary impacts from these losses include lower recruitment in large-seeded plants (Culot *et al.* 2017), which greatly impede forest regeneration (Osazuwa-Peters *et al.* 2015; Gardner *et al.* 2019) and carbon stocking (Peres *et al.* 2016; Bello *et al.* 2015, Osuri *et al.* 2016).

To our knowledge, only two studies have directly evaluated the impacts of selective logging on the mass-abundance relationship of ecological communities, both on avian communities (Srinivasan 2013; Sreekar *et al.* 2015), and these showed contrasting results. Srinivasan (2013) found that the mass-abundance relationship of understory insectivorous bird communities (body size ranging 6.1 g – 71.3 g) became more negative (i.e. fewer larger bodied species and more smaller bodies species) as logging intensity increased in the Himalaya. This decrease in abundance of larger species and subsequent increase in abundance of smaller species is due to density compensation. It occurs when resource declines cause larger species to become rarer, allowing smaller species to access resources previously monopolized by larger species and increase in abundance (MacArthur *et al.* 1972). In contrast, Sreekar *et al.* (2015) found no changes in the mass-abundance relationship between primary forests, degraded forests and agricultural lands in Sri Lanka, which was likely due to the high species turnover observed in each land-use type. The high species turnover likely led to a like-for-like replacement of lost species with similar sized species, thus maintaining the mass-abundance relationship in these land-use types. These contrasting results invoke the need for a meta-analysis, where data from appropriate studies across the tropics will be used to determine the global trend of this relationship.

We investigated the impacts of selective logging on the mass-abundance scaling of avian communities—which are well-known taxonomically (Jetz *et al.* 2012), good indicators of responses to environmental change in other taxa (Edwards *et al.* 2014a) and important for ecosystem functioning (Sekercioglu 2006)—by conducting a meta-analysis to examine the overall pan-tropical trend of this relationship. We use the local size-density relationship (LSDR) between the average body mass of a species and the abundance of the species, with all abundances coming from localised study areas. We measured the slope of the upper bound of this mass-abundance relationship (Srinivasan 2013) since the upper bound represents the maximum potential abundance of a species of a certain body size, typically between the 75th percentile to the 95th percentile of the mass-abundance relationship. This upper bound is measured because: (1) the LSDR is determined by processes that influence resource allocation between species (White *et al.* 2007) and, therefore, the upper bound is likely to be energetically limiting (Blackburn *et al.* 1992); and (2) local assemblages tend to contain species with lower population sizes compared to larger global-scale communities (Brown *et al.* 1995) as they contain only a subset of the global population size. We tested the hypothesis that logging typically decreased the upper-bound slope of the mass abundance relationship, relative to primary forest, due to disproportionate effects on the abundance of large-bodied species (Srinivasan 2013). We also investigated the impacts of selective logging on mass-abundance scaling within different avian foraging guilds, given that guilds differ in their rates of energy consumption as well as energy availability (Russo *et al.* 2003), and that foraging guilds often respond differently to land-use change (Sreekar *et al.* 2015).

## 3.3 Materials & Methods

### 3.3.1 Data collection

Data were obtained from 30 studies (19 studies using mist-netting methods and 11 studies using point-count methods) that contained information on abundance or capture rate for avian species in both selectively logged forests and old-growth primary forest controls across the tropics (Figure 3.1, Table B.1, Table B.2). The online Web of Science database was used to search for studies with the keywords ["selective logging" OR forestry OR "secondary forest" OR "regenerating forest"] AND [bird\* OR avian OR aves] AND [mass OR abundance OR number OR "capture rate" OR density]. This search was refined by [tropic\*] and ["mist-net" OR "point-count"] resulting in 80 156 studies. We further refined the search to only include studies with topics such as environmental sciences, ecology, forestry, zoology and biodiversity conservation, leaving us with 525 studies. We then supplemented the search using two more Google Scholar searches with the keywords; search 1: "selective logging", bird\*, avian, aves, mass, abundance, number, "capture rate", density, "mist-net\*", "point-count\*", tropic\*; search 2: "regenerating forest, bird\*, avian, aves, mass, abundance, number, "capture rate", density, "mist-net\*", "point-count\*", tropic\*. Search 1 resulted in 774 studies and search 2 returned 215 studies. This left us with a total of 1514 studies and after removing duplicates, we were left with 1395 studies. Excluding studies based on title reduced the collection to 676 studies and excluding the remaining studies based on abstract resulted in 211 studies. All searches were conducted between 4th April 2019 to 18th April 2019.

Of these 211 studies, studies were only included during full-text screening if they were (i) conducted in the tropics (between 23.43706°N and 23.43706°S), (ii) conducted in closed-canopy forests, (iii) used mist-netting or point-counts to sample birds, (iv) presented species-specific abundance estimates in both selectively logged forests and old-growth primary forests, and (v) mist-net and point-count datasets (if both included) could be separated. This resulted

in a total of 47 studies, for one of which the author no longer had the abundance dataset, another one for which the sole author (Johns 1996) was uncontactable, and for 15 of which we did not get a response from the authors we contacted.

This left us with 30 studies (19 mist-netting studies and 11 point-count studies; see Table B.1 and Table B.2 for information on each study). Where available, mass was obtained from individual studies, and for studies in which no information on mass was provided (or where masses were missing for some species), we used Dunning's CRC Handbook of Avian Body Masses (2008) and Handbook of the birds of the world alive (del Hoyo *et al.* 2017). The data from two of these studies (Wunderle *et al.* 2006; Hawes *et al.* 2008) were split and analysed separately as they contained data from different habitats, where each habitat type contained a distinct avian community. This resulted in 21 separate mist-netting studies.

### 3.3.2 Quantile regression

The mist-netting data and point-count data were analysed separately. To study the impacts of selective logging on the mass-abundance scaling of avian communities across the tropics, a meta-analysis was conducted on differences in the slope of the upper bound of mass-abundance relationships between logged forests and primary forest controls. The abundance or capture rate for each species was standardised within each study and within each habitat type (primary or logged forest) to obtain the relative standardised abundance:

$$\text{Relative Standardised Abundance} = \frac{x - \bar{x}}{\sigma}$$

$x$  = Abundance

$\bar{x}$  = Mean abundance

$\sigma$  = Standard deviation of abundance



Using relative standardized abundance rather than abundance or capture rate will affect the intercept but not the slope of the mass-abundance relationship (N.B. Similar results were produced when running the analysis on either the relative standardized abundance or on abundance and capture rates; Figure B.11). For each study and habitat type (primary forest or logged forest), the slopes of the upper bound of the mass-abundance relationship was estimated using quantile regressions in the R software (R Core Team 2019) package `quantreg` (Koenker 2017). Quantile regression enables the quantification of information from the boundaries of polygonal relationships (Scharf *et al.* 1998) and can identify factors that limit species' responses (Vaz *et al.* 2008). Standardised relative abundance was  $\log_{10}(y + 1)$  transformed in the mist-net data and  $\log_{10}(y+2)$  transformed in the point-count data, while species mass was  $\log_{10}$  transformed to obtain a straight line upper bound on the mass-abundance relationship. The upper bound of the polygonal mass-abundance relationship is likely to represent an energetic limit on abundance (Blackburn & Gaston 1997).

### 3.3.3 Meta-analysis

For each paired logged and primary slope estimate, the mean difference effect size, Hedges'  $g$  was calculated using the `compute.es` package (Del Re 2013). Studies were weighted by the inverse of their variance so that smaller studies or those with high uncertainty contribute less to estimated effects. The average effect size was then calculated using the random-effects model in the `MAd` package (Del Re & Hoyt 2014). To test for the effect of elevation and geographic region (continent) on the effect sizes, a meta-regression was performed with elevation and continent using the `MAd` package (Del Re & Hoyt 2014). The extent of heterogeneity was tested using the  $I^2$ -statistic.

Publication bias was tested for using two methods in the `metafor` package (Viechtbauer 2010). Firstly, publication bias was examined visually using a funnel plot of effect size (Figure

B.9, Figure B.10) and the second method was using Rosenthal's Fail-Safe N analysis. This meta-analysis was repeated using slope estimates from a range of regression quantiles (0.75, 0.8, 0.85, 0.9, 0.95). All analyses were done using the R software (R Core Team 2017).

### 3.3.4 Guild analyses

To examine the impacts of selective logging on the mass-abundance scaling of different species foraging guilds, each species was first assigned to a foraging guild (Insectivore, Frugivore, Omnivore, Carnivore, Granivore; see Table B.3 for more information) based on the categorisation used in the EltonTraits 1.0 database (Wilman *et al.* 2014). This resulted in only three foraging guilds, Insectivore, Frugivore and Omnivore, containing enough data after removing studies where there were less than ten species per study and per habitat type (i.e. less than ten species in either primary forest or logged forest). The above meta-analysis methods were then conducted separately for Insectivore, Frugivore and Omnivore foraging guilds. The resulting studies for each guild are as follows, Insectivore: 19 mist-netting studies and eleven point-count studies; Frugivore: ten mist-netting studies and seven point-count studies; Omnivore: nine mist-netting studies and seven point-count studies.

## 3.4 Results

There was a small degree of between-study heterogeneity ( $I^2$ : 0.004% - 33.43%) in the 0.75 quantile models (Mist-net: Frugivore; Point-count: Overall, Frugivore), 0.8 quantile models (Point-count: Frugivore, Omnivore), 0.85 quantile models (Point-count: Frugivore, Omnivore), 0.9 quantile models (Mist-net: Frugivore, Omnivore; Point-count: Overall, Frugivore, Omnivore) and 0.95 quantile models (Mist-net: Overall, Frugivore, Omnivore; Point-count: Overall, Insectivore, Frugivore, Omnivore). However, there was a large degree of uncertainty in these  $I^2$  estimates, which is to be expected due to the small amount of studies.

Publication bias was detected for the 0.95 quantile Overall model (Mist-net:  $p=0.044$ , Fail-safe  $N=2$ , Figure B.9; Point-count:  $p=0.01$ , Fail-safe  $N=11$ , Figure B.10), the 0.9 Omnivore model (Mist-net:  $p=0.033$ , Fail-safe  $N=3$ , Figure B.9) and the 0.95 Omnivore model (Mist-net:  $p=0.032$ , Fail-safe  $N=3$ , Figure B.10).

### 3.4.1 Mist-net studies

Selective logging did not affect the mass-abundance scaling of the Overall avian community across all regression quantiles ( $p>0.05$ ; Figure 3.2, Figure 3.3a, Figure B.1). Confidence intervals for these effect sizes overlapped zero in all cases (Table 3.1), indicating considerable between-study uncertainty in the strength of the effects of logging on mass-abundance scaling. Mass-abundance relationships did not vary significantly in relation to elevation or study continent ( $p>0.05$ ).

Examining the effect of selective logging on the mass-abundance relationship at the Insectivore and Frugivore foraging guild level showed similar results across all regression quantiles ( $p>0.05$ ; Figure 3.2, Figure 3.3b, Figure 3.3c, Figure B.2, Figure B.3). Again, confidence intervals for these effect sizes overlapped zero in all cases (Table 3.1). The effect sizes for the Insectivore guild were also not affected by elevation and study continent ( $p>0.05$ ). However, effect sizes for the Frugivore guild were associated with study continent in the 0.75 quantile (Asia having a significant negative effect size: mean Hedges'  $g$  [ $\pm 95\%$  CI] =  $-0.42$  [ $-0.834, -0.009$ ],  $p=0.045$ ) and 0.95 quantile (South America having a significant positive effect size: mean Hedges'  $g$  [ $\pm 95\%$  CI] =  $0.53$  [ $0.037, 1.013$ ],  $p=0.035$ ), as well as by elevation in the 0.95 quantile where there is a significant positive effect at zero elevation (mean Hedges'  $g$  [ $\pm 95\%$  CI] =  $0.31$  [ $0.017, 0.606$ ],  $p=0.038$ ). In the Omnivore guild, the mass-abundance relationship at the 0.9 quantile became significantly more negative in selectively logged forests (mean Hedges'  $g$  [ $\pm 95\%$  CI] =  $-0.20$  [ $-0.388, -0.017$ ],  $p=0.033$ ; Table 3.1, Figure B.4c) with

all other quantiles showing no effect of selective logging (Table 3.1, Figure 3.3d, Figure B.4). Elevation and study continent did not affect the mass-abundance scaling of the Omnivore communities.

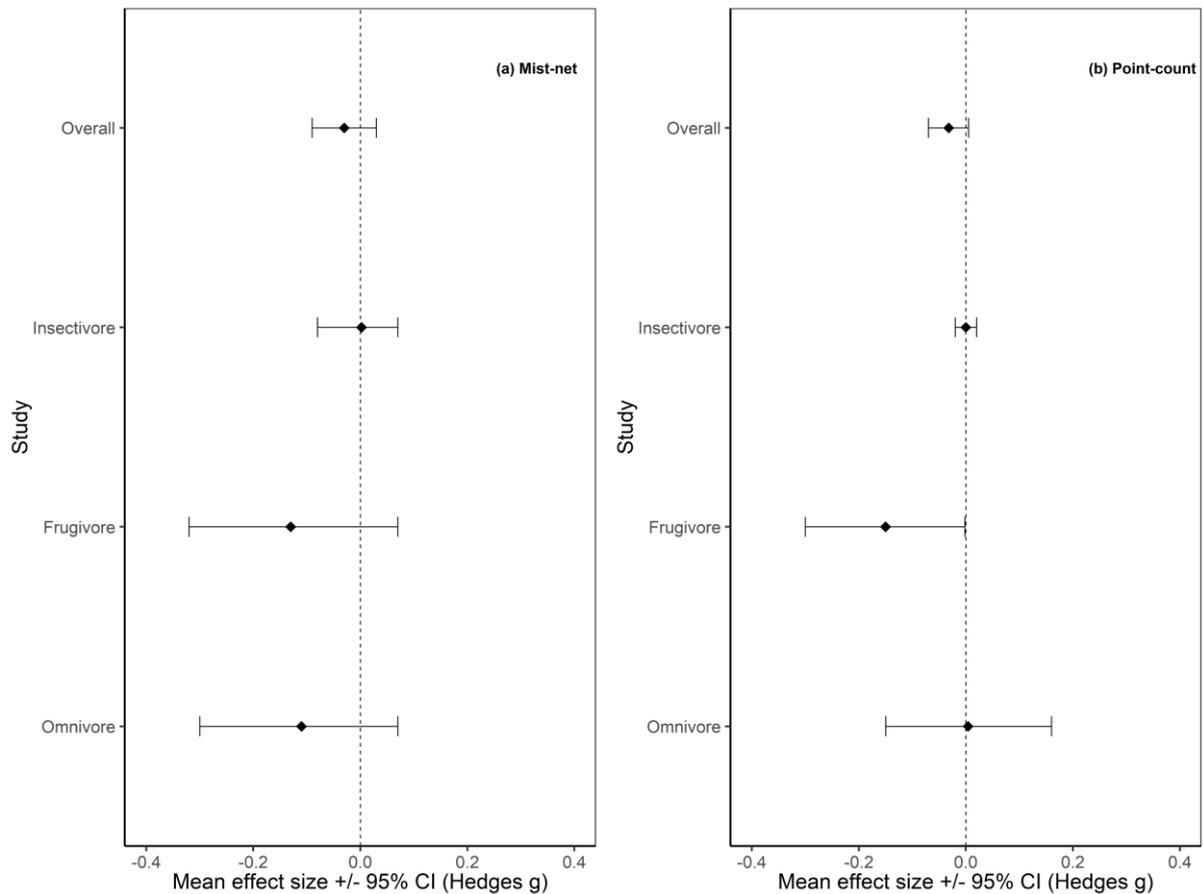


Figure 3.2. Overall effect sizes of all studies combined in each category: Overall (all data), Insectivore, Frugivore and Omnivore; with their respective 95% confidence intervals. Effect sizes are from the 0.75 regression quantile for (a) Mist-net studies and (b) Point-count studies.

### 3.4.2 Point-count studies

There was no effect of selective logging on the mass-abundance scaling of the Overall bird community (Table 3.2, Figure 3.2, Figure 3.4a, Figure B.5) except in the 0.95 quantile where the mass-abundance slope was significantly more negative in selectively logged forests (mean Hedges'  $g$  [ $\pm 95\%$  CI] = -0.05 [-0.07, -0.03],  $p < 0.001$ ; Table 3.2, Figure B.5d). When

elevation and continent were both taken into account, only the African continent had a significant positive effect size (mean Hedges'  $g$  [ $\pm 95\%$  CI] = 0.28 [0.028, 0.540],  $p=0.030$ ) at the 0.75 quantile.

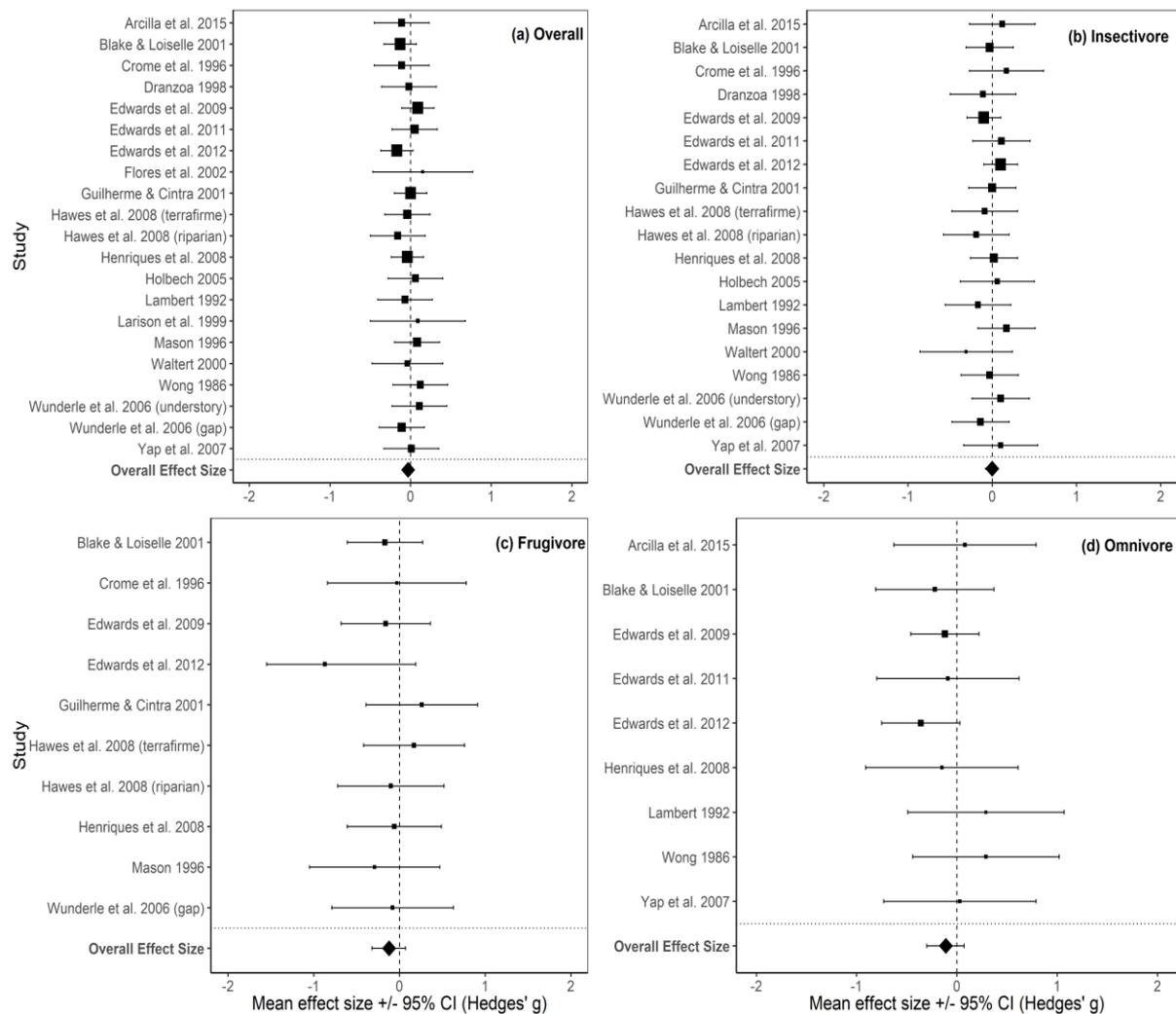


Figure 3.3. The effect sizes of each mist-net study and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the 0.75 regression quantile for (a) Overall, (b) Insectivore foraging guild, (c) Frugivore foraging guild and (d) Omnivore foraging guild.

At the foraging guild level, the mass-abundance relationships of the Insectivore and Omnivore communities were unaffected by selective logging ( $p>0.05$ ; Table 3.2, Figure 3.2,

Insectivore: Figure 3.4b, Figure B.6, Omnivore: Figure 3.4d, Figure B.8) and there was no influence of elevation and study continent ( $p>0.05$ ).

Table 3.1. The average Hedges'  $g$  effect sizes of each mass-abundance regression quantile and the 95% confidence interval for each effect size from the mist-net data. Results are shown for the whole dataset (Overall) and for each foraging guild (Insectivore, Frugivore and Omnivore). Significant effect sizes are highlighted in bold.

<b>Overall</b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	-0.029	-0.090	0.032
0.80	-0.030	-0.091	0.031
0.85	-0.054	-0.115	0.007
0.90	-0.052	-0.112	0.009
0.95	-0.059	-0.120	0.002
<b>Guild: <i>Insectivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	0.002	-0.076	0.071
0.80	0.005	-0.068	0.078
0.85	0.007	-0.081	0.066
0.90	0.009	-0.064	0.083
0.95	-0.020	-0.094	0.053
<b>Guild: <i>Frugivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	-0.125	-0.315	0.066
0.80	0.001	-0.190	0.192
0.85	0.100	-0.090	0.291
0.90	0.102	-0.089	0.293
0.95	0.127	-0.065	0.318
<b>Guild: <i>Omnivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	-0.111	-0.297	0.074
0.80	-0.149	-0.334	0.037
0.85	-0.176	-0.362	0.009
<b>0.90</b>	<b>-0.202</b>	<b>-0.388</b>	<b>-0.017</b>
0.95	-0.180	-0.366	0.005

Contrarily, the mass-abundance scaling of Frugivores was significantly more negative in selectively logged forests in the 0.75 (mean Hedges'  $g$  [ $\pm 95\%$  CI] = -0.15 [-0.299, -0.002],  $p=0.047$ ; Figure 2), 0.8 (mean Hedges'  $g$  [ $\pm 95\%$  CI] = -0.17 [-0.321, -0.024],  $p=0.023$ ) and

0.95 (mean Hedges'  $g$  [ $\pm 95\%$  CI] = -0.17 [-0.313, -0.016],  $p=0.030$ ) quantiles (Table 3.2, Figure 3.4c, Figure B.7). However, elevation and study continent did not affect these mass-abundance relationships ( $p>0.05$ ).

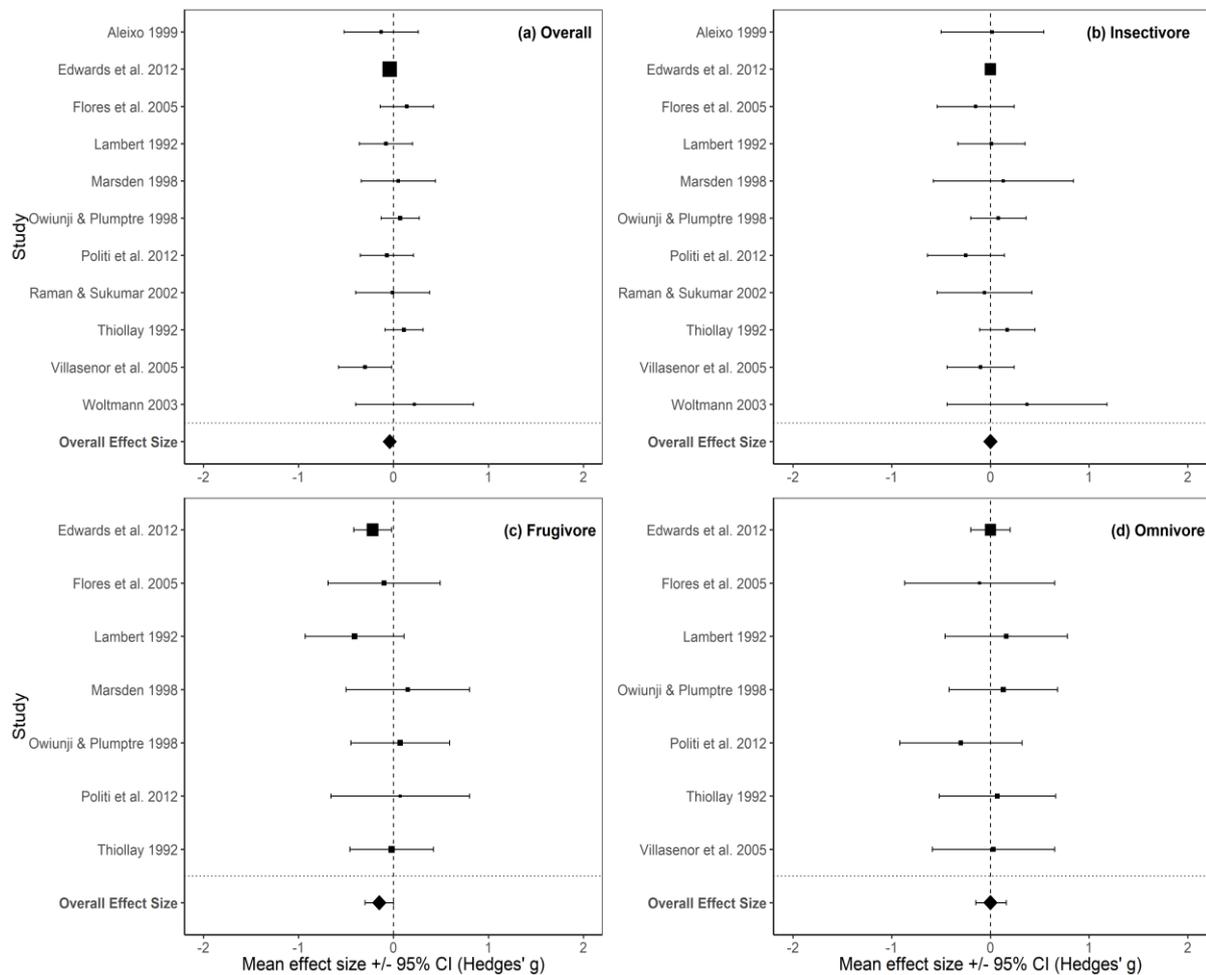


Figure 3.4. The effect sizes of each point-count study and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the 0.75 regression quantile for (a) Overall, (b) Insectivore foraging guild, (c) Frugivore foraging guild and (d) Omnivore foraging guild.

### 3.5 Discussion

We investigated how selective logging affects the mass-abundance relationship in avian communities across the tropics, finding that communities sampled by mist-netting largely experienced no effect of selective logging on these relationships, except in the Omnivore

communities, where the mass-abundance relationship became more negative in selectively logged forests. On the other hand, we found that the mass-abundance relationship of the overall communities sampled by point-counts was more negative in logged forests. This was likely driven by the Frugivore communities, which were the only foraging guild to have a more negative mass-abundance relationship in selectively logged forests.

Table 3.2. The average Hedges'  $g$  effect sizes of each mass-abundance regression quantile and the 95% confidence interval for each effect size from the point-count data. Results are shown for the whole dataset (Overall) and for each foraging guild (Insectivore, Frugivore and Omnivore). Significant effect sizes are highlighted in bold.

<b>Overall</b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	-0.032	-0.070	0.005
0.80	-0.010	-0.029	0.009
0.85	-0.011	-0.063	0.042
0.90	0.000	-0.020	0.019
<b>0.95</b>	<b>-0.05</b>	<b>-0.070</b>	<b>-0.030</b>
<b>Guild: <i>Insectivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	0.000	-0.019	0.020
0.80	0.009	-0.028	0.011
0.85	0.001	-0.019	0.020
0.90	0.010	-0.033	0.052
0.95	0.001	-0.018	0.021
<b>Guild: <i>Frugivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
<b>0.75</b>	<b>-0.150</b>	<b>-0.299</b>	<b>-0.002</b>
<b>0.80</b>	<b>-0.172</b>	<b>-0.321</b>	<b>-0.024</b>
0.85	-0.007	-0.156	0.141
0.90	-0.112	-0.261	0.037
<b>0.95</b>	<b>-0.165</b>	<b>-0.313</b>	<b>-0.016</b>
<b>Guild: <i>Omnivore</i></b>			
<b>Quantile</b>	<b>Average Effect Size</b>	<b>95% CI</b>	
0.75	0.004	-0.152	0.159
0.80	0.028	-0.127	0.184
0.85	-0.029	-0.285	0.227
0.90	-0.070	-0.301	0.160
0.95	-0.025	-0.299	0.249

This increased negative slope in the mass-abundance relationship could indicate a loss of larger species or a rise in the number of small species (Srinivasan 2013), potentially signalling changes in resource and energy partitioning between species, with downstream impacts on ecosystem functioning.

Srinivasan (2013) found that the mass-abundance relationship of understory avian insectivores became steeper and more negative as logging intensity increased. This was thought to be due to multiple factors such as resource depletion and density compensation. As resources decline in degraded habitats, disproportionately vulnerable larger species may decrease in abundance and thus free up resources for smaller species to thus increase in abundance. Hunting could also be a factor leading to declines in larger species, as selectively logged forests tend to have increased hunting pressure due to more accessibility via logging roads (Sheil & Meijaard 2005).

Different functional groups consume energy at different rates and have different amounts of energy available to them in their habitat (Marquet 2002; Ernest *et al.* 2003) and although species which forage on fruits and nectar (Frugivore guild) tend to thrive in degraded forests compared to species which forage on invertebrates (Insectivore guild) (Greenberg *et al.* 1997; Sreekar *et al.* 2015), we observe that the mass-abundance relationship of Frugivore point-count communities were affected by selective logging and not the Insectivore communities. This could indicate greater vulnerability of larger frugivore species, perhaps because large fruiting trees tend to be removed during the logging process and require a longer period of time to regenerate (Burivalova *et al.* 2015). Furthermore, some large frugivore species, such as the Helmeted Hornbill (*Rhinoplax vigil*), are particularly threatened by hunting due to their value for meat, ornamental feathers or ivory-like casque (Bennett *et al.* 1997; Beastall *et al.* 2016). The change in the mass-abundance relationship in these frugivore communities could precipitate important changes in seed dispersal services within logged forest ecosystems.

On the other hand, our results show that many mass-abundance relationships in the mist-net and point-count communities are robust to selective logging activities. Many studies from freshwater, intertidal and marine ecosystems have shown that the mass-abundance relationship is robust to disturbances (Marquet *et al.* 1990; Jonsson *et al.* 2005; O'Gorman & Emmerson 2011). O'Gorman and Emmerson (2011) found that the mass-abundance relationship in marine food webs were robust to disturbances due to higher species turnover in the disturbed communities. One potential mechanism is structural changes in habitat or food webs produce new size-abundance niches that could be exploited by new species. Similarly, there could be a replacement of species with similar body sizes after logging, allowing the community to maintain energy and structural stability within the system (Damuth 1981, 1987; Marquet *et al.* 1990; Jonsson *et al.* 2005).

Sreekar *et al.* (2015) also found no difference in the mass-abundance relationship of avian communities between primary forests and selectively logged forests in southern India. Sreekar *et al.* (2015) suggested that this similarity was due to high species turnover in logged forests, as the avian communities change in response to altered environments. They observed a higher proportion of insectivores in primary forests than logged forests and a higher proportion of insectivores in the understory primary forest community than the logged community. Given that there is a limited amount of energy available within a logged habitat, it is perhaps unsurprising that mass-abundance relationships are not consistently affected as communities adapt to the amount of available energy. Nevertheless, previous studies showing marked changes in avian community structure following logging, such as changes in community composition (Burivalova *et al.* 2014; Edwards *et al.* 2014a), suggest that other ecosystem properties in logged forests may be different from that of primary forests, representing an important topic for future studies. These different responses found between Srinivasan (2013) and Sreekar *et al.* (2015) may be due to the degree of habitat variation. For instance, Srinivasan

(2013) sampled across a gradient of selective logging intensities, while this study and Sreekar *et al.* (2015) sampled across a gradient of distinct habitats which are more drastically different from each other. In the two distinct habitats, the logged forest communities could have had time to reach a new state of energy and structural equilibrium that still adheres to the power law  $N \propto M^b$ , which describes the mass-abundance relationship, where  $N$  is species abundance and  $M$  is the species' body mass. Thus, both logged and primary forests in this case would have similar mass-abundance slopes.

### 3.5.1 Synthesis and Applications

Our study suggests that logging only significantly alters the avian mass-abundance relationships of selected Frugivore and Omnivore communities in tropical forests. Inclusion of point-count studies in the meta-analysis was important as these detected some changes in the mass-abundance relationship that the mist-net studies failed to capture, especially in the avian communities living above the understory (i.e. mid-storey and canopy species). The mist-net communities represent the understory bird communities and allowed the detection of cryptic and quiet understory species, which would have gone undetected using point-count techniques. The lack of impacts on understorey communities in the mist-net studies may be due to mist-nets only detecting a subset of bird sizes, making it difficult to detect abundance changes in species at the upper extreme of the size spectrum.

The impacts experienced by these communities could be minimised by restoring selectively logged forests with native fruiting trees, especially those bearing larger fruits. The results also show that logging does not change the mass-abundance relationship of the majority of the avian communities which adds weight to the evidence that avian communities are relatively robust to selective logging, with species and communities exhibiting some flexibility to adapt to modified environments and, in doing so, maintaining ecosystem functioning (Ewers

*et al.* 2015), which is crucial in an epoch of global change. These results also underscore the high conservation value of logged tropical forests (Edwards *et al.* 2011), indicating that an urgent conservation priority is the protection of these cost-effective habitats from further degradation and deforestation, allowing enhanced area of forest protection, buffering of primary forest reserves and maintenance of landscape-scale connectivity (Edwards *et al.* 2014b).

### **3.6 Data availability**

Data available from Figshare: <https://doi.org/10.15131/shef.data.11590902.v1>.

### **3.7 Acknowledgements**

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## Chapter 4

# Tropical selective logging alters local-scale movement of understory avian communities



Green broadbill (*Calyptomena viridis*)

This chapter has been submitted to Ecology as:

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## 4.1 Abstract

Selective logging dominates the tropical forest landscape at the expense of pristine old-growth forests. Despite the structural damage incurred by selective logging, these forests can still retain a substantial amount of biodiversity. However, our understanding of how selective logging impacts the mechanistic processes underpinning biodiversity change is scant. Movement is a vital mechanistic process, determining an organism's survival, growth, and breeding, underpinning demographic changes and many fundamental ecological and evolutionary mechanisms. Movement varies depending on food resource and availability, the degree of species' dietary flexibility, and thus a species' trophic position, which is often higher in logged versus old-growth forest. We assessed how tropical selective logging impacts local movements of understory avian species in Sabah, Malaysian Borneo. We determined whether these movement patterns relate to species' conservation status, traits, logging sensitivity and species' changes in trophic positions. We used a capture-mark-recapture methodology and a hierarchical Bayesian analytical framework to model maximum observed local movement distances, accounting for spatial sampling heterogeneity. Across the community of 71 species, we found a higher mean probability of moving shorter distances (up to 200 m) in logged forests, while movement probability was higher at longer distances (above 200 m) in unlogged forests. Shifts in movement patterns after logging may be due to increased understory density (favouring most understory species), altered resource distribution, predation risks, or smaller home-range sizes. Species' conservation status, body mass, foraging guild, sensitivity to logging and trophic position were unrelated to the magnitude of movement change. These results indicate that persistence of understory species after logging may depend on plasticity in movement behaviour, conferring resilience to habitat degradation. This underscores the potential for selectively logged forests to retain high conservation value and lends further support for their protection.

## 4.2 Introduction

Tropical forests are increasingly degraded worldwide, contributing to carbon emissions (Pearson *et al.* 2017) and threatening many species in biodiversity hotspots (Myers *et al.* 2000). Over 403 million hectares of tropical forests are slated for selective logging at the expense of pristine old-growth forests (Asner *et al.* 2009; Blaser *et al.* 2011), although the true extent is much higher due to the vast area of undocumented, illegal logging (Lawson & MacFaul 2010; Pacheco *et al.* 2016). Selective logging alters the forest structure, leaving a fragmented canopy, compacted soil along skid trails, and a denser understory dominated by early successional and climbing vegetation that can impede forest regeneration, enduring for decades (Putz *et al.* 2008; Hawthorne *et al.* 2012; Osazuwa-Peters *et al.* 2015).

Despite alterations in forest structure, a substantial amount of species and functional diversity is retained after selective logging (Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014b), although community composition is altered as forest-interior species decline and edge-tolerant species increase (Edwards *et al.* 2011). However, our understanding of how selective logging impacts the mechanistic processes underpinning biodiversity change is scant (Cosset *et al.* 2019). Movement is a vital mechanistic process, determining an organism's survival, growth, and breeding (Faccio, Gabriel & Pizo 2018), underpinning demographic changes and many fundamental ecological and evolutionary mechanisms (Hanski 1998; Postma & van Noordwijk 2005). Within an animal's home range—the area where an animal tracks resources to meet its needs (Burt 1943)—movement can be driven by the abundance and distribution of resources (Hansbauer *et al.* 2008a; Morrison *et al.* 2010; Chasar *et al.* 2014), habitat structure (Vieira & Scariot 2006), and predator or mate encounters (Fortin *et al.* 2005; Hua & Sieving 2016). Considering movement can improve predictions of long-term population persistence (Kokko & Lopez-Sepulcre 2006; Doligez & Part 2008; Robertson *et al.* 2018),

species conservation status (Schaub *et al.* 2010), and conservation action efficiency (Lieury *et al.* 2015).

Structural changes in selectively logged forests not only affect the abundance or distribution of resources, but also likely affect the ability of animals to effectively detect and move towards their essential resources and to evade predators (Curran & Leighton 2000; Vieira & Scariot 2006; Wells *et al.* 2006). Previous work used spool-and-line or telemetry techniques to assess how logging impacts movement patterns, tending to focus on a single species of mammal (Colón *et al.* 2002; Wong *et al.* 2004; Wells *et al.* 2008; but see Wells *et al.* 2006) or bird (Dale & Slembe 2005). All mammal studies showed no impact of selective logging on home-range size, movement rates or patterns, but instead found that movement strategies were affected by the heterogeneous structure of logged forest microhabitats and associated food distribution. Conversely, the understory passerine red-tailed bristlebill (*Bleda syndactyla*) in Uganda had higher movement rates and larger home-ranges in unlogged forests as their preferred dense understory habitat was scattered, compared to logged forests (Dale & Slembe 2005). Understanding the community-wide impacts of logging on species' movement, including on habitat-sensitive rare species, thus remains a major knowledge gap.

Previous modelling approaches to examining community-wide movement patterns have involved using linear models with species as random effects (e.g. Tucker *et al.* 2018) or separately estimating responses for each species (e.g. Wells *et al.* 2006). These methods tend to suffer from sparse data for the large number of rare species detected in the community, but recent advances in joint species modelling have helped overcome this by allowing species- and community-level responses to be estimated simultaneously in a hierarchical framework (Ovaskainen *et al.* 2019). This allows more accurate estimations for rarer species, by allowing species-level effects to be partially informed by community-level patterns (Warton *et al.* 2015; Saracco *et al.* 2018; Ovaskainen *et al.* 2019; Ramos *et al.* 2020).

The impact of logging on local movements might vary depending on how logging affects the distribution of food resources, and in turn the degree of species' dietary flexibility, as measured by a species' trophic position (Edwards *et al.* 2013; Hamer *et al.* 2015). Many Bornean birds feed from higher trophic positions in logged than unlogged forests, indicating more protein-rich diets (i.e. more invertebrate and less fruit or insectivores consuming more predatory arthropods or elevated trophic positions of invertebrate prey) in logged forests (Edwards *et al.* 2013). Because a greater proportion of fruits are produced by lianas during the non-masting years in logged forests, these denser patches of tangles would likely require movement between patches (Marshall *et al.* 2020) whereas a more permanent source of invertebrate prey might require less movement (Doherty *et al.* 2019). Changes in movement, resources, and consequently trophic position, could have repercussions on species' survival and thus abundance, potentially leading to long-term declines in populations of species otherwise thought to persist after logging (Gray *et al.* 2006; Hamer *et al.* 2015; Messina *et al.* 2020b).

Here, we (1) assess how tropical selective logging impacts the local movements of understory avian species, (2) determine whether species traits or conservation status are important determinants of movement patterns, (3) determine if differences in movement patterns are related to species' sensitivity to selective logging, and (4) determine whether movement patterns relate to changes in avian species' trophic positions. Birds are our study taxa as they are important for ecosystem processes (Sekercioglu 2006), and they are good indicators of overall forest health and of responses in other taxa (Edwards *et al.* 2014a). We develop a novel hierarchical modelling framework to estimate movement rates at both species- and community-levels, adapting recent developments in joint species occupancy modelling to allow more efficient statistical use of multispecies movement data (Ovaskainen *et al.* 2019). This study represents the first empirical community assessment of the impacts of tropical

selective logging on the movement patterns of whole ecological communities (71 species in 19 families).

## 4.3 Materials & Methods

### 4.3.1 Study site

The study was conducted in the global biodiversity hotspot of Northern Borneo in the Malaysian state of Sabah (Myers *et al.* 2000). Two habitat types (unlogged, old-growth forest and twice-logged, selectively logged forest) were sampled in the Yayasan Sabah (YS) concession, a ~1 million hectare contiguous forest block comprised of mostly lowland evergreen forest dominated by dipterocarp tree species (Dipterocarpaceae) (Newbery *et al.* 1992), which are highly valuable timber (Fisher *et al.* 2011a). Within the YS concession, we focused on logged forests in the 126,846 ha Ulu-Segama Forest Reserve (USFR) (4° 57' N, 117° 55' E). The first logging cycle was carried out from 1976 to 1991, with trees >0.6 m DBH extracted, yielding 73 to 166 m<sup>3</sup> of timber per hectare (Edwards *et al.* 2011). The second logging cycle was then conducted in the logged forests of the USFR between 2001 and 2007, with trees >0.4 m DBH extracted, yielding 15 to 72 m<sup>3</sup> per hectare (Edwards *et al.* 2011). The YS concession also contains the unlogged old-growth forests of the 45 200 ha Danum Valley Conservation Area (DVCA) and Palum Tambun Watershed Reserve (4° 55' N, 117° 40' E), adjacent to USFR, which we used as our unlogged forest controls.

### 4.3.2 Avifaunal sampling

We sampled the understory avian community using mist-netting techniques in a capture-mark-recapture methodology. In each habitat type (i.e. logged and unlogged forests), three sampling plots were established with each plot at least 1.83 km apart (4.95 km ± 1.26 km:

unlogged = 6.23 km  $\pm$  2.28 km; logged = 3.67 km  $\pm$  1.04 km). Each plot contained three 250 m transects, placed 250 m apart in parallel.

Fifteen 12 m mist-nets were placed end-to-end on each transect, allowing 70 m in total of extra space to avoid placing mist-nets over very steep gullies and fallen tree trunks. Mist-netting was conducted from 06:00 to 12:00 for two consecutive days, with each plot sampled three times (approximately monthly) from early June to early September each year from 2014 to 2018. Mist-netting was not conducted in heavy rain, high winds or when elephants were in the vicinity, thus equating to 38,835 mist-net hours in total (unlogged: 20,300 mist-net hours, logged: 18,535 mist-net hours).

To determine the movement patterns of birds, each transect was divided into five zones, each containing three mist-nets and with 50 m  $\pm$  1.2 m distance between the centre of each zone. This design allows us to detect cross-transect movements within plots, ranging up to 538 m (Figure C.1). Birds captured were identified to species, tagged with a uniquely numbered leg ring, sexed, aged, and released at the mist-net of capture within the zone. In total, 4922 individual birds comprising 119 species were captured between 2014 and 2018, of which 1225 individuals of 71 species were recaptured at least once. All mist-netting and bird ringing procedures conformed to set guidelines by the British Trust for Ornithology.

### 4.3.3 Movement kernel models

To determine how selective logging impacts the local movements of understory avian species within home ranges, we excluded long-distance movements that are likely to arise from other processes (natal or breeding dispersal), where there were only 15 such events observed. We restricted our dataset to only include within-plot movements (i.e. movements ranging up to 538 m), leaving 1210 individuals of 71 species. The distance moved by each individual bird

from a point of origin to the point  $x, y$  on a two-dimensional plane is called the amplitude,  $r$ , calculated using the Pythagorean theorem,  $r = \sqrt{x^2 + y^2}$ . We used the maximum distance moved,  $r$ , between any two capture locations for each individual bird to model movements with respect to habitat type (logged or unlogged forest). Maximum distance moved was used to indicate the observed potential for an individual to move a certain maximum distance within its home-range. Individual birds that were only recaptured within their original transect zone were assigned a maximum distance  $r$  of 12.5 m, which is half the buffer radius, as it is impossible for an individual to not move at all.

The hierarchical modelling framework developed here consists of two components: (1) the ‘state’ component, and (2) the ‘observation’ component. For the ‘state’ component, we use movement kernels to model the probability density of movement across different distances, and how this varies across species and habitats (Nathan *et al.* 2012). Movement kernels assume that the farther the distance, the lower the probability the subject moves at that distance. They not only describe the process of moving, but also reflect decisions made in response to food acquisition, predator avoidance and finding mates and suitable habitats.

We fitted four different movement kernel probability density functions (Rayleigh, Gamma, Log-normal and Cauchy), representing different hypotheses about the distribution of underlying movement distances (Van Houtan *et al.* 2007). The Rayleigh distribution has probability density function:

$$f(r; \sigma) = \frac{r}{\sigma^2} e^{-r^2/2\sigma^2}, \quad r \geq 0, \quad \sigma > 0,$$

where  $\sigma$  is the shape parameter which varies by both species  $s$  and habitat  $h$ . It is a thin-tailed distribution, where it decays faster than or at the same rate as an exponential, and thus assumes that larger movement distances are unlikely.

The Gamma distribution has probability density function:

$$f(r; \alpha, \beta) = \frac{1}{\beta^\alpha \Gamma(\alpha)} r^{\alpha-1} e^{-r/\beta}, \quad r \geq 0, \quad \alpha > 0, \quad \beta > 0,$$

where the shape parameter,  $\alpha$ , and the rate parameter,  $\beta$ , varies by both species  $s$  and habitat  $h$ . Its tail tends to have a slower decay compared to the Rayleigh distribution.

Heavy-tailed distributions are probability distributions whose tails decay slower than an exponential. These distributions, such as the Log-normal and Cauchy distribution, allow for movements at larger distances. The Cauchy distribution is also a fat-tailed distribution (a subclass of heavy-tailed distribution) where its tail decays following a power law. The Log-normal distribution, however, is not a fat-tailed distribution as its tail decays faster than a power law.

The Log-normal distribution has probability density function:

$$f(r; \mu, \sigma) = \frac{1}{r\sigma\sqrt{2\pi}} e^{\left(-\frac{(\ln r - \mu)^2}{2\sigma^2}\right)}, \quad r > 0, \quad \mu \in (-\infty, +\infty), \quad \sigma > 0,$$

where  $r$  is the distance moved,  $\mu$  is the location parameter and  $\sigma$  is the shape parameter. The shape parameter,  $\sigma$ , and location parameter,  $\mu$ , varies by both species  $s$  and habitat  $h$ .

The Cauchy distribution has probability density function:

$$f(r; x_0, \gamma) = \frac{1}{\pi} \left( \frac{\gamma}{(r - x_0)^2 + \gamma^2} \right), \quad r \in \mathbb{R}, \quad x_0 \in (-\infty, +\infty), \quad \gamma > 0,$$

where the scale parameter,  $\gamma$ , varies by both species  $s$  and habitat  $h$  and the location parameter,  $x_0$ , was set to zero to obtain the positive half of the Cauchy distribution.

Movement kernels can be heavily biased by spatial sampling effort, as only a subset of possible movements distances is observable for each marked individual (Van Houtan *et al.* 2007). The ‘observation’ component of the hierarchical model accounts for this, by modelling the observation process alongside the true movement process in a state-space formulation (Patterson *et al.* 2008), where for each individual we model the likelihood that the true

maximum distance was greater than the observed maximum  $r_i$ , within the range of observable distances under our sampling design. We define the probability of observing a given maximum movement distance  $r$  as the proportion of space within an annulus of radius  $r$  that intersects our sampled area (Van Houtan *et al.* 2007). Using ArcMap 10.6 (ESRI 2018), we apply buffers of radius 25 m around each transect to represent this sampled space (reflecting an assumption that individuals within 25m of a mist-net have high probability of capture) and an annulus ring width of 1m centred around the centre of the capture zone where the given individual was captured (Figure C.2). The radius size of the annulus ring reflects the maximum distance observed  $r$  for that given individual. We then calculate the area of sampled space within that annulus ring across all transects, and divided this by the total area of that annulus ring to give the  $Wr$ , the probability of observing a movement at distance  $r$  for a given individual:

$$Wr = \frac{\text{Area sampled within annulus at distance } r}{\text{Total area in annulus at distance } r}$$

The intersection of the annulus ring with the sampled space represents the likelihood that an individual, moving distance  $r$  from its former capture location, comes within the sampled space. An annulus ring width of 1m was used because we wanted to reduce the error of intersected space by producing as close as possible the maximum distance moved  $r$  (N.B. other annulus ring widths were tested, up to 12.5m which is half the buffer radius, and there were little differences in the resulting  $Wr$  values).

For each individual,  $i$ , we then model whether each observable movement distance  $r$  (ranging from the observed maximum  $r_i$  up to the observable limit  $\max(r)$ , 538m) is the true maximum distance moved by that individual (1) or not (0) as a Bernoulli trial:

$$p_{r_i:\max(r)} \sim \text{Bernoulli}(X_{s,h,r_i:\max(r)})$$

where  $X_{s,h,r_i:\max(r)}$  are movement probabilities for species  $s$  in habitat  $h$  for the range of observable distances  $r_i:\max(r)$ , given by the probability density function for a given movement kernel.

A matrix containing the observed data was constructed with rows for individuals and columns for all the possible observable distance levels. Binary values were supplied to the matrix to indicate whether an individual was observed moving a certain distance  $r$  (1) or not (0). Another matrix of similar structure to the observed data was produced for  $Wr$ , the probability of observing a movement at distance  $r$  for a given individual. These  $Wr$  values were supplied for distance levels from the individual's observed maximum distance to the observable maximum distance limit (538m) for each individual. We then model our observed data as Bernoulli trials:

$$d_{r_i:\max(r)} \sim \text{Bernoulli}(w_{r_i:\max(r)} \times p_{r_i:\max(r)})$$

where  $d_{r_i:\max(r)}$  is the matrix containing the observed data,  $w_{r_i:\max(r)}$  is the matrix containing the probabilities of observing movements to distances greater than  $r_i$  up to the observable limit (538m), and  $p_{r_i:\max(r)}$  is the corresponding binary value 0 or 1 indicating whether individual  $i$  moved these distances (1) or not (0), as given by the movement kernel above. The model thus estimates if each individual in reality moved further than its observed maximum distance, but was unobserved given the arrangement of sampled space around its initial capture location (Van Houtan *et al.* 2007).

Models were fitted using the software JAGS (Plummer 2003) through the R version 3.6.2 (R Core Team 2019) packages *rjags* (Plummer 2019) and *R2jags* (Su & Yajima 2015). We used non-informative (vague) priors and hyperpriors for all parameters. Under the hierarchical formulation, priors represent species-level movement parameters, which are drawn from community-level hyper-priors, allowing maximum use of information across the dataset (Ovaskainen *et al.* 2019). Models were run using Markov chain Monte Carlo (MCMC)

methods with three parallel chains, 30 000 iterations, a burn-in of 20 000 iterations and thinned by 10. Model convergence was assessed using the Gelman-Rubin potential scale reduction parameter,  $R_{hat}$ , where values close to 1 indicate that the model converged (Gelman & Rubin 1992).  $R_{hat}$  values between 1.0 and 1.05 were accepted. We conducted posterior predictive checks for each model (Figure C.11; Figure C.12; Figure C.13) by first computing the observed mean probability densities for each observed maximum distance. The same was then done for a simulated dataset using parameters sampled from the posterior distribution. Bayesian p-values were then computed, where values close to 0 or 1 indicated a doubtful fit and values close to 0.5 indicated a good fit (Gelman *et al.* 1996). We used best-fitting models, with the lowest deviance information criterion (DIC) value (Spiegelhalter *et al.* 2002), for subsequent inference (Table 4.1; Table C.2). The probability of each species moving distances from 1 m to 538 m was predicted from each model. Differences in movement probabilities between habitats for each species were considered to be statistically significant if the 95% credible interval of the posterior distribution for habitat differences in parameter estimates did not overlap zero. The model R scripts can be found in the Supplementary Material (Appendix C.3).

We also re-ran the above models only including the more common species occurring in both habitat types to test model sensitivity to the inclusion of data-poor species. First, we included only species with at least one individual in each habitat type, which resulted in 1165 individuals comprising 43 species in the total dataset. Second, we included only the commonest species, i.e. species with at least 5 individuals per habitat type, comprising 1035 individuals of 25 species.

To determine if recapture rate was biased by habitat type, we examined whether habitat type (logged or unlogged forests) affected the number of recaptures per transect for all species combined, as well as testing for effects of understory habitat structure, including percentage ground vegetation cover (1.5 m above ground), percentage understory vegetation cover (15 m

above ground), tree stand basal area (m<sup>2</sup>/ha) of circumference >0.6 m and sapling stand basal area (m<sup>2</sup>/ha) of circumference between 0.1 – 0.6, (see Appendix C.4 for more information).

Table 4.1. Bayesian model performance for the movement kernel model of 71 species using probability density function (pdf) for the Cauchy distribution, Rayleigh distribution, Gamma distribution and Log-normal distribution. Models with the lowest DIC values are the most parsimonious and models with less than 2  $\Delta$ DIC are considered equally parsimonious. DIC = Deviance Information Criterion,  $\Delta$ DIC = the DIC difference between the best model and that stated model, pD = the effective number of parameters, Rhat = Rhat statistic close to 1 indicates that the model converged. Rhat values up to 1.05 were accepted. All parameters in each model had Rhat values less than the maximum presented below.

<b>Distribution</b>	<b>DIC</b>	<b><math>\Delta</math>DIC</b>	<b>pD</b>	<b>Rhat</b>
Cauchy	3976.1	0.00	0.2	<1.03
Log-normal	3977.3	1.20	0.4	<1.008
Gamma	3977.5	1.40	0.4	<1.05
Rayleigh	3978.1	2.00	0.4	<1.27

#### 4.3.4 Species conservation status and traits

To investigate whether species of higher conservation concern or species with certain traits determine the magnitude of their change in movement between habitat types, we first obtained movement probability estimates for each species from the best-fitting movement kernel model (i.e. Cauchy distribution model). The effect of logging on movement for each species was calculated by subtracting mean movement probability estimates at 1 m intervals from 0 to 538m in unlogged forests from those in logged forests. These resulting values were standardised (mean=0, standard deviation=1) and then averaged to give a single mean movement change estimate for each species. Species' conservation status were obtained from the IUCN Red List, their foraging guild data were obtained from the Elton Traits 1.0 database (Wilman *et al.* 2014) and species body mass (g) data were obtained from Dunning's CRC

Handbook of Avian Body Masses (2008) and Handbook of the Birds of the World Alive (del Hoyo *et al.* 2017) (species information in Table C.1).

We used linear regression models in R version 3.6.2 (R Core Team 2019). A global model was fitted using change in movement probability between logged and unlogged forests as a function of species' body mass (g), species' conservation status, and species' foraging guild. Model was checked for normality and heteroscedasticity. To determine which metrics were important determinants of the change in movement probabilities, we compared all possible variable combinations of the global model, using the *dredge* function from the MuMIn package (Barton 2019). The most parsimonious model has the lowest AICc value (Anderson 2008) and models with less than 2  $\Delta$ AICc are considered to be equally parsimonious (Table C.3). The most parsimonious models were then fitted separately.

### 4.3.5 Species' logging sensitivity analysis

We determined whether differences in movement patterns are related to species' sensitivity to selective logging by first calculating the Relative Population Abundance (RPA) index for each species as a measure of a species' logging sensitivity (Messina *et al.* 2020):

$$RPA = \frac{\text{Abundance in logged forest} - \text{Abundance in unlogged forest}}{\text{Abundance in logged forest} + \text{Abundance in unlogged forest}}$$

Sampling effort was taken into account in the abundance data for each species in each habitat type (abundance/number of mist-net hours). The RPA index is the inverse of the logging sensitivity index (Hamer *et al.* 2015) where positive values indicate that the species has higher abundance in logged forests compared to unlogged forests (vice versa) and it has a theoretical range from -1 (species occurring only in unlogged forests) to +1 (species occurring only in logged forests). The movement probability estimates were again obtained for each species from the best-fitting movement kernel model (i.e. Cauchy distribution model). The effect of logging

on movement for each species was calculated using the same procedure as the previous analysis on species conservation status and traits, and these resulting values were also standardised. A linear regression was then fitted with change in movement probability as a function of the RPA index. The model was checked for normality and heteroscedasticity.

### 4.3.6 Trophic position analysis

To examine whether species with higher trophic positions had higher or reduced amount of changes in movement probabilities between logged and unlogged forests (and vice versa), we directly obtained trophic position values, calculated from isotope values, for 34 species from Edwards *et al.* (2013). The movement probability estimates were obtained for each species from the best-fitting movement kernel model (i.e. Cauchy distribution model). The effect of logging on movement for each species was calculated using the same procedure as the previous analysis on species conservation status and traits, and these resulting values were also standardised. Change in trophic position was then calculated by subtracting the trophic position in unlogged forests from those in logged forests. A linear regression was then fitted with change in movement probability as a function of change in trophic position. The model was checked for normality and heteroscedasticity.

## 4.4 Results

A total of 4922 individual birds comprising 119 species were captured between 2014 and 2018, of which 1210 individuals of 71 species were recaptured at least once and used in this study. We found no impact of habitat type or any understory habitat metric on species recapture rates per transect (Appendix C.4).

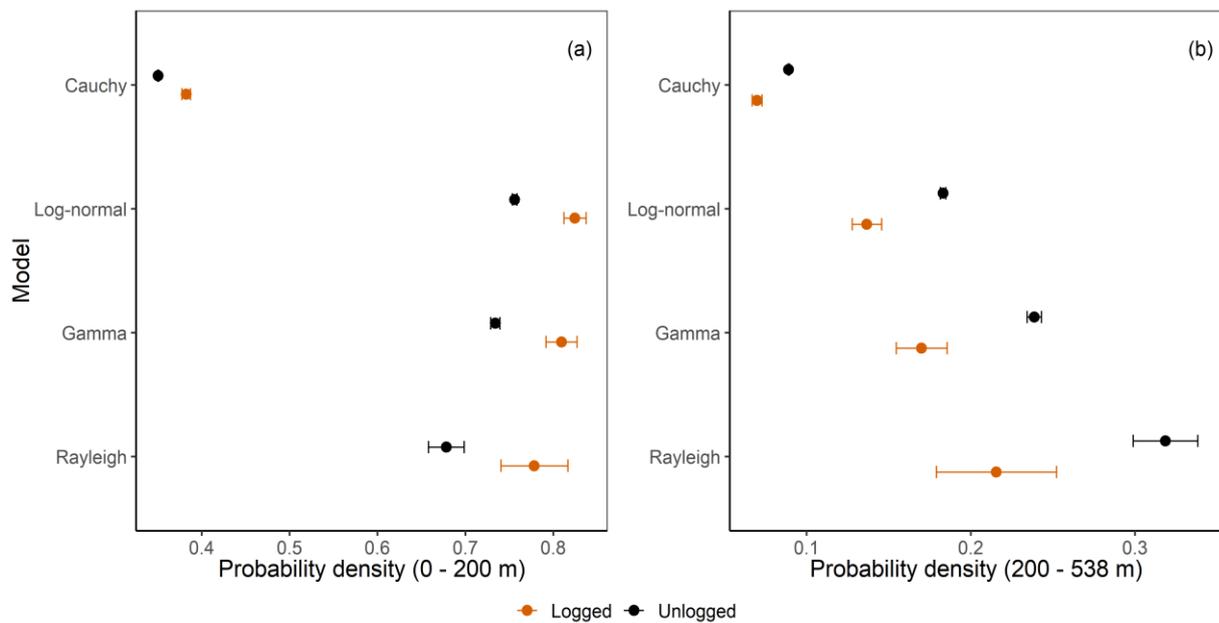


Figure 4.1. Mean probability density from all four models (Cauchy, Log-normal, Gamma, Rayleigh) containing 71 species combined for distances between (a) 0 m to 200 m and (b) 200 m to 538 m, with 95% credible intervals. Only the positive half of the Cauchy probability density function was used in the model.

#### 4.4.1 Movement patterns

Across the full dataset (71 species), the three heavier-tailed movement kernel models had relatively small differences with  $\Delta$ DIC values within 2.00 (Table 4.1) and showed similar patterns of community-level movement with respect to habitat (Figure 4.1; Figure 4.2; Figure C.4). The thin-tailed Rayleigh distribution model did not converge, suggesting poor fit to the data. For simplicity, we base further inference on the model with lowest DIC, which was the Cauchy kernel distribution. The understory community, in combination, had a higher probability of moving shorter distances (up to 200 m) in logged forests compared to unlogged forests (Cauchy: logged: mean probability = 0.382, 95% CI = 0.377 to 0.387, unlogged: mean probability = 0.350, 95% CI = 0.350 to 0.351; Figure 4.1a; Figure 4.2). The opposite pattern occurred at distances above 200 m, where the probability of moving larger distances was higher

in unlogged forests compared to logged forests (Cauchy: logged: mean probability = 0.070, 95% CI = 0.067 to 0.073, unlogged: mean probability = 0.0891, 95% CI = 0.0886 to 0.0894; Figure 4.1b; Figure 4.2).

Modelling movement probabilities of species with at least one observation in each habitat type (43 species model set) and the commonest species in the dataset (25 species model set) showed similar results to the full analysis, suggesting that community-level inferences were not sensitive to the inclusion of data-poor species (Table C.2; Figure C.3; Figure C.5; Figure C.6). Again, these models had a higher probability of moving shorter distances (up to 200 m) in logged versus unlogged forests (43 species Cauchy model: logged: mean probability = 0.382, 95% CI = 0.374 to 0.390, unlogged: mean probability = 0.351, 95% CI = 0.350 to 0.353) (25 species Cauchy model: logged: mean probability = 0.383, 95% CI = 0.371 to 0.396, unlogged: mean probability = 0.351, 95% CI = 0.349 to 0.353) (Figure C.3; Figure C.5; Figure C.6), and the reverse pattern at distances above 200 m (43 species Cauchy model: logged: mean probability = 0.070, 95% CI = 0.065 to 0.075, unlogged: mean probability = 0.0884, 95% CI = 0.0877 to 0.0892) (25 species Cauchy model: logged: mean probability = 0.069, 95% CI = 0.062 to 0.077, unlogged: mean probability = 0.089, 95% CI = 0.088 to 0.090) (Figure C.3; Figure C.5; Figure C.6).

At the species level, the results from the 71 species model set concur with those of the 43 species and 25 species model sets. Differences in movement probabilities between habitat types are only significant for seven insectivorous species (six of those seven species in the 25 species model set; Table C.1; Figure C.7), where 95% credible intervals for the difference in scale parameter,  $\gamma$ , between habitat types did not overlap zero (BCBAB: *Pellorneum nigrocapitatum*, CWBAB: *Cyanoderma erythropterum*, GHBAB: *Stachyris poliocephala*, HBAB: *Malacocincla sepiaria*, RCBAB: *Malacopteron magnum*, STBAB: *Pellorneum*

*malaccense*, YRFLPEC: *Prionochilus xanthopygius*) (Table C.1; Figure 4.3; Figure 4.4; Figure C.7).

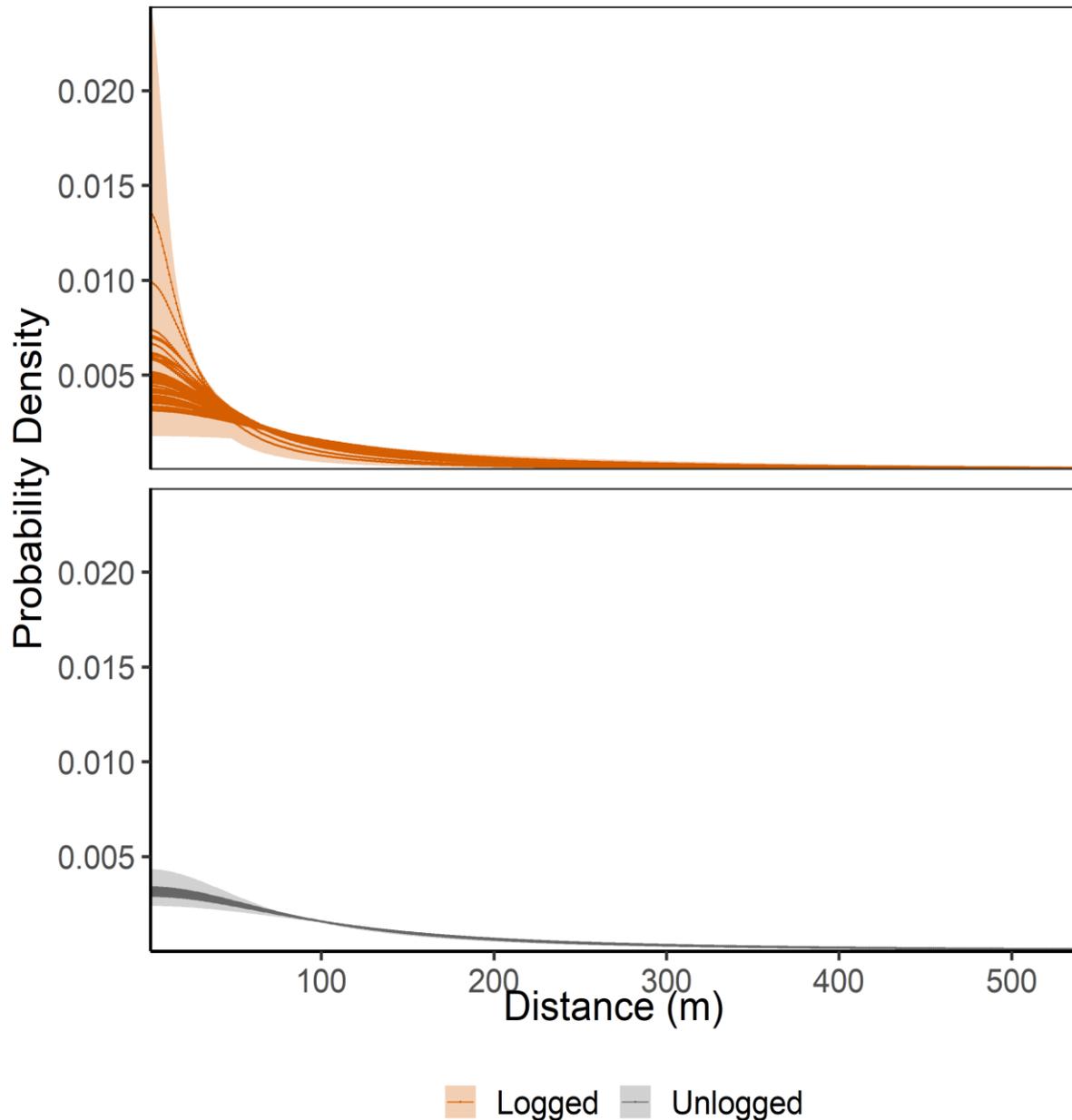


Figure 4.2. Posterior means with 95% credible intervals for movement kernels of all species fitted with the Cauchy probability density function in the 71 species model set given a certain maximum distance moved in each habitat type (logged or unlogged). Each line is for a separate species.

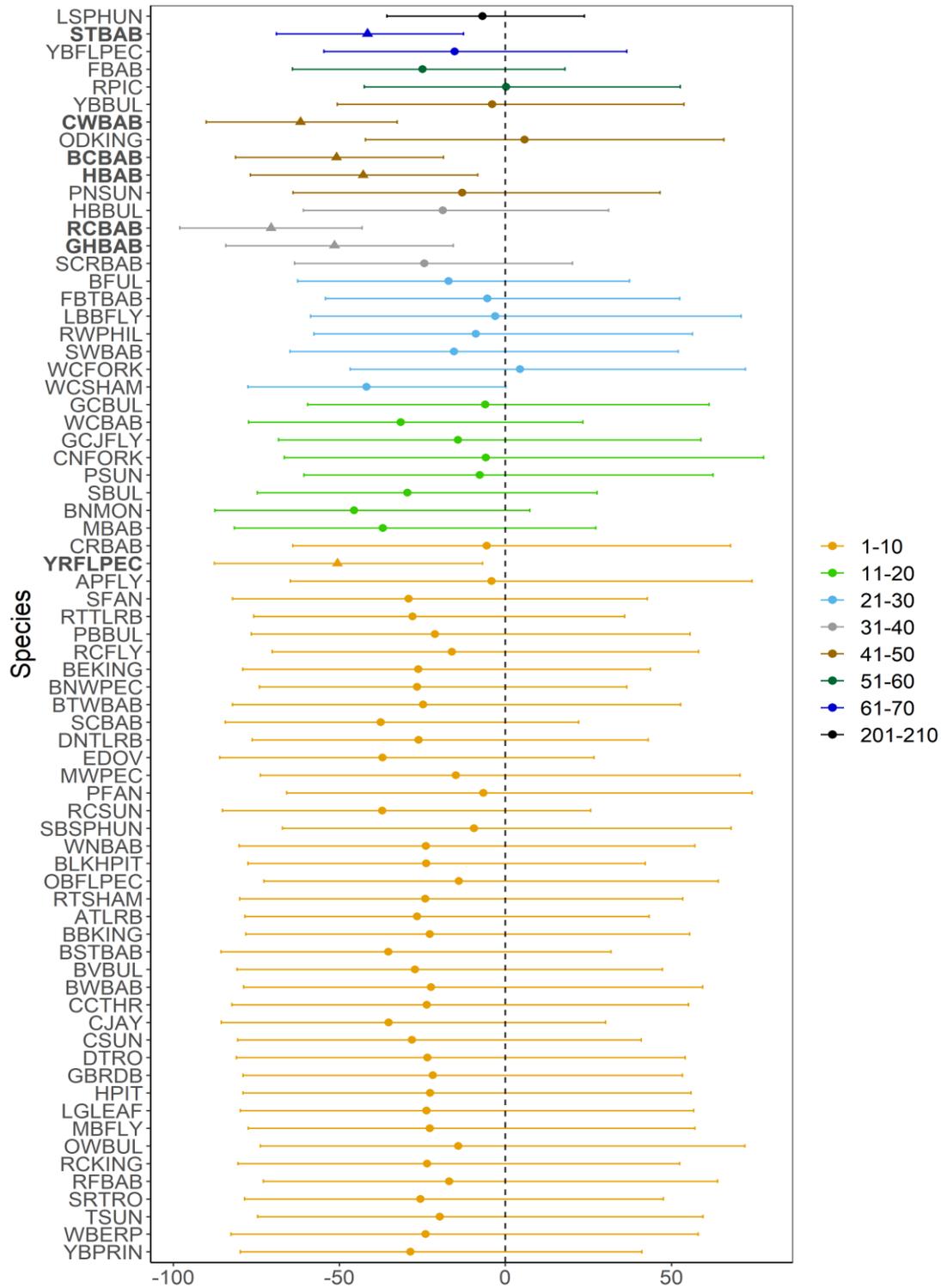


Figure 4.3. Posterior distributions (mean and 95% credible interval) for the difference in scale parameter,  $\gamma$ , between habitat types (logged and unlogged), of the Cauchy probability density function in the 71 species model set. 95% credible intervals not overlapping zero are considered to be statistically significant. Species with statistically significant movement changes are highlighted in bold. Sample sizes for each species are colour coded. Species names are substituted with the species' code (species information in Table C.1).

## 4.4.2 Species conservation status and traits

The most parsimonious models ( $<2 \Delta AICc$ ) were the null model and the model including only species' body mass ( $F = 0.32$ ,  $df = 1,69$ ,  $p = 0.57$ ) (Table C.3; Figure C.8), indicating that across all 71 species, species' conservation status, body mass and foraging guild did not determine the magnitude of their change in movement between habitat types.

## 4.4.3 Species' logging sensitivity

Species' sensitivity to selective logging (RPA index) was not related to the magnitude of change in movement probability between logged and unlogged forests for all species ( $y = 0.003x - 0.0003$ ,  $F=0.34$ ,  $df=1,69$ ,  $p=0.56$ ; Figure C.10).

## 4.4.4 Trophic position

Trophic position data was obtained for 34 of the 71 species included in the model. Overall, species' change in trophic position between logged and unlogged forests were not important determinants for the extent of change in movement probabilities between logged and unlogged forests for all species combined ( $y = 0.02 - 0.05x$ ,  $F=2.10$ ,  $df=1,32$ ,  $p=0.16$ ; Figure C.9).

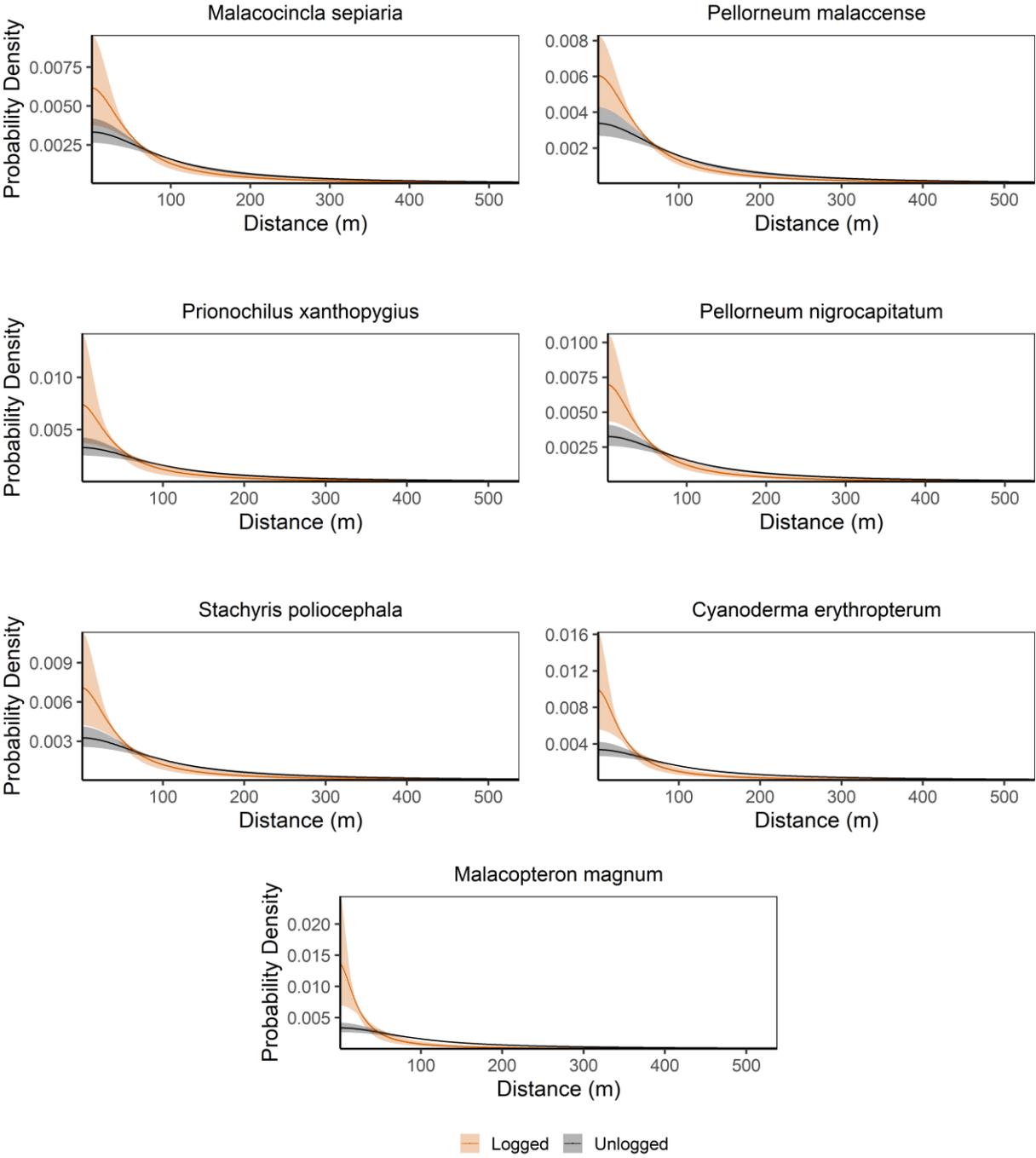


Figure 4.4. Posterior means with 95% credible intervals for movement kernels, of species with significantly different movement probabilities between logged and unlogged forests, fitted with the Cauchy probability density function in the 71 species model set given a certain maximum distance moved in each habitat type (logged or unlogged).

## 4.5 Discussion

We assessed how tropical selective logging impacts the local movements of understory avian species by comparing relative movement rates in unlogged and logged forests. We found that including communities with different species into the model (71 species model set) produced similar results to the models (43 species and 25 species model set) that only included communities of species occurring in both logged and unlogged forests. On average across the understory community, individuals had a higher probability of moving shorter distances (up to around 200 m) in logged forests compared to unlogged forests, while movement probability was higher at longer distances (above 200 m) in unlogged forests compared to logged forests. Species' conservation status, body mass, foraging guild, sensitivity to logging and trophic position did not determine the magnitude of their change in movement between habitat types, suggesting that movement plasticity and dietary plasticity are not directly linked (Edwards *et al.* 2013). Moving shorter distances could be indicative of higher fitness due to less energy expended to obtain resources (Cattarino *et al.* 2016), although this is not always the case (Doherty *et al.* 2019).

### 4.5.1 Movement patterns

The higher probability of moving shorter distances in logged forests and moving longer distances in unlogged forests could be due to the distribution of the preferred habitat type of these understory species. Understory specialist birds tend to prefer dense understories (Fagan *et al.* 2016) and these dense habitats generally occur throughout logged forests, while they are more patchily distributed in unlogged forests, as observed for red-tailed bristlebill (*Bleda syndactyla*) in Uganda (Dale & Slembe 2005). Furthermore, some species move shorter distances in their preferred habitat (Hansbauer *et al.* 2008a), which is likely resource driven

(Hansbauer *et al.* 2008b; Lees & Peres 2009; Rehm *et al.* 2018). For many understory species, the dense understory of logged forests might also provide additional cover from predators (Loveridge *et al.* 2016).

Higher predation risks could increase the likeliness of understory species to move shorter distances in logged forests (Cooper & Francis 1998; Thiollay 1999; Pangau-Adam, Waltert & Muhlenberg 2006; Ewers *et al.* 2015). Borah *et al.* (2018) suggested that lower participation in mixed flocks by understory birds, relative to mid-canopy species, could be explained by the higher availability of predator refugia in the understory, reducing the pressure for cooperative vigilance. Birds enter mixed-species flocks during times of low resource or high predation risks as flocking can have anti-predator benefits (Goodale & Kotagama 2005), thus allowing more foraging time. Moving larger distances might increase predation risks of understory species, and thus denser understories in logged forest could mean that active evasion of predators through movement is reduced (Loveridge *et al.* 2016). Structural differences in logged forests may also alter predation risk perception (Hua & Sieving 2016), with consequent impacts on movement.

Another potential explanation for reduced movement is that species occur at higher densities in logged forests and thus have smaller home-range sizes. Dale & Slembe (2005) also found smaller home range sizes and higher densities of red-tailed bristlebill (*Bleda syndactyla*) in logged forests compared to unlogged forests. Logged forests tend to have more understory arthropod prey (Edwards *et al.* 2012) and small-sized fruits, especially from pioneer trees (Levey 1988; Wells & Bagchi 2005) that are usually spatially clumped (Condit *et al.* 2002), potentially reducing the need for logged forest understory species to travel far to acquire food.

The more heterogeneous distribution of resources in unlogged forests may also lead to larger home range sizes and, hence, longer distances travelled in unlogged forests so that species can meet their survival needs (Hansbauer *et al.* 2008a; Hansbauer *et al.* 2008b; Mokross

*et al.* 2018). Despite the increase in food resources in degraded habitats, such as logged forests, some species may experience lower survival probabilities (Bailey & King 2019) due to factors like increased predation risks, more resource competition, or lower habitat quality. This could occur if habitats become ‘ecological traps’ (Gilroy & Sutherland 2007) where habitat quality declines without changes in the relative attractiveness of the habitat.

## **4.5.2 Species conservation status, traits, sensitivity and trophic position**

We found that species of high conservation concern are equally likely to have similar movement patterns to those of low conservation concern and species traits, such as body mass and foraging guild, did not influence the extent of change in movement of our understory species. This, however, was not supported by Ramos *et al.* (2020) where avian species movement patterns in a fragmented landscape were dependent on their body mass and diet. For example, larger species and frugivores moved greater distances (Ovaskainen *et al.* 2019), owing to the lack of predictability of fruit resource production. Species that were more sensitive to logging were not more likely have greater or smaller movement changes compared to species which were more robust to logging, suggesting that movement as a mechanistic process does not directly underpin the relative population abundance of a species in logged forests.

Previous work has shown that understory species in our study community tend to feed higher up the food chain in logged forests (Edwards *et al.* 2013) but we did not find a link between the likeliness of species with higher trophic position change with more or less movement change. This could indicate behavioural plasticity (Schleuning *et al.* 2011), as species that change their movement to a higher extent may be doing so in order to keep exploiting the same prey type, which is distributed differently in degraded habitats. Some Malaysian avian species alter their foraging techniques in response to forest structure changes,

increasing foraging efficiency (Mansor *et al.* 2018). Changes in movement probabilities in logged forests could be driven by the distribution and/or availability of nesting sites, occurrence of competitors, predation risks or food resource availability, but the lack of association with trophic position shifts suggest that it is not associated with changing prey type.

### **4.5.3 Conclusions**

In conclusion, species' movement probabilities were higher at shorter distances in logged forests and movement probabilities were higher at longer distances in unlogged forests, where these differences were significant for seven insectivorous species. The magnitude of movement changes were not related to species conservation status, traits (i.e. body mass and foraging guild), sensitivity to logging and trophic position, suggesting that these traits and dietary plasticity are not directly linked to movement plasticity. The presence of multiple red-listed species within our sample underscores the potential for selectively logged forests to retain high conservation value and lending further support for their protection for biodiversity conservation (Edwards *et al.* 2011). However, we remain unsure if survival and recruitment in logged forest are at, below, or above replacement level, and populations might be sustained by immigration from surrounding 'source' unlogged forests, that produce a surplus of dispersing individuals (Gilroy & Edwards 2017). Future studies are now needed to examine how selective logging impacts species survival and recruitment, in combination with movement patterns, especially for rare and endangered species.

## **4.6 Data availability**

Data will be made available from Figshare upon publication

.

## 4.7 Acknowledgements

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## Chapter 5

# Apparent survival of tropical understory birds after selective logging



Bornean banded pitta (*Hydrornis schwaneri*)

This chapter is currently in preparation for submission:

**Cosset, C.C.P., Gilroy, J.J., Tomassi, S., Benedick, S., Nelson, L., Cannon, P.G., Messina, S., Kaputa, M., Fandrem, M., Madrid, R.S., Lello-Smith, A., Pavan, L., King, B., Fogliano, R., Hackney, T.B., Gerald, E., Chai, J.Y.-W., Cros, E., Chong, Y.Y., Tan, C.H., Chai, R.R., Cheoh, C.O. & Edwards, D.P. Apparent survival of tropical understory birds after selective logging.**

## 5.1 Abstract

Across the tropics, forest degradation is primarily driven by selective logging, with over 400 million hectares slated for logging. In the short term, selective logging maintains species richness, underpinned by changes in species' abundance from more to less common. A key issue is that species retention does not guarantee long-term population viability. Assessments of species survival rates, which determine population size and long-term population viability, are severely lacking in selectively logged forest. Another important consideration is El Niño events, which are extreme manifestations of climate change and have been shown to increase the detrimental impacts of selective logging. In this first empirical community assessment of its kind, we assessed (1) the survival rates of 71 species of tropical understory birds in lowland selective logged and unlogged old-growth forests of Sabah, Malaysian Borneo, a global biodiversity hotspot, and (2) determined how the 2015-16 El Niño event affected species survival in these logged and unlogged forests. We used a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework to estimate habitat-specific survival at the community and species levels for each habitat type. We found similar apparent survival probabilities across all 71 understory avian species in both unlogged and logged forests. This may be due to species ecological traits and physiological coping mechanisms that enable survival in degraded habitats. Moreover, the absence of an effect on species' survival from the 2015-16 El Niño supports the notion that selectively logged forests are thermally buffered from climate change impacts. Although uncertainties in the survival estimates exist as a result of low recapture rates and model limitations, the continued presence of multiple species of conservation concern as well as forest specialist species provides support for the long-term potential of selectively logged forests to maintain high conservation value. Our findings thus underscore the importance of protecting selectively logged forests for biodiversity conservation.

## 5.2 Introduction

Across the tropics, forest degradation is primarily driven by selective logging activities (Kissinger *et al.* 2012, Edwards *et al.* 2014b). Over 400 million hectares of the world's tropical forests are assigned for selective logging activities, mainly located in lowland forests in Southeast Asia, the Congo and the Amazon (Asner *et al.* 2009, Blaser *et al.* 2011). Selective logging activities will continue to increase as timber demands are predicted to double by 2030 and increase six-fold by 2060 (FAO 2009, Raunikar *et al.* 2010).

In the short term (ie up to ~20 years post-logging), selectively logged forests retain substantial biodiversity, especially with reduced-impact harvest techniques and at lower harvest intensity (Edwards *et al.* 2011, Burivalova *et al.* 2014). Species richness and functional diversity is largely maintained after selective logging with some losses in forest specialist species (Edwards *et al.* 2014b). However, species' abundance and community composition are altered after selective logging (Edwards *et al.* 2011, Edwards *et al.* 2014b) and shifts in species' food webs lead to birds feeding higher up in the food chain in selectively logged forests (Edwards *et al.* 2013).

Current knowledge on the impacts of selective logging mostly cover its short-term impacts such as the maintenance of much species and ecosystem function after selective logging (Edwards *et al.* 2014b) with changes in community composition and species' abundance as forest-specialist species are more negatively affected than generalist species (Edwards *et al.* 2011). Protecting selectively logged forests for biodiversity conservation has become a potential solution to the current biodiversity and ecosystem crises, especially because they can be cheaper to conserve than old-growth due to reduced timber revenues (Fisher *et al.* 2011b) and can expand and connect existing protected areas (Edwards *et al.* 2014b).

A key issue with current studies is that the retention of high species richness or abundance after selective logging does not determine population viability in the long term (Cosset *et al.*

2019). For instance, high population abundance may be caused by multiple factors, including source-sink dynamics (Gilroy & Edwards 2017) and ecological traps (Gilroy & Sutherland 2007). Thus, our understanding of the impacts of selective logging and subsequent conservation policy may be flawed.

Survival determines population size and long-term population viability (Saether and Bakke 2000). Assessments of species survival rates are lacking in biodiversity hotspot areas (Cosset *et al.* 2019). Selective logging can affect individual survival by altering food and breeding resources, predator communities, competition and parasite load (Visco *et al.* 2015, Tchoumbou *et al.* 2020). Moreover, habitat degradation creates more open canopies, changes forest structure and alters resources, which can exacerbate the effects of climate change, as climate change further alters habitat quality and resources (Wolfe *et al.* 2015, Woodworth *et al.* 2018). The survival of some species may be more affected by habitat degradation compared to others depending on their degree of specialisation to that habitat type (Burivalova *et al.* 2015, Srinivasan 2019, Wolfe *et al.* 2020).

A key question is how selective logging impacts animal species survival rates in lowland tropical forests. There appears to be no such study in lowland tropical forests, however, in montane Hawaiian forests, selective logging had no impact on the survival of Elepaio flycatcher bird populations (*Chasiempis sandwichensis*), despite a lower carrying capacity observed in logged sites (VanderWerf 2004). This species appears to have adapted to their disturbed environment by increasing territory sizes to locate sufficient resources for survival. In subtropical montane forest of the eastern Himalayas, survival rates of avian species across the understory community in the selectively logged forests were trait dependent, where solitary foragers and non-migratory species had lower survival probabilities in selectively logged compared to intact forests (Srinivasan 2019). There is thus an urgent need to assess the

community-wide impacts of tropical selective logging on species' survival in lowland forests, including on habitat-sensitive rare species.

Selectively logged forests have often been considered to be more threatened by climate change due to the interactions between multiple drivers of biodiversity loss (Mantyka-pringle *et al.* 2012, Sirami *et al.* 2017, but see Senior *et al.* 2018). El Niño events are an extreme manifestation of climate change and have been shown to increase the detrimental impacts of selective logging (Nepstad *et al.* 1999, França *et al.* 2020). Hence, how would El Niño events interact with selective logging to affect species' survival?

We assessed (1) the survival rates of tropical understory avian species in the lowland selective logged and unlogged old-growth forests of Sabah, Malaysian Borneo, a global biodiversity hotspot (Myers *et al.* 2000), and (2) determined how the 2015-16 El Niño event affected species survival in selectively logged and unlogged forests. Birds are used as our study taxa as they are important for many ecosystem processes (Sekercioglu 2006) and are reliable indicators of responses in other taxa and overall ecosystem health (Edwards *et al.* 2014a). We used a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework (Royle 2008), adapted from (Munoz *et al.* 2018), to estimate habitat-specific survival at the community and species levels for each habitat type (selectively logged and unlogged forests). This study represents the first empirical community assessment of selective logging impacts on species survival rates in tropical lowland forests (71 species in 19 families).

## 5.3 Materials & Methods

### 5.3.1 Study site

This study site was situated in the global biodiversity hotspot of Northern Borneo in the Malaysian state of Sabah (Myers *et al.* 2000). Sampling occurred in two habitat types (unlogged, old-growth forest and twice-logged, selectively logged forest) located in the

Yayasan Sabah (YS) concession, a ~1 million hectare contiguous forest area comprised of mostly lowland evergreen forest dominated by highly valuable timber tree species (Dipterocarpaceae) (Newbery *et al.* 1992, Fisher *et al.* 2011a).

We sampled in the unlogged old-growth forests, used as controls, of the 45 200 ha Danum Valley Conservation Area (DVCA) and Palum Tambun Watershed Reserve (4° 55' N, 117° 40' E), within the YS concession. Our selectively logged forests within the YS concession were concentrated in the 126,846 ha Ulu-Segama Forest Reserve (USFR) (4° 57' N, 117° 55' E), adjacent to DVCA. The first logging cycle in this area extracted trees >0.6 m DBH, yielding 73 to 166 m<sup>3</sup> of timber per hectare, occurring from 1976 to 1991 (Edwards *et al.* 2011). Eleven years later, from 2001 to 2007, the second logging cycle was conducted with trees >0.4 m DBH extracted, yielding 15 to 72 m<sup>3</sup> per hectare (Edwards *et al.* 2011).

### 5.3.2 Avifaunal sampling

The understory avian community was sampled using mist-netting techniques in a capture-mark-recapture methodology. Three sampling plots were created in each habitat type (i.e. selectively logged and unlogged forests), where plots were spaced at least 1.83 km apart (4.95 km ± 1.26 km: unlogged = 6.23 km ± 2.28 km; logged = 3.67 km ± 1.04 km). Three parallel 250 m transects, 250 m apart, were set up in each plot (Figure D.1). Each transect contained fifteen 12 m mist-nets placed successively, with an additional 70 m in total of extra space between the mist nets to avoid placing them over fallen tree trunks or very steep gullies. Mist-netting was conducted over two consecutive days from 06:00 to 12:00, with sampling occurring three times in each plot (approximately monthly) from early June to early September, primarily the non-breeding period for birds, yearly from 2014 to 2018. We did not conduct mist-netting during heavy rain, high winds or when elephants were in the vicinity, thus

equating to 38,835 mist-net hours in total (unlogged: 20,300 mist-net hours, logged: 18,535 mist-net hours).

Captured birds were identified to species, tagged with a uniquely numbered leg ring, sexed, aged, and released at the mist-net of capture within the zone. Individuals only caught once were not included in this study as they are considered to be transients (Pradel *et al.* 1997). All mist-netting and bird ringing procedures conformed guidelines of the British Trust for Ornithology.

### 5.3.2 Survival modelling

To determine the effects of habitat type on adult avian survival, juveniles were removed from the dataset as there are age-specific differences in survival probabilities between juveniles and adults (Munoz *et al.* 2018) and sample sizes of juveniles were too small to model in most species, leaving 1112 individuals comprising 71 species. Species-specific arrays with 3-dimensions (individuals x occasions x species) were constructed for the capture histories of each individual, containing the number of secondary occasions (months: June, July and August) that the individual is captured in for each primary occasion (year) for each species. Another 3-dimensional array of similar structure to the capture histories was built for the habitat covariate data, containing information about the habitat type (1 = logged, 2 = unlogged, 3 = unknown; primary occasions after first capture when the individual was not recaptured were assigned the habitat type '3') in which each individual was caught at each primary occasion and for each species. Two individuals were recaptured in different habitat types within the same year and they were assigned the habitat type in which they were first captured for that specific year. All primary occasions (years) before first capture for each individual are filled with NAs (see Appendix D.3 for data structure).

We estimated habitat-specific survival using a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework (Royle 2008), adapted from (Munoz *et al.* 2018), which estimates apparent survival at the community level and at the species-level for each habitat type (selectively logged and unlogged). We assume that species survival rates and recapture probabilities would be more similar within species (i.e. between habitats) rather than between species (i.e. within habitats). Therefore, species-level parameters are from a statistical distribution of the logit transformation with a survival or recapture probability intercept and habitat effects. The intercepts and habitat effects are random effects with hyper-parameters describing species averages and among species heterogeneity within their community, and the habitat effect averages and heterogeneity, respectively:

$$\text{logit}(\Phi_{s,\text{log}}) = \text{lphi}_s$$

$$\text{logit}(\Phi_{s,\text{unl}}) = \text{lphi}_s + \text{beta1}_s$$

$$\text{lphi}_s \sim \text{Normal}(\mu_\phi, \sigma_\phi)$$

$$\text{beta1}_s \sim \text{Normal}(\mu_{\text{beta1}}, \sigma_{\text{beta1}})$$

$$\text{logit}(p_{s,\text{log}}) = \text{lp}_s$$

$$\text{logit}(p_{s,\text{unl}}) = \text{lp}_s + \text{beta2}_s$$

$$\text{lp}_s \sim \text{Normal}(\mu_p, \sigma_p)$$

$$\text{beta2}_s \sim \text{Normal}(\mu_{\text{beta2}}, \sigma_{\text{beta2}})$$

where species-specific estimates  $\Phi_{s,\text{log}}$  and  $\Phi_{s,\text{unl}}$  are survival in selectively logged and unlogged forests, respectively, and,  $p_{s,\text{log}}$  and  $p_{s,\text{unl}}$  are recapture probability in selectively logged and unlogged forests, respectively, for each species,  $s$ . The hyperparameters  $\mu_\phi$  and  $\sigma_\phi$  represent the community-level mean and variance survival parameters and, hyperparameters  $\mu_p$  and  $\sigma_p$  are the equivalents for recapture probability. Hyperparameters

$\mu_{beta1}$  and  $\sigma_{beta1}$  or  $\mu_{beta2}$  and  $\sigma_{beta2}$  represent the community-level habitat effect averages and variances.

The CJS model consists of modeling the individual state and the observation process, both of which are only defined for primary occasions after the first capture occasion (year) as it conditions on the first capture. For each species, the individual state is modelled as a Bernoulli trial. This state process contains two components. The first component being the initial state:

$$z_{i,f} = 1$$

where,  $z_{i,t}$  is the latent variable describing the “alive state” for individual  $i$  at time  $t$ ; 1 meaning the individual is alive and 0 for a dead individual.  $f_i$  is observed data representing the time when individual  $i$  was first caught. Thus, the state of individual  $i$  at first capture is always 1.

The second component is the individual transition states at subsequent captures from time  $t$  to time  $t + 1$  modelled as Bernoulli trials:

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(z_{i,t} \times \Phi_{X(i,t,s)})$$

where probability  $\Phi_{i,t}$  varies from  $(t = 1, \dots, T - 1)$ ;  $T$  being the last capture occasion (year).

If an individual is alive at time  $t$ ,  $z_{i,f} = 1$ , it survives to time  $t + 1$  with probability  $\Phi_{X(i,t)}$ .

The habitat covariate array,  $X_{i,t,s}$ , is used to model habitat type effects on avian survival, where there are three states – selectively logged, unlogged and unknown with values 1, 2 and 3 respectively. The unknown state, 3, is not observed and is modelled using the mixture approach adapted from Munoz *et al.* (2018):

$$\Phi_{s,3} = \omega_s \times \Phi_{s,1} + (1 - \omega_s) \times \Phi_{s,2}$$

where the species-specific survival for individuals in unknown habitat,  $\Phi_{s,3}$ , is a weighted average of survival in selectively logged forests,  $\Phi_{s,1}$ , and survival in unlogged forests,  $\Phi_{s,2}$ .

Weights are the proportions of individuals in selectively logged forests,  $\omega$ , and unlogged forests,  $1 - \omega$ .

The observation process for each species is modelled as a Binomial model with three trials, representing the total number of secondary capture occasions (June, July and August):

$$y_{i,t,s} \sim \text{Binomial}(z_{i,t} \times p_{X(i,t,s)}, 3)$$

where  $y_{i,t,s}$  is the array of capture histories and  $p_{i,t}$ , varies from  $(t = 2, \dots, T)$ . If an individual is alive at time  $t$ , it is recaptured at time  $t$  with probability  $p_{X(i,t,s)}$ . The X habitat covariate array,  $X_{i,t,s}$ , is used to model habitat type effects on avian recapture probability. The same mixture approach above is done for recapture probability of individuals in unknown habitat,  $p_{s,3}$ :

$$p_{s,3} = \omega_s \times p_{s,1} + (1 - \omega_s) \times p_{s,2}$$

We also fitted a second model in which we hypothesised that survival rates may vary between El Niño and non-El Niño years and between habitat types (selectively logged and unlogged forests). We first obtained precipitation data (mm) for each year (2014 to 2018) from the weather station at the DVCA, and then standardised the precipitation data so that it had a mean of zero and a standard deviation of 1. The El Niño model is similar to the model above except that survival varies by primary occasion and a precipitation term is added to the survival logit transformed distribution:

$$\text{logit}(\Phi_{t,s,\text{log}}) = \text{lphi}_s + \text{beta3} * \text{precipitation}_t$$

$$\text{logit}(\Phi_{t,s,\text{unl}}) = \text{lphi}_s + \text{beta1}_s + \text{beta3} * \text{precipitation}_t$$

$$\text{lphi}_s \sim \text{Normal}(\mu_\Phi, \sigma_\Phi)$$

$$\text{beta1}_s \sim \text{Normal}(\mu_{\text{beta1}}, \sigma_{\text{beta1}})$$

$$\text{beta3} \sim \text{Normal}(\mu_{\text{beta3}}, \sigma_{\text{beta3}})$$

where species-specific survival estimates  $\Phi_{t,s,habitat}$  vary by habitat type (selectively logged or unlogged forests) and primary occasion (years 2014 to 2018) (see Appendix D.3 for model code).

To test the robustness of our results, we fitted two more models with only the most common species in our dataset. We only included species with more than 20 individuals which left a total of 843 individuals from 18 species used in these two models. The first of these two models was a multi-species model and is identical to the model excluding El Niño effects. In the second model, we ran single-species models, similar to the model excluding El Niño effects but excluding the hierarchical structure.

All models were fitted using the software JAGS (Plummer 2003) through the R version 3.6.3 (R Core Team 2020) packages *rjags* (Plummer 2019) and *R2jags* (Su & Yajima 2015). We used non-informative (vague) priors for all parameters running models using Markov chain Monte Carlo (MCMC) methods with three MCMC chains, 100 000 iterations, a burn-in of 60 000 iterations and thinned by 5. Model convergence were assessed using the Gelman-Rubin potential scale reduction parameter,  $R_{hat}$  (Gelman & Rubin 1992). Chains were considered to have converged when values were close to 1 but values up to 1.05 were accepted.

We evaluated goodness-of-fit for each model using the Freeman-Tukey statistic by simulating expected data from the model and comparing it to the observed data (Royle *et al.* 2014). Bayesian p-values were then computed, where values above 0.9 or below 0.1 indicated a doubtful fit and values close to 0.5 indicated a perfect fit (Gelman *et al.* 1996). Differences in survival estimates between habitat types were considered to be statistically significant if the 95% credible interval of the posterior distribution for habitat differences in parameter estimates did not overlap zero. Model R code can be found in the Supplementary Material (Appendix D.3).

## 5.4 Results

Across five years (2014 to 2018), a total of 4922 individual birds from 119 species were captured, where, 1112 adult individuals comprising 71 species from 19 families were recaptured at least once and fulfilled the inclusion criteria for this study. Of these, 15 species were recaptured only in selectively logged forest and 14 species only in unlogged forest (Table D.1). Bayesian p-values for the model excluding El Niño effects, including El Niño effects, the multi-species model and the single-species model are 0.282, 0.282, 0.288 and 0.287 respectively.

Both models excluding and including the effects of El Niño showed no differences in apparent survival probability between selectively logged and unlogged forests for any species (Figure 5.1; Figure 5.3; Figure D.2). Model comparisons demonstrate that both models had

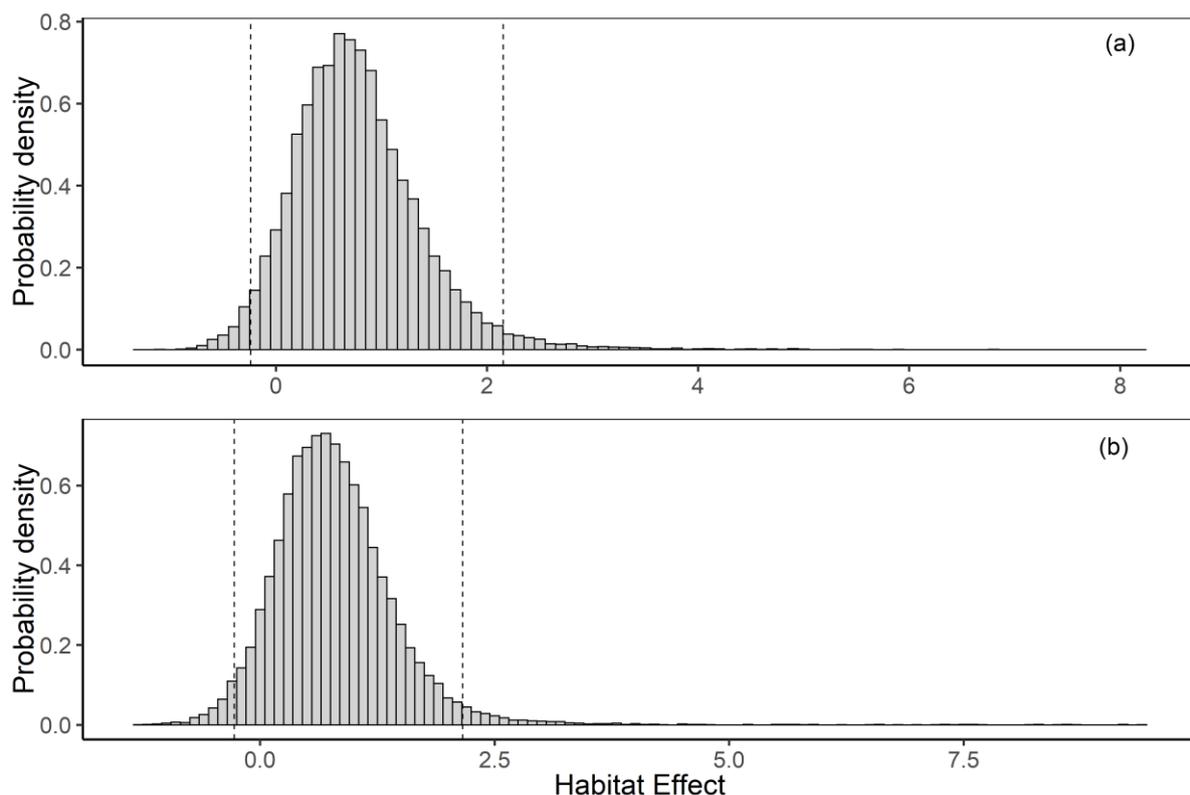


Figure 5.1. Posterior distribution for the community-level mean habitat effect on adult apparent survival,  $\mu_{beta1}$ , under the model excluding El Niño effects (a) and including El Niño effects (b). Vertical dashed lines show the 95% credible interval limits. 95% credible intervals including zero are considered to be not statistically significant.

similar precision in species-specific estimates (Figure 5.2). There was no effect of habitat type (selectively logged or unlogged forest) on the survival estimates on the overall community for both models. This is shown by the posterior distribution for the community-level mean habitat effect on adult apparent survival,  $\mu_{beta1}$ , where the 95% credible interval included zero (Model without El Niño: mean = 0.77, 95% CI = -0.24 – 2.15; El Niño model: mean = 0.79, 95% CI = -0.28 – 2.16; Figure 5.1). Furthermore, there is no effect of precipitation on species survival in the model including El Niño effects, shown by the community-level mean precipitation effect on adult apparent survival,  $\mu_{beta3}$ , where the 95% credible interval included zero (mean = 0.20, 95% CI = -0.15 – 0.54).

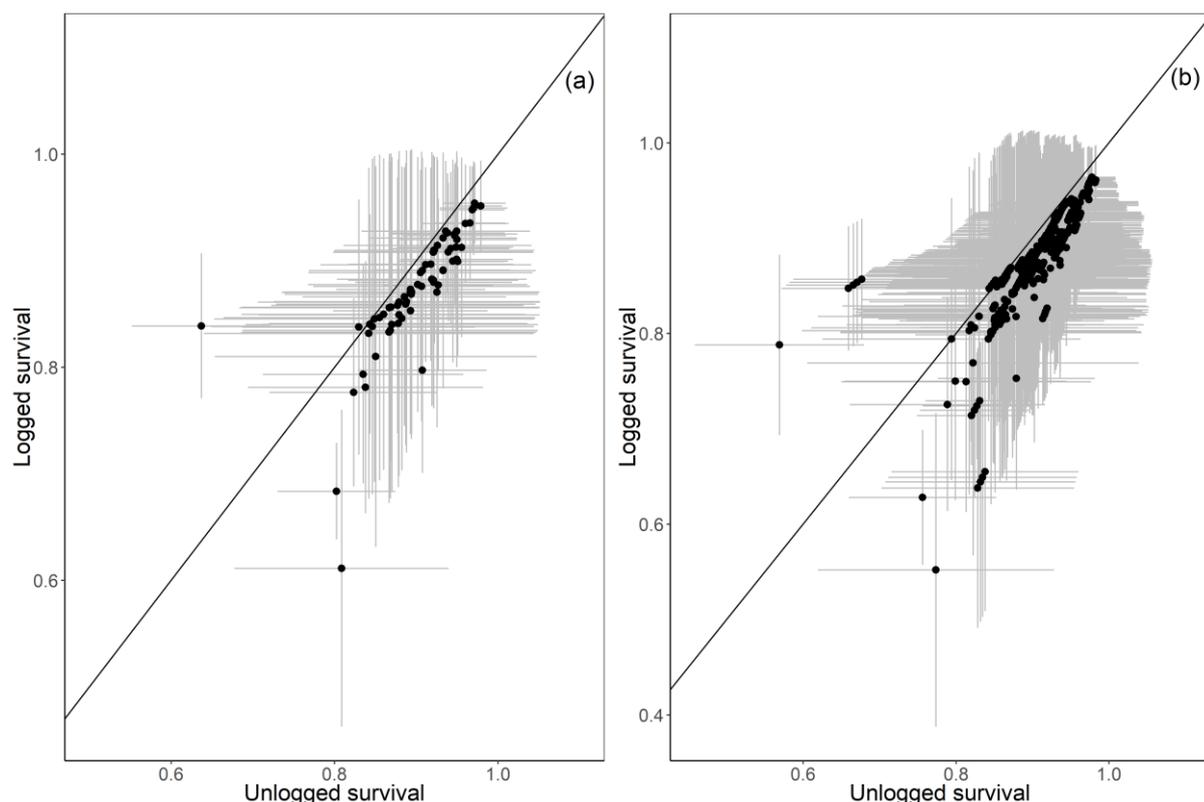


Figure 5.2. Comparison of selectively logged forest and unlogged forests adult apparent survival estimates, with standard deviation values represented by the grey lines, for all species in the model excluding El Niño effects (a) and including El Niño effects (b). Lines correspond to the identity line  $y=x$ .

Across the community, mean species survival estimates ranged from 0.61 – 0.95 in selectively logged forests and 0.64 - 0.98 in unlogged forests for the model excluding El Niño effects (Table D.1). For the model including El Niño effects, mean species survival estimates ranged from 0.55 – 0.96 in selectively logged forests and 0.57 – 0.98 in unlogged forests. In comparison, other studies of apparent survival rates on similar sized avian species in Malaysia reported estimates ranging from 0.5 – 0.85 (Martin *et al.* 2017, Boyce *et al.* 2020). At the species-level, survival probability was similar in both selectively logged and unlogged forests for all species in both models excluding and including El Niño effects (Figure 5.3; Figure D.2). For each species, 95% credible intervals of the posterior means for the difference between mean adult apparent survival in selectively logged forest  $\Phi_{s,1}$  and unlogged forest  $\Phi_{s,2}$  overlapped zero.

The multi-species and single-species models including only the most common species (i.e. more than 20 individuals per species) showed similar results to the models including all 71 species (Figure D.3). The apparent survival estimates of all species were not significantly different between habitat types, except for *Prionochilus maculatus* which had a significantly higher survival estimate in selectively logged forest for the single-species model only (Figure D.3).

## 5.5 Discussion

The emerging global restoration agenda, motivated by international initiatives, such as the Bonn Challenge and potentially lucrative carbon markets, has led to a policy focus on the restoration and protection of degraded tropical forests for biodiversity and ecosystem recovery (Blaser *et al.* 2011, Ciccarese *et al.* 2012). Protecting selectively logged forests requires a comprehensive understanding of its effectiveness for biodiversity conservation in the long-term. We investigated the impacts of tropical selective logging on the survival of understory

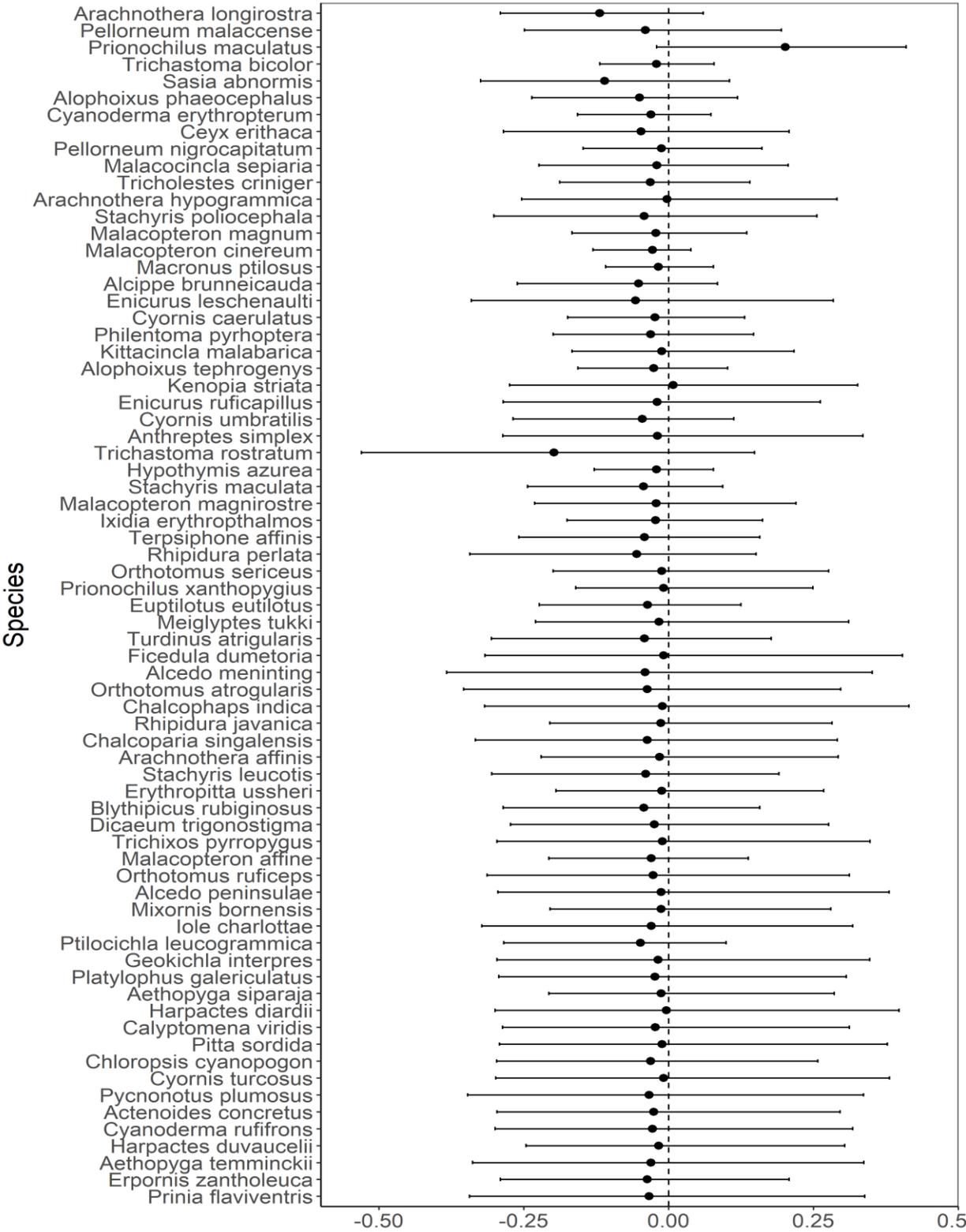


Figure 5.3. Posterior means with 95% credible intervals, from the model excluding El Niño effects, for the difference between mean adult apparent survival in selectively logged forest  $\Phi_{s,1}$  and unlogged forest  $\Phi_{s,2}$  for each species. 95% credible intervals including zero are considered to be not statistically significant. Species are ordered by sample size from largest (top) to smallest.

avian species by estimating adult apparent survival probability in selectively logged and unlogged old-growth forests and determined the effects of the 2015-16 El Niño event on species survival in selectively logged and unlogged forests. Adult apparent survival probabilities were similar in both selectively logged and unlogged forests at both the community and species levels, indicating that our sampled avian community had some ability to adapt to degraded forests, likely by obtaining sufficient resources in logged forests. The 2015-16 El Niño event did not seem to have any impact on species' survival in selectively logged and unlogged forests, due to selectively logged forests being potential refuges in the events of climate change (Senior *et al.* 2018).

Being understory specialist species, our sampled avian community are likely more resilient to changes in selectively logged forests. Selectively logged forests have widely available dense understory (Dale *et al.* 2000), which is preferred by many of these species (Fagan *et al.* 2016). A preference for denser understories could be resource driven (Loiselle & Blake 1993, Chatterjee & Basu 2018), although many bird species exhibit plasticity in their foraging behaviour (Mansor *et al.* 2018) and are able to supplement their diet using different food resources based on their availability (Price *et al.* 2003, Carnicer *et al.* 2009). For example, understory avian species in Bornean selectively logged tropical forests had higher trophic levels than in unlogged forests, indicating more protein rich diets (Edwards *et al.* 2013). Another benefit of a denser understory is the additional protection from predators for many understory species (Loveridge *et al.* 2016, Hua & Sieving 2016, Pillay *et al.* 2019).

The ability of understory avian species to survive in the altered environment of selectively logged forests may largely depend on their traits (Burivalova *et al.* 2015, Srinivasan 2019). Smaller frugivores, carnivores, insectivores and larger omnivores tend to persist in logged forests (Burivalova *et al.* 2015), with several of these traits possessed by some of our study species. Furthermore, nectarivores initially increase in abundance after selective logging

(Burivalova *et al.* 2015) which could explain the unaffected survival levels in our study as sampling occurred only seven years after selective logging activities ceased in 2007. Mixed-species flocking participation is also an important trait that aids species' survival in selectively logged forests, exhibited by 17 species in our study. (Srinivasan 2019) found higher survival probabilities in understory avian species that participated in mixed-species flocks in more heavily selectively logged montane forests compared to more intact forests. Avian species in selectively logged forests also have different regulation of oxidative status, a physiological mechanism enabling these species to survive in altered environments (Messina *et al.* 2020a).

The last selective logging activity ceased in 2007, seven years before sampling in this study was conducted. The understory avian community was sampled in these forests shortly after from 2007 to 2009 (Edwards *et al.* 2011) and compared to the logged community sampled in this study, there was a similar set of species caught, of which we were able to include most of these species in the model. This is not surprising considering that disturbance-tolerant species do well in selectively logged forests, proliferating in place of rarer forest-specialist species (Newbold *et al.* 2014). However, there is some evidence of species previously only caught in unlogged forests between 2007 and 2009, returning to selectively logged forests in this study, for example, *Aethopyga temminckii* and *Rhipidura perlata*. Furthermore, species that tend to prefer unlogged forests, such as *Kenopia striata* and *Stachyris maculata*, were found in selectively logged forests both in the 2007 to 2009 dataset as well as in this study.

The lack of difference in survival probabilities between selectively logged and unlogged forests may be due to uncertainty in the estimates of survival probabilities generated by low recapture rates (Tinoco *et al.* 2019). Obtaining a robust number of recaptures remains a challenge for many mist-netting studies, even for those with over a decade of sampling (Tinoco *et al.* 2019). However, we found no variation in species-level survival probability or confidence intervals with increasing recaptures: thus, even *Arachnothera longirostra*, *Prionochilus*

*maculatus* and *Pellorneum malaccense* with 532, 182 and 154 recaptures respectively still revealed no impacts of logging on survival. These models are unable to distinguish between deaths and permanent emigration. Permanent emigration may be of higher occurrence from logged forests to unlogged forests, as observed by (Srinivasan *et al.* 2015). Future studies are required to integrate dispersal parameters into the model to generate more accurate survival estimates.

The lack of an effect that the 2015-16 El Niño event had on species' survival suggests that selectively logged forests have the potential to be thermally buffered from the impacts of climate change, providing refuge for many species (Senior *et al.* 2018). This is in contrast to studies finding that changes in the structure of selectively logged forests, i.e. lower and more fragmented canopy with large gaps in the forest (Okuda *et al.* 2003, Ewers *et al.* 2015), lead to increased day-time temperatures and changes in the number of "cool" microhabitats (Saner *et al.* 2009, Scheffers *et al.* 2014, Carlson *et al.* 2017). Therefore, having detrimental impacts on biodiversity (Nepstad *et al.* 1999, França *et al.* 2020). Instead, a recent study by Senior *et al.* (2018) conducted in our study site found that selectively logged forests had similar thermal buffering abilities to unlogged old-growth forests, with comparable amounts of microclimates, and similar macroclimate and microclimate temperatures. Furthermore, it has been shown that the presence of more novel habitats in selectively logged forests allows them to be thermally buffered, thus providing biodiversity with protection from climate change (Holting *et al.* 2016).

### **5.5.1 Conclusions**

Similar apparent survival probabilities of understory avian species in both unlogged and selectively logged forests could indicate long-term resilience to logging impacts (Rutt *et al.* 2019). Furthermore, the absence of an effect to species' survival from the 2015-16 El Niño

supports the notion that selectively logged forests are thermally buffered from climate change impacts, allowing selectively logged forests to maintain biodiversity despite climate change (Senior *et al.* 2018). However, there are uncertainties in the survival estimates as a result of low recapture rates or model limitations in differentiating deaths from permanent emigration. Uncertainties aside, the continued presence of multiple species of conservation concern as well as forest specialist species in our sampled community provides further support for the potential of selectively logged forests to maintain high conservation value. This underscores the importance of their protection to bolster biodiversity conservation (Edwards *et al.* 2014b).

## **5.6 Data availability**

Data will be made available from Figshare upon publication.

## **5.7 Acknowledgements**

We thank the Leverhulme Centre for Advanced Biological Modelling for a PhD studentship awarded to C.C.P.C. and the Rufford Foundation for funding two years of fieldwork. We thank Yayasan Sabah, Danum Valley Management Committee, the State Secretary, Sabah Biodiversity Centre, Sabah Chief Minister's Department, and the Economic Planning Unit of the Prime Minister's Department for permission to conduct research in Sabah. We also thank the Borneo Rainforest Lodge, Glen Reynolds, and the Royal Society's Southeast Asian Rainforest Research Program (SEARRP) for site access and logistical support, and Amy Donnison, Sylwia Zbijewska and all Universiti Malaysia Sabah and Universiti Malaysia Sarawak undergraduate interns who contributed to fieldwork.

## Chapter 6

### General Discussion



Danum Valley at dawn.

## 6.1 Summary

Solving the global biodiversity crisis requires the prioritization of nature conservation and habitat protection initiatives due to limited available funds (McCarthy *et al.* 2012; Waldron *et al.* 2013). Prioritizing conservation programs in the tropics would target the greatest number of threatened species, whilst improving local and global ecosystem services. Land-use change, predominantly due to deforestation and forest degradation in the tropics (Gibson *et al.* 2011; Armenteras *et al.* 2017), to meet global resource demands is the key driver of biodiversity loss (Sala *et al.* 2000). Tropical forest degradation is primarily driven by selective logging activities (Kissinger, Herold & De Sy 2012; Edwards *et al.* 2014b), which, in turn, is a catalyst for deforestation (Shearman, Bryan & Laurance 2012). With degraded forests increasingly dominating the tropical forest landscape, a global restoration agenda to restore and protect degraded tropical forests for biodiversity and ecosystem recovery has developed (Blaser *et al.* 2011; Ciccarese, Mattsson & Pettenella 2012).

Selectively logged tropical forests have been proposed as a good candidate for forest protection and restoration efforts (Meijaard & Sheil 2007; Edwards *et al.* 2014b) as these forests harbour a substantial amount of biodiversity and ecosystem functions compared to other tropical land-uses (Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014b). However, there first needs to be a comprehensive understanding of the effectiveness of selectively logged forest to maintain biodiversity and their associated ecosystem processes in the long-term. Most work on selective logging impacts on biodiversity examines species richness, abundance and community composition (Gibson *et al.* 2011; Putz *et al.* 2012; Burivalova, Sekercioglu & Koh 2014), which can conceal underlying impacts. It is important that we examine the impacts of logging on processes that underpin these biodiversity changes such as vital rates (i.e. survival, reproductive success and movement) and underlying community function (i.e. mass-abundance scaling). Vital rates can inform us about long-term

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population viability (Saether & Bakke 2000; Haridas *et al.* 2013), while underlying community function such as the mass-abundance scaling of communities can inform us about energy flow and ecosystem functioning (White *et al.* 2007).

The over-arching aim of this thesis was to determine the long-term ecological value of selectively logged tropical forests, by assessing how selective logging affects underlying community and vital rate responses such as (1) the mass-abundance scaling of avian communities, (2) the local movements of avian species, and (3) the survival rates of avian species. I first conducted a literature review in Chapter 2 to examine the state of our current knowledge on how tropical land-use change impacts species' vital rates (i.e. survival, reproductive success and movement) across the tropics. I found that empirical research on species' vital rates across taxa and regions were greatly lacking, with some biases toward birds and mammals and land-use transitions, including fragmentation and agriculture (Cosset, Gilroy & Edwards 2019). There is also considerable between-species variation in vital rate responses to land-use change, which could reflect trait-based differences in species sensitivity, complex context dependencies (e.g., between-region variation), or inconsistency in study methodologies. The lack of information on vital rate impacts of anthropogenic disturbance makes it difficult to draw definite conclusions about the magnitude of threats to tropical ecosystems under anthropogenic pressures.

For the rest of the thesis, I focused explicitly on tropical selective logging, which I found in Chapter 2 (Cosset, Gilroy & Edwards 2019) was one of the land-uses that severely lacked information about the underlying responses of biodiversity. In Chapter 3, I investigated the impacts of selective logging on the mass–abundance scaling of avian communities, an underlying community level response, by conducting a meta-analysis to examine its pantropical trend. There were no consistent effects of selective logging on mass–abundance scaling relative to old-growth unlogged forests in all 19 mist-netting studies,

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except for the omnivore guild where there were fewer larger-bodied species after logging (Cosset *et al.* 2020). Across eleven point-count studies, there was a more negative relationship in the whole community after logging, likely driven by the frugivore guild, showing a similar pattern (Cosset *et al.* 2020). Limited effects of logging on mass–abundance scaling may suggest high species turnover in logged communities, with like-for-like replacement. Contrarily, the increased negative mass–abundance relationship found in some logged communities could result from resource depletion, density compensation, or increased hunting; potentially indicating downstream impacts on ecosystem functions.

In Chapters 4 and 5, I used field data from a capture-mark-recapture mist-netting methodology of understory birds from Borneo to assess underlying species’ vital rate responses (i.e. local movements and survival) to selective logging at the community and species level. To assess local avian movements, in Chapter 4 I developed hierarchical Bayesian models, adapting recent developments in joint species occupancy modelling, to compare local movement patterns in selectively logged and unlogged old-growth forests. Across the community of 71 species, I found a higher mean probability of moving shorter distances (up to 200 m) in logged forests, while movement probability was higher at longer distances (above 200 m) in unlogged forests. Shifts in movement patterns after logging may be due to increased understory density (favouring most understory species), altered resource distribution, predation risks, or smaller home-range sizes.

It is important to note that different types of movement, such as local-scale movement, natal dispersal movement or breeding dispersal movement, would produce different movement kernels. This is because movement kernels not only describe the process of moving, but also incorporate other processes such as foraging, predator avoidance, and refuge, mate and habitat search (Nathan *et al.* 2012; Robertson *et al.* 2018). Here, I focused on local-scale movement to represent movement within a species’ home-range which

includes processes such as foraging, refuge search and predator avoidance. It is also difficult to determine the start and end of a movement event and thus, the only way to detect a movement event is to identify deviations from what would be deemed ‘normal’ behaviour (Nathan *et al.* 2012). Therefore, in this thesis, I assessed deviations in movement in selectively logged forests from those in unlogged forests. Furthermore, not all probability density functions are appropriate for the type of movement assessed. This was the case for the Rayleigh distribution model which did not converge, suggesting poor fit to the data. Overall, in analysing species movements, it was unclear what were the mechanisms behind these movement changes or the demographic implications on these species. Future studies should have clear expectations about the what changes in movement can inform about species’ persistence or species’ demographic rates.

Finally, to determine avian survival rates, in Chapter 5, I developed a multi-species hierarchical Cormack-Jolly-Seber (CJS) model in a Bayesian framework, adapting recent works, to compare habitat-specific survival at the community and species levels in selectively logged and unlogged old-growth forests. Similar apparent survival probabilities were observed across all 71 understory avian species in both unlogged and logged forests, potentially due to species’ traits and physiological mechanisms that allow their survival in degraded habitats. Furthermore, there was no effect of El Niño in species’ survival rates.

It should be highlighted that modelling El Niño impacts on survival could also be achieved by adding a time variable instead of including a precipitation effect. Allowing survival to vary by time alone would be sufficient to show different survival rates between years. Furthermore, the consistency seen in the results may be due to the hierarchical component of the model, where species level estimates are informed by the overall community-level means. However, the results from the hierarchical models in Chapter 5

show similar results to the single-species model, without the hierarchical component, suggesting that our modelling approach is robust.

The results from this thesis, specifically those of Chapter 4 and 5 on avian species' local movements and survival, have limited generalisability across spatial scales and species (Coutts *et al.* 2016). Since the robustness of extrapolating is limited, more studies or data is required to fill in these gaps. However, this is may be impractical in many cases due to insufficient resources (McCarthy *et al.* 2012). It would thus be more effective to have specific indicators of ecosystem degradation which can be reliably extrapolated to wider spatial scales or across species, and of which obtaining and analysing data is economical and time efficient. An example of such efforts is the development of Essential Biodiversity Variables (EBVs) which can detect ecological changes at meaningful temporal and spatial scales, and can be measured and modelled practically across different ecosystems (Jetz *et al.* 2019). Furthermore, developing a consistent, integrated and scalable framework for monitoring ecosystem changes is important for assessing EBVs. Guerra *et al.* (2019) developed a scalable framework for identifying and assessing EBVs which builds on socio-ecological knowledge at the systems-level, the associated models and the data required. In this framework, knowledge on all components of the system allows for the identification of important EBVs that meet conservation needs at various scales. These efforts would allow for more efficient monitoring and a smoother transition from science to policy or decision-making processes.

In the rest of this chapter, I synthesise my results along with those from the literature to illustrate the overall ecological value of selectively logged forests. The chapter concludes with post-logging management and policy recommendations for integrating sustainable management of timber concessions with biodiversity conservation, and directions for future research.

## 6.2 Ecological value of selectively logged forests

Overall, selectively logged forests retain substantial biological value, affecting some species more than others depending on their traits. They also maintain much ecosystem services despite having a modified forest structure. The intensity of selective logging also has a role to play with more adverse impacts at higher logging intensities or when using conventional logging techniques (Bicknell *et al.* 2014; Burivalova, Sekercioglu & Koh 2014; Martin *et al.* 2015). Selective logging changes multiple aspects of the forest structure. It fragments and reduces the height and density of the forest canopy (Okuda *et al.* 2003), damages the soil and neighbouring vegetation (Putz *et al.* 2008), and has a denser understory covered with early successional non-tree plant species, all of which hinder forest regeneration (Hawthorne *et al.* 2012; Osazuwa-Peters, Chapman & Zanne 2015; Gaudi *et al.* 2019). Moreover, selective logging alters all stages of the seedling recruitment process, thus reducing tree recruitment and tree abundance (Pillay *et al.* 2018). Selectively logged forests have more liana vines and a different composition which has negative implications on timber value and carbon storage (Magrath *et al.* 2016). Plant and tree species richness shift after selective logging (Gatti *et al.* 2015; Martin *et al.* 2015) with some studies showing that tree species richness is highest at intermediate logging levels (Imai *et al.* 2016). Over time, however, the floristic composition of selectively logged forests can move towards pre-logging levels provided logging activities are at lower intensities (Gaudi *et al.* 2019).

Biodiversity patterns in selectively logged forests show similar levels of species richness (between 85% to 100% of bird, mammal, plant and invertebrate) to old-growth pristine forests (Putz *et al.* 2012; Martin *et al.* 2015), some of which are species of conservation concern (Iris *et al.* 2018; Hearn *et al.* 2019). The community composition of mammals, birds, plants and invertebrates, however, change after selective logging and is underpinned by shifts in species abundances (Edwards *et al.* 2011; Burivalova, Sekercioglu &

Koh 2014; Osazuwa-Peters *et al.* 2015; Wearn *et al.* 2017). This could be on some part due to community assembly processes being affected in selectively logged forests (Wearn *et al.* 2019). These patterns in biodiversity are more apparent at higher logging intensities (Burivalova, Sekercioglu & Koh 2014; Martin *et al.* 2015; Ross *et al.* 2018), whereas impacts are minimal using reduced-impact logging techniques (Bicknell, Struebig & Davies 2015; Milheiras *et al.* 2020). Furthermore, these responses are species dependent, where some species survive better than others in selectively logged forests due to their traits (Burivalova *et al.* 2015; Costantini, Edwards & Simons 2016). Some species have better physiological coping mechanisms to environmental stressors (Franca *et al.* 2016; Messina *et al.* 2020) or have behavioural plasticity that enable them to persist in degraded forests (Hua & Sieving 2016).

Ecosystem processes, and functional and phylogenetic diversity are largely retained in selectively logged forests (Edwards *et al.* 2014b; Chapman *et al.* 2018; Ding *et al.* 2019), with some taxa being more adversely impacted than others (Ernst, Linsenmair & Rodel 2006; Edwards *et al.* 2014b). However, there are some alterations in processes such as species interactions, nutrient cycling and seed dispersal. In Borneo, avian species have been found to feed at higher trophic positions (i.e. they have a higher protein diet), which alters species' abundances (Edwards *et al.* 2013; Hamer *et al.* 2015), and soil microbiome network complexity increases, with implications on soil microbe interactions (Tripathi *et al.* 2016). Dung beetle-mediated soil bioturbation in the Brazilian Amazon was affected, especially at higher logging intensities (Franca *et al.* 2017), while biogeochemical nutrient cycling in Borneo has been shown to be impacted in Bornean logged forests (Both *et al.* 2017). Moreover, species-specific seed dispersal distances were altered even at low-intensity logging (Nunez *et al.* 2019) and animal-dispersed seed size decreased after logging (Yguel *et al.* 2019). Climate change can alter floristic composition of forests and thus affect

biodiversity over time (Gaui *et al.* 2019). However, selectively logged forests can provide biodiversity with protection from climate change as they are thermally buffered due to the availability of novel habitats (Holting, Bovolo & Ernst 2016; Senior *et al.* 2018).

Ecological processes underpinning biodiversity change in selectively logged forests vary in responses depending on the studied species, as found in Chapter 2 (Cosset, Gilroy & Edwards 2019). I find that the mass-abundance relationship of avian communities remain relatively robust to selective logging (Chapter 3; Cosset *et al.* 2020) and that Bornean understory avian species are able to maintain their survival rates (Chapter 5) in selectively logged forests despite having shifts in their local movement patterns (Chapter 4). Taken together, these results highlight the potential of selectively logged forests to retain ecological value over time, however, the coping mechanisms which allow species to persist in these forests remains to be identified. There are also some losses in ecological value after selective logging and these can be recovered through post-logging management interventions.

### **6.3 Post-logging management & policy recommendations**

Post-logging management interventions can restore the lost ecological value from selective logging (Cerullo & Edwards 2019). The main goal of post-logging restoration (i.e. ecosystem restoration, timber enhancement, carbon enhancement or ecosystem service enhancement) is important because if the focus is on timber or carbon enhancement, the associated restoration techniques may have adverse effects on biodiversity (Edwards *et al.* 2009; Cosset & Edwards 2017; O'Brien *et al.* 2017). In terms of recovering lost biodiversity and ecosystem functions after selective logging, ecosystem restoration interventions represent the most ideal outcomes (Cerullo & Edwards 2019). Firstly, protecting selectively logged forests from further degradation and deforestation is vital for avoiding further adverse impacts on biodiversity (Meijaard & Sheil 2007; Edwards *et al.* 2014b; Chapter 3; Chapter 4;

Chapter 5). Logged forests are up to 400% more likely to be deforested for conversion to more lucrative agricultural lands compared to old-growth pristine forests (Asner *et al.* 2006). Deforestation for farmland conversion results in a significant loss of biodiversity (Gibson *et al.* 2011; Wilcove *et al.* 2013). Ecosystem restoration activities could also involve restoring habitat components, such as streams and vital microhabitats, that have been damaged during logging (Luke *et al.* 2017a; Cerullo & Edwards 2019). Logged forest streams have been found to contain significantly reduced anuran density, larval dragonfly abundance and species richness with shifts in community composition (Seshadri 2014; Luke *et al.* 2017b) compared to those of unlogged old-growth forests.

Key ecosystem restoration activities typically involve (1) liberation cutting of competing vegetation such as vines and early successional plants, and (2) enrichment planting of lost timber trees and a variety of species important for wildlife (Kobayashi 2007). Planting large fruiting trees is vital for larger frugivores which tend to be more vulnerable as shown in Chapter 3. Liberation cutting of liana vines can increase canopy tree reproduction and tree species diversity (Schnitzer & Carson 2010; Leon *et al.* 2018). Enrichment planting and liberation cutting have also been shown to have little to no impacts on invertebrates or avian species of conservation concern (Ansell, Edwards & Hamer 2011; Edwards *et al.* 2012). However, at high liberation cutting intensities, the removal of vital foraging and nesting substrates from vines and understory vegetation can negatively affect biodiversity (Cosset & Edwards 2017). It is thus crucial that the optimal intensity for liberation cutting is applied to minimise biodiversity impacts (Ansell, Edwards & Hamer 2011).

Forest and landscape restoration funds could motivate non-timber focused post-logging interventions, such as ecosystem restoration, ecosystem service and carbon enhancement, to be applied within past production forests. Additionally, commercial investments could create self-funded post-logging restoration where governments encourage corporate investment by

providing subsidies, tax breaks, loans or direct payments to make restoration economically more favourable (Brancalion *et al.* 2017). Due to the substantial amount of biodiversity and ecosystem processes maintained in selectively logged forests (Edwards *et al.* 2014b), payments for ecosystem services funds could be directed towards post-logging restoration in sustainably managed timber concessions (Cerullo & Edwards 2019). The current forest and landscape restoration (FLR) approach prioritizes both biodiversity conservation and people's livelihoods (Stanturf, Palik & Dumroese 2014) and, therefore, these funds could be used for post-logging restoration within active logging concessions to improve both ecosystem benefits and provide local communities with employment in silviculture. Post-logging management funds would also require the prioritisation of intervention activities within the logged forest landscape of differing degrees of degradation. Consideration for prioritisation should include the various environmental, social and economic costs and benefits of different restoration activities (Budiharta *et al.* 2014), as well as the benefits of avoiding deforestation for agriculture (Cerullo & Edwards 2019).

Designing and managing logging concessions to minimise adverse biodiversity impacts (e.g. Chapter 3 and 4) is an ongoing challenge. One such currently debated proposed solution is the land-sparing or land-sharing approach (Edwards *et al.* 2014c; Piloniot *et al.* 2019). The land-sparing approach involves the intensification of logging using a smaller land area to meet demands, while leaving a larger area of untouched forests for biodiversity. This approach could be beneficial for biodiversity at the landscape level by (1) deterring hunting or illegal logging with the presence of forest officers, (2) limiting forest access from concentrating roads to within logged areas only, and (3) preserving pristine forest habitat for habitat sensitive species (Gaveau *et al.* 2013; Kleinschroth, Healey & Gourlet-Fleury 2016; Cerullo & Edwards 2019). Land-sparing logging in Borneo has been shown to have more benefits for dung beetles, birds and leaf-litter ants compared to the land-sharing approach

(Edwards *et al.* 2014c). Coupling timber enhancement activities to ensure sufficient timber yields over time with the land-sparing approach could prevent the remaining pristine old-growth forests from being logged (Cerullo & Edwards 2019). On the contrary, land-sharing logging involves logging a larger area at low-intensities while maintaining some old-growth habitat features for biodiversity. This approach can also benefit biodiversity if reduced impact logging (RIL) is conducted in combination with having a secure land tenure (Griscom *et al.* 2018). Incorporating timber enhancement activities into management plans would help maintain timber yields and thus prevent future logging intensification to meet timber demands (Cerullo & Edwards 2019). Future research is critically needed to determine the environmental, carbon, economic and timber trade-offs of different logging management approaches and post-logging interventions to inform on designing logging concessions for minimising biodiversity impacts.

At the commercial level, transnational corporations that run logging concessions have the power to drastically change timber forestry practices instead of maintaining damaging “cut-and-run” practices (Laurance 2000). These corporations engage in governance directly, have a network of well-connected subsidiaries, manage important areas and may be involved throughout the timber supply chains (Moog, Spicer & Bohm 2015; Osterblom *et al.* 2017). Timber demands are predicted to increase and therefore, industrial logging of tropical forests is expected to endure (FAO 2009; Raunikar *et al.* 2010). It is thus vital that logging malpractices are prevented and instead that logging concessionaires uphold sustainable management and “cut-and-stay” mentalities (Cerullo & Edwards 2019). Governments could issue long-lasting timber exploitation licences, based on a concessionaire’s track record for sustainable management, instead of short-term licences, to encourage “cut-and-stay” mentalities (FAO 2016). This can be cemented by introducing laws and enforcement to ensure application of post-logging interventions and motivate commercial investment in long-

term timber sustainability (FAO 2016). Building science-business initiatives and implementing high certification standards are key for shifting business norms towards environmentally sustainable practices (Moog, Spicer & Bohm 2015; Osterblom *et al.* 2017). Sustainably managed logging concessions would thus be significant components for enhancing biodiversity conservation outside protected areas (Gaveau *et al.* 2013).

## 6.4 Conclusions & future directions

The protection and retention of old-growth pristine tropical forests is still a priority for biodiversity conservation (Gibson *et al.* 2011; Chapter 2). Nevertheless, with degraded forests increasingly dominating the tropical forest landscape, increasing attention is being placed on protecting and restoring degraded forests for multiple biodiversity and human benefits (Edwards *et al.* 2014b). The results from this thesis suggest limited impacts on avian species and communities. This highlights the potential high ecological value maintained in selectively logged forests over time, and thus, lends further support for the effectiveness of protecting these forests for biodiversity conservation. Furthermore, post-logging management interventions can restore ecological value lost from selective logging (Cerullo & Edwards 2019). Integrating this with various restoration funds, long-term commercial investments and effective governance will further drive transformative change for the long-term environmentally sustainable management of logging concessions. Key future research to inform efforts on improving the biodiversity-friendliness of logged forest management include (1) improving the accuracy of species' survival estimates by integrating dispersal parameters into the model to be able to distinguish between death and emigration, (2) establishing long-term monitoring of underlying ecological mechanisms and ecosystem services in logged forests, and (3) determining the environmental, carbon, economic and timber trade-offs of different logging management approaches and post-logging interventions

to inform on designing logging concessions for mutual conservation, economic or social benefits.

# Appendix A

## Supporting information for Chapter 2

### Appendix A.1. Complete list of studies on vital rates.

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## Appendix A.2. Supplementary tables

Table A.1. Number of studies with positive, negative and varying responses to land-use change, grouped by elevation.

<b>Elevation</b>	<b>Survival</b>	<b>Reproductive success</b>	<b>Movement</b>	<b>Response</b>
Lowland	0	4	13	Positive
	1	6	12	Negative
	2	3	9	Varies
Submontane	0	4	1	Positive
	2	4	4	Negative
	0	0	1	Varies
Montane	2	4	0	Positive
	0	3	1	Negative
	0	0	1	Varies

# Appendix B

## Supporting information for Chapter 3

### Appendix B.1. Supplementary tables

Table B.1. Information of all mist-net studies including continent where the study was conducted, type of logging conducted in the study sites and the proportion of each guild in each study.

Study	Continent	Logging type	Guild proportions	
			Foraging Guild	Proportion
Arcilla N, Holbech LH, O'Donnell S. 2015. Severe declines of understory birds following illegal logging in Upper Guinea forests of Ghana, West Africa. <i>Biological Conservation</i> 188:41-49.	Africa	<ul style="list-style-type: none"> <li>• Conventional logging</li> <li>• Salvage logging</li> </ul>	Insectivore	0.68
			Frugivore	0.10
			Omnivore	0.20
			Carnivore	0.02
			Granivore	0.00
Blake JG, Loiselle BA. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: Perspectives from mist nets and point counts. <i>Auk</i> 118:304-326.	Central America	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.57
			Frugivore	0.24
			Omnivore	0.13
			Carnivore	0.03
			Granivore	0.03
Crome FHJ, Thomas MR, Moore LA. 1996. A novel Bayesian approach to assessing impacts of rain forest logging. <i>Ecological Applications</i> 6:1104-1123.	Australia	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.66
			Frugivore	0.19
			Omnivore	0.14
			Carnivore	0.02
			Granivore	0.00
Dranzoa C. 1998. The avifauna 23 years after logging in Kibale National park, Uganda. <i>Biodiversity and Conservation</i> 7:777-797.	Africa	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.64
			Frugivore	0.13
			Omnivore	0.14
			Carnivore	0.01

			Granivore	0.09
			Insectivore	0.68
Edwards DP, Ansell FA, Ahmad AH, Nilus R, Hamer KC. 2009. The Value of Rehabilitating Logged Rainforest for Birds. <i>Conservation Biology</i> 23:1628–1633.	Asia	• Conventional logging	Frugivore	0.08
			Omnivore	0.23
			Carnivore	0.01
			Granivore	0.00
Edwards DP, Larsen TH, Docherty TDS, Ansell FA, Hsu WW, Derhe MA, Hamer KC, Wilcove DS. 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. <i>Proceedings of the Royal Society B-Biological Sciences</i> 278:82-90.	Asia	• Conventional logging	Insectivore	0.71
			Frugivore	0.09
			Omnivore	0.17
			Carnivore	0.02
			Granivore	0.02
Edwards DP, Woodcock P, Edwards FA, Larsen TH, Hsu WW, Benedick S, Wilcove S. 2012. Reduced-impact logging and biodiversity conservation: a case study from Borneo. <i>Ecological Applications</i> 22:561–571.	Asia	• Conventional logging • Reduced-impact logging	Insectivore	0.69
			Frugivore	0.08
			Omnivore	0.21
			Carnivore	0.01
			Granivore	0.01
Flores B, Rumiz DI, Fredericksen TS, Fredericksen NJ. 2002. El uso de claros de aprovechamiento forestal por la avifauna de un bosque semideciduo chiquitano de Santa Cruz, Bolivia. <i>Hornero</i> 17: 61-69.	South America	• Conventional logging	Insectivore	0.66
			Frugivore	0.26
			Omnivore	0.06
			Carnivore	0.00
			Granivore	0.02
Guilherme E, Cintra R. 2001. Effects of intensity and age of selective logging and tree girdling on an understory bird community composition in Central Amazonia, Brazil. <i>Ecotropica</i> 7:77-92.	South America	• Conventional logging	Insectivore	0.79
			Frugivore	0.15
			Omnivore	0.05
			Carnivore	0.01
			Granivore	0.00
Hawes J, Barlow J, Gardner TA, Peres CA. 2008. The value of forest strips for understory birds in an Amazonian plantation landscape. <i>Biological Conservation</i> 141:2262-2278.	South America	• Conventional logging	Insectivore	0.60
			Frugivore	0.26
			Omnivore	0.09
			Carnivore	0.02
			Granivore	0.03
Henriques LMP, Wunderle Jr. JM, Oren DC, Willig MR. 2008. Efeitos da exploração madeireira de baixo impacto sobre uma comunidade de aves de sub-bosque na	South America	• Conventional logging	Insectivore	0.74
			Frugivore	0.14
			Omnivore	0.07

Floresta Nacional do Tapajós, Pará, Brasil. Acta Amazonica 38:267-290.			Carnivore	0.03
			Granivore	0.01
Holbech LH. 2005. The implications of selective logging and forest fragmentation for the conservation of avian diversity in evergreen forests of south-west Ghana. Bird Conservation International 15:27-52.	Africa	<ul style="list-style-type: none"> <li>• Conventional logging</li> <li>• Salvage logging</li> </ul>	Insectivore	0.71
			Frugivore	0.09
			Omnivore	0.17
			Carnivore	0.02
			Granivore	0.01
Lambert FR. 1992. The Consequences of Selective Logging for Bornean Lowland Forest Birds. Phil. Trans. R. Soc. Lond. B. 335:443-457.	Asia	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.71
			Frugivore	0.11
			Omnivore	0.18
			Carnivore	0.00
			Granivore	0.00
Larison B, et al. 1999. Biotic Surveys of Bioko and Rio Muni, Equatorial Guinea, Biodiversity Support Program, USA.	Africa	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.67
			Frugivore	0.14
			Omnivore	0.14
			Carnivore	0.02
			Granivore	0.03
Mason D. 1996. Responses of venezuelan understory birds to selective logging, enrichment strips, and vine cutting. Biotropica 28:296-309.	South America	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.74
			Frugivore	0.14
			Omnivore	0.07
			Carnivore	0.03
			Granivore	0.01
Waltert M. 2000. Forest management and the distribution of understorey birds in the Bossematié Forest, eastern Ivory Coast. Ostrich 71:295-299.	Africa	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.68
			Frugivore	0.08
			Omnivore	0.18
			Carnivore	0.01
			Granivore	0.04
Wong M. 1986. Trophic organization of understory birds in a Malaysian dipterocarp forest. Auk 103:100-116.	Asia	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.74
			Frugivore	0.07
			Omnivore	0.17
			Carnivore	0.01
			Granivore	0.01
Wunderle JM, Henriques LMP, Willig MR. 2006. Short-term responses of birds to forest gaps and understory: An assessment of	South America	<ul style="list-style-type: none"> <li>• Conventional logging</li> </ul>	Insectivore	0.75
			Frugivore	0.15

reduced-impact logging in a lowland Amazon forest. <i>Biotropica</i> 38:235-255.		• Reduced-impact logging	Omnivore	0.06
			Carnivore	0.03
			Granivore	0.01
Yap CAM, Sodhi NS, Peh KSH. 2007. Phenology of tropical birds in Peninsular Malaysia: Effects of selective logging and food resources. <i>Auk</i> 124:945-961.	Asia	• Conventional logging	Insectivore	0.67
			Frugivore	0.09
			Omnivore	0.22
			Carnivore	0.03
			Granivore	0.00

Table B.2. Information of all point-count studies including continent where the study was conducted, type of logging conducted in the study sites and the proportion of each guild in each study.

Study	Continent	Logging type	Guild proportions	
			Foraging Guild	Proportion
Aleixo A. 1999. Effects of selective logging on a the Brazilian Atlantic bird community in forest. <i>The Condor</i> <b>101</b> :537-548.	South America	•Conventional logging	Insectivore	0.53
			Frugivore	0.21
			Omnivore	0.16
			Carnivore	0.04
			Granivore	0.07
Edwards DP, Woodcock P, Edwards FA, Larsen TH, Hsu WW, Benedick S, Wilcove S. 2012. Reduced-impact logging and biodiversity conservation: a case study from Borneo. <i>Ecological Applications</i> <b>22</b> :561–571.	Asia	•Conventional logging	Insectivore	0.66
			Frugivore	0.16
			Omnivore	0.17
			Carnivore	0.01
			Granivore	0.00
Flores B, Rumiz DI, Blate GM. 2005. Estructura de la vegetación y de la comunidad de aves en un bosque intervenido de la Chonta, Guarayos, Santa Cruz. <i>Rev. Bol. Ecol.</i> <b>18</b> : 33- 50.	South America	•Conventional logging	Insectivore	0.53
			Frugivore	0.26
			Omnivore	0.14
			Carnivore	0.01
			Granivore	0.05
Lambert FR. 1992. The Consequences of Selective Logging for Bornean Lowland Forest Birds. <i>Phil. Trans. R. Soc. Lond. B.</i> <b>335</b> :443-457.	Asia	•Conventional logging	Insectivore	0.60
			Frugivore	0.23
			Omnivore	0.15
			Carnivore	0.01
			Granivore	0.01
Marsden SJ. 1998. Changes in Bird Abundance Following Selective Logging on Seram, Indonesia. <i>Conservation Biology</i> <b>12</b> :605-611.	Asia	•Conventional logging	Insectivore	0.32
			Frugivore	0.37
			Omnivore	0.16
			Carnivore	0.05
			Granivore	0.10
Owiunji I, Plumtre AJ. 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. <i>Forest Ecology and Management</i> <b>108</b> :115–126.	Africa	•Conventional logging	Insectivore	0.61
			Frugivore	0.19
			Omnivore	0.16
			Carnivore	0.01
			Granivore	0.04
Politi N, Hunter Jr M, Rivera L. 2012. Assessing the effects of selective logging on birds in Neotropical piedmont and cloud montane forests. <i>Biodiversity Conservation</i> <b>21</b> :3131-3155.	South America	•Conventional logging	Insectivore	0.57
			Frugivore	0.14
			Omnivore	0.21
			Carnivore	0.02
			Granivore	0.06
Raman TRS, Sukumar R. 2002. Responses of tropical rainforest birds to abandoned plantations,	Asia		Insectivore	0.64
			Frugivore	0.12

edges and logged forest in the Western Ghats, India. <i>Animal Conservation</i> <b>5</b> :201–216.		•Conventional logging	Omnivore	0.22
			Carnivore	0.01
			Granivore	0.00
Thiollay JM. 1992. Influence of Selective Logging on Bird Species Diversity in a Guianan Rain Forest. <i>Conservation Biology</i> <b>6</b> :47–63.	South America	•Conventional logging	Insectivore	0.57
			Frugivore	0.25
			Omnivore	0.14
			Carnivore	0.00
			Granivore	0.04
Villaseñor JF, Sosa N, Villaseñor L. 2005. Effects of Selective Logging on Birds in the Sierra de Coalcomán, Sierra Madre del Sur, Michoacán, Western Mexico. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191. 381–390.	South America	•Conventional logging	Insectivore	0.62
			Frugivore	0.10
			Omnivore	0.18
			Carnivore	0.02
			Granivore	0.09
Woltmann S. 2003. Bird community responses to disturbance in a forestry concession in lowland Bolivia. <i>Biodiversity and Conservation</i> <b>12</b> :1921–1936.	South America	•Conventional logging	Insectivore	0.62
			Frugivore	0.24
			Omnivore	0.14
			Carnivore	0.00
			Granivore	0.00

Table B.3. Information about the foraging guild classes assigned to each species. The categorisation of each foraging guild is based on the EltonTraits 1.0 database (Wilman *et al.* 2014)

<b>Foraging Guild</b>	<b>EltonTraits 1.0 Category</b>	<b>Diet</b>
Insectivore	Invertebrate	Invertebrates
Frugivore	FruaNect	Fruits and Nectar
Omnivore	Omnivore	Consisting of less than or equal to 50% of all four categories (Invertebrate, FruitNect, VertFishScav, PlantSeed)
Carnivore	VertFishScav	Vertebrates, Fish and Carrion
Granivore	PlantSeed	Plants and Seeds

## Appendix B.2. Supplementary figures

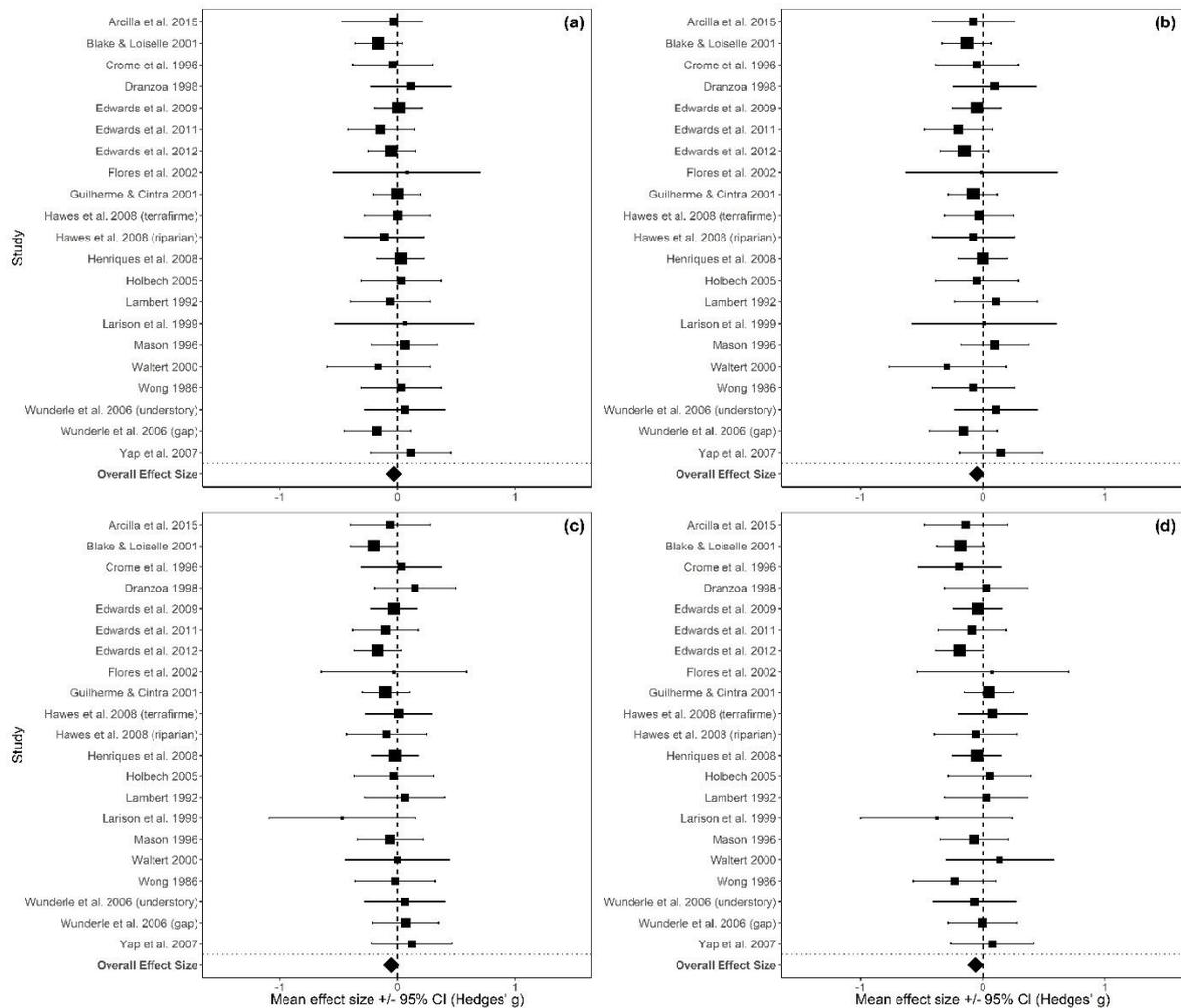


Figure B.1. The effect sizes of each mist-net study from the *Overall* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

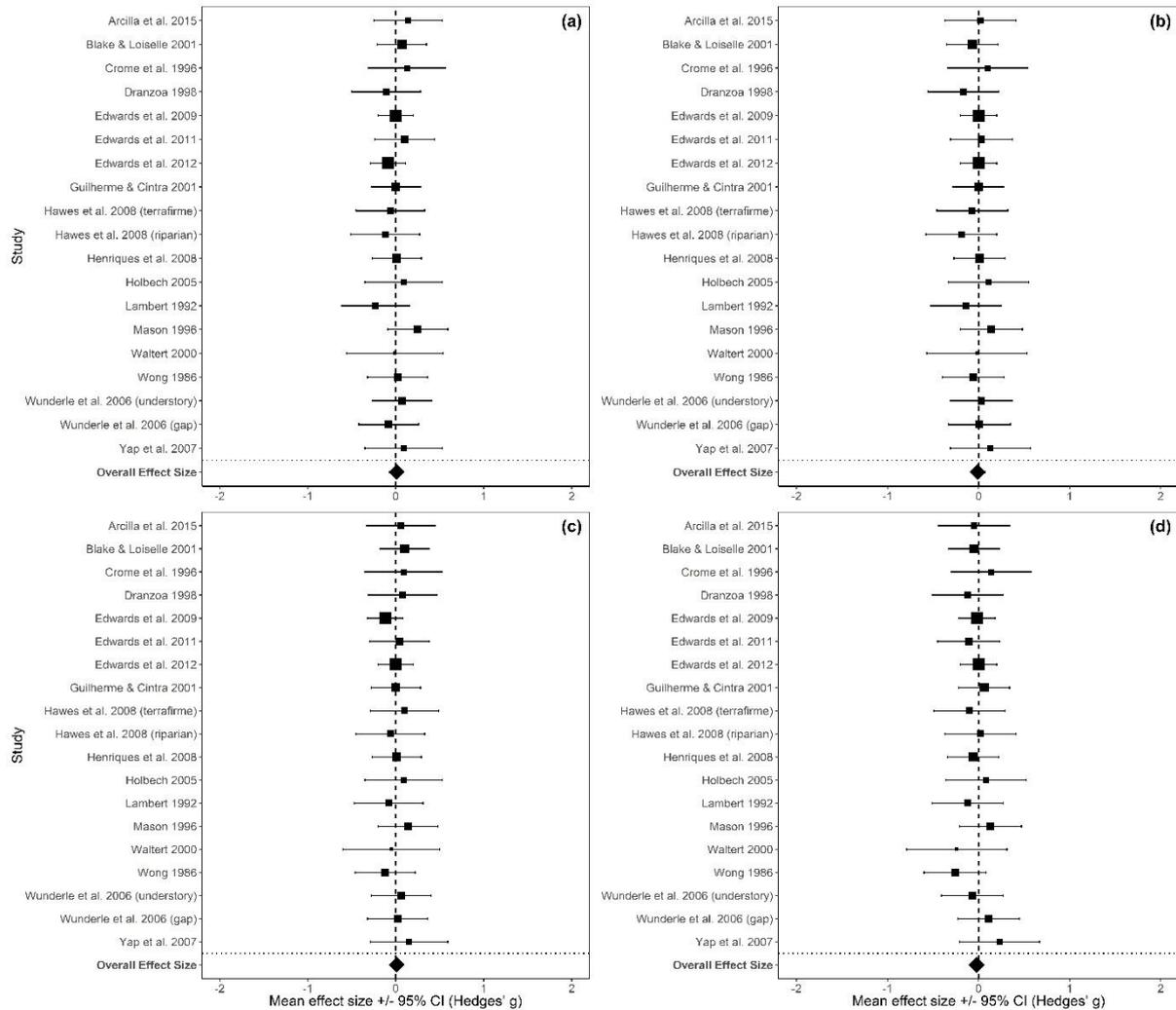


Figure B.2. The effect sizes of each mist-net study from the *Insectivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

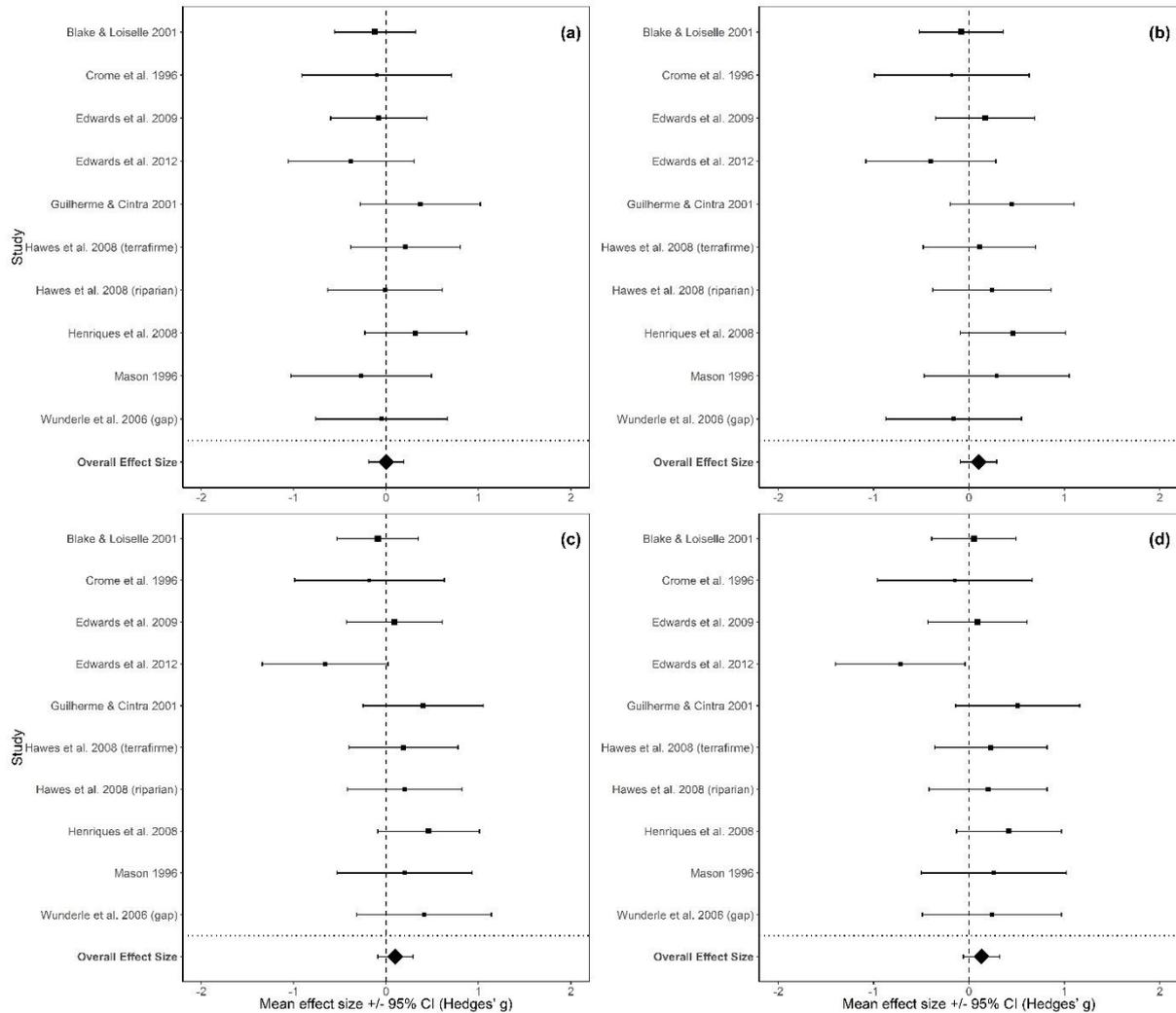


Figure B.3. The effect sizes of each mist-net study from the *Frugivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

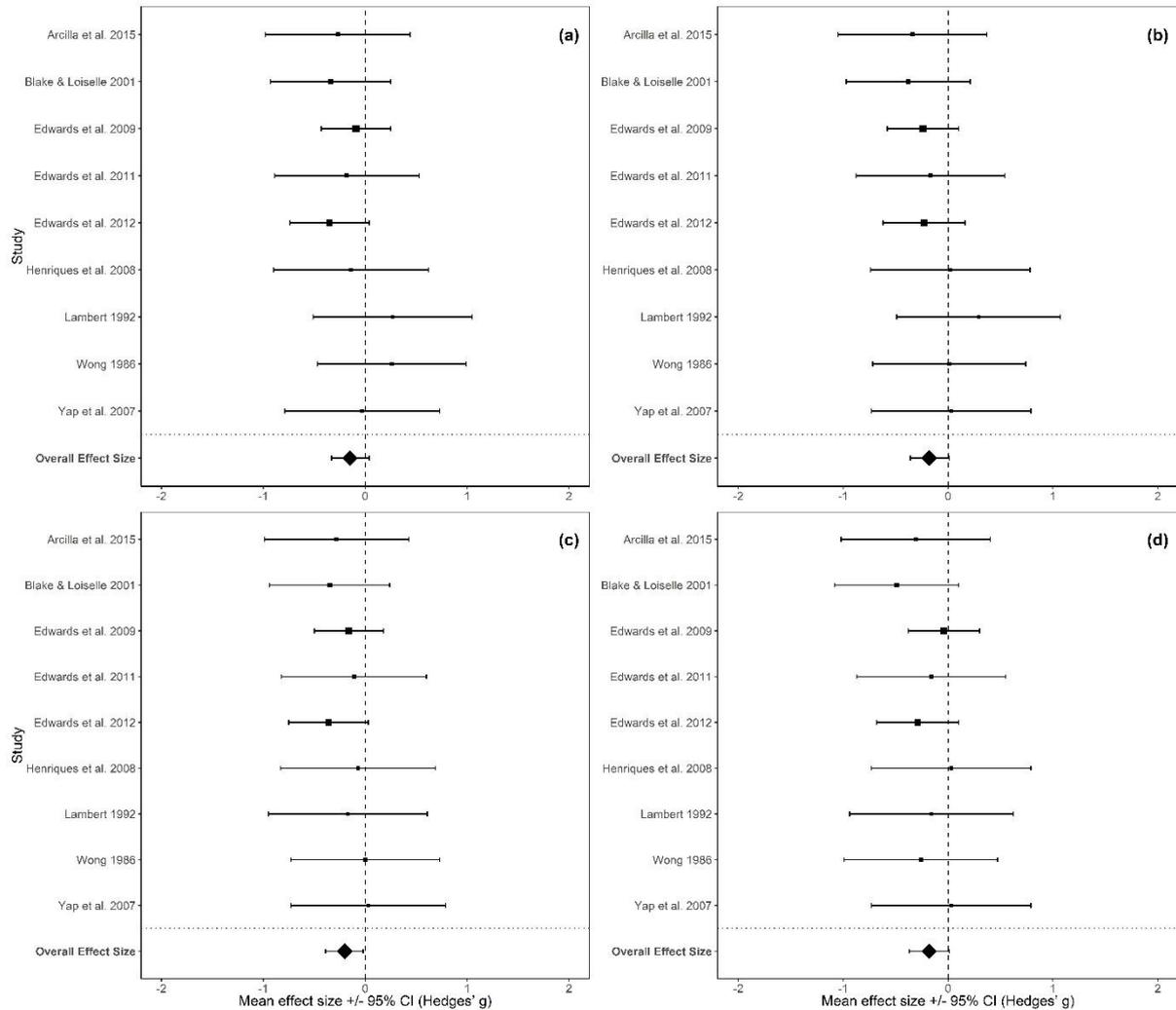


Figure B.4. The effect sizes of each mist-net study from the *Omnivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

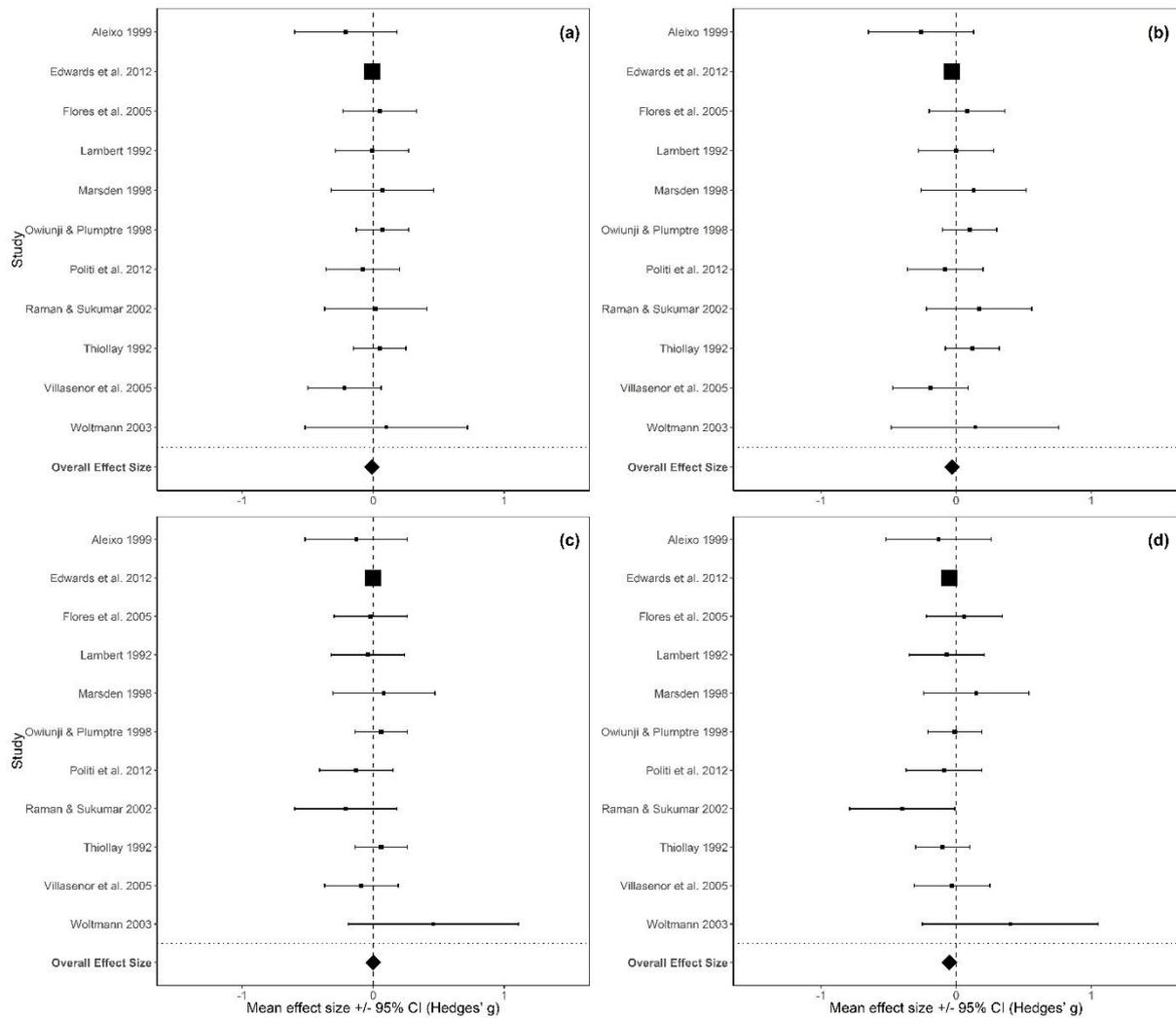


Figure B.5. The effect sizes of each point-count study from the *Overall* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

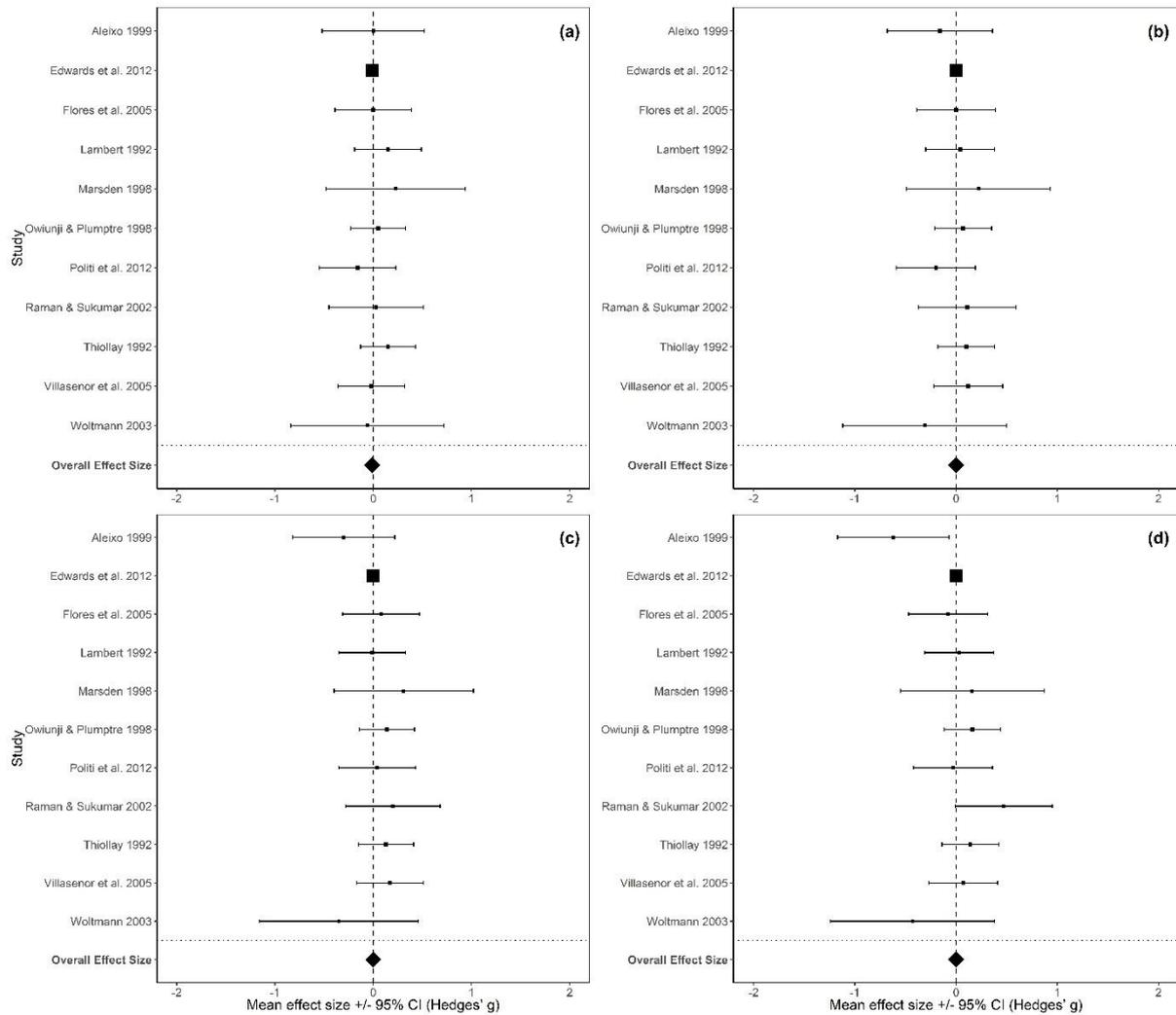


Figure B.6. The effect sizes of each point-count study from the *Insectivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

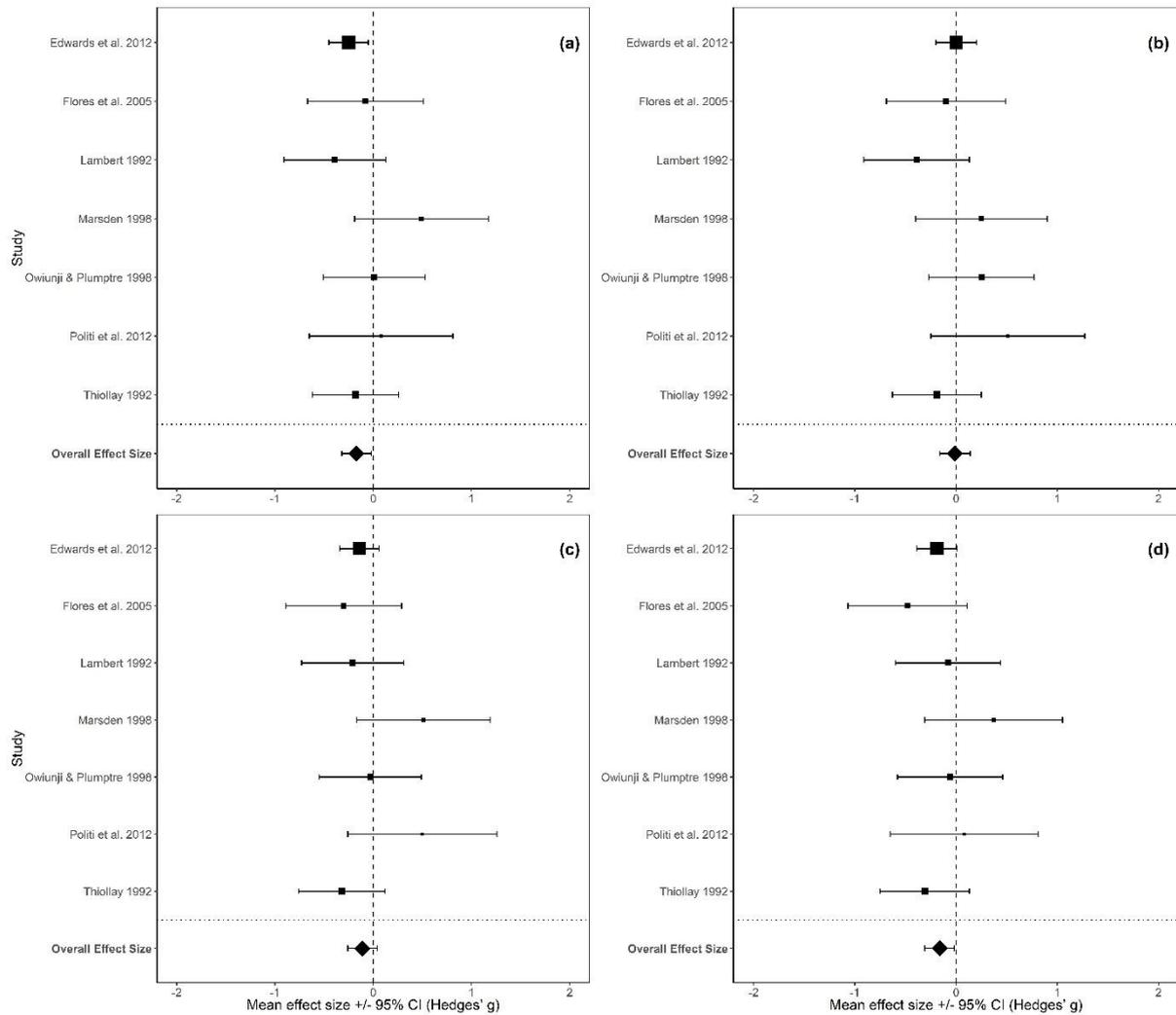


Figure B.7. The effect sizes of each point-count study from the *Frugivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

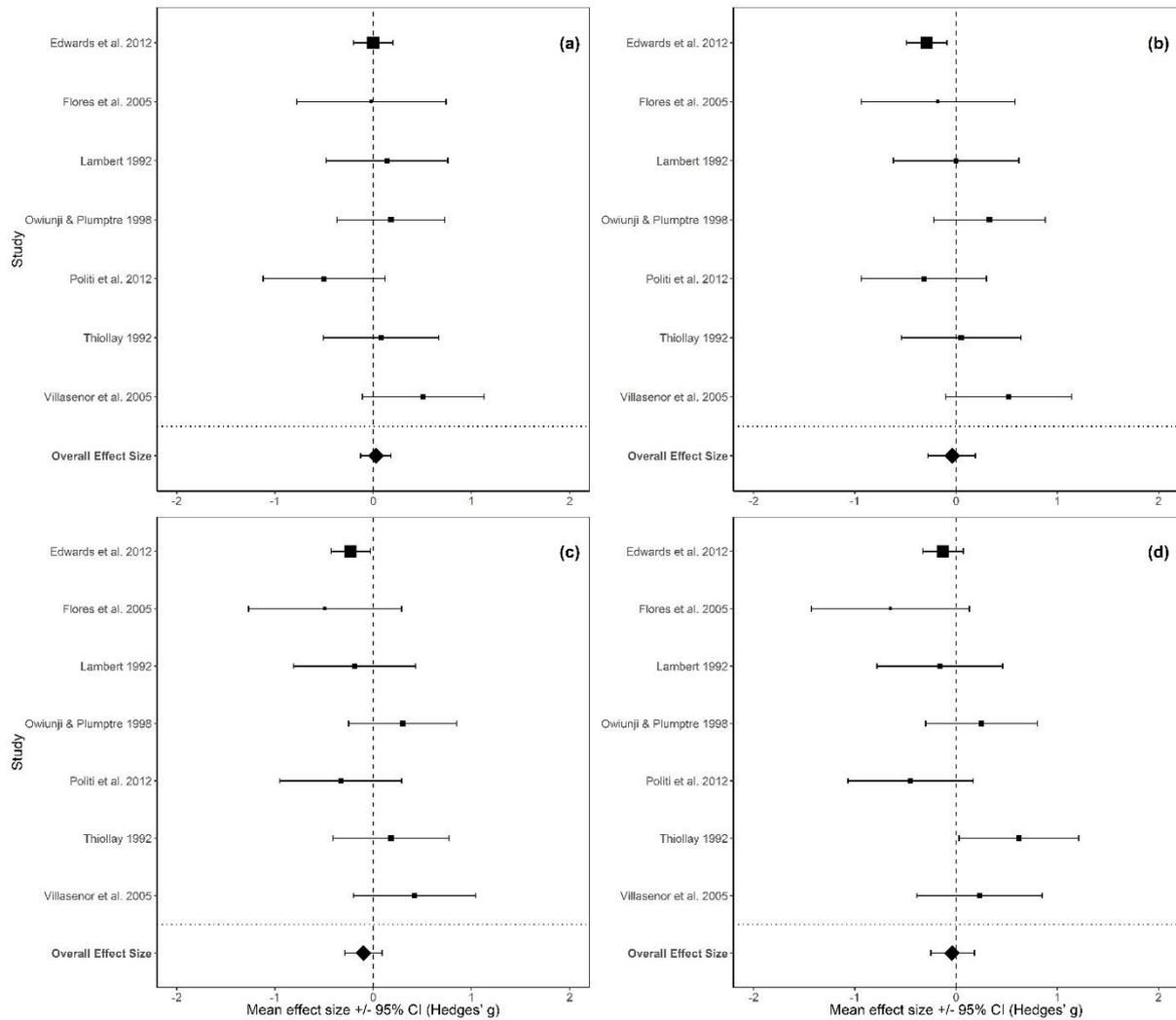


Figure B.8 The effect sizes of each point-count study from the *Omnivore* analysis and the overall effect size with their respective 95% confidence intervals. The size of the points corresponds to each study's respective weights. Effect sizes are from the (a) 0.80, (b) 0.85, (c) 0.90 and (d) 0.95 regression quantile.

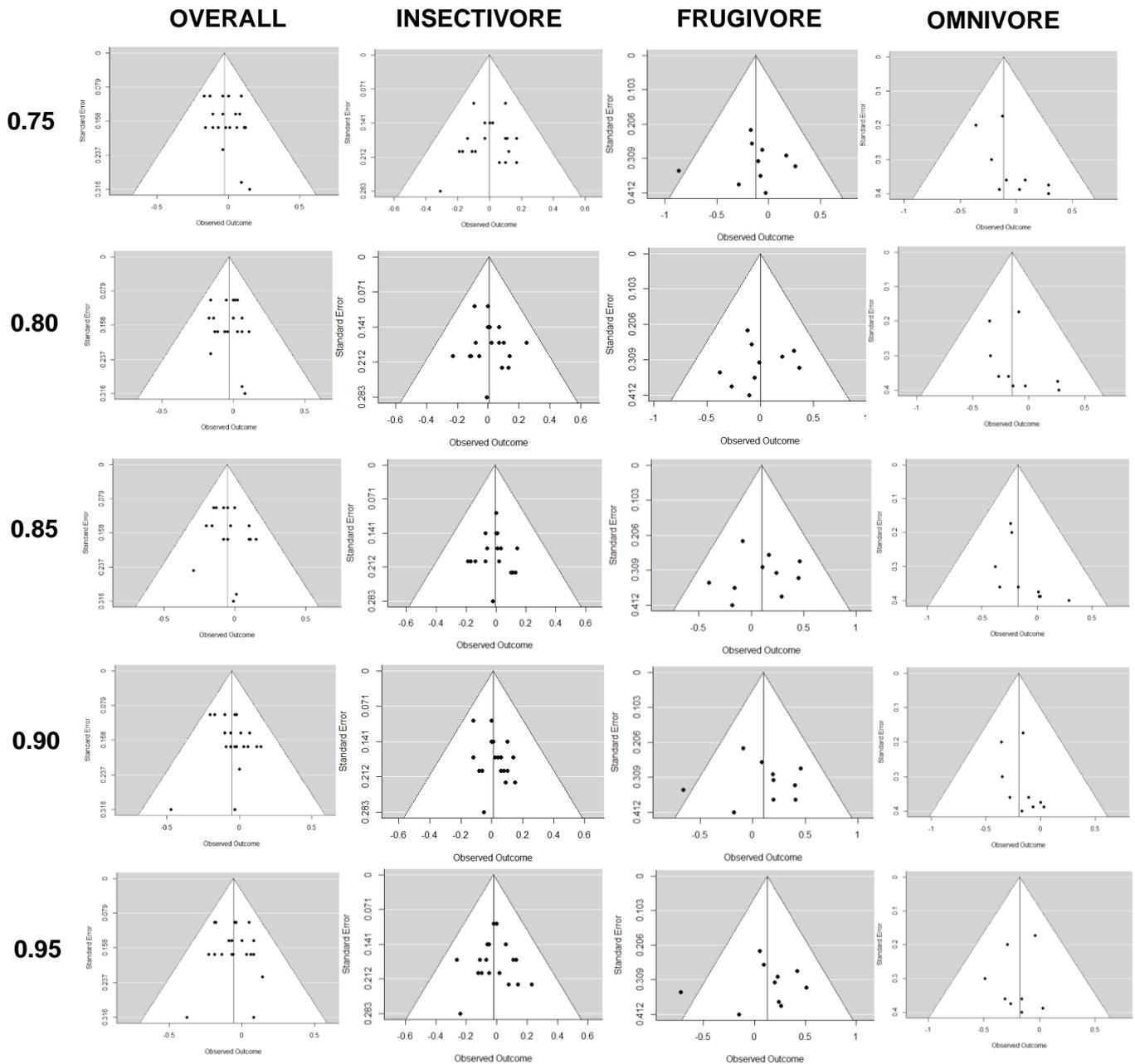


Figure B.9. Funnel plots of effect sizes (0.75, 0.8, 0.85, 0.9, 0.95 quantiles) for each mist-net study *Overall* and foraging guilds (*Insectivore*, *Frugivore* and *Omnivore*).

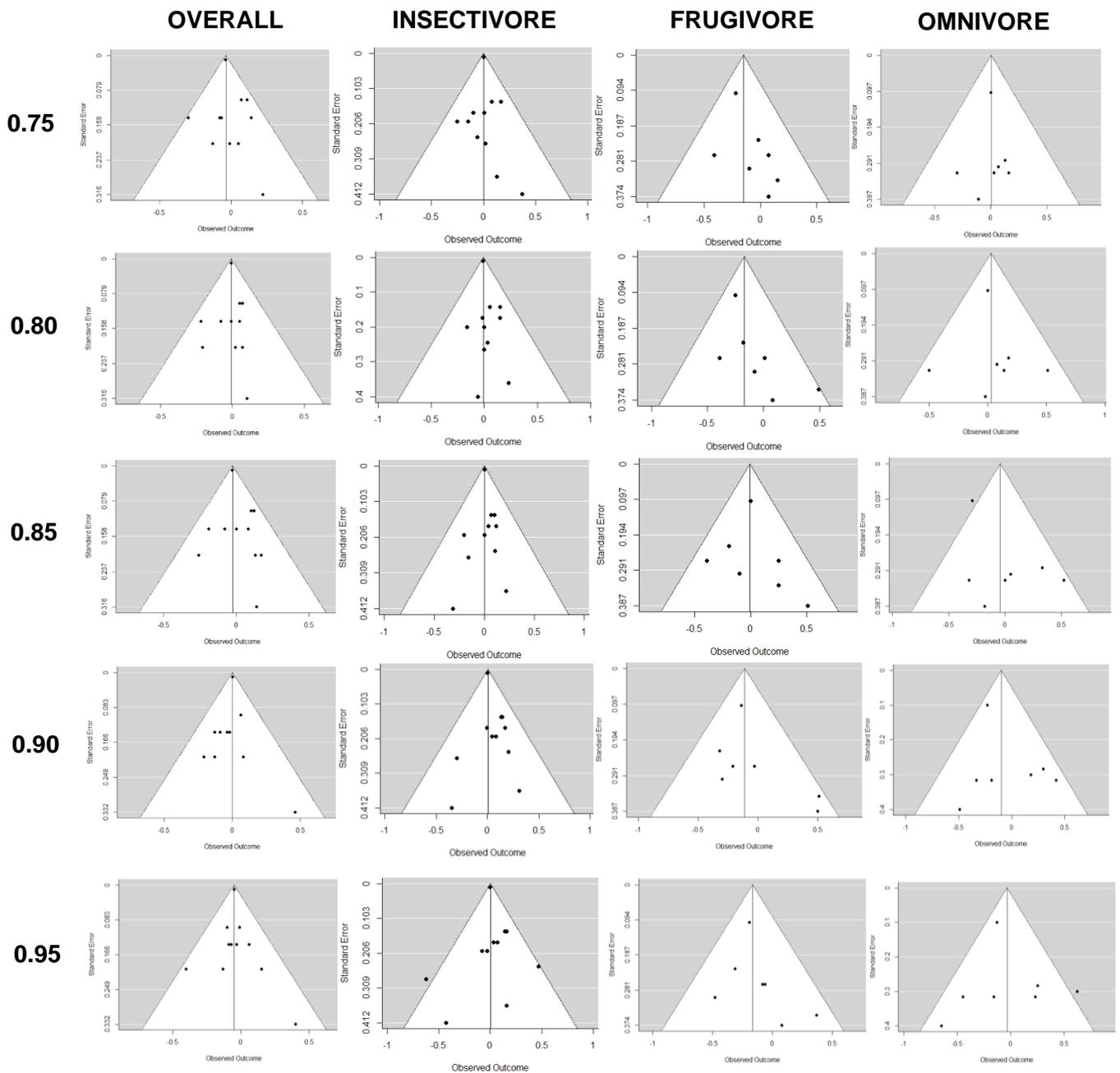


Figure B.10. Funnel plots of effect sizes (0.75, 0.8, 0.85, 0.9, 0.95 quantiles) for each point-count study *Overall* and foraging guilds (*Insectivore*, *Frugivore* and *Omnivore*).

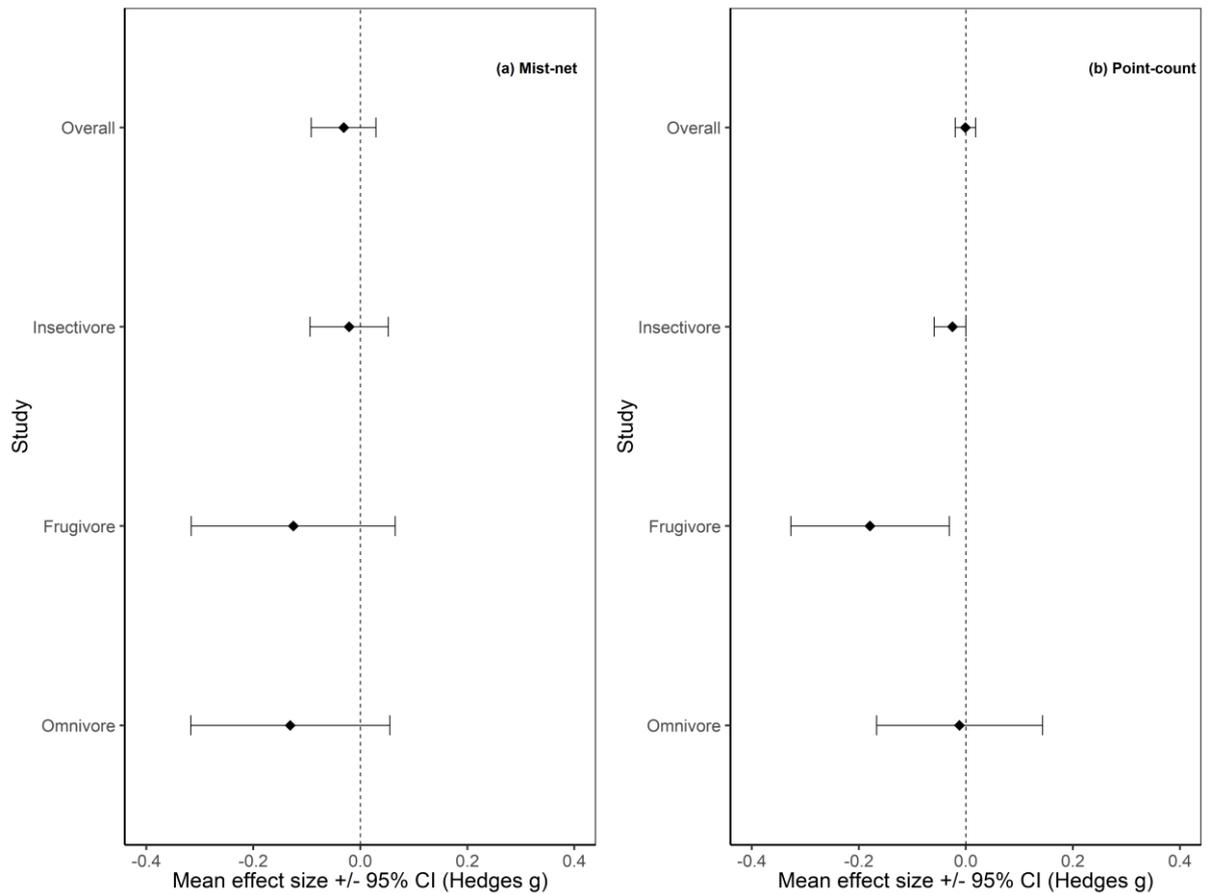


Figure B.11. Overall effect sizes of all studies combined in each category: Overall (all data), Insectivore, Frugivore and Omnivore; with their respective 95% confidence intervals. Effect sizes are from the 0.75 regression quantile for (a) Mist-net studies and (b) Point-count studies, using raw abundance or capture rate data.

# Appendix C

## Supporting information for Chapter 4

### Appendix C.1. Supplementary tables

Table C.1. Species, foraging guild, family and conservation status information (IUCN status) for all 71 species. Species showing significant movement changes between logged and unlogged forests in the 71 species, 43 species and 25 species model set are indicated. Family and foraging guild data were obtained from the Elton Traits 1.0 database (Wilman *et al.* 2014). LC = Least Concern, NT = Near Threatened, VU = Vulnerable.

Species	Species Code	Foraging Guild	Family	IUCN status	Movement change		
					71 sp	43 sp	25 sp
<i>Terpsiphone affinis</i>	APFLY	Invertebrate	Monarchidae	LC	No	No	-
<i>Orthotomus ruficeps</i>	ATLRB	Invertebrate	Sylviidae	LC	No	-	-
<i>Alcedo peninsulae</i>	BBKING	VertFishScav	Alcedinidae	NT	No	-	-
<i>Pellorneum nigrocapitatum</i>	BCBAB	Invertebrate	Timaliidae	LC	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Alcedo meninting</i>	BEKING	VertFishScav	Alcedinidae	LC	No	-	-
<i>Alcippe brunneicauda</i>	BFUL	Invertebrate	Timaliidae	NT	No	No	No
<i>Erythropitta ussheri</i>	BLKHPIT	Invertebrate	Pittidae	NT	No	-	-
<i>Hypothymis azurea</i>	BNMON	Invertebrate	Monarchidae	LC	No	No	No
<i>Meiglyptes tukki</i>	BNWPEC	Invertebrate	Picidae	NT	No	-	-
<i>Mixornis bornensis</i>	BSTBAB	Invertebrate	Timaliidae	LC	No	-	-
<i>Turdinus atrigularis</i>	BTWBAB	Invertebrate	Timaliidae	NT	No	-	-
<i>Iole charlottae</i>	BVBUL	Omnivore	Pycnonotidae	NT	No	-	-
<i>Ptilochla leucogrammica</i>	BWBAB	Invertebrate	Timaliidae	VU	No	-	-
<i>Geokichla interpres</i>	CCTHR	Invertebrate	Turdidae	NT	No	-	-
<i>Platylophus galericulatus</i>	CJAY	Invertebrate	Corvidae	NT	No	-	-
<i>Enicurus ruficapillus</i>	CNFORK	Invertebrate	Muscicapidae	NT	No	No	-
<i>Stachyris maculata</i>	CRBAB	Invertebrate	Timaliidae	NT	No	No	-

<i>Aethopyga siparaja</i>	CSUN	Omnivore	Nectariniidae	LC	No	-	-
<i>Cyanoderma erythropterum</i>	CWBAB	Invertebrate	Timaliidae	LC	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Orthotomus atrogularis</i>	DNTLRB	Invertebrate	Sylviidae	LC	No	No	-
<i>Harpactes diardii</i>	DTRO	Invertebrate	Trogonidae	NT	No	-	-
<i>Chalcophaps indica</i>	EDOV	Omnivore	Columbidae	LC	No	No	-
<i>Trichastoma bicolor</i>	FBAB	Invertebrate	Timaliidae	LC	No	No	No
<i>Macronus ptilosus</i>	FBTBAB	Invertebrate	Timaliidae	NT	No	No	No
<i>Calyptomena viridis</i>	GBRDB	FruaNect	Eurylaimidae	NT	No	-	-
<i>Alophoixus tephrogenys</i>	GCBUL	Omnivore	Pycnonotidae	LC	No	No	No
<i>Cyornis umbratilis</i>	GCJFLY	Invertebrate	Muscicapidae	NT	No	No	-
<i>Stachyris poliocephala</i>	GHBAB	Invertebrate	Timaliidae	LC	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Malacocincla sepiaria</i>	HBAB	Invertebrate	Timaliidae	LC	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Tricholestes criniger</i>	HBBUL	Omnivore	Pycnonotidae	LC	No	No	No
<i>Pitta sordida</i>	HPIT	Invertebrate	Pittidae	LC	No	-	-
<i>Cyornis caerulatus</i>	LBBFLY	Invertebrate	Muscicapidae	VU	No	No	No
<i>Chloropsis cyanopogon</i>	LGLEAF	FruaNect	Chloropseidae	NT	No	-	-
<i>Arachnothera longirostra</i>	LSPHUN	Omnivore	Nectariniidae	LC	No	No	No
<i>Malacopteron magnirostre</i>	MBAB	Invertebrate	Timaliidae	LC	No	No	-
<i>Cyornis turcosus</i>	MBFLY	Invertebrate	Muscicapidae	NT	No	-	-
<i>Blythipicus rubiginosus</i>	MWPEC	Invertebrate	Picidae	LC	No	No	-
<i>Dicaeum trigonostigma</i>	OBFLPEC	FruaNect	Dicaeidae	LC	No	No	-
<i>Ceyx erithaca</i>	ODKING	Invertebrate	Alcedinidae	LC	No	No	No
<i>Pycnonotus plumosus</i>	OWBUL	FruaNect	Pycnonotidae	LC	No	-	-
<i>Euptilotus eutilotus</i>	PBBUL	Omnivore	Pycnonotidae	NT	No	No	-
<i>Rhipidura javanica</i>	PFAN	Invertebrate	Rhipiduridae	LC	No	-	-
<i>Arachnothera hypogrammica</i>	PNSUN	Omnivore	Nectariniidae	LC	No	No	No
<i>Anthreptes simplex</i>	PSUN	FruaNect	Nectariniidae	LC	No	No	-
<i>Malacopteron magnum</i>	RCBAB	Invertebrate	Timaliidae	NT	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Ficedula dumetoria</i>	RCFLY	Invertebrate	Muscicapidae	LC	No	No	-
<i>Actenoides concretus</i>	RCKING	Invertebrate	Alcedinidae	NT	No	-	-
<i>Chalcoparia singalensis</i>	RCSUN	Invertebrate	Nectariniidae	LC	No	No	-
<i>Cyanoderma rufifrons</i>	RFBAB	Invertebrate	Timaliidae	LC	No	-	-
<i>Sasia abnormis</i>	RPIC	Invertebrate	Picidae	LC	No	No	No
<i>Trichixos pyrropygus</i>	RTSHAM	Invertebrate	Muscicapidae	NT	No	-	-

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<i>Orthotomus sericeus</i>	RTTLRB	Invertebrate	Sylviidae	LC	No	No	-
<i>Philentoma pyrhoptera</i>	RWPHIL	Invertebrate	Tephrodornithidae	LC	No	No	No
<i>Arachnothera affinis</i>	SBSPHUN	Invertebrate	Nectariniidae	LC	No	-	-
<i>Ixidia erythroptalmos</i>	SBUL	Omnivore	Pycnonotidae	LC	No	No	-
<i>Malacopteron affine</i>	SCBAB	Invertebrate	Timaliidae	NT	No	No	-
<i>Malacopteron cinereum</i>	SCRBAB	Invertebrate	Timaliidae	LC	No	No	No
<i>Rhipidura perlata</i>	SFAN	Invertebrate	Rhipiduridae	LC	No	No	-
<i>Harpactes duvaucelii</i>	SRTRO	Invertebrate	Trogonidae	NT	No	-	-
<i>Pellorneum malaccense</i>	STBAB	Invertebrate	Timaliidae	NT	<b>Yes</b>	<b>Yes</b>	<b>Yes</b>
<i>Kenopia striata</i>	SWBAB	Invertebrate	Timaliidae	NT	No	No	No
<i>Aethopyga temminckii</i>	TSUN	Omnivore	Nectariniidae	LC	No	-	-
<i>Erpornis zantholeuca</i>	WBERP	Invertebrate	Timaliidae	LC	No	-	-
<i>Trichastoma rostratum</i>	WCBAB	Invertebrate	Timaliidae	NT	No	No	No
<i>Enicurus leschenaulti</i>	WCFORK	Invertebrate	Muscicapidae	LC	No	No	No
<i>Kittacincla malabarica</i>	WCSHAM	Invertebrate	Muscicapidae	LC	No	No	No
<i>Stachyris leucotis</i>	WNBAB	Invertebrate	Timaliidae	NT	No	-	-
<i>Alophoixus phaeocephalus</i>	YBBUL	Omnivore	Pycnonotidae	LC	No	No	No
<i>Prionochilus maculatus</i>	YBFLPEC	Fruinect	Dicaeidae	LC	No	No	No
<i>Prinia flaviventris</i>	YBPRIN	Invertebrate	Cisticolidae	LC	No	-	-
<i>Prionochilus xanthopygius</i>	YRFLPEC	Fruinect	Dicaeidae	LC	<b>Yes</b>	<b>Yes</b>	-

---

Table C.2: Bayesian model performance for the movement kernel models using probability density function (pdf) for the Cauchy distribution, Rayleigh distribution, Gamma distribution and Log-normal distribution. Models with the lowest DIC values are the most parsimonious and models with less than 2  $\Delta$ DIC are considered equally parsimonious. DIC = Deviance Information Criterion,  $\Delta$ DIC = the DIC difference between the best model and that stated model, pD = the effective number of parameters, Rhat = Rhat statistic close to 1 indicates that the model converged. Rhat values up to 1.05 were accepted. All parameters in each model had Rhat values less than the maximum presented below.

<b>Model set: 43 species</b>				
<b>Distribution</b>	<b>DIC</b>	<b><math>\Delta</math>DIC</b>	<b>pD</b>	<b>Rhat</b>
Cauchy	3812.4	0.00	0.2	<1.05
Log-normal	3813.5	1.10	0.3	<1.03
Gamma	3813.7	1.30	0.3	<1.017
Rayleigh	3814.4	2.00	0.4	<1.05
<b>Model set: 25 species</b>				
<b>Distribution</b>	<b>DIC</b>	<b><math>\Delta</math>DIC</b>	<b>pD</b>	<b>Rhat</b>
Cauchy	3390.3	0.00	0.1	<1.04
Log-normal	3391.4	1.10	0.3	<1.007
Gamma	3391.5	1.20	0.3	<1.008
Rayleigh	3392.1	1.80	0.3	<1.05

Table C.3. Model selection of linear models. Models were selected for change in movement probability between logged and unlogged forests in relation to species' body mass (g), species' conservation status, and species' foraging guild, based on their AICc values. The null model did not include any of the predictor variables. Foraging guild data were obtained from the Elton Traits 1.0 database (Wilman *et al.* 2014) and species body mass data were obtained from Dunning's CRC Handbook of Avian Body Masses (2008) and Handbook of the Birds of the World Alive (del Hoyo *et al.* 2017). Mass = species' body mass (g), IUCN status = species' conservation status, Guild = species' foraging guild. Most parsimonious models are highlighted in boldface type. df = degrees of freedom, logLik = Log-likelihood, AICc = Akaike information criterion for small sample sizes,  $\Delta$ AICc = the AICc difference between the best model and that stated model, Weight = AICc weights.

<b>Model</b>	<b>df</b>	<b>logLik</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>Weight</b>
<b>NULL</b>	2	140.12	-276.06	0.00	0.56
<b>Mass</b>	3	140.28	-274.21	1.85	0.22
IUCN status	4	140.75	-272.89	3.17	0.12
IUCN status + Mass	5	140.87	-270.81	5.25	0.04
Guild	5	140.81	-270.69	5.37	0.04
Guild + Mass	6	140.95	-268.59	7.47	0.01
Guild + IUCN status	7	141.52	-267.27	8.79	0.007
Guild + IUCN status + Mass	8	141.67	-265.02	11.04	0.002

## Appendix C.2. Supplementary figures

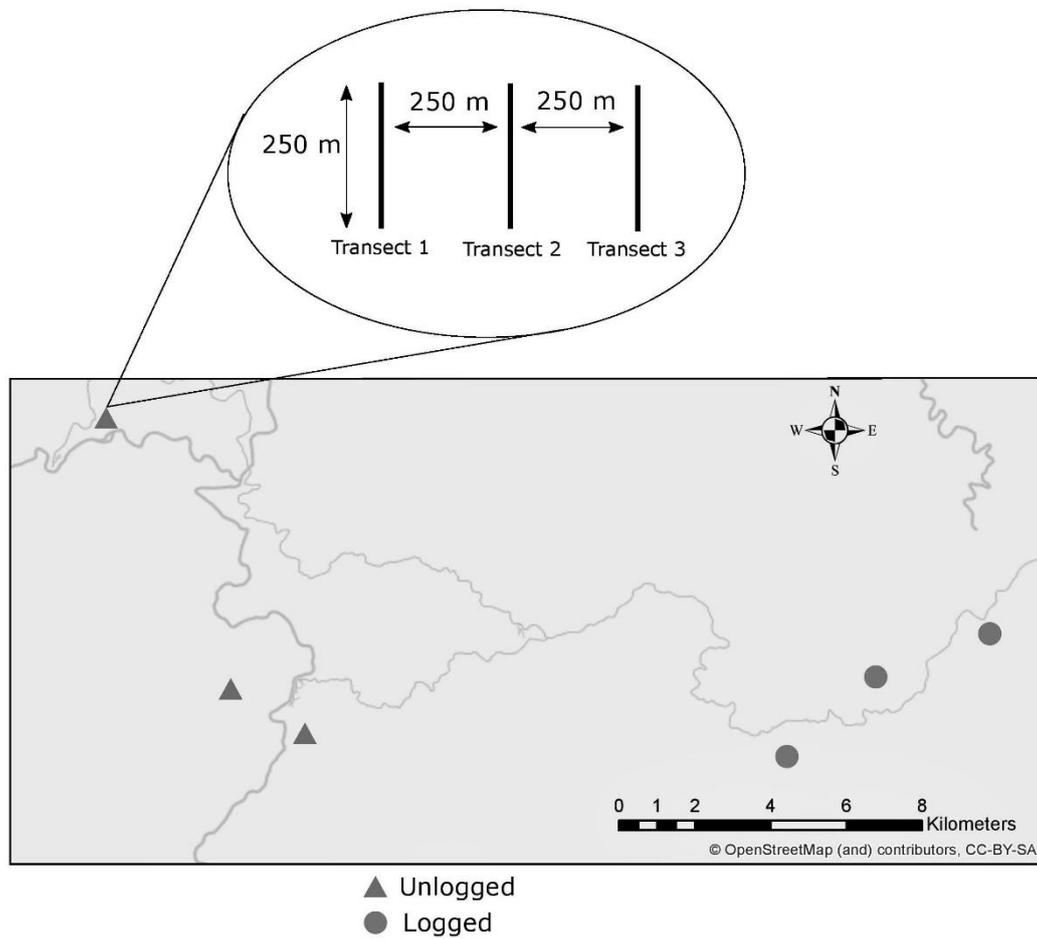


Figure C.1. Locations of our six sampling plots (three in unlogged old-growth forests; three in twice-logged forests) with the mist-netting transect set up in each plot.

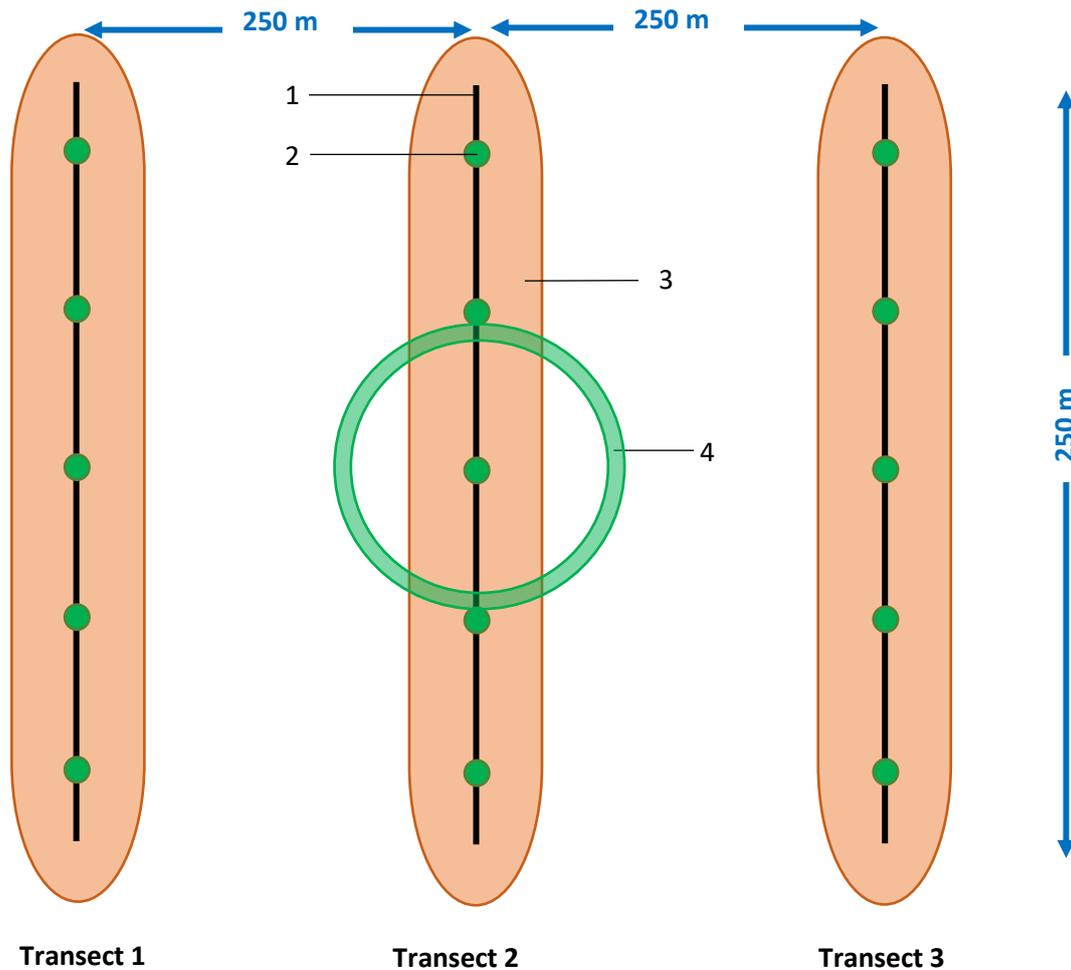


Figure C.2. Example of the buffers and annulus ring set up in a plot using ArcMap 10.6 (ESRI 2018) to calculate  $Wr$ , the probability of observing a movement at distance  $r$  for a given individual. **1**: transect lines each containing 15 mist-nets; **2**: centre of each capture zone (1 – 5), the distance between the centres of each capture zone is  $50\text{m} \pm 1.2\text{m}$ ; **3**: buffer of radius 25 m around each transect to represent the sampled space; **4**: annulus ring of 1m width centred around the centre of the capture zone where the given individual was captured, shown here is the annulus ring of 50m radius as this given individual had a maximum distance moved,  $r$ , of 50m. The area of sampled space within that annulus ring across all transects was divided by the total area of that annulus ring to give the  $Wr$ .

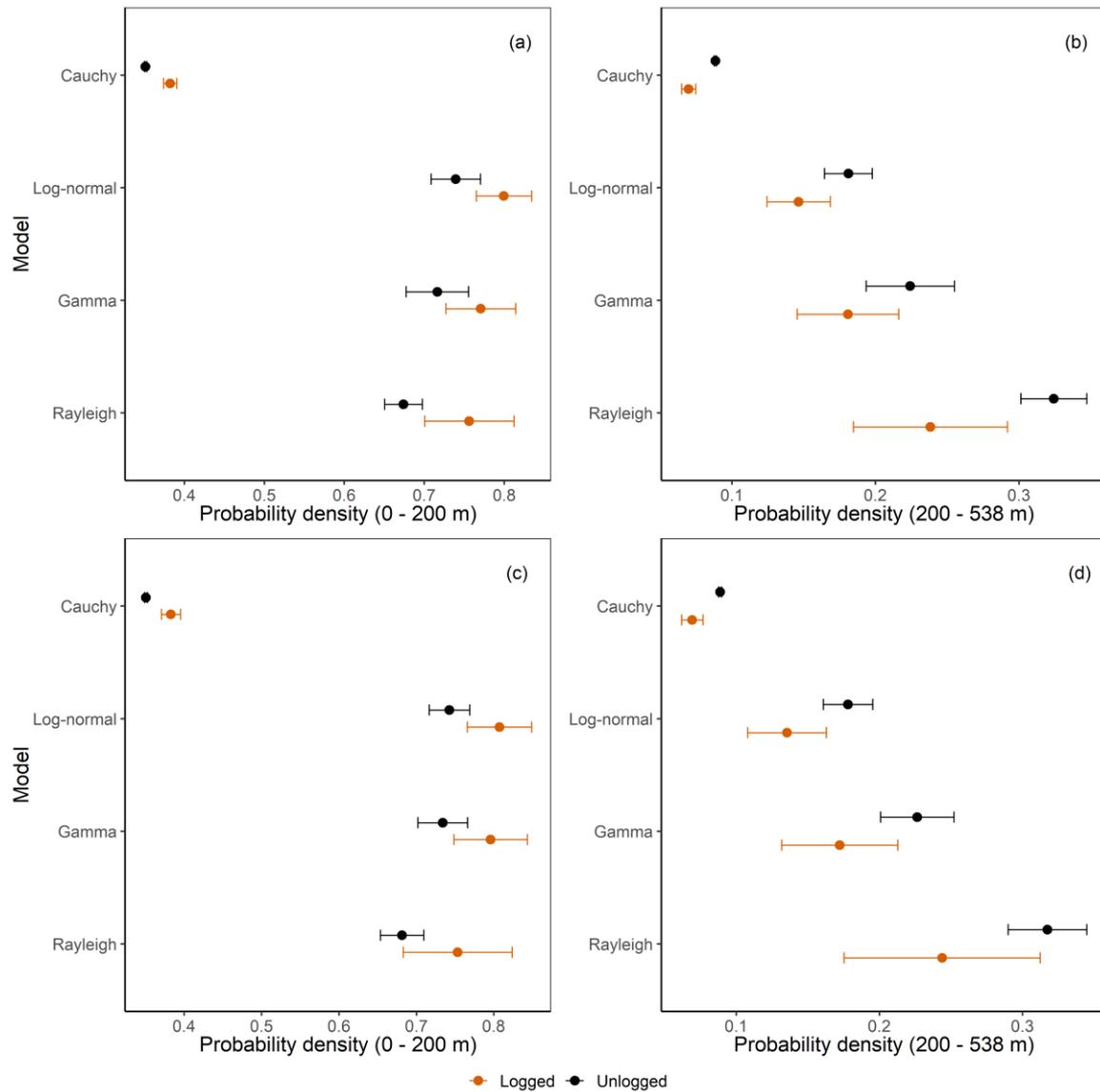


Figure C.3. Mean probability density from all four models (Cauchy, Log-normal, Gamma, Rayleigh) for distances between 0 m to 200 m, and, 200 m to 538 m, with 95% credible intervals. (a) & (b) 43 species combined; (c) & (d) 25 species combined. Only the positive half of the Cauchy probability density function was used in the model.

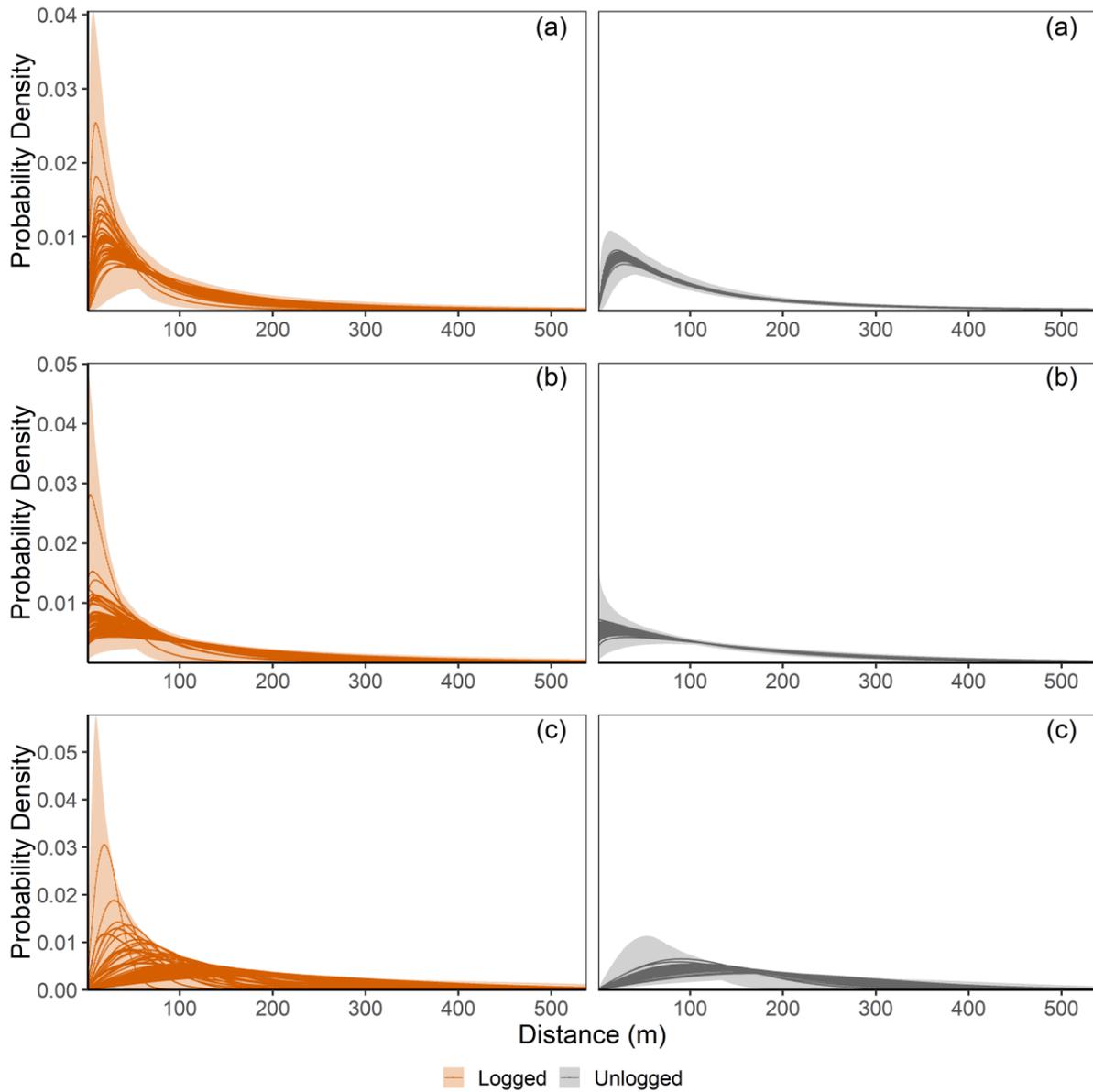


Figure C.4. Posterior means with 95% credible intervals for movement kernels of all species fitted with the (a) Log-normal, (b) Gamma, and (c) Rayleigh probability density function in the 71 species model set given a certain maximum distance moved in each habitat type (logged or unlogged). Each line is for a separate species.

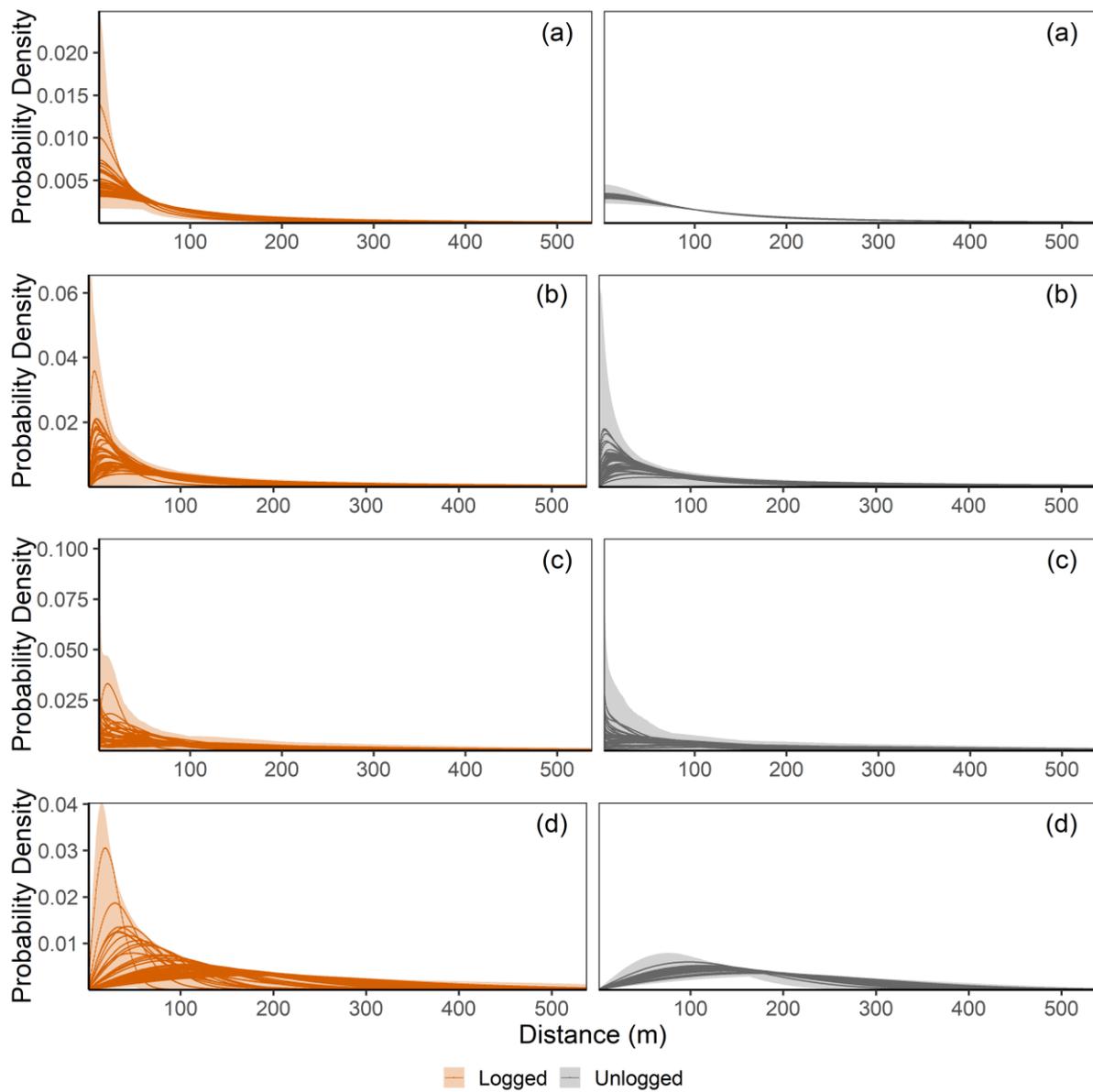


Figure C.5. Posterior means with 95% credible intervals for movement kernels of all species fitted with the (a) Cauchy, (b) Log-normal, (c) Gamma, and (d) Rayleigh probability density function in the 43 species model set given a certain maximum distance moved in each habitat type (logged or unlogged). Each line is for a separate species.

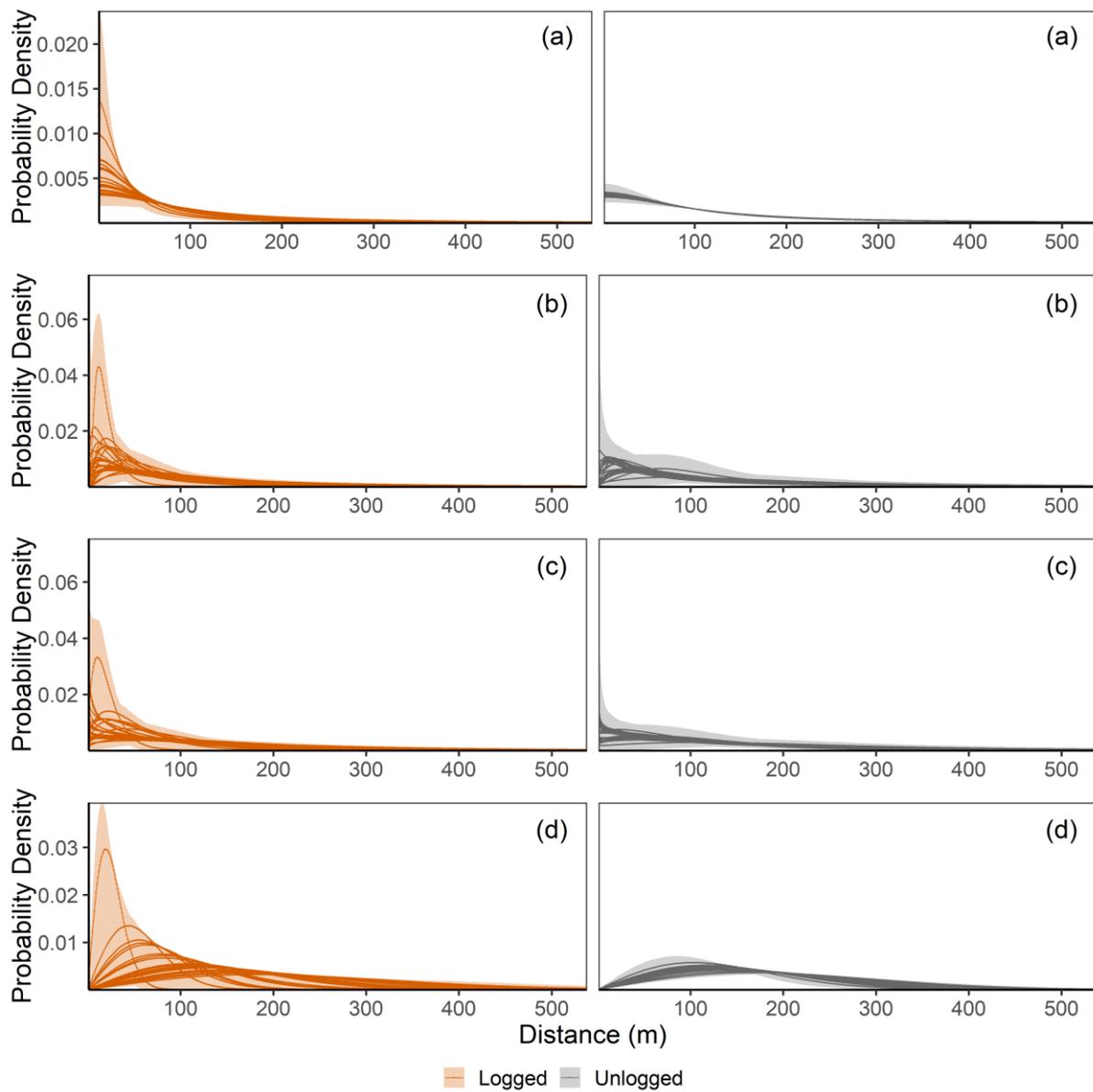


Figure C.6. Posterior means with 95% credible intervals for movement kernels of all species fitted with the (a) Cauchy, (b) Log-normal, (c) Gamma, and (d) Rayleigh probability density function in the 25 species model set given a certain maximum distance moved in each habitat type (logged or unlogged). Each line is for a separate species.

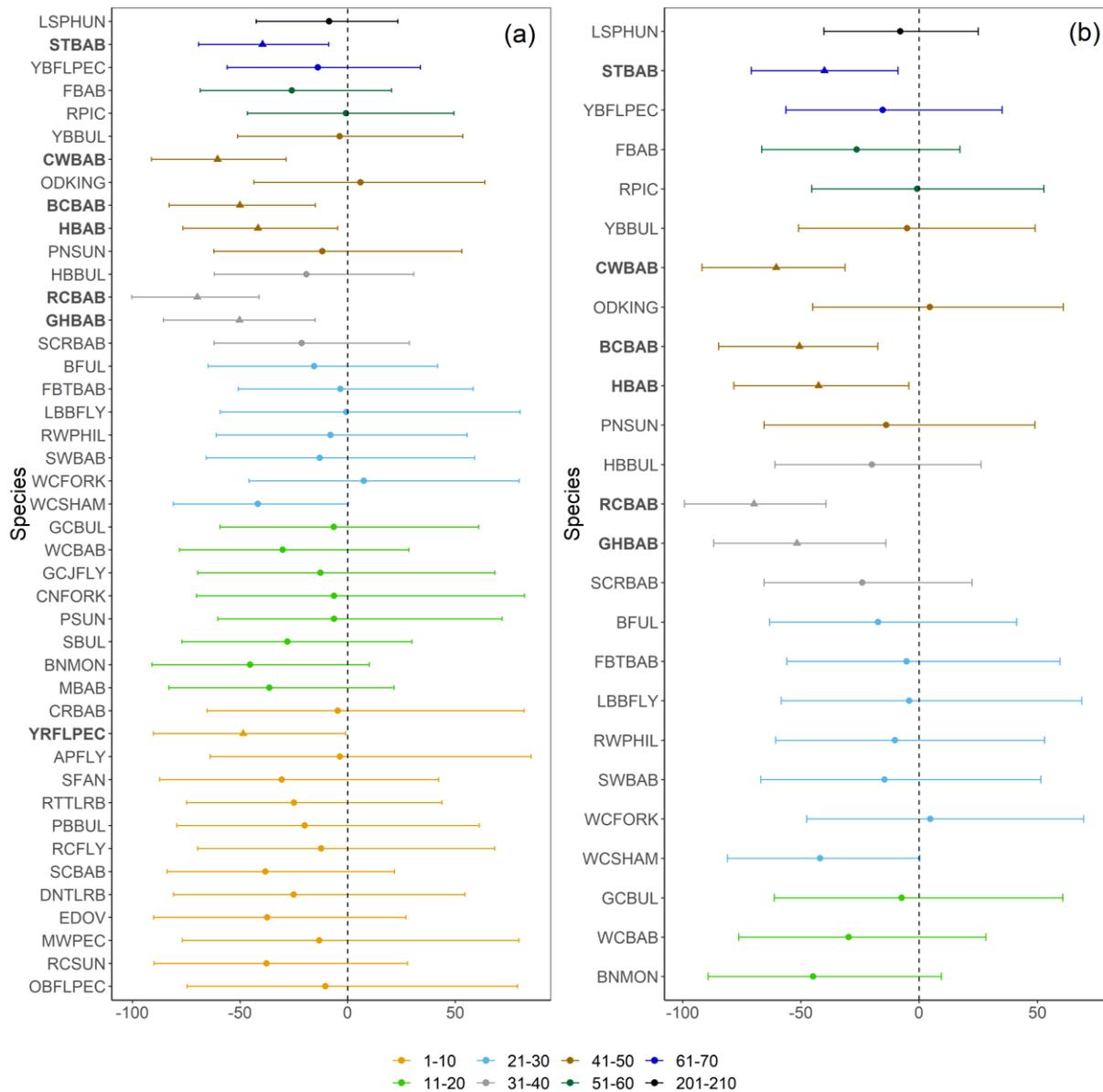


Figure C.7. Posterior distributions (mean and 95% credible interval) for the difference in scale parameter,  $\gamma$ , between habitat types (logged and unlogged), of the Cauchy probability density function in the (a) 43 species model set and (b) 25 species model set. 95% credible intervals not overlapping zero are considered to be statistically significant. Species with statistically significant movement changes are highlighted in bold. Sample sizes for each species are colour coded. Species names are substituted with the species' code (species information in Table C.1).

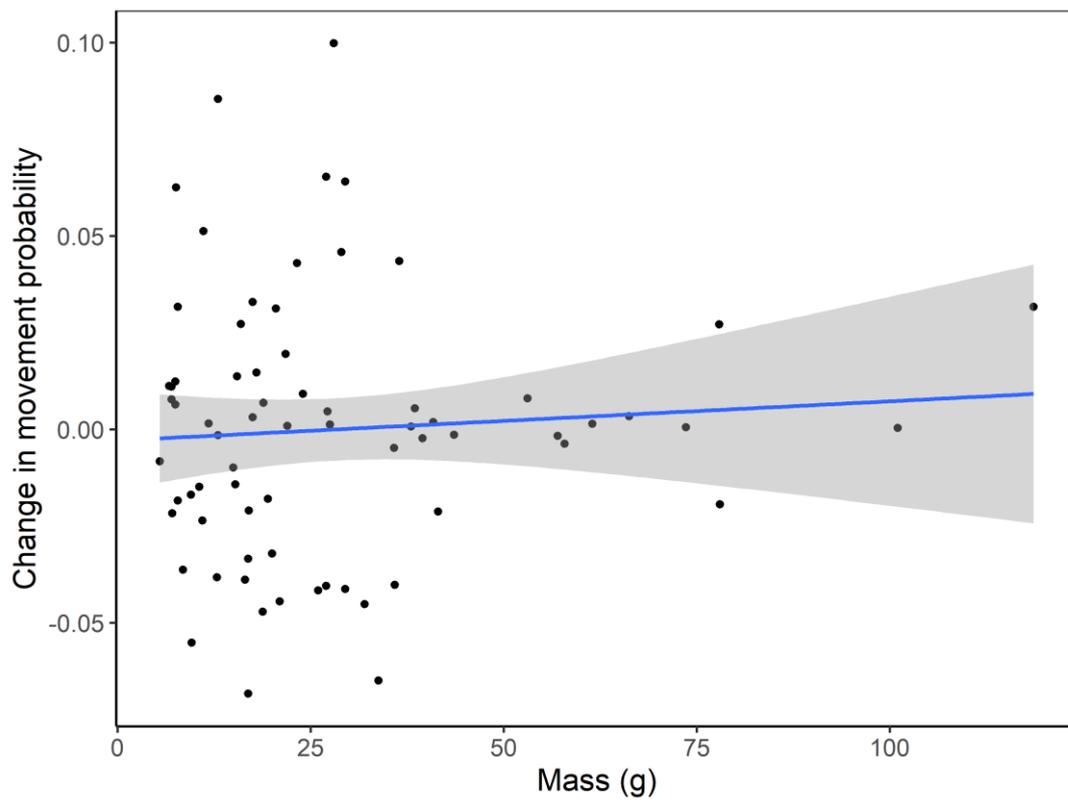


Figure C.8. Species traits and conservation status effects on the changes in movement probabilities between logged and unlogged forests. Species' body mass ( $p=0.57$ ) did not determine the magnitude of change in movement probabilities between logged and unlogged forests. Individual points represent the mean change in movement probabilities across distances 1 – 538 m between logged and unlogged forests for each species. Fitted lines are predictions from the linear regression with 95% confidence intervals.

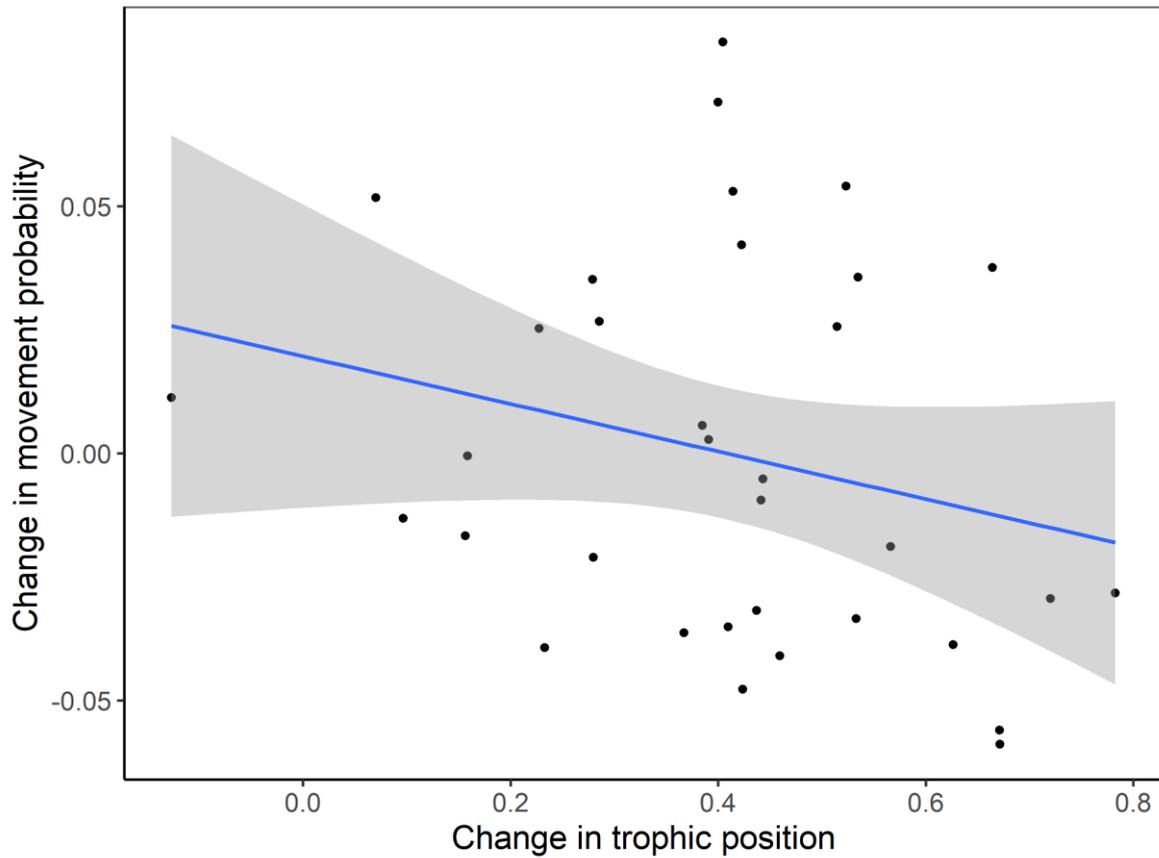


Figure C.9. Species change in movement probabilities between logged and unlogged forests in relation to species change in trophic position between logged and unlogged forests for all 34 species. The magnitude of a species' change in trophic position did not determine the magnitude of change in movement probabilities between logged and unlogged forests ( $p=0.157$ ). Individual points represent the mean change in movement probabilities across distances 1 – 538 m between logged and unlogged forests for each species. Fitted lines are predictions from the linear regression with 95% confidence intervals.

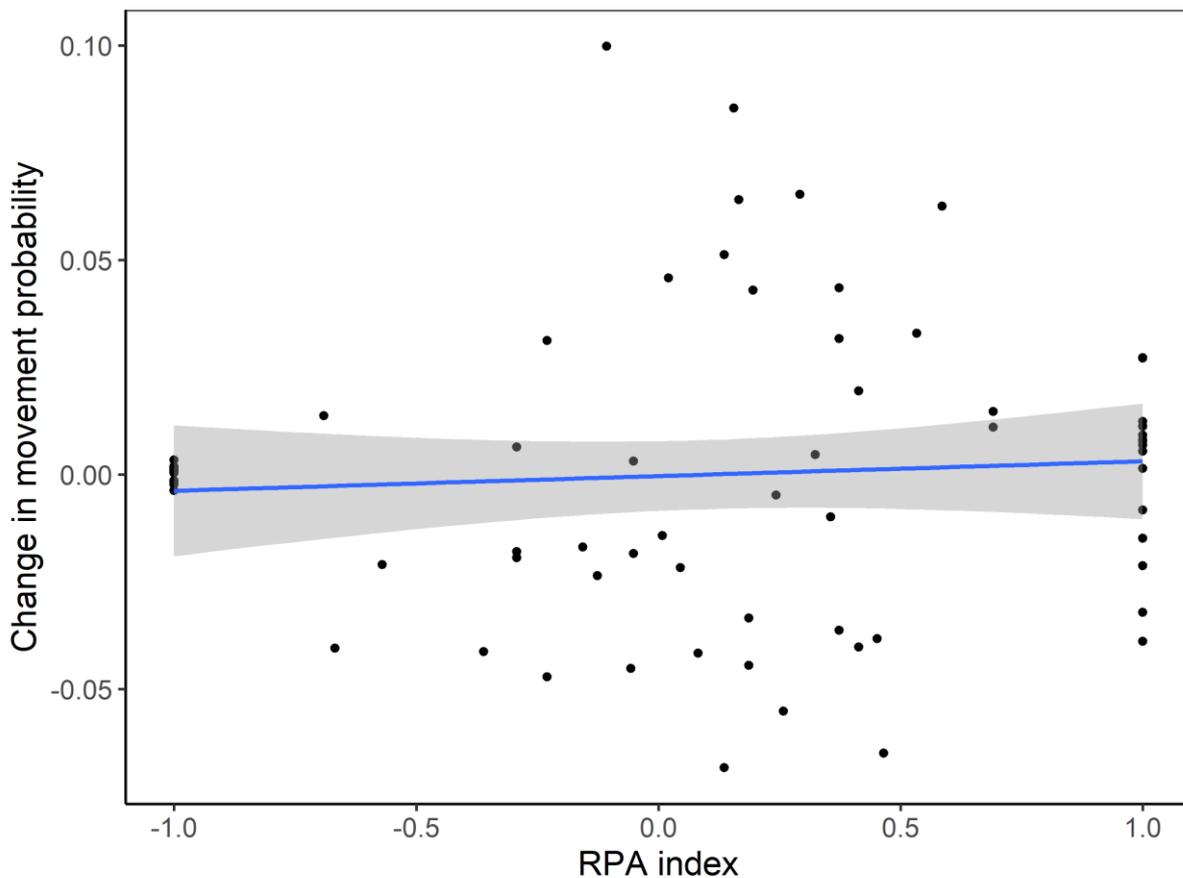


Figure C.10. Species change in movement probabilities between logged and unlogged forests in relation to species' Relative Population Abundance (RPA) Index for all 71 species. A species' RPA index did not determine the magnitude of change in movement probabilities between logged and unlogged forests ( $p=0.564$ ). Individual points represent the mean change in movement probabilities across distances 1 – 538 m between logged and unlogged forests for each species. Fitted lines are predictions from the linear regression with 95% confidence intervals.

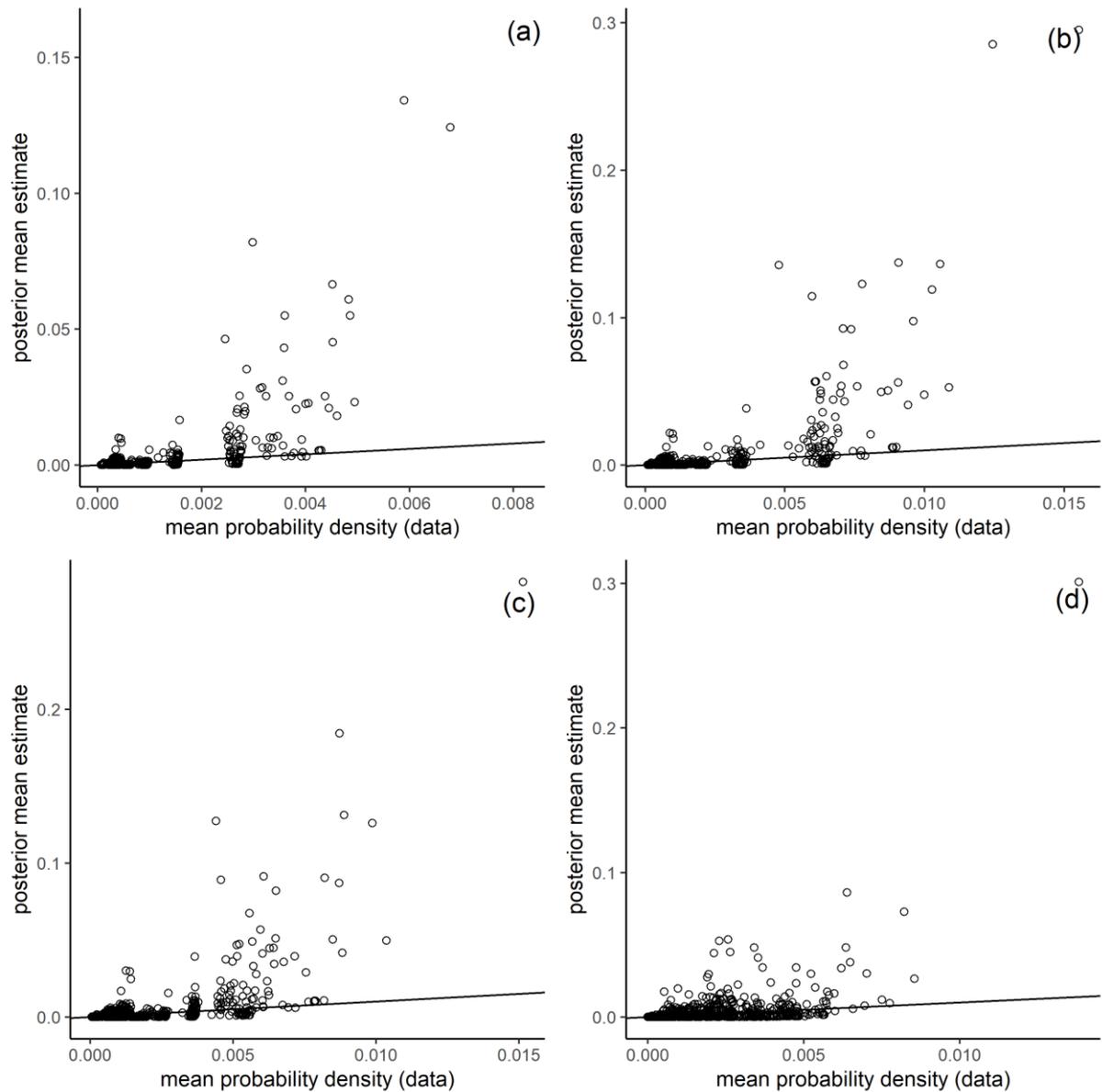


Figure C.11. Posterior predictive checks for the 71 species model set fitted with the (a) Cauchy (Bayesian p-value: 0.70), (b) Log-normal (Bayesian p-value: 0.71), (c) Gamma (Bayesian p-value: 0.71), and (d) Rayleigh (Bayesian p-value: 0.71) probability density function. Each panel compares the observed mean probability densities for a certain maximum distance moved to the posterior mean estimates. Each point corresponds to one species given a certain maximum distance moved. Lines correspond to the identity line  $y=x$ .

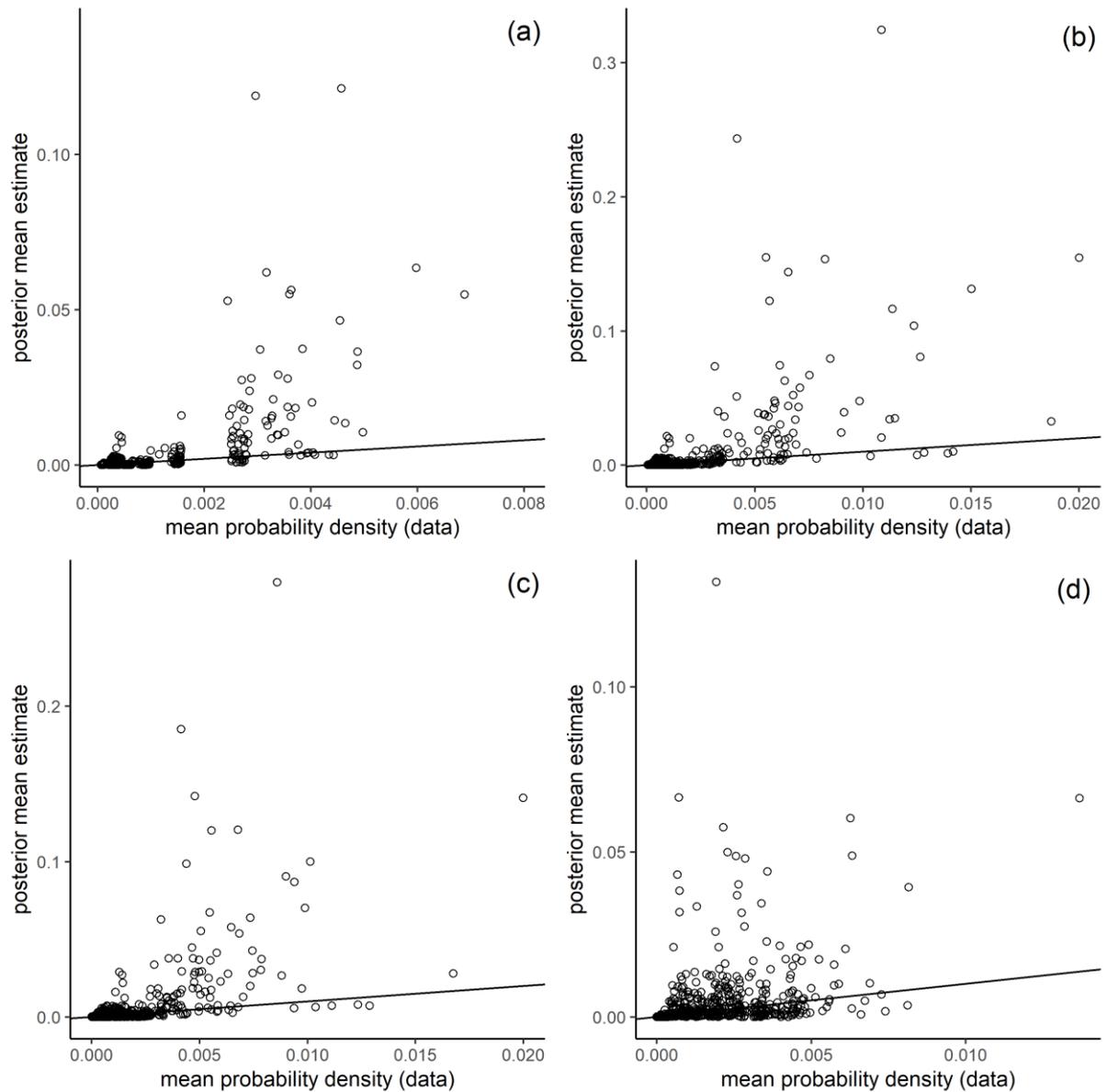


Figure C.12. Posterior predictive checks for the 43 species model set fitted with the (a) Cauchy (Bayesian p-value: 0.55), (b) Log-normal (Bayesian p-value: 0.53), (c) Gamma (Bayesian p-value: 0.51), and (d) Rayleigh (Bayesian p-value: 0.51) probability density function. Each panel compares the observed mean probability densities for a certain maximum distance moved to the posterior mean estimates. Each point corresponds to one species given a certain maximum distance moved. Lines correspond to the identity line  $y=x$ .

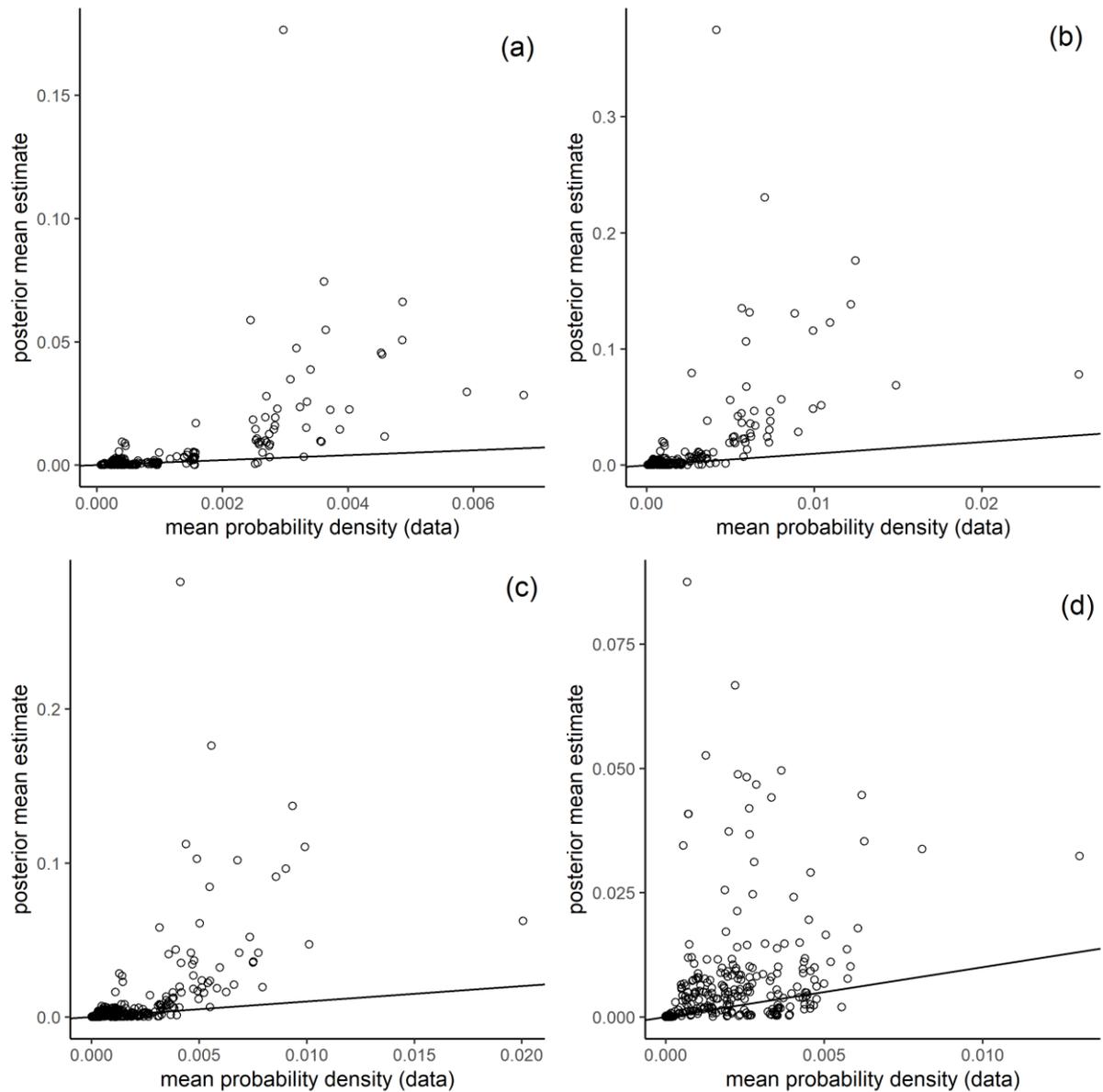


Figure C.13. Posterior predictive checks for the 25 species model set fitted with the (a) Cauchy (Bayesian p-value: 0.35), (b) Log-normal (Bayesian p-value: 0.33), (c) Gamma (Bayesian p-value: 0.33), and (d) Rayleigh (Bayesian p-value: 0.29) probability density function. Each panel compares the observed mean probability densities for a certain maximum distance moved to the posterior mean estimates. Each point corresponds to one species given a certain maximum distance moved. Lines correspond to the identity line  $y=x$ .

## Appendix C.3. Model code for Bayesian movement model

### Model Code (Cauchy distribution)

```

# location parameter --> b
# scale parameter --> a

# nspecies = total number of species.
# nhabs = total number of habitat types.
# ndists = total number of observable distances.
# possdists = vector of all observable distances.
# ninds = total number of individuals.
# obs.sp = vector of species number assigned to each corresponding individual
# obs.hab = vector of habitat number assigned to each corresponding individual (1=logged,
                                                2=unlogged)

# distobs = a matrix supplied as data where rows are individuals and columns are the
            possdists distance levels, and for each individual all values are zero except
            the column of their observed maximum distance, which gets a 1.
# weights = a corresponding data matrix (matching distobs) with the weight,  $w_r$ , for distance
            levels ranging from the observed maximum distance to the observable
            maximum distance limit (i.e. 538m), for each individual.
# truedist = a latent matrix (not supplied as data) that holds the 'true' maximum distances.
# max.r[i] = the observed maximum distance level for individual i. max.r isn't the distance,
            it is the column number (or value of possdists) corresponding to that
            distance.

### Model
bayesmod <- function(){

### State component:
  for(i in 1:nspecies){
    for(j in 1:nhabs){
      for(k in 1:ndists){
        X[i,j,k] <- (1/3.14159)*(a[s[i],habitat[j]]/((possdists[k]-
            b[s[i],habitat[j]])^2+(a[s[i],habitat[j]]^2))) # Cauchy distribution pdf
      }
    }
  }

### Observation component:
  for(i in 1:ninds){
    for(k in max.r[i]:ndists){
      truedist[i,k] ~ dbern(X[obs.sp[i],obs.hab[i],k])
      distobs[i,k] ~ dbern(weights[i,k]*truedist[i,k]) # distobs can only be 1 if truedist is 1
      sim.distobs[i,k] <- weights[i,k]*mu[obs.sp[i],obs.hab[i],k] # this will simulate an
          #equivalent dataset from the model parameters
    }
  }

### priors ###
  for(k in 1:nspecies){
    a[k,1] ~ dgamma(com.alpha[1],tau.alpha[1])
    a[k,2] ~ dgamma(com.alpha[2],tau.alpha[2])
    b[k,1] <- 0 # Location parameter set to zero to get the positive half of the Cauchy pdf.
  }
}

```

```

b[k,2] <- 0 # Location parameter set to zero to get the positive half of the Cauchy pdf.
}

### community level hyperpriors ###
com.alpha[1] ~ dunif(0,100)
tau.alpha[1] ~ dunif(0,100)
com.alpha[2] ~ dunif(0,100)
tau.alpha[2] ~ dunif(0,100)

### get model-predicted values to use in constructing movement kernels
for(i in 1:538){ # distance from 1 m to 538 m
  for(k in 1:nspecies){
    mu_log[i,k] <- (1/3.14159)*(a[k,1]/((i-b[k,1])^2+(a[k,1]^2)))
    mu_pri[i,k] <- (1/3.14159)*(a[k,2]/((i-b[k,2])^2+(a[k,2]^2)))
    a_diff[i,k] <- a[k,1] - a[k,2]
  }
}

jags.data <- list('max.r' = max.r,
                 'possdists' = possdists,
                 'ndists' = length(unique(data_summ$max.r)),
                 'weights' = as.matrix(weights),
                 'distobs' = as.matrix(distobs),
                 'ninds' = ninds,
                 'nspecies' = nspecies,
                 'nhabs' =2,
                 'habitat' = c(1,2),
                 's' = 1:nspecies,
                 'obs.sp' = obs.sp,
                 'obs.hab' = obs.hab)

### Initial values for truedist
init.truedist <- as.matrix(distobs)
for(i in 1:ninds){
  if(max.r[i]>1){
    init.truedist[i,1:(max.r[i]-1)]<-NA
  }
}
inits = function(){
  list(truedist = init.truedist)
}

```

---

## Appendix C.4. Methods and Results for recapture rate analysis

### Recapture rate analysis

To examine how habitat type and understory habitat metrics affect the number of recaptures per transect, the number of recaptures per transect for all 71 species was calculated across all plots in both logged and unlogged forests. Understory habitat metrics were obtained from (Senior *et al.* 2018) who conducted habitat structure surveys in the same area as this study was conducted. The habitat metrics included were percentage ground vegetation cover (1.5 m above ground), percentage understory vegetation cover (15 m above ground), tree stand basal area ( $\text{m}^2/\text{ha}$ ) of circumference  $>0.6$  m and sapling stand basal area ( $\text{m}^2/\text{ha}$ ) of circumference between 0.1 – 0.6 m. These habitat metrics were measured either on one of the transects in the plot or on a nearby transect, between 250 m – 810 m to the next nearest transect. Each of these habitat metrics were estimated for our transects by calculating the mean of these habitat metrics, taken from the nearest surveyed transect, and applying it across the three transects for all six plots separately.

We used generalized linear models (GLM) using the *glm* function in R version 3.6.2 (R Core Team 2019). A global model was fitted using the number of recaptures per transect as a function of habitat type (logged vs unlogged forest), percentage ground vegetation cover, percentage understory vegetation cover, tree stand basal area and sapling stand basal area. Model assumptions were checked. A Quasipoisson error distribution and log link was used to deal with overdispersion in the data. To determine which habitat metrics were important determinants of the number of recaptures per transect, we compared all possible variable combinations of the global model, using the *dredge* function from the *MuMIn* package (Barton 2019). The most parsimonious model has the lowest AIC value (Anderson 2008) and models

with less than 2  $\Delta$ AIC were considered to be equally parsimonious. The most parsimonious models were then fitted separately.

## Recapture rate results

A total of 1210 recaptured individual birds from 71 species were recorded in this movement study. Mean number of recaptures per transect in logged and unlogged forests were 180 recaptures and 150 recaptures respectively (Table C.4). The most parsimonious models ( $<2$   $\Delta$ AIC) were the NULL model and the models including only sapling stand basal area (GLZ: Estimate =  $1.42\text{E-}3$ , SE =  $1.24\text{E-}3$ ,  $t = 1.14$ ,  $p = 0.27$ ), tree stand basal area (GLZ: Estimate =  $-2.62\text{E-}5$ , SE =  $2.35\text{E-}5$ ,  $t = -1.12$ ,  $p = 0.28$ ) and ground vegetation cover (GLZ: Estimate =  $-8.61\text{E-}3$ , SE =  $8.31\text{E-}3$ ,  $t = -1.04$ ,  $p = 0.32$ ) separately (Table C.5; Figure C.11) indicating that the number of recaptures per transect were not affected by habitat type or any of the understory habitat metrics.

Table C.4. Mean number of recaptures per transect for all 71 species in unlogged and twice-logged forests.

Habitat	Recaptures per transect			Mean recaptures per transect
	Plot 1	Plot 2	Plot 3	
Unlogged	156.3	152.7	141.0	150.0
Logged	191.3	131.3	213.3	179.9

Table C.5. Model selection of generalized linear models. Models were selected for number of recaptures per transect in relation to habitat type (logged or unlogged forests), percentage ground vegetation cover (1.5 m above ground), percentage understory vegetation cover (15 m above ground), tree stand basal area ( $\text{m}^2/\text{ha}$ ) of circumference  $>0.6$  m and sapling stand basal area ( $\text{m}^2/\text{ha}$ ) of circumference between 0.1 – 0.6 m, based on their QAICc values. The null model did not include any of the predictor variables. Habitat = habitat type, Ground = percentage ground vegetation cover, Understory = percentage understory vegetation cover, Tree = tree stand basal area, Sapling = sapling stand basal area. Most parsimonious models are highlighted in boldface type. df = degrees of freedom, logLik = Log-likelihood, QAICc = quasi- Akaike information criterion for small sample sizes,  $\Delta\text{QAICc}$  = the QAICc difference between the best model and that stated model, Weight = QAICc weights.

<b>Model</b>	<b>df</b>	<b>logLik</b>	<b>QAICc</b>	<b><math>\Delta\text{QAICc}</math></b>	<b>Weight</b>
<b>NULL</b>	1	-366.50	28.72	0.00	0.241
<b>Sapling</b>	2	-348.28	30.38	1.66	0.105
<b>Tree</b>	2	-348.96	30.42	1.70	0.103
<b>Ground</b>	2	-351.33	30.58	1.86	0.095
Habitat	2	-353.66	30.73	2.01	0.088
Understory	2	-357.07	30.95	2.23	0.079
Sapling + Tree	3	-336.18	32.84	4.12	0.031
Ground + Understory	3	-338.13	32.97	4.25	0.029
Ground + Sapling	3	-339.71	33.07	4.36	0.027
Sapling + Understory	3	-341.36	33.18	4.46	0.026
Habitat + Sapling	3	-345.39	33.44	4.73	0.023
Ground + Tree	3	-345.87	33.48	4.76	0.022
Tree + Understory	3	-348.68	33.66	4.94	0.020
Habitat + Tree	3	-348.89	33.67	4.96	0.020
Ground + Habitat	3	-350.00	33.75	5.03	0.020

---

Habitat + Understory	3	-353.25	33.96	5.24	0.018
Ground + Tree + Understory	4	-321.94	35.67	6.95	7.47E-03
Habitat + Sapling + Tree	4	-328.71	36.11	7.39	5.99E-03
Ground + Habitat + Understory	4	-332.98	36.39	7.67	5.21E-03
Ground + Sapling + Tree	4	-334.89	36.52	7.80	4.89E-03
Sapling + Tree + Understory	4	-335.87	36.58	7.86	4.74E-03
Ground + Sapling + Understory	4	-336.57	36.63	7.91	4.63E-03
Ground + Habitat + Sapling	4	-339.47	36.82	8.10	4.21E-03
Habitat + Sapling + Understory	4	-340.96	36.91	8.20	4.01E-03
Ground + Habitat + Tree	4	-345.44	37.21	8.49	3.46E-03
Habitat + Tree + Understory	4	-348.68	37.42	8.70	3.12E-03
Habitat + Sapling + Tree + Understory	5	-320.47	39.96	11.24	8.75E-04
Ground + Habitat + Sapling + Tree	5	-320.51	39.96	11.24	8.74E-04
Ground + Habitat + Tree + Understory	5	-321.35	40.02	11.30	8.50E-04
Ground + Sapling + Tree + Understory	5	-321.58	40.03	11.31	8.44E-04
Ground + Habitat + Sapling + Understory	5	-325.89	40.31	11.59	7.33E-04
Ground + Habitat + Sapling + Tree + Understory	6	-320.45	45.14	16.42	6.56E-05

---

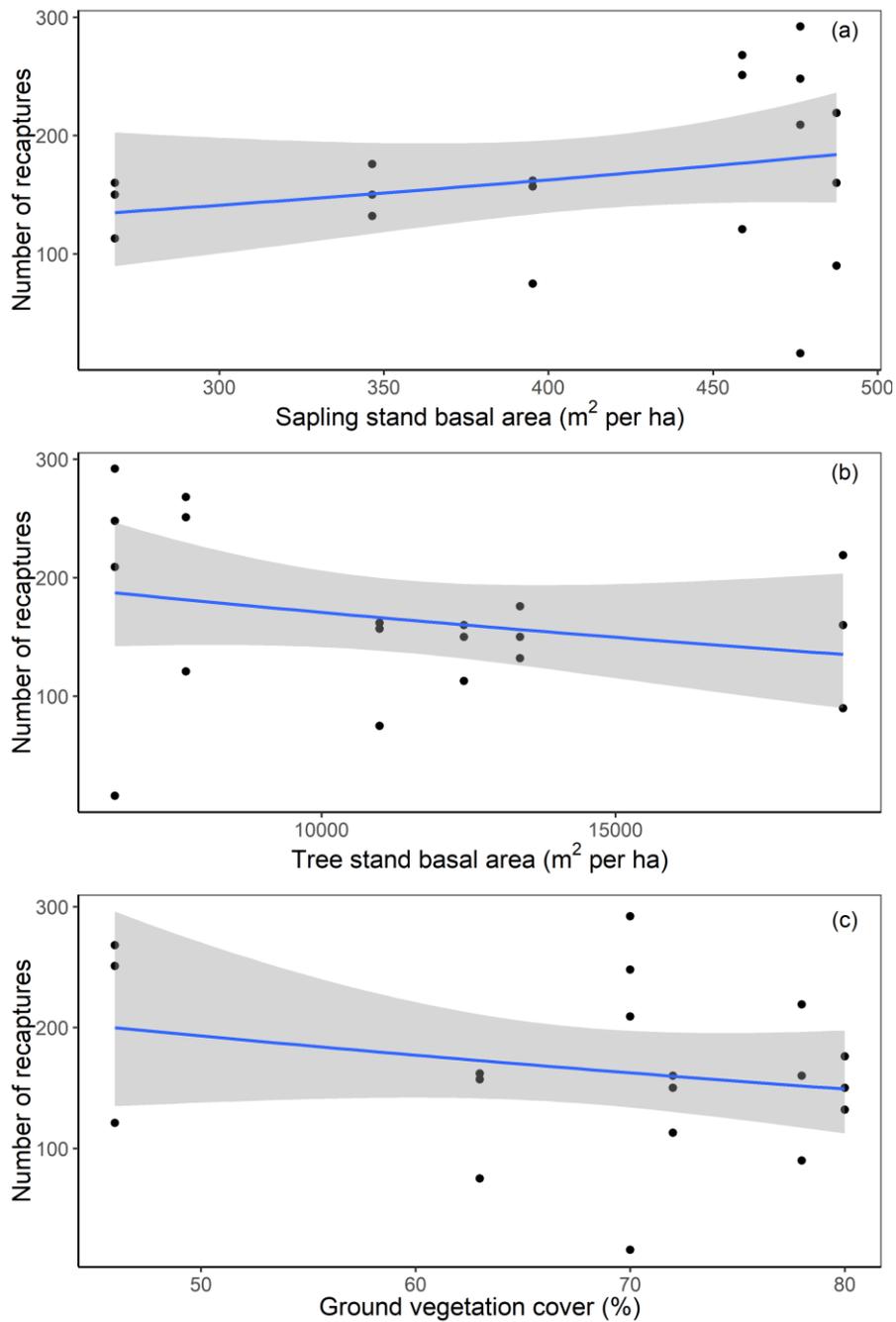


Figure C.14. Understory habitat structure effects on the number of recaptures per transect. The number of recaptures per transect was not significantly affected by (a) sapling stand basal area ( $p=0.271$ ), (b) tree stand basal area ( $p=0.28$ ), or (c) ground vegetation cover ( $p=0.315$ ). Fitted lines are predictions from the GLZ taking into account overdispersion with 95% confidence intervals.

# Appendix D

## Supporting information for Chapter 5

### Appendix D.1. Supplementary tables

Table D.1. Species, foraging guild, family, conservation status information (IUCN status) and mean apparent survival estimates ( $\pm$  sd) from the model excluding El Niño for all 71 species. Family and foraging guild data were obtained from the Elton Traits 1.0 database (Wilman *et al.* 2014). LC = Least Concern, NT = Near Threatened, VU = Vulnerable. Species recaptured in logged forest only are highlighted in bold and species recaptured in unlogged forest only are underlined.

Species	Species Code	Foraging Guild	Family	IUCN status	Mean survival $\pm$ sd	
					Logged	Unlogged
Terpsiphone affinis	APFLY	Invertebrate	Monarchidae	LC	0.89 $\pm$ 0.09	0.93 $\pm$ 0.08
<b>Orthotomus ruficeps</b>	<b>ATLRB</b>	Invertebrate	Sylviidae	LC	0.86 $\pm$ 0.14	0.89 $\pm$ 0.16
<u>Alcedo peninsulae</u>	<u>BBKING</u>	VertFishScav	Alcedinidae	NT	0.86 $\pm$ 0.14	0.87 $\pm$ 0.18
Pellorneum nigrocapitatum	BCBAB	Invertebrate	Timaliidae	LC	0.93 $\pm$ 0.06	0.94 $\pm$ 0.07
<b>Alcedo meninting</b>	<b>BEKING</b>	VertFishScav	Alcedinidae	LC	0.81 $\pm$ 0.18	0.85 $\pm$ 0.20
Alcippe brunneicauda	BFUL	Invertebrate	Timaliidae	NT	0.90 $\pm$ 0.09	0.95 $\pm$ 0.06
<b>Erythropitta ussheri</b>	<b>BLKHPIT</b>	Invertebrate	Pittidae	NT	0.91 $\pm$ 0.08	0.93 $\pm$ 0.11
Hypothymis azurea	BNMON	Invertebrate	Monarchidae	LC	0.95 $\pm$ 0.04	0.97 $\pm$ 0.04
<b>Meiglyptes tukki</b>	<b>BNWPEC</b>	Invertebrate	Picidae	NT	0.89 $\pm$ 0.10	0.91 $\pm$ 0.14
<b>Mixornis bornensis</b>	<b>BSTBAB</b>	Invertebrate	Timaliidae	LC	0.91 $\pm$ 0.09	0.92 $\pm$ 0.12
<u>Turdinus atrigularis</u>	<u>BTWBAB</u>	Invertebrate	Timaliidae	NT	0.88 $\pm$ 0.12	0.92 $\pm$ 0.10
<b>Iole charlottae</b>	<b>BVBUL</b>	Omnivore	Pycnonotidae	NT	0.85 $\pm$ 0.15	0.88 $\pm$ 0.17
<u>Ptilocichla leucogrammica</u>	<u>BWBAB</u>	Invertebrate	Timaliidae	VU	0.90 $\pm$ 0.10	0.95 $\pm$ 0.07
<u>Geokichla interpres</u>	<u>CCTHR</u>	Invertebrate	Turdidae	NT	0.86 $\pm$ 0.14	0.88 $\pm$ 0.17
<b>Platylophus galericulatus</b>	<b>CJAY</b>	Invertebrate	Corvidae	NT	0.87 $\pm$ 0.13	0.89 $\pm$ 0.16
Enicurus ruficapillus	CNFORK	Invertebrate	Muscicapidae	NT	0.87 $\pm$ 0.12	0.89 $\pm$ 0.12

<i>Stachyris maculata</i>	CRBAB	Invertebrate	Timaliidae	NT	0.91 ± 0.08	0.96 ± 0.06
<b><i>Aethopyga siparaja</i></b>	<b>CSUN</b>	Omnivore	Nectariniidae	LC	0.91 ± 0.09	0.92 ± 0.12
<i>Cyanoderma erythropterum</i>	CWBAB	Invertebrate	Timaliidae	LC	0.94 ± 0.05	0.97 ± 0.04
<i>Orthotomus atrogularis</i>	DNTLRB	Invertebrate	Sylviidae	LC	0.84 ± 0.15	0.88 ± 0.16
<u><i>Harpactes diardii</i></u>	<u>DTRO</u>	Invertebrate	Trogonidae	NT	0.85 ± 0.15	0.85 ± 0.20
<i>Chalcophaps indica</i>	EDOV	Omnivore	Columbidae	LC	0.83 ± 0.16	0.84 ± 0.20
<i>Trichastoma bicolor</i>	FBAB	Invertebrate	Timaliidae	LC	0.95 ± 0.04	0.97 ± 0.04
<i>Macronus ptilosus</i>	FBTBAB	Invertebrate	Timaliidae	NT	0.95 ± 0.04	0.97 ± 0.04
<u><i>Calyptomena viridis</i></u>	<u>GBRDB</u>	FruiTect	Eurylaimidae	NT	0.87 ± 0.13	0.89 ± 0.16
<i>Alophoixus tephrogenys</i>	GCBUL	Omnivore	Pycnonotidae	LC	0.93 ± 0.06	0.96 ± 0.05
<i>Cyornis umbratilis</i>	GCJFLY	Invertebrate	Muscicapidae	NT	0.90 ± 0.10	0.94 ± 0.07
<i>Stachyris poliocephala</i>	GHBAB	Invertebrate	Timaliidae	LC	0.79 ± 0.10	0.83 ± 0.12
<i>Malacocincla sepiaria</i>	HBAB	Invertebrate	Timaliidae	LC	0.87 ± 0.08	0.89 ± 0.09
<i>Tricholestes criniger</i>	HBBUL	Omnivore	Pycnonotidae	LC	0.91 ± 0.06	0.94 ± 0.07
<u><i>Pitta sordida</i></u>	<u>HPIT</u>	Invertebrate	Pittidae	LC	0.86 ± 0.14	0.87 ± 0.18
<i>Cyornis caerulatus</i>	LBBFLY	Invertebrate	Muscicapidae	VU	0.92 ± 0.06	0.95 ± 0.06
<u><i>Chloropsis cyanopogon</i></u>	<u>LGLEAF</u>	FruiTect	Chloropseidae	NT	0.88 ± 0.13	0.91 ± 0.13
<i>Arachnothera longirostra</i>	LSPHUN	Omnivore	Nectariniidae	LC	0.68 ± 0.05	0.80 ± 0.07
<i>Malacopteron magnirostre</i>	MBAB	Invertebrate	Timaliidae	LC	0.90 ± 0.09	0.92 ± 0.10
<u><i>Cyornis turcosus</i></u>	<u>MBFLY</u>	Invertebrate	Muscicapidae	NT	0.85 ± 0.15	0.85 ± 0.19
<u><i>Blythipicus rubiginosus</i></u>	<u>MWPEC</u>	Invertebrate	Picidae	LC	0.89 ± 0.11	0.93 ± 0.09
<i>Dicaeum trigonostigma</i>	OBFLPEC	FruiTect	Dicaeidae	LC	0.88 ± 0.12	0.90 ± 0.13
<i>Ceyx erithaca</i>	ODKING	Invertebrate	Alcedinidae	LC	0.78 ± 0.09	0.82 ± 0.10
<b><i>Pycnonotus plumosus</i></b>	<b>OWBUL</b>	FruiTect	Pycnonotidae	LC	0.83 ± 0.16	0.87 ± 0.18
<i>Euptilotus eutilotus</i>	PBBUL	Omnivore	Pycnonotidae	NT	0.91 ± 0.08	0.95 ± 0.07
<b><i>Rhipidura javanica</i></b>	<b>PFAN</b>	Invertebrate	Rhipiduridae	LC	0.91 ± 0.09	0.92 ± 0.12
<i>Arachnothera hypogrammica</i>	PNSUN	Omnivore	Nectariniidae	LC	0.84 ± 0.10	0.84 ± 0.13
<i>Anthreptes simplex</i>	PSUN	FruiTect	Nectariniidae	LC	0.86 ± 0.12	0.88 ± 0.15
<i>Malacopteron magnum</i>	RCBAB	Invertebrate	Timaliidae	NT	0.93 ± 0.06	0.95 ± 0.06
<i>Ficedula dumetoria</i>	RCFLY	Invertebrate	Muscicapidae	LC	0.84 ± 0.16	0.85 ± 0.20
<u><i>Actenoides concretus</i></u>	<u>RCKING</u>	Invertebrate	Alcedinidae	NT	0.87 ± 0.14	0.89 ± 0.15
<i>Chalcoparia singalensis</i>	RCSUN	Invertebrate	Nectariniidae	LC	0.85 ± 0.14	0.88 ± 0.15
<b><i>Cyanoderma rufifrons</i></b>	<b>RFBAB</b>	Invertebrate	Timaliidae	LC	0.86 ± 0.13	0.89 ± 0.16
<i>Sasia abnormis</i>	RPIC	Invertebrate	Picidae	LC	0.80 ± 0.10	0.91 ± 0.08

---

<u>Trichixos pyrropygus</u>	<u>RTSHAM</u>	Invertebrate	Muscicapidae	NT	0.85 ± 0.15	0.86 ± 0.17
Orthotomus sericeus	RTTLRB	Invertebrate	Sylviidae	LC	0.91 ± 0.08	0.92 ± 0.12
Philentoma pyrhoptera	RWPHIL	Invertebrate	Tephrodornithidae	LC	0.91 ± 0.07	0.94 ± 0.07
<b>Arachnothera affinis</b>	<b>SBSPHUN</b>	Invertebrate	Nectariniidae	LC	0.90 ± 0.09	0.91 ± 0.13
Ixidia erythroptalmos	SBUL	Omnivore	Pycnonotidae	LC	0.93 ± 0.07	0.95 ± 0.08
Malacopteron affine	SCBAB	Invertebrate	Timaliidae	NT	0.92 ± 0.08	0.95 ± 0.07
Malacopteron cinereum	SCRBAB	Invertebrate	Timaliidae	LC	0.95 ± 0.04	0.98 ± 0.03
Rhipidura perlata	SFAN	Invertebrate	Rhipiduridae	LC	0.87 ± 0.13	0.93 ± 0.09
<b>Harpactes duvaucelii</b>	<b>SRTRO</b>	Invertebrate	Trogonidae	NT	0.89 ± 0.11	0.91 ± 0.14
Pellorneum malaccense	STBAB	Invertebrate	Timaliidae	NT	0.85 ± 0.09	0.89 ± 0.09
Kenopia striata	SWBAB	Invertebrate	Timaliidae	NT	0.84 ± 0.12	0.83 ± 0.14
<b>Aethopyga temminckii</b>	<b>TSUN</b>	Omnivore	Nectariniidae	LC	0.84 ± 0.16	0.87 ± 0.18
<u>Erpornis zantholeuca</u>	<u>WBERP</u>	Invertebrate	Timaliidae	LC	0.88 ± 0.12	0.92 ± 0.12
Trichastoma rostratum	WCBAB	Invertebrate	Timaliidae	NT	0.61 ± 0.15	0.81 ± 0.13
Enicurus leschenaulti	WCFORK	Invertebrate	Muscicapidae	LC	0.78 ± 0.12	0.84 ± 0.14
Kittacincla malabarica	WCSHAM	Invertebrate	Muscicapidae	LC	0.92 ± 0.06	0.93 ± 0.09
<u>Stachyris leucotis</u>	<u>WNBAB</u>	Invertebrate	Timaliidae	NT	0.88 ± 0.12	0.92 ± 0.10
Alophoixus phaeocephalus	YBBUL	Omnivore	Pycnonotidae	LC	0.88 ± 0.08	0.93 ± 0.07
Prionochilus maculatus	YBFLPEC	FruNect	Dicaeidae	LC	0.84 ± 0.07	0.64 ± 0.08
<b>Prinia flaviventris</b>	<b>YBPRIN</b>	Invertebrate	Cisticolidae	LC	0.83 ± 0.16	0.87 ± 0.18
Prionochilus xanthopygius	YRFLPEC	FruNect	Dicaeidae	LC	0.93 ± 0.07	0.94 ± 0.10

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## Appendix D.2. Supplementary figures

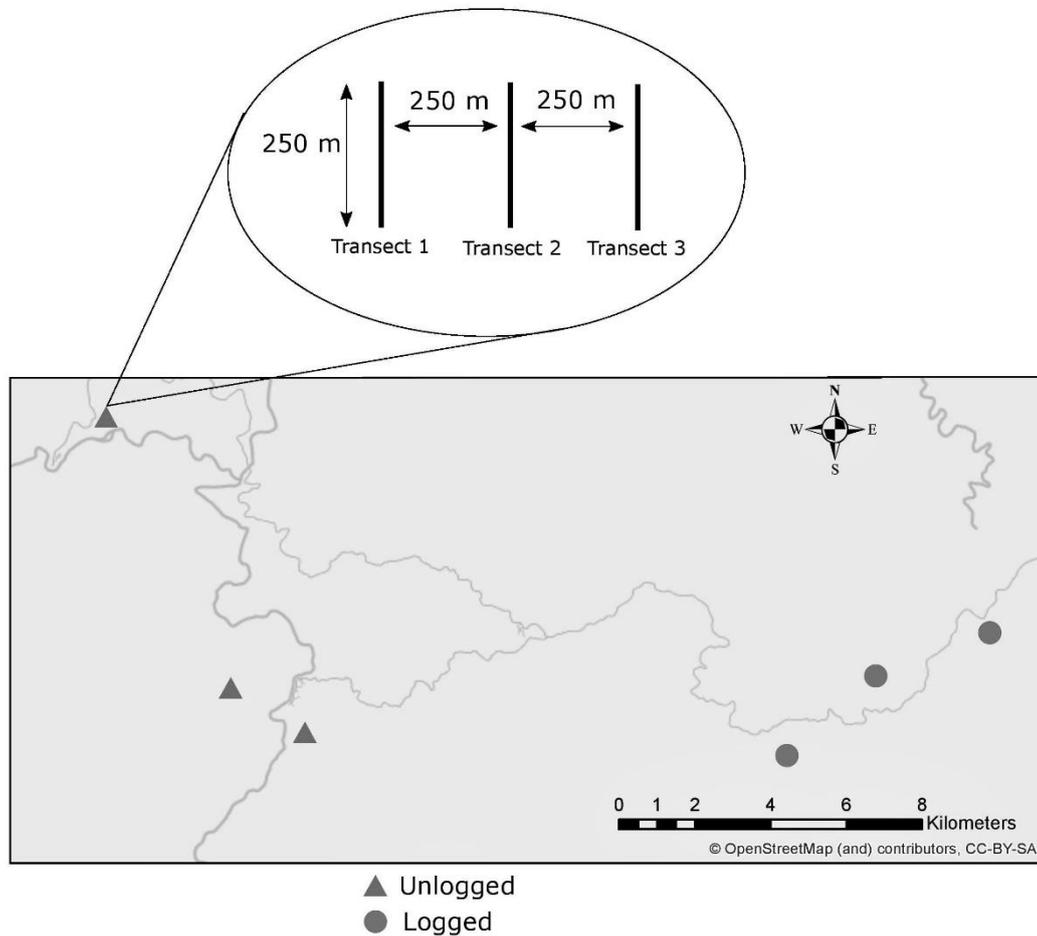


Figure D.1. Locations of our six sampling plots (three in unlogged old-growth forests; three in twice-logged forests) with the mist-netting transect set up in each plot.

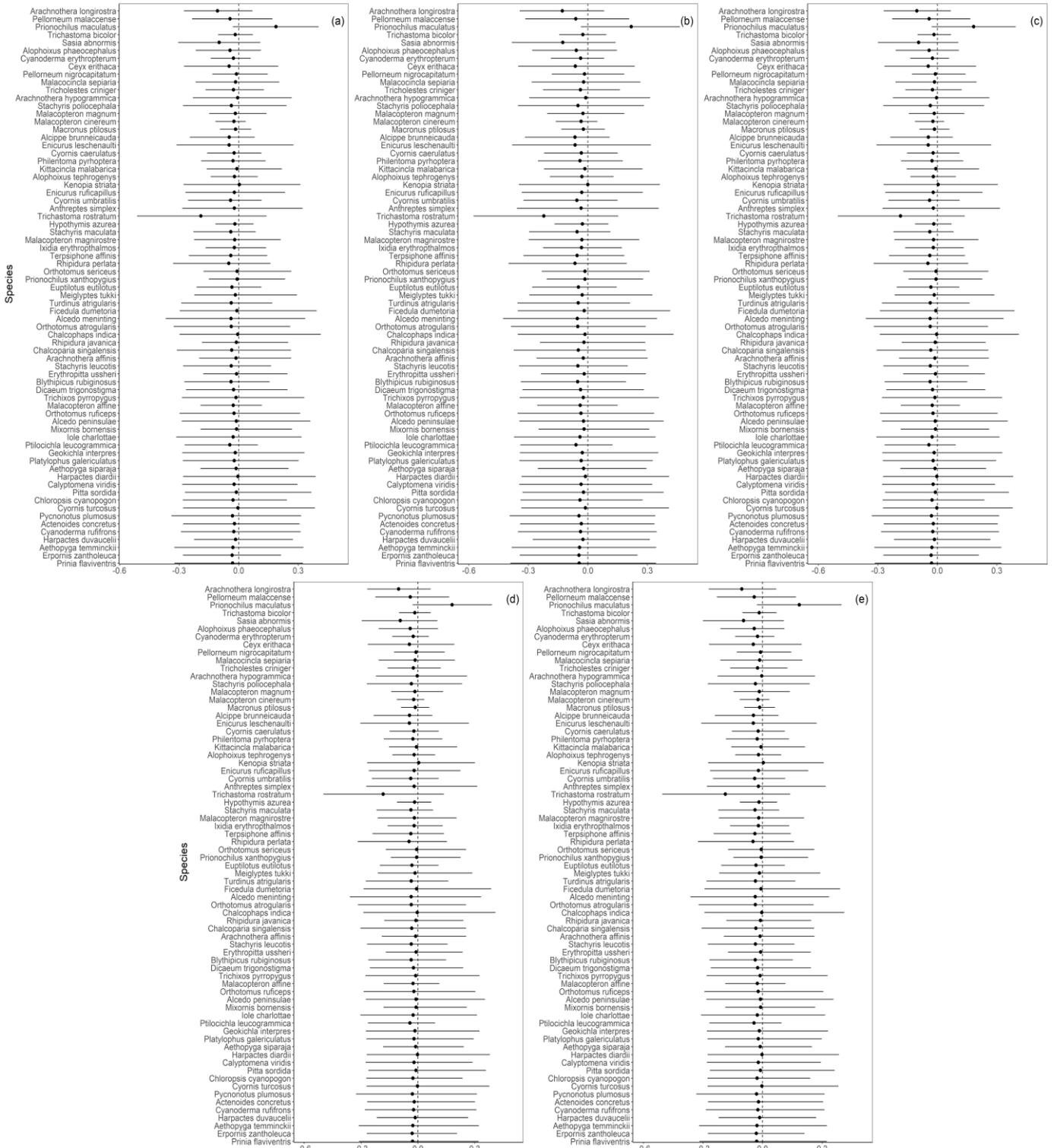


Figure D.2. Posterior means with 95% credible intervals, from the model including El Niño effects, for the difference between mean adult apparent survival in selectively logged forest  $\Phi_{s,1}$  and unlogged forest  $\Phi_{s,2}$  for each species and each year: (a) 2014, (b) 2015, (c) 2016, (d) 2017 and (e) 2018. 95% credible intervals including zero are considered to be not statistically significant. Species are ordered by sample size from largest (top) to smallest.

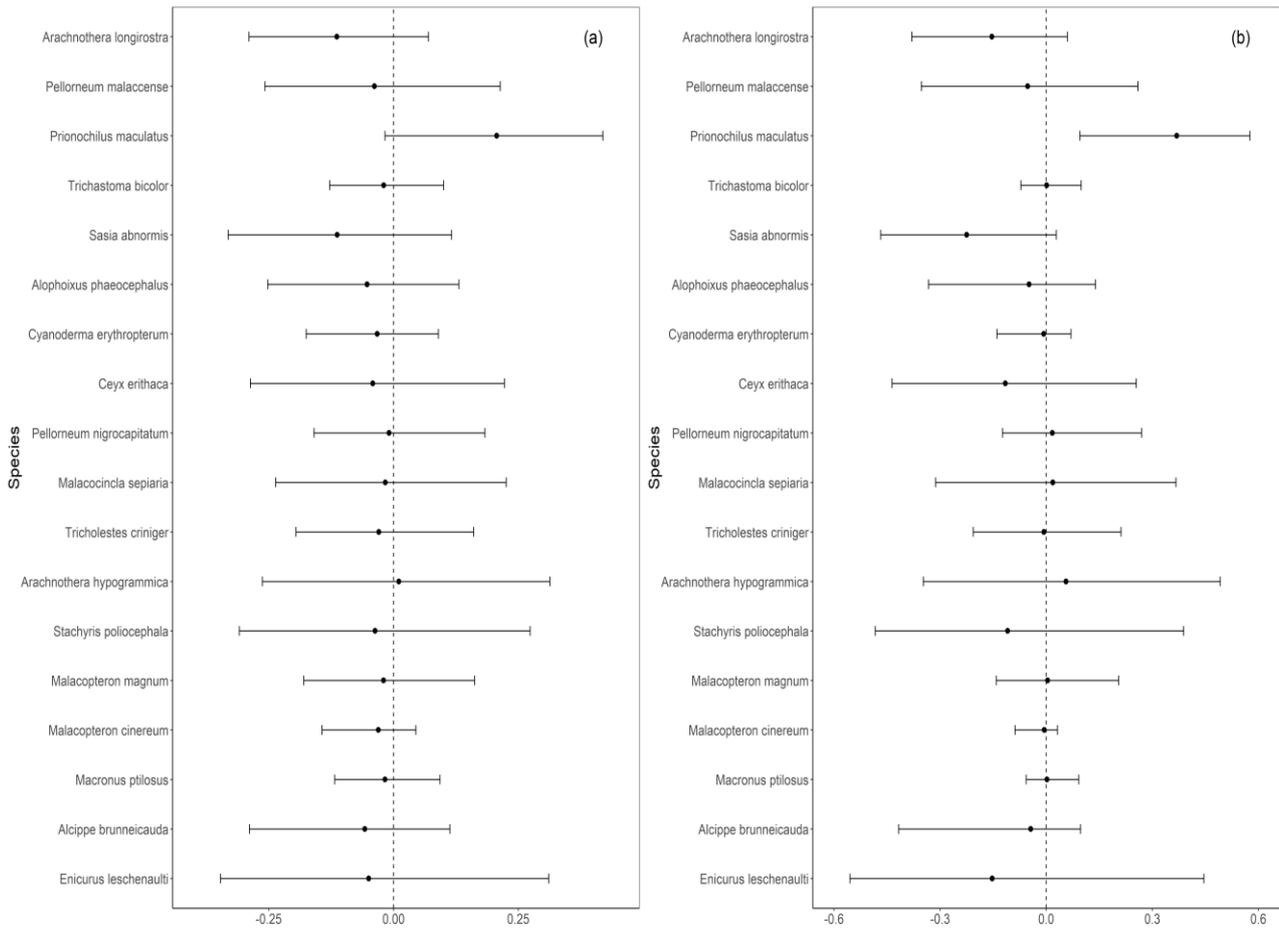


Figure D.3. Posterior means with 95% credible intervals, from the models containing only the most common species: (a) multi-species model, (b) single-species model, for the difference between mean adult apparent survival in selectively logged forest  $\Phi_{s,1}$  and unlogged forest  $\Phi_{s,2}$  for each species. 95% credible intervals including zero are considered to be not statistically significant. Species are ordered by sample size from largest (top) to smallest.

## Appendix D.3. Model code for survival model

### Model Code

##### JAGS INPUT DATA:

# **y capture histories (3D array)** = number of secondary occasions (months: June, July and August) an individual is captured in for each primary occasion (year) for each species (zero if no individuals captured). First dimension corresponds to the number of individuals of the species with the most caught individuals. For species with less individuals, the extra individual rows are filled with NAs.

*# Data structure: num [1:182, 1:5, 1:71] 1 1 0 0 0 0 0 NA NA NA ...*

# **x habitat covariate (3D array)** = Identical in structure to the y capture histories array but instead, it contains information about the habitat type (1 = logged, 2 = unlogged, 3 = unknown) in which each individual was caught at each primary occasion (year) and for each species. All primary occasions (years) before first capture are filled with NAs.

*# Data structure: num [1:182, 1:5, 1:71] 2 1 NA NA NA NA NA NA NA NA*

# **first matrix** = first primary occasion (year) individual was caught

*# Data structure: num [1:182, 1:71] 1 1 2 3 5 4 2 NA NA NA ...*

# **M vector (length 71)** = the sample size (number of individuals) for each species.

*# Data structure: num [1:71] 7 1 1 38 3 22 2 11 4 1 ...*

# **Year** = number of primary occasions (years)

# **N** = number of species

# **omega** = proportion of individuals for each species in logged forest

*# Data structure: num [1:71] 0.571 1 0 0.553 1 ...*

# **precip vector (length 5)** = precipitation data in mm for each primary occasion (years 2014 to 2018). Precipitation data is standardised (mean = 0 and s.d. = 1).

*# Data structure: num [1:5] 0.227 -1.766 0.503 0.655 0.381*

```

##### SURVIVAL MODEL (WITHOUT EL NIÑO) #####
# phi = survival
# p = recapture probability

bayesmod <- function(){

  for(n in 1:N){ # Loop over each species
    # survival parameters:
    logit(phi[n,1]) <- lphi[n] # logit survival for logged forest
    logit(phi[n,2]) <- lphi[n] + beta1[n] # logit survival for unlogged
                                     # forest with habitat effect

    # Mixture model for survival of individuals with unknown
    # habitat (habitat=3)
    phi[n,3] <- omega[n]*phi[n,1] + (1-omega[n])*phi[n,2]

    # Recapture probability parameters:
    logit(p[n,1]) <- lp[n] # logit recapture probability for logged
                          # forest
    logit(p[n,2]) <- lp[n] + beta2[n] # logit recapture probability for
                                     # unlogged forest with habitat
                                     # effect

    # Mixture model for recapture probability of individuals with
    # unknown habitat (habitat=3)
    p[n,3] <- omega[n]*p[n,1] + (1-omega[n])*p[n,2]

    # Priors:
    lphi[n] ~ dnorm(mu.lphi,tau.lphi) # survival intercept
    beta1[n] ~ dnorm(mu.beta1,tau.beta1) # survival habitat effect

    lp[n] ~ dnorm(mu.lp,tau.lp) # recapture probability intercept
    beta2[n] ~ dnorm(mu.beta2,tau.beta2) # recapture probability habitat
                                     # effect
  } #n

  # Hyperpriors:
  mu.lphi ~ dnorm(0,0.0001) # mean community survival
  tau.lphi ~ dunif(0,1) # community survival variance

  mu.beta1 ~ dnorm(0,0.0001) # community habitat effect for survival
  tau.beta1 ~ dunif(0,1)

  mu.lp ~ dnorm(0,0.0001) # mean community recapture probability
  tau.lp ~ dunif(0,1) # community recapture probability variance

```

```

mu.beta2 ~ dnorm(0,0.0001) # community habitat effect for recapture
                                # probability
tau.beta2 ~ dunif(0,1)

for(n in 1:N){ # Loop over each species
  for (i in 1:M[n]){ # Loop over every individual in each species

    # Latent state at first capture
    z[i,first[i,n],n] <- 1

    for (t in (first[i,n]+1):Year){ # Loop over years after first
                                    # capture

      # Individual transition states from t to t+1 for all t>fi
      z[i,t,n] ~ dbern(phiUP[i,t,n])
      phiUP[i,t,n] <- z[i,t-1,n] * phi[n,X[i,t-1,n]]

      # Observation process
      y[i,t,n] ~ dbinom(mu2[i,t,n],3) # number of trials=3; number of
                                        # secondary occasions (months) in a primary
                                        # occasion (year)
      newy[i,t,n] ~ dbinom(mu2[i,t,n],3) # generate simulated expected
                                          # data for posterior predictive
                                          # check
      mu2[i,t,n] <- z[i,t,n] * p[n,X[i,t,n]]
    } #t
  } #i
} #n

# Compute habitat differences in survival for each species
for(n in 1:N){
  sp.diff.mean[n] <- phi[n,1] - phi[n,2]
}
}

```

```
##### SURVIVAL MODEL (WITH EL NIÑO) #####
# phi = survival
# p = recapture probability

bayesmod <- function(){

  for(n in 1:N){ # Loop over each species
    for(Y in 1:Year){ # Loop over each year

      # Survival parameters:
      logit(phi[Y,n,1])<- lphi[n] + beta3*precip[Y] # logit survival for
        # logged forest with precipitation effect
      logit(phi[Y,n,2])<- lphi[n] + beta1[n] + beta3*precip[Y] # logit
        # survival for unlogged forest with habitat
        # and precipitation effect

        # Mixture model for survival of individuals with unknown
        # habitat (habitat=3)
      phi[Y,n,3] <- omega[n]*phi[Y,n,1] + (1-omega[n])*phi[Y,n,2]
    }#Y

    # Recapture probability parameters:
    logit(p[n,1])<- lp[n] # logit recapture probability for logged
      # forest
    logit(p[n,2])<- lp[n] + beta2[n] # logit recapture probability for
      # unlogged forest with habitat effect

      # Mixture model for recapture probability of individuals
      # with unknown habitat (habitat=3)
    p[n,3] <- omega2[n]*p[n,1] + (1-omega2[n])*p[n,2]

    # Priors:
    lphi[n] ~ dnorm(mu.lphi,tau.lphi) # survival intercept
    beta1[n] ~ dnorm(mu.beta1,tau.beta1) # survival habitat effect

    lp[n] ~ dnorm(mu.lp,tau.lp) # recapture probability intercept
    beta2[n] ~ dnorm(mu.beta2,tau.beta2) # recapture probability habitat
      # effect

    }#n
    beta3 ~ dnorm(mu.beta3,tau.beta3) # survival precipitation effect

    # Hyperpriors
    mu.lphi ~ dnorm(0,0.0001) # mean community survival
    tau.lphi ~ dunif(0,1) # community survival variance

    mu.beta1 ~ dnorm(0,0.0001) # community habitat effect for survival
    tau.beta1 ~ dunif(0,1)
  }
}
```

```

mu.lp ~ dnorm(0,0.0001) # mean community recapture probability
tau.lp ~ dunif(0,1) # community recapture probability variance

mu.beta2 ~ dnorm(0,0.0001) # community habitat effect for recapture
# probability
tau.beta2 ~ dunif(0,1)

mu.beta3 ~ dnorm(0,0.0001) # community precipitation effect for
# survival
tau.beta3 ~ dunif(0,1)

for(n in 1:N){ # Loop over each species
  for (i in 1:M[n]){ # Loop over every individual in each species

    # Latent state at first capture
    z[i,first[i,n],n] <- 1

    for (t in (first[i,n]+1):Year){ # Loop over years after first
      # capture

      # Individual transition states from t to t+1 for all t>fi
      z[i,t,n] ~ dbern(phiUP[i,t,n])
      phiUP[i,t,n] <- z[i,t-1,n] * phi[t-1,n,X[i,t-1,n]]

      # Observation process
      y[i,t,n] ~ dbinom(mu2[i,t,n],3)
      newy[i,t,n] ~ dbinom(mu2[i,t,n],3) # generate simulated expected
      # data for posterior predictive check
      mu2[i,t,n] <- z[i,t,n] * p[n,X[i,t,n]]
    } #t
  } #i
} #n

# Compute habitat differences in survival for each species
for(Y in 1:Year){
  for(n in 1:N){
    sp.diff.mean[n] <- phi[Y,n,1] - phi[Y,n,2]
  } #n
} #Y
}

```

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