



Norwegian University of Life Sciences  
Faculty of Environmental Sciences  
and Natural Resource Management

Philosophiae Doctor (PhD)  
Thesis 2023:6

# Effects of selective logging on Amazonian wildlife

Effekten av selektiv hogst på viltpopulasjoner  
i Amazonas

Elildo Alves Ribeiro de Carvalho Jr



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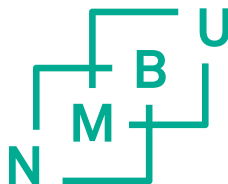
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Philosophiae Doctor (PhD) Thesis  
Elildo Alves Ribeiro de Carvalho Jr

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# 1 List of papers

This PhD thesis consists of the following papers (1-4):

## **Paper 1**

Carvalho Jr EAR, Nienow SS, Bonavigo PH, Haugaasen T (2021) Mammal responses to reduced-impact logging in Amazonian forest concessions. *Forest Ecology and Management* 496:119401. <https://doi.org/10.1016/j.foreco.2021.119401>

## **Paper 2**

Carvalho EAR, Mendonça EN, Martins A, Haugaasen T. (2020) Effects of illegal logging on Amazonian medium and large-sized terrestrial vertebrates. *Forest Ecology and Management* 466:118105. <https://doi.org/10.1016/j.foreco.2020.118105>

## **Paper 3**

Carvalho EAR, Mendonça EN, Martins A, Haugaasen T. (2022) Current status of the Critically Endangered Black-winged Trumpeter *Psophia obscura* in one of its last strongholds. *Bird Conservation International* 1-14. <https://doi.org/10.1017/S0959270922000077>

## **Paper 4**

Carvalho EAR, Hawes JE, Haugaasen T. (2022) Potential losses of animal-dispersed trees due to selective logging in Amazonian forest concessions. *Trees, Forests and People* 9:100316. <https://doi.org/10.1016/j.tfp.2022.100316>

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## 2 Abstract

Selective logging of tropical forests is rapidly expanding, making it inevitable that future tropical landscapes will be dominated by production forests. Any biodiversity conservation strategy must consider the potential and limitations of these forests for conservation. This thesis investigates the prospects of wildlife conservation in forest landscapes subjected to contrasting logging regimes in the Brazilian Amazon. Data comes from two case studies representing legally and illegally logged landscapes: Jamari National Forest, where forest concessions operate under reduced-impact logging (RIL), and Gurupi Biological Reserve, which was illegally logged for several decades until very recently. Manuscript 1 uses camera traps to investigate RIL effects on the medium- to large-sized mammal assemblage in Jamari. Site-level species richness was negatively related to logging intensity, and positively related to density of logging roads. However, no individual species responded significantly to these factors and all species were retained in the landscape, suggesting that RIL may be a reasonable compromise between production and conservation. Manuscript 2 uses camera traps to assess effects of past illegal logging on the assemblage of medium- to large-sized mammals and birds in Gurupi. Illegal logging had a negligible effect on species relative abundances, suggesting that even illegally logged forests retain conservation value, provided they are protected from further impacts. Manuscript 3 uses a five-year camera-trap monitoring data to assess the status and trends of a Critically Endangered bird, the Black-winged Trumpeter (*Psophia obscura*), at Gurupi. Results show that the species is a habitat specialist that prefers areas with more than a decade of post-logging recovery and with a structure like mature forest. In addition, occupancy rates of the species remained stable throughout the study, demonstrating that even illegally logged forests can play a role in the conservation of this forest specialists. The fourth and final chapter uses data from forest inventories conducted by concession companies to estimate losses of animal-dispersed trees resulting from direct harvest in Jamari RIL concessions. Animal-dispersed trees dominate the forest but are significantly less targeted for logging than abiotically-dispersed trees. Still, at least ten percent of the large animal-dispersed trees were lost in the landscape, indicating that even low logging intensities can reduce frugivore resources. Taken together, the results indicate that although both legal and illegal harvesting have impacts on medium- to large-sized vertebrates, these are generally moderate so that logged forest landscapes retain their full species complement. However, the case studies are best-case scenarios coming

from protected areas, which underlines the importance of protecting logged forests from additional anthropogenic impacts to maintain their conservation value.

### 3 Norsk sammendrag

Selektiv hogst av tropiske skoger utvides raskt, noe som gjør det uunngåelig at fremtidige tropiske landskap vil bli dominert av produksjonsskog. Enhver strategi for bevaring av biologisk mangfold må ta hensyn til potensialet og begrensningene til disse skogene. Denne oppgaven undersøker utsiktene for bevaring av dyreliv i skoglandskap utsatt for kontrasterende hogstregimer i den brasilianske Amazonas. Data kommer fra to case-studier som representerer landskap med lovlig og ulovlig tømmerhogst: Jamari National Forest, hvor skogkonsesjoner opererer under bærekraftig tømmerhogst, og Gurupi Biological Reserve, som ble ulovlig hugget i flere tiår inntil helt nylig. Manuskript 1 bruker kamerafeller for å undersøke effekter av bærekraftig hogst på mellomstore til store pattedyr i Jamari. Artsrikdom på stedsnivå var negativt relatert til hogstintensitet, og positivt relatert til veitetthet. Imidlertid reagerte ingen individuelle arter signifikant på de samme faktorene, og alle arter ble beholdt i landskapet, noe som tyder på at bærekraftig tømmerhogst kan være et rimelig kompromiss mellom produksjon og bevaring. Manuskript 2 bruker kamerafeller for å vurdere effekten av tidligere ulovlig hogst på mellomstore og store pattedyr og fugler i Gurupi. Ulovlig hogst hadde en ubetydelig effekt på artssamfunnet og arters relative abundans, noe som tyder på at selv ulovlig hogst beholder sin bevaringsverdi, forutsatt at de er beskyttet mot ytterligere påvirkninger. Manuskript 3 bruker en femårig kamerafelle-studie for å vurdere statusen og trendene til en kritisk truet fugl, den svartvingede trompetisten (*Psophia obscura*), i Gurupi. Resultatene bekrefter at arten er en habitatspesialist som foretrekker områder der gjenveksten har kommet lengst etter hogst og som har en struktur som moden skog. I tillegg forble arten stabil gjennom hele studien, noe som viser at til og med ulovlig hogd skog kan spille en rolle i bevaringen av denne skogspesialisten. Det fjerde og siste kapittelet bruker data fra skogregistreringer utført av tømmerhogstselskaper for å estimere tap av trær som har frukt og frø spredt av dyr, som følge av tømmerhogst i Jamari. Trær som har frø spredt av dyr dominerer skogen, men er betydelig mindre utsatt for hogst enn trær som har frø som blir spredt abiotisk. Likevel gikk minst ti prosent av de store dyrespredte trærne tapt i landskapet, noe som indikerer at selv lave hogstintensiteter kan redusere frukt-ressursene. Samlet indikerer resultatene at selv om både lovlig og ulovlig tømmerhogst har innvirkning på middels til store virveldyr, er disse generelt moderate slik at skoglandskapet beholder sitt fulle arts-komplement. Case-studiene er imidlertid best-case-scenarier som kommer fra

verneområder, noe som understreker viktigheten av å beskytte hugget skog mot ytterligere menneskeskapte påvirkninger for å opprettholde deres bevaringsverdi.

## 4 Synopsis

### 4.1 Tropical forests: global relevance and threats

Tropical forests play a disproportionate role in providing biodiversity, ecosystem services and human welfare on a global scale. They are the most biodiverse terrestrial ecosystems on earth, covering approximately seven percent of the land surface but harbouring more than half of all living species (Gallery, 2014; Raven et al., 2020; Primack & Morrison, 2013). They regulate temperature, wind and rainfall patterns at local, regional and global scales (Sheil, 2018; Bonan, 2008; Arraut et al., 2012; Foley et al., 2007; Richter, 2016). Tropical forests account for more than one-third of global gross primary productivity (Beer et al., 2010), two-thirds of terrestrial biomass (Pan et al., 2013) and one quarter of the carbon in the biosphere (Bonan, 2008). They ameliorate climate change by sequestering a large fraction of global fossil fuel carbon emissions (Houghton et al., 2015; Hubau et al., 2020) – although this is being increasingly offset by deforestation (Saatchi et al., 2011; Pan et al., 2011). Tropical forests provide food, fuel, medicines, building materials, environmental services and cultural values for countless peoples around the world (Newton et al., 2016; Chao, 2012), with up to 800 million people depending on these forests for their subsistence and livelihoods (FAO & UNEP, 2020; Chao, 2012; Chomitz, 2007; Newton et al., 2016).

As an ever-growing human population and rising *per capita* consumption rates translate into increasing demand for land and resources, tropical forests are under increasing pressure. The global demand for food is expected to rise by 70 percent until the middle of the century (Balmford et al., 2012) while demand for industrial forest products such as timber will exceed production in the 2020s (Sloan & Sayer, 2015). Most of this increasing demand has been met by expanding agricultural and extractive activities in the tropics (Gibbs et al., 2010; Köhl et al., 2015; Phalan et al., 2013; Pendrill et al., 2022).

Tropical forests already lost more than one-third of their original cover (Hansen et al., 2020). Additionally, forest degradation, by which anthropogenic impacts reduce or severely constrain ecological processes shaping forest dynamics (Ghazoul et al., 2015), is a serious problem. In many areas, degradation rates surpass forest loss (van Lierop et al., 2015; Matricardi et al., 2020; Gaveau et al., 2014; Vancutsem et al., 2021). At the global level, more than half of the remaining forests therefore only have medium to low ecosystem integrity (Grantham et al., 2020; Ghazoul, 2015) or are recovering from past disturbances (Pan et al., 2013). These disturbed forests have substantially lower biodiversity levels than primary forests (Gibson et al., 2011; Barlow et al., 2016).

Drivers of forest degradation include fragmentation, logging, fires, hunting, invasive species and climate change (Lewis et al., 2015; Galetti & Dirzo, 2013; Laurance, 1998; Coe et al., 2013; Matricardi et al., 2020). Degradation levels depend on the extent to which disturbances affect forest state (i.e., its composition, structure and function) and resilience (i.e., their ability to return to pre-disturbance states) (Ghazoul et al., 2015). Forests are resilient to moderate disturbance, but severe or chronic disturbances may arrest succession, leading to irreversible change. For example, interactions between climate change, deforestation, logging and fires create positive feedbacks that result in irreversible ecosystem transition in Amazonia (Cochrane et al., 1999; Nepstad et al., 2008; Nobre & Borma, 2009; Barlow & Peres, 2008).

## **4.2 Selective logging**

Selective logging is the most profitable intervention in tropical forests after clear-cutting (Putz et al., 2001; Ghazoul, 2015) and is expanding due to increasing demand and prices (Sloan & Sayer, 2015; Masiero et al., 2015). The forest products sector accounts for one percent of the world's GDP (Contreras-Hermosilla et al., 2007; Arce, 2019) and the annual trade of tropical wood products surpasses 25 billion USD (Poker & MacDicken, 2016). Yet, the trade is even greater as these estimates do not consider domestic markets which often comprise the largest share. For example, more than 90



percent of the timber harvested in Brazil goes to the domestic market (Farani & Oliveira, 2019).

In view of such large demand, it is no surprise that selective logging became a dominant land use in tropical forests. In Brazilian Amazonia, the logged area surpasses deforestation (Asner et al., 2005, 2006; Matricardi et al., 2020), while in Borneo most forests have already been logged (Gaveau et al., 2014) and in Gabon more than half of forests are within logging concessions (Karsenty & Hardin, 2017). Globally, one quarter of tropical forests have already been explored for timber and another quarter is targeted for future exploration, amounting to 400 million hectares of “production forests” (Blaser et al., 2011; Poker & MacDicken, 2016).

Selective logging is a controversial use of tropical forest resources. On the one hand, it is a profitable activity that brings social benefits such as jobs and revenue. The forestry sector creates more than 60 million formal and informal jobs around the world (Arce, 2019) and accounts for more than 15 billion USD in annual government revenue (Whiteman et al., 2015). In Brazil, selective logging creates four million jobs (Sociedade Brasileira de Silvicultura, 2008) while in Brazilian Amazonia it is the third most important economic activity, accounting for 2,3 billion USD in revenue (Ghazoul, 2015) and creating 380,000 jobs (Keller et al., 2007).

Another positive point is that timber is (at least in principle) a renewable resource, making production forests an alternative to secure forested landscapes and avoid deforestation in the long-run (Edwards et al., 2014). Logged forests often retain similar ecosystem services and much of the biodiversity found in undisturbed forests, so they can have high conservation value in themselves (Clark et al., 2009; Edwards et al., 2014; Gaveau et al., 2013; Putz et al., 2012; Berry et al., 2010).

However, selective logging has its downsides. Benefits tend to concentrate in the hands of a few and not be shared with local communities, which may end up losing resources and ecosystem services (Obidzinski & Kusters, 2015; Rist et al., 2012). Logging degrades forests and is often followed by secondary anthropogenic impacts (Foley et

al., 2007; Nepstad et al., 1999), and in some cases logged forests become carbon sources (Huang & Asner, 2010; Ellis et al., 2019; Pearson et al., 2014). Finally, despite the proclaimed ideal of sustainable forest management, logging is often practised as a mining of a non-renewable resource (Putz et al., 2001). When exhausted of timber, forests become vulnerable to conversion to other land uses. Logging is thus often a prelude to deforestation (Asner et al., 2006; Shearman et al., 2012).

### **4.3 Impacts of logging on forests**

Logging impacts go well beyond direct timber removal and include collateral damage from tree felling, winching and skidding, road opening, clearing for log landings and damming of streams (Uhl & Vieira, 1989; Verissimo et al., 1992). Indeed, more trees die from collateral damage than from direct harvest (Uhl et al., 1991; Verissimo et al., 1992). For every tree harvested by conventional logging in Amazonia another 25 were destroyed (Verissimo et al., 1992; Uhl et al., 1991). Collateral damage often surpasses 50 percent of residual forests in Indonesia and Malaysia (Pinard et al., 1995; Kartawinata et al., 2001) and range between 10 and 20 percent in the Congo basin (Karsenty, 2016; Pérez et al., 2005).

It's not just the trees that are affected. Logging operations disrupt forest soils (Hattori et al., 2013; McNabb et al., 1997) and increase water and sediment run-off (Douglas et al., 1993; Bruijnzeel, 2004; Hartanto et al., 2003). Logging disturbs forest microclimates, at least in the short-term (Senior et al., 2018; Mollinari et al., 2019). Finally, in its wake logging brings a host of secondary impacts that are often more severe than logging itself. These include human colonization, hunting, biological invasions and increased vulnerability of forests to fire (Foley et al., 2007; Nepstad et al., 1999; Van Vliet & Nasi, 2008). Many of these secondary impacts are facilitated by the road network that is created to support logging operations (Kleinschroth & Healey, 2017; Laurance et al., 2009; Bicknell et al., 2015a; Siegert et al., 2001).

In practice, impact levels will depend on site characteristics, operational practices and harvest levels, which are highly variable among regions. For instance, harvest intensities in the Congo basin are typically low at less than two trees ha<sup>-1</sup> (10-13 m<sup>3</sup> ha<sup>-1</sup>) (White, 1994; Pérez et al., 2005; Karsenty, 2016) while in Amazonia they range between three and nine trees ha<sup>-1</sup> (18-62 m<sup>3</sup> ha<sup>-1</sup>) (Uhl & Vieira, 1989; Verissimo et al., 1992). Harvest intensities tend to be higher in Southeast Asia, where the dominance of dipterocarp trees allows for much higher harvest levels, reaching up to 20 trees ha<sup>-1</sup> (60-150m<sup>3</sup> ha<sup>-1</sup>) (Edwards et al., 2012; Pinard et al., 1995; Kartawinata et al., 2001).

#### **4.4 Illegal logging**

Illegal logging refers to logging that violates laws and regulations concerning the felling of trees (Ravenel & Granoff, 2004). It can occur at any phase of forest management, from planning to execution to commercialization (Bisschop, 2012). The activity is difficult to quantify so estimates of its scale are highly variable (Contreras-Hermosilla et al., 2007). The proportion of illegal timber in the global market has been estimated at 15 to 30 percent (Nellemann et al., 2012; Hirschberger, 2008), reaching up to 90 percent in some tropical countries (Scotland & Ludwig, 2002; Smith, 2004; Glastra, 2007; Lowe et al., 2016). Global annual losses for states, industry and forest owners due to illegal logging were estimated at 15 billion USD (Hirschberger, 2008; Blaser & Zabel, 2016). Illegal activities deprive governments of resources that could be used to improve forest management or social benefits. It fosters corruption and is associated with other crimes (Hirschberger, 2008). Illegal logging disrespects protected areas and the rights of indigenous and rural communities (Watson, 1996; Pedlowski et al., 2005). It depreciates market prices and reduce the competitiveness of more environmentally friendly operations (Lima et al., 2018; Bisschop, 2012).

There is no fundamental difference between impacts of legal and illegal logging on forests (Pacheco et al., 2016). Yet illegal logging tends to be more damaging to forests due to predatory practices such as the harvest of more trees, of more species, of smaller diameters, with no mitigation for collateral damage (Ravenel & Granoff, 2004; Putz et

al., 2008). In addition, illegal loggers tend to harvest the same stands repeatedly without reusing the infrastructure created during their previous forays, increasing impacts on the forest (Gerwing, 2002; Nepstad et al., 1999).

## **4.5 Reduced-impact logging**

If properly managed, production forests can retain much of their conservation value, providing ecosystem services and expanding the network of protected natural habitats (Clark et al., 2009; Edwards et al., 2014; Gaveau et al., 2013; Edwards et al., 2011). A promising management alternative is reduced-impact logging (RIL), a set of principles aiming to maximize efficiency while mitigating undesirable outcomes (Lima et al., 2018; Putz et al., 2008, 2012). Typical RIL features include capacity building, pre-harvest tree inventory and infrastructural planning, vine cutting, directional tree felling, best practices in winching and skidding, and post-harvest closure (Schulze et al., 2008; Pinard et al., 1995). It tends to fare better than conventional logging, causing less damage to vegetation, biodiversity and the physical environment (Chaudhary et al., 2016; Bicknell et al., 2015b; Burivalova et al., 2019). RIL also provides better economic and social outcomes (Holmes, 2016, 2014; Holmes et al., 2002), release less carbon (Ellis et al., 2019) and present higher rates of biomass and timber recovery (Vidal et al., 2016).

## **4.6 Vertebrate responses to logging**

Vertebrates are key components of tropical forest ecosystems, affecting vegetation dynamics, nutrient flow and energy cycling (Lacher et al., 2019; Sobral et al., 2017; Rosin et al., 2017; Terborgh et al., 2008). Maintaining healthy vertebrate populations is essential to maintain forest integrity and to ensure the long-term viability of timber production, as most tropical trees are dispersed by vertebrates (Sheil & van Heist, 2000; Rosin, 2014; Hammond et al., 1996; Forget et al., 2007).

How species respond to logging will depend on their ecological characteristics and requirements, such as affinity to primary forest, dependence on canopy resources, degree of trophic or ecophysiological specialization, sensitivity to hunting, territoriality, demography, and others (Ochoa, 1997; Meijaard & Sheil, 2008; Meijaard et al., 2005). It is not easy to generalize on vertebrate responses to logging, as demonstrated by the lack of consistence among studies (Gibson et al., 2011; Burivalova et al., 2014; Putz et al., 2012; Bawa & Seidler, 1998). This is not surprising given the wide variation across studies in response metrics, sampling design, local environmental characteristics, harvest methods and intensities, recovery times, etc. (Meijaard et al., 2005; Putz et al., 2000; Gibson et al., 2011). In addition, pseudoreplication and sampling biases may confound interpretation of results (Laufer et al., 2013; Ramage et al., 2013) and reviews often lump together a wide range of taxa, masking patterns (Gibson et al., 2011).

Despite these caveats, some broad patterns are discernible. In general, species with narrow ecological niches such as habitat and dietary specialists are the most sensitive to logging (Edwards et al., 2013; Newbold et al., 2013; Meijaard & Sheil, 2008). This includes many canopy and closed-forest specialists as well as strict frugivores, carnivores or insectivores and species that depend on critical resources at some stage of their life cycle (Newbold et al., 2013; Meijaard & Sheil, 2008). For example, cavity-nesting birds (Costantini et al., 2016; Schaaf et al., 2021), large raptors that require emergent trees for nesting (Miranda et al., 2020) and large frugivore primates (Johns & Skorupa, 1987; Felton et al., 2010) all tend to be vulnerable to the loss of large trees due to logging. However, as exemplified by the contrasting responses of specialized frugivore birds and bats, these generalizations are not rigid. Whereas birds tend to be negatively affected (Gray et al., 2007; Chaves et al., 2017) bats tend to benefit from logging (Peters et al., 2006; Castro & Michalski, 2014; Clarke et al., 2005).

Habitat and food generalists tend to be resilient and sometimes they even benefit from logging (Johns, 1988; Plumptre & Reynolds, 1994; Johns & Skorupa, 1987; Tobler et al., 2018; Davies et al., 2001). For example, generalist herbivores such as forest ungulates

and elephants are attracted to logged areas thanks to the vigorous plant regrowth found near gaps (Barnes et al., 1997; Struhsaker et al., 1996; Fragoso et al., 1991; Davies et al., 2001). Omnivores and non-strict insectivores benefit from the increased insect biomass that is often observed at disturbed areas (Lambert et al., 2006). Many widely distributed, large-sized terrestrial vertebrates which occur in a variety of environments are ecologically flexible and resilient to moderate disturbance (Tobler et al., 2018; Roopsind et al., 2017; Magintan et al., 2017; Azevedo-Ramos et al., 2006). Still, they may be vulnerable to secondary impacts such as increased hunting pressure in residual forests (Brodie et al., 2015b; Roopsind et al., 2017).

## 4.7 Objectives

The main goal of this thesis is to provide a better understanding of the effects of legal and illegal logging regimes on Amazonian medium- to large-sized terrestrial vertebrates (i.e., mammals and birds, Table 1; Figures 1 and 2). More specifically, the study aimed to:

- i. Assess the effects of RIL on an assemblage of medium- to large-sized mammals in south-western Amazonia (paper 1);
- ii. Assess the effects of illegal logging on an assemblage of medium- to large-sized mammals and birds in eastern Amazonia (paper 2);
- iii. Assesses the status and trends of a Critically Endangered bird, the Black-winged trumpeter *Psophia obscura*, in an illegally logged forest in eastern Amazonia (paper 3);
- iv. Assess potential impacts of RIL on the numbers of animal-dispersed trees in south-western Amazonia forest concessions (paper 4).

Table 1. Vertebrate species (medium- to large-sized birds and non-volant mammals) included in the papers constituting this thesis and the papers in which the species were included.

<b>Class</b>	<b>Order</b>	<b>Family</b>	<b>Species</b>	<b>Paper</b>	
Aves	Galliformes	Cracidae	<i>Mitu tuberosum</i>	2	
			<i>Penelope</i> spp.	2	
		Odontophoridae	<i>Odontophorus gujanensis</i>	2	
	Gruiformes	Psophiidae	<i>Psophia obscura</i>	2,3	
			Tinamiformes	Tinamidae	<i>Crypturellus</i> spp.
	<i>Tinamus</i> spp.	2			
	Mammalia	Carnivora	Canidae	<i>Atelocynus microtis</i>	1
Felidae				<i>Leopardus pardalis</i>	1,2
				<i>Leopardus wiedii</i>	1,2
			<i>Panthera onca</i>	1,2	
			<i>Puma concolor</i>	1,2	
<i>Puma yagouaroundi</i>			1		
Mustelidae			<i>Eira barbara</i>	1,2	
			Procyonidae	<i>Nasua nasua</i>	1,2
				<i>Procyon cancrivorus</i>	1
Cetartiodactyla			Cervidae	<i>Mazama americana</i>	1,2
				<i>Mazama nemorivaga</i>	1,2
			Tayassuidae	<i>Pecari tajacu</i>	1,2
				<i>Tayassu pecari</i>	1,2
Cingulata		Dasypodidae	<i>Dasypus</i> spp.	1,2	
			<i>Priodontes maximus</i>	1,2	
Didelphimorphia		Didelphidae	<i>Didelphis marsupialis</i>	1,2	
Perissodactyla		Tapiridae	<i>Tapirus terrestris</i>	1,2	
Pilosa		Myrmecophagidae	<i>Myrmecophaga tridactyla</i>	1,2	
			<i>Tamandua tetradactyla</i>	1,2	
Rodentia		Cuniculidae	<i>Cuniculus paca</i>	1,2	
	Dasyproctidae		<i>Dasyprocta prymnolopha</i>	2	
		<i>Dasyprocta variegata</i>	1		

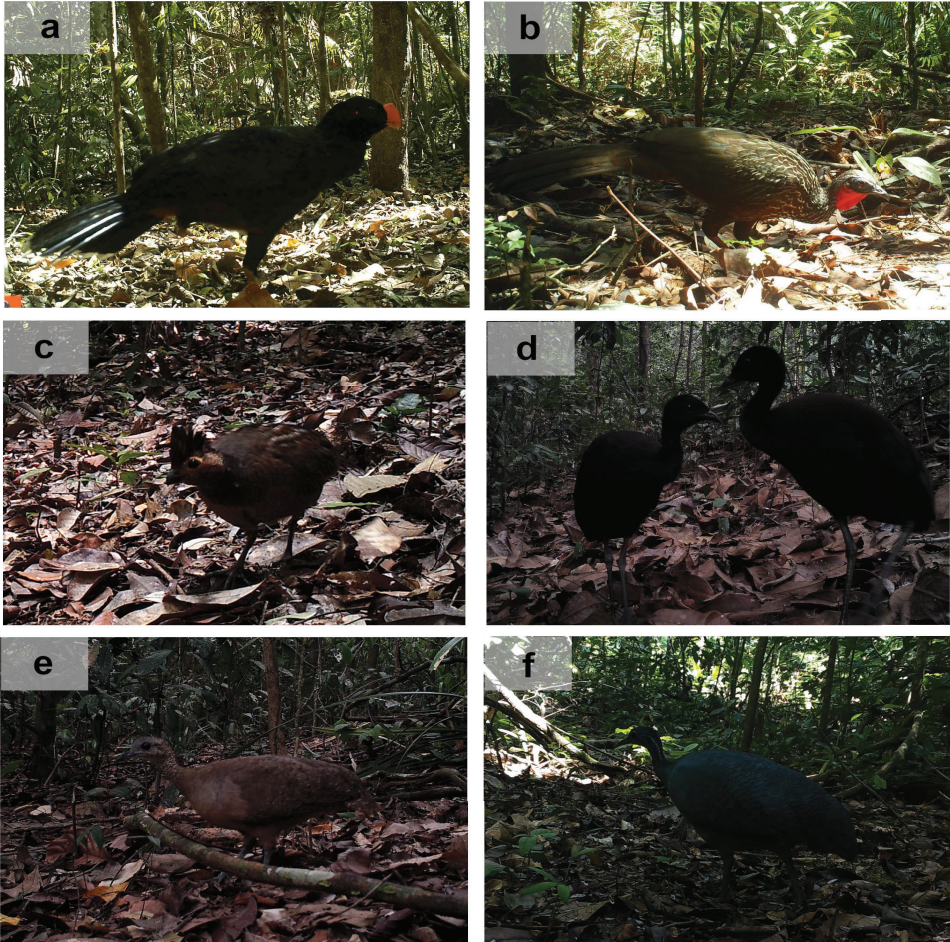


Figure 1: Examples of birds included in the papers constituting this thesis (Latin names of species in parenthesis): a. Razor-billed Curassow (*Mitu tuberosum*); b. Rusty-margined Guan (*Penelope superciliaris*); c. Marbled Wood-quail (*Odontophorus gujanensis*); d. Black-winged Trumpeter (*Psophia obscura*); e. Great Tinamou (*Tinamus major*); f. Grey Tinamou (*Tinamus tao*).





Figure 2: Examples of mammals included in the papers constituting this thesis (Latin names of species in parenthesis): a. Short-eared Dog (*Atelocynus microtis*); b. Jaguar (*Panthera onca*); c. Amazonian Brown Brocket (*Mazama nemorivaga*); d. Lowland Tapir (*Tapirus terrestris*); e. Giant Armadillo (*Priodontes maximus*); f. Black-rumped Agouti (*Dasyprocta prymnolopha*).

## 4.8 Materials and Methods

### *Study areas*

Data used in this thesis was collected at two protected areas in Brazilian Amazonia (Fig. 3), each subjected to a different type of logging. What follows is a brief description of these areas, for more details please refer to the corresponding papers.

Jamari National Forest (Fig. 3) is a 220,000 ha protected area located in south-western Amazonia. Approximately half of the reserve has been allocated as concessions for logging of commercial timber species  $\geq 50$  cm in diameter at breast height, to be explored under RIL techniques (Kauai et al., 2019; Mollinari et al., 2019). Operations started in 2010 and two concessions are currently active. Jamari was the study site for papers 1 and 4.

Gurupi Biological Reserve (Fig. 3 and 4) is a 271,000 ha strictly protected area located in extreme eastern Amazonia. Though formally protected, the reserve was subjected to over three decades of illegal logging and other anthropogenic pressures (Fig. 5). However, the reserve still safeguards a significant portion of the regional biodiversity, including the full complement of medium- to large-sized terrestrial vertebrates (Carvalho Jr. et al., 2020; Lopes & Ferrari, 2000; Lima et al., 2014; Mendonça et al., 2021). Recently, strategic enforcement expelled illegal loggers from sectors of the reserve, creating an opportunity to investigate the effects of previous illegal logging on wildlife, the theme of papers 2 and 3.



Figure 3: Map of northern South America depicting the two study areas in Amazonia: (1) Jamari National Forest; (2) Gurupi Biological Reserve.



Figure 4: A dirt road cutting through Gurupi Biological Reserve (Photo: Flávio K. Ubaid).



Figure 5: Illegally logged timber in a log yard at Gurupi Biological Reserve (Photo: ICMBio).

### *Data collection*

Papers 1 to 3 used wildlife data collected by camera-traps at Gurupi and Jamari as part of the Brazilian *in situ* monitoring program of Federal Protected Areas (Programa Monitora) (Roque et al., 2018). Sampling at both sites followed the standardized Tropical Ecology Assessment and Monitoring (TEAM) protocol for terrestrial vertebrates (Rovero & Ahumada, 2017). In brief, the protocol provides for the deployment of at least 60 camera-traps distributed in one to several arrays with a density of one camera per 2 km<sup>2</sup>. Cameras are attached to trees at knee-height (Fig. 6) and are set to operate for at least 30 days during the local dry season. The minimum TEAM guidelines were duly followed, yet details of implementation varied between sites. More details are provided in the individual papers.



Figure 6: Paulo H. Bonavigo deploys a camera trap at Jamari National Forest (Photo: Natieli Q. Ignácio).

Paper 4 relied on data from forestry surveys conducted by concession companies at Jamari National Forest. In the surveys, field teams identified, measured and mapped all

trees with diameter at breast height (dbh)  $\geq 40$  cm within production areas (Pinagé et al., 2016), excluding gallery forests along streams and non-timber species such as palms. Trees were identified in the field by parataxonomists, using common names later converted to taxonomic binomials by concession technicians (Netto et al., 2017; Kauai et al., 2019; Muhlbauer & Madeflona, 2009). Surveys were conducted before harvest and the dataset was updated after harvest to indicate the fate (logged or not) of each individual tree.

Papers 1 to 3 relate wildlife data provided by camera-traps to site-level explanatory variables representing logging impacts and other factors deemed relevant. The list of explanatory variables included third party data (e.g., maps of harvested trees and road infrastructure produced by concession companies, used in papers 1 and 4, Fig. 7), data extracted from satellite imagery (e.g., indices of past logging, used in papers 2 and 3), *in situ* measurements of forest structure (e.g., tree density and basal area, used in papers 2 and 3, Fig. 8), public access databases (e.g., forest cover from the MapBiomias monitoring system (<https://mapbiomas.org/>), Souza et al., 2020), used in papers 2 and 3). Table 2 lists all variables used, and more precise details are provided in the individual papers.



Figure 7: Map of an annual production unit within a concession at Jamari, showing (a) the location of harvested trees and (b) the logging road network.



Figure 8: Walison Silva, Ana M. Andrade and Carolina Melo collect data on forest structure at Gurupi (Photo: E. Carvalho Jr).

## Data analysis

Table 2 presents a short summary of the analyses and variables used in each paper. More details on statistical analyses are provided in the corresponding papers.

Table 2. Summary of analysis and variables used in each paper.

Paper	Response variable	Explanatory variables	Analyses
1	Occupancy	i) logging status (unlogged/logged)	Multi-species occupancy model (MSOM) Generalized linear model (GLM)
	Detection	ii) logging intensity	
	Species richness	iii) road density	
2	Relative abundance	i) number of logging bouts	Hierarchical model of species communities (HMSC)
		ii) post-logging recovery time	
		iii) edge index	
		iv) fire index	
3	Occupancy	i) elevation	Multi-season occupancy model
	Detection	ii) distance to water	
	Apparent survival	iii) distance to edge	
	Apparent mortality	iv) tree density	
	Turnover	v) basal area	
		vi) post-logging recovery time	
		vii) number of logging bouts	
4	Number of trees		T-test
	Basal area of trees	i) dispersal syndrome	Chi-squared test of homogeneity
	Proportion of trees from different dispersal syndromes.	ii) tree fate (logged/unlogged)	



## 4.9 Results and discussion

Here I present the main results of papers 1 to 4 and, where relevant, discuss how they relate to each other. A more detailed discussion of the results in the context of the current literature is provided in each paper.

### *Paper 1*

In paper 1 we found that site-level mammal species richness in Jamari forest concessions was negatively affected by logging intensity, and positively affected by density of logging roads. Whereas the negative effect of logging intensity is consistent with a recent meta-analysis on biodiversity responses to gradients of logging intensity (Burivalova et al., 2014), it contrasts with several studies reporting little or no effect of logging on large tropical mammals (Azevedo-Ramos et al., 2006; Bicknell & Peres, 2010; Laufer et al., 2015; Tobler et al., 2018). Perhaps this is because most previous studies on this group treated logging as a binary, homogeneous form of land use, whereas we are among the first to sample across gradients of logging intensity. The spatial refinement of our data allowed us to detect localized effects that would otherwise go unnoticed if we had treated the landscape in a binary way or aggregated the data at larger scales.

The positive relationship between roads and species richness is unexpected to some extent, as many of the negative effects of logging, especially secondary ones such as human encroachment and hunting, are associated with roads (Kleinschroth et al., 2016; Kleinschroth & Healey, 2017; Bicknell et al., 2015a). However, roads can also benefit wildlife by increasing habitat heterogeneity and providing enhanced food resources and movement corridors (Kleinschroth & Healey, 2017; Tobler et al., 2018). The result therefore indicates that concessions were successful in controlling negative secondary impacts associated with roads while facilitating their positive effects.

Despite their significant effect on site-level species richness, neither logging intensity nor road density significantly affected the occupancy rate of any individual species,

which seems counterintuitive. Nevertheless, most species tended to respond to these variables in the same direction observed for species richness. Given that richness is the sum of all species occurrences, even small changes in occupancy probabilities can affect richness if they occur in tandem for most species. An interesting consequence is that variation in site-level richness does not stem from the consistent loss or gain of any set of species, so that the full complement of species is retained in the landscape even in the face of moderate site-level species loss.

The overall conclusion is that RIL has relatively moderate effects on the medium- to large-sized mammal assemblage, confirming that it may be a reasonable compromise between the often-conflicting interests of production and conservation (Edwards et al., 2014; Burivalova et al., 2019).

### *Paper 2*

As far as we know, paper 2 was the first assessment of the effects of illegal logging on Amazonian vertebrates. Here we found that illegal logging (quantified as the number of logging bouts and post-logging recovery time) had a negligible effect on the relative abundance of the studied species. This was evidenced both by the low overall explanatory power of the model and the fact that virtually no species responded significantly to these variables. In this paper, we also evaluated if species traits (taxonomic class, body mass and dietary guild) mediate their responses to logging. Again, we found little support for any trait effect on species responses. In part, this stems from the small range of variation in species responses (as they were not affected by the predictors); other possible reasons are discussed in the paper.

The above results agree with most previous studies that reported resiliency of large tropical vertebrates to selective logging (Azevedo-Ramos et al., 2006; Tobler et al., 2018; Meijaard & Sheil, 2008). A possible explanation for this is that most of these vertebrates are habitat generalists and therefore flexible to moderate habitat disturbance. For example, most species included in this paper are widely distributed and occur in different vegetation types and successional stages (Redford & da Fonseca,

1986; Parry et al., 2007; Norris et al., 2008). However, this speculation refers mostly to habitat and the study includes at least a few specialists (e.g. the bird *Psophia obscura*, see discussion on paper 3 below).

Results from paper 2 should be interpreted with caution as there are several caveats. The study setting represents a best-case scenario as the study area has a continuous forest cover, is under enforced protection and has been spared from secondary logging impacts, which are often the most harmful to wildlife (Brodie et al., 2015b; Zimmerman & Kormos, 2012). The study lacked unlogged control sites and site-level logging impacts were quantified using relatively coarse indices, which was inevitable given that illegal logging leaves no systematic records of harvest levels. In view of this, the main conclusion to be drawn is that even illegally logged forests can retain much of their conservation value, especially if they are protected from further impacts.

A cursory comparison between the results of papers 1 and 2 may give the impression that illegal logging equals RIL, as both had only minor effects on the target species. However, this would be hasty, as the studies differ in relevant aspects that preclude direct comparisons. For example, even though both studies used the same sampling protocol for vertebrates, they differ in the way that predictor and response variables were measured and in their analytical approaches. Paper 1 used occupancy as the response variable, whereas paper 2 used relative abundance. Paper 1 accounted for imperfect detection while paper 2 did not. As for predictor variables, paper 1 benefited from high-resolution data on harvest intensities and road infrastructure provided by concession companies, while paper 2 was restricted to relatively coarse indices of logging impacts. In addition, sites differ in other aspects, such as mean post-logging recovery time and natural features.

More studies are clearly needed to contrast the effects of legal and illegal logging practices on wildlife. For these studies to be comparable, it is essential that they use more refined, and preferably standardized, measurements of harvest intensities, collateral damage and impact gradients across the landscape. It is also important that

these studies are carried out in less favourable settings, for example in fragmented landscapes outside protected areas.

### *Paper 3*

Paper 3 revisits the illegally logged Gurupi Biological Reserve, this time to investigate the occupancy status and trends of a Critically Endangered bird, the Black-winged trumpeter (*Psophia obscura*). Regarding occupancy patterns, we confirmed that the species is an interior-forest specialist that avoids sites with a disturbed forest structure, such as recently logged sites with high densities of small trees (del Hoyo et al., 2020; Portes et al., 2011; Moura et al., 2014). As for temporal trends, we found stable occupancy rates for the species throughout the five-year study period (2016-2020) and that this stability derived mainly from high between-year survival rates. The overall conclusion is that the species is doing well in the reserve – although these trends should be interpreted cautiously as the study length was relatively short, amounting to approximately one generation of the species (Bird et al., 2020). For example, the IUCN Red List guidelines requires a time series longer than three generations or 10 years as input to categorize a species (Rodrigues et al., 2006).

As in paper 2, the above results reaffirm the value of illegally logged forests for conservation, provided they are protected from additional impacts. This is consistent with other studies showing that logged areas provide habitat for endangered and vulnerable birds (Edwards et al., 2011) and mammals (Brodie et al., 2015a; Clark et al., 2009). That such areas have a role to play is particularly important for this species given that much of its remaining population is in private areas, many of which have been selectively logged (Lees et al., 2012). Finally, the study also confirms that habitat quality of such areas tends to improve over time so even interior-forest specialists can return to using them after a while.

### *Paper 4*

The loss of food resources is one of the mechanisms proposed to explain negative effects of logging on wildlife (Heydon & Bulloh, 1997; Johns, 1992). Paper 4 uses an indirect approach to assess potential impacts of logging on frugivorous vertebrates, by quantifying the loss of animal-dispersed (endozoochorous and synzoochorous) trees resulting from harvest in RIL forest concessions at Jamari. We found that most individual trees and most of the basal area of the pre-harvest forest belong to animal-dispersed genera, as is typical in tropical forests (ter Steege et al., 2013; Jansen & Zuidema, 2001). However, despite their predominance these trees were much less explored than abiotically-dispersed trees either in absolute or relative terms – in agreement with data on global timber market (Jansen & Zuidema, 2001).

Still, at least ten percent of all large animal-dispersed trees were lost across the landscape, with site-level (50 ha plots) losses sometimes exceeding a third of all animal-dispersed trees. The conclusion is that logging may deplete frugivore resources in residual forests and this may have negative consequences for frugivore populations (Johns, 1992). However, this inference is based on indirect measures and does not consider potentially confounding factors. For example, on the one hand losses of fruit trees can be even greater due to collateral damage resulting from exploitation; on the other hand, residual forest may experience increases in fruit production due to compensatory mechanisms (Davies et al., 2001; Clarke et al., 2005). Therefore, further studies are needed to assess the dynamics of fruit production in residual forests and how frugivores perceive and react to these changes.

#### **4.10 Concluding remarks and perspectives**

This thesis adds to our understanding of vertebrate conservation in selectively logged tropical forests. The results indicate that medium- to large-sized vertebrates are mostly resilient to legal RIL as well as to illegal logging. As discussed above, with a few exceptions, virtually all species included in this study were insensitive to logging, at least in the way its impacts were quantified in the papers that make up this thesis. In

addition, both the legally logged Jamari National Forest and the illegally logged Gurupi Biological Reserve retain their full complement of medium to large vertebrate species, demonstrating that logged landscapes hold considerable value for wildlife conservation.

A key factor enabling the persistence of these animals appears to be the control of secondary impacts such as human settlement, hunting, forest fragmentation and fires. It is well known that many impacts of logging are indirect, arising from these factors (Zimmerman & Kormos, 2012; Lhoest et al., 2020). The study areas in this thesis are both within formally protected areas that are under active enforcement either by government agencies or by private concession companies. A measure that seems to be particularly effective and that applies to both cases is the closure of access roads, a major vector of spread for secondary impacts (Kleinschroth & Healey, 2017). This likely favoured the preservation of wildlife in the studied landscapes. However, this also limits the generality of the conclusions as both study sites represent best-case scenarios, which are unlikely to be matched in most logged rainforest landscapes.

In most of this thesis, logging was treated as a single and broad type of human impact, measurable through simple indices such as harvest intensity or number of logging bouts. However, the precise mechanisms and processes by which logging affects wildlife remains poorly understood (Meijaard et al., 2005; Messina et al., 2018; Bousfield et al., 2020). For example, logging effects may be mediated by changes in forest structure (affecting the ability of animals to move or hide, e.g. McLean et al., 2016), resource availability (changing the spatiotemporal availability of food and shelter, e.g. Felton et al., 2010; Hamer et al., 2015; Schaaf et al., 2021), and microclimate (harming or benefiting species depending on their physiological tolerances, e.g. Beaudrot et al., 2019). These different factors may affect populations in a myriad of direct and indirect, positive and negative, ways. Disentangling their effects is a much-needed line of research that can help to improve management and restoration techniques in production areas (Sheil & van Heist, 2000; Meijaard et al., 2005).

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## 6 Papers



# Paper I





# Mammal responses to reduced-impact logging in Amazonian forest concessions

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## ABSTRACT

Production forests are a dominant feature of most tropical forest landscapes and it is therefore important to understand the effects of timber extraction on the resident fauna. Here we investigate the effects of reduced-impact logging (RIL) on medium- to large-sized terrestrial mammals in two Jamari National Forest logging concessions, south-western Brazilian Amazonia. We used camera traps to survey the terrestrial mammal fauna. Bayesian multi-species occupancy models (MSOMs) were performed to assess the effect of logging intensity and density of logging roads on site-level species richness, occupancy and detection rates. Species richness was negatively affected by logging status and by increasing logging intensity, and positively affected by road density. Occupancy and detection rates of individual species were largely unrelated to model predictors, although responses across species tended to be consistent with that observed for species richness. Despite negative effects of logging on species richness, no individual species were lost at the landscape level, suggesting that concessions managed under RIL techniques may be a reasonable compromise between economic and conservation interests.

## 1. Introduction

Logged forests represent an increasing share of global tropical forest cover (Asner et al., 2009). Approximately one quarter of the world's tropical forests have already been explored for timber, and another quarter is targeted for future exploration, amounting to 400 million hectares of forests for production (Poker and MacDicken, 2016). Even though logging is a relatively benign form of land use compared to deforestation, it is still a relevant form of forest degradation (Asner et al., 2006) and industrial logging has been identified as the leading cause of global primary forest disturbance (Potapov et al., 2017).

If properly managed, production forests can retain much of their conservation value, providing ecosystem services and supporting the network of available wildlife habitat (Clark et al., 2009; Edwards et al., 2014a). For instance, logging impacts can be greatly reduced by the adoption of reduced-impact logging (RIL), a set of principles designed to maximize efficiency while mitigating undesirable outcomes (Lima et al., 2018; Putz et al., 2012, 2008). Typical RIL features include capacity

building, improved inventory and infrastructural planning to reach target trees and optimize skidding routes, and the adoption of measures to reduce collateral damage, such as pre-felling vine cutting and directional felling to avoid pulling down non-target trees (Schulze et al., 2008). As a result, RIL is not only less damaging to the remaining vegetation, biodiversity and the physical environment (Bicknell et al., 2015b; Burivalova et al., 2019; Chaudhary et al., 2016), but also tends to provide better economic and social outcomes than conventional logging (Holmes, 2014; Holmes et al., 2002).

Medium- and large-bodied terrestrial mammals are key components of tropical forest ecosystems, affecting processes such as vegetation dynamics, seed dispersal, nutrient flow and energy cycling (Galetti et al., 2015; Gardner et al., 2019; Lacher et al., 2019; Markl et al., 2012; Rosin et al., 2017; Sobral et al., 2017). Maintaining healthy mammal populations is essential not only to maintain ecosystem integrity of logged forests, but also to ensure timber regeneration and the long-term viability of production, as most potential timber species are dispersed by vertebrates (Forget et al., 2007; Hammond et al., 1996; Rosin, 2014;

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Sheil and van Heist, 2000). Understanding how logging affects mammals can help to clarify the role of production forests in balancing wildlife conservation with economically productive activities.

Previous studies show that medium- and large-bodied terrestrial mammals are often ecologically flexible and resilient to logging (Azevedo-Ramos et al., 2006; Magintan et al., 2017; Roopsind et al., 2017; Tobler et al., 2018). For example, this group includes many habitat generalists, omnivores and generalist browser/frugivores that are resilient to disturbance and may even benefit from plant regrowth found in and around logging gaps and along roads (e.g. Brodie et al., 2015, Davies et al., 2016; Plumptre and Reynolds, 1994; Tobler et al., 2018). In fact, it is the secondary effects of logging, such as hunting and human colonization, that have the greatest negative impact on these animals (Costantini et al., 2016; Lhoest et al., 2020; Zimmerman and Kormos, 2012).

Reviews assessing the effects of logging on mammal species richness have generally reported negligible effects (Berry et al., 2010; Gibson et al., 2011; Putz et al., 2012), although a recent and more refined meta-analysis assessing responses along gradients of logging intensities found that increasing logging intensities depress mammal species richness (Burivalova et al., 2014). However, most of the mammal data used in this meta-analysis referred to bats and small mammals, probably because most studies on medium- to large-bodied mammals did not survey a gradient of logging intensity, but rather treated logging as a uniform land use (Burivalova et al., 2014).

In the Brazilian Amazon, the area affected by logging surpasses the area deforested (Asner et al., 2006, 2005; Matricardi et al., 2020). Each year, more than 6000 km<sup>2</sup> of forests are logged in the region (Matricardi et al., 2020), most under conventional techniques that are highly damaging to forests (Asner et al., 2006; Schulze et al., 2008) if not outright illegal (Lima et al., 2018). To improve environmental standards and compliance within the timber sector, the Brazilian government adopted a policy of concessions that to date has granted more than one million hectares of public forests to private enterprise (Azevedo-Ramos et al., 2015; Bauch et al., 2009). All concessions are located in National

Forests – sustainable use protected areas that allow for different types of human use, but also serves the purpose of biodiversity conservation (Rylands and Brandon, 2005). For this reason, maintaining ecosystem health within concessions is crucial (Azevedo-Ramos et al., 2015).

Here we investigate how medium- and large-bodied terrestrial mammals respond to reduced-impact logging in two forest concessions located within a National Forest in south-western Brazilian Amazonia. More specifically, we assess the effects of logging status, logging intensity and density of logging roads on mammal species richness, species occupancy and detection rates.

## 2. Methods

### 2.1. Study area

Jamari National Forest (JNF) is a 220,000 ha protected area located in south-western Brazilian Amazonia (Fig. 1). Climate is tropical monsoonal with mean annual temperatures > 26 °C and mean annual rainfall ranging between 2200 and 2500 mm (Alvares et al., 2013). The area is covered by dense evergreen tropical forest with patches of open forest; elevation ranges between 100 and 300 m a.s.l. (IBAMA, 2005). Approximately half of JNF has been allocated as concessions for logging of commercial timber species > 40 cm in diameter at breast height (Kauai et al., 2019; Mollinari et al., 2019). Operations started in 2010 and two concessions are currently active. Each concession is divided into annual production units (APUs) that are explored under RIL techniques in rotation cycles of 25 to 30 years. Maximum allowed harvest is 25 m<sup>3</sup> ha<sup>-1</sup> (Locks and Matricardi, 2019), but actual harvest levels are usually lower, ranging between 10 and 15 m<sup>3</sup> ha<sup>-1</sup> (Pinagé et al., 2016).

### 2.2. Mammal sampling

Camera-trap surveys were performed to sample terrestrial mammals during the 2017 and 2018 dry season (June–December). Sampling was conducted as part of the Brazilian *in situ* monitoring program of Federal

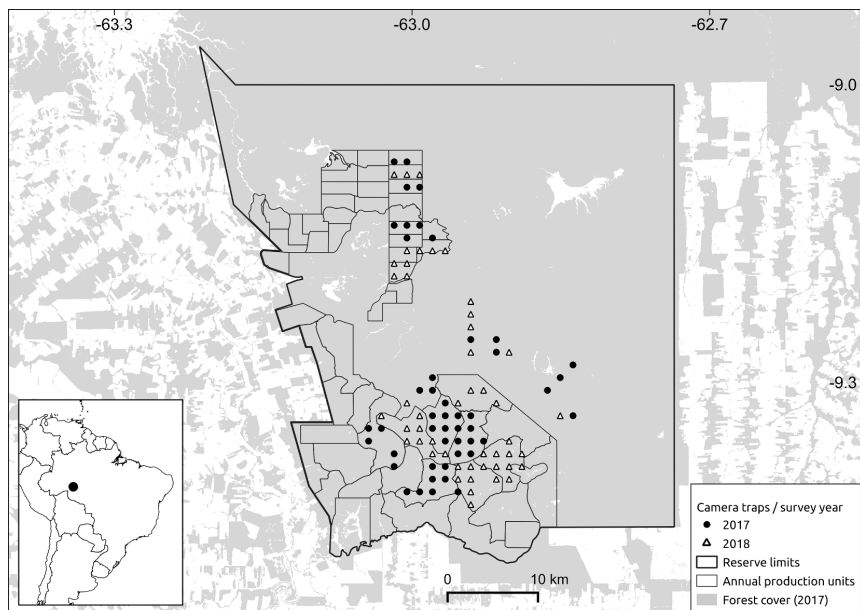


Fig. 1. Map of Jamari National Forest in south-western Brazilian Amazonia, showing the Annual Production Units within concession areas and the distribution of camera-trap stations (forest cover from MapBiomas, <http://mapbiomas.org>).

Protected Areas (Programa Monitora), following the Tropical Ecology Assessment and Monitoring (TEAM) protocol for vertebrates (Jansen et al., 2014). We deployed 95 camera-traps equipped with passive infrared sensors (Bushnell Trophy Cam) distributed in a grid with a density of one camera station per 2 km<sup>2</sup> (47 stations in 2017 and 48 in 2018, Fig. 1, Suppl. Mat. Table S1). We deployed cameras on suitable trees as close as possible to predefined grid locations and never placed cameras on roads. Camera locations included unlogged sites outside concessions as well as unlogged and logged sites within concessions. We deployed cameras at knee height and perpendicular to the ground and cleared the vegetation directly in front of the cameras. Images were processed in the wild.ID software using the IUCN as a taxonomic authority (Fegraus et al., 2011). For the analysis, we only included terrestrial mammals  $\geq 500$  g body mass. Due to difficulty with identification, we lumped *Dasypus novemcinctus* and *D. kappleri* as *Dasypus* spp., and *Mazama americana* and *M. nemorivaga* as *Mazama* spp. for the analysis. To increase detection probabilities and facilitate model convergence in the occupancy analysis, we collapsed data into five-day sampling occasions (Otis et al., 1978).

### 2.3. Environmental variables

We quantified a set of environmental variables to represent site-level logging impacts with potential to affect the mammalian fauna: (1) *Logging status* is a binary variable indicating whether a site has been logged or not. (2) *Logging intensity* is the aggregated basal area of all harvested trees within 500 m buffers centred on camera trap locations. Logging intensities at sampling locations ranged from 0.25 to 1.6 m<sup>2</sup> ha<sup>-1</sup> (mean = 0.83), amounting to approximately 5 to 25 m<sup>3</sup> ha<sup>-1</sup> in volume. (3) *Road density* is the summed length of all road segments (skid trails excluded) within 500 m buffers centred on camera trap locations, divided by buffer area. Road densities at sampling locations ranged between zero and 63 m ha<sup>-1</sup> (mean = 23.7). We assume variables 1, 2 and 3 can potentially affect both species occupancy and detection rates, as they may influence not only their spatial distribution but also their abundance and/or activity levels. We did not include hunting as an additional model predictor because concessions control access to most of the area and hunting levels are low.

In addition to the variables described above, we included random factors in our models to control for spatial and temporal autocorrelation between sites: (4) *APU* is the Annual Production Unit where each camera was placed and (5) *sampling year* is a binary factor indicating if the site was sampled in 2017 or 2018. Finally, we used (6) mean Julian *date* of sampling occasion as a proxy for the progression of dry season during sampling. Predictors were uncorrelated (Suppl. Mat. Table S2) and were standardized before analysis.

### 2.4. Species richness and occupancy

Species richness, occupancy and detection rates were estimated using Bayesian multi-species occupancy models (MSOM; Devarajan et al., 2020; Dorazio et al., 2006). This approach combines community and species-level attributes in a single framework that accounts for imperfect detection and provides better parameter estimates than alternative methods (Dorazio et al., 2006; Kéry and Schaub, 2012; Zipkin et al., 2010, 2009). In the model, the latent state variable occurrence of species *i* at site *j* is specified as a Bernoulli outcome governed by occupancy probability of species *i* at site *j*:  $z_{ij} \sim \text{Bern}(\psi_{ij})$ . Imperfect observation of  $z_{ij}$  may bias estimation of  $\psi_{ij}$ , so the observation process is specified as a Bernoulli outcome governed by  $z_{ij}$  times detection probability for species *i* at site *j* during survey *k*:  $y_{i,j,k} \sim \text{Bern}(z_{ij} \times p_{i,j,k})$  (Kéry and Royle, 2008; Kéry and Schaub, 2012).

The model can incorporate predictors for  $\psi$  and  $p$  by means of logit link functions (Dorazio et al., 2006; Kéry and Schaub, 2012). We ran two alternative models. In model 1, we evaluated the effect of logging status on species occupancy, and the effects of status and dates on species

detection, using the following specifications:

$$\text{logit}(\psi_{ij}) = \alpha_0 + \alpha_1 \text{APU}_j + \alpha_2 \text{year}_j + \alpha_3 \text{status}_j \quad (1)$$

$$\text{logit}(p_{i,j,k}) = \beta_0 + \beta_1 \text{status}_j + \beta_2 \text{date}_{j,k} \quad (2)$$

In model 2, we evaluated the effect of logging intensity and road density on species occupancy, and logging intensity, road density and dates on species detection, using the following specifications:

$$\begin{aligned} \text{logit}(\psi_{ij}) = & \alpha_0 + \alpha_1 \text{APU}_j + \alpha_2 \text{year}_j + \alpha_3 \text{loggingintensity}_j \\ & + \alpha_4 \text{roaddensity}_j \end{aligned} \quad (3)$$

$$\text{logit}(p_{i,j,k}) = \beta_0 + \beta_2 \text{loggingintensity}_j + \beta_3 \text{roaddensity}_j + \beta_4 \text{date}_{j,k} \quad (4)$$

In both models, we used the parameter-expanded data augmentation technique to estimate species richness while accounting for unobserved species (Kéry and Schaub, 2012). We added 10 additional all-zero observation histories, corresponding to “potential”, undetected species, to the dataset and fitted a zero-inflated version of the model to it. We added an indicator variable  $w_i$  to the occurrence process so that  $z_{ij}$  became a Bernoulli outcome governed by  $\psi_{ij} \times w_i$ , where  $w_i$  is a Bernoulli outcome governed by the inclusion probability  $\Omega$ :  $w_i \sim \text{Bern}(\Omega)$  (Kéry and Schaub, 2012; Zipkin et al., 2010). We then estimated global and local species richness by summing the estimated  $w_i$  from all “species” in the augmented dataset (Kéry and Schaub, 2012; Zipkin et al., 2010). We stress that we estimate relative, not “true” species richness, as some species were lumped for analysis and we only refer to species detectable by camera-traps (Guillera-Arroita et al., 2019).

We fitted the models in JAGS (Plummer, 2015) using the *R2jags* package (Su and Yajima, 2012). We used non-informative priors for all the parameters and ran three chains with 100,000 Markov Chain Monte Carlo (MCMC) iterations with a burn-in of 50,000 and a thinning rate of 100. We evaluated parameter convergence using the Gelman-Rubin diagnostic (Gelman and Shirley, 2011) and visual inspection of trace plots. We considered that there was support for a covariate effect when the 95% posterior credible interval (CI) for the parameter did not include zero. We used generalized linear models to assess the relationship between site-level estimated species richness and logging status (model 1) or logging intensity and road length (model 2). Data and codes used in the MSOM analysis are available at <https://github.com/ICMBio-CENAP/Mammal-responses-logging-concessions>.

## 3. Results

A total of 15,789 images corresponding to 1805 independent (>60-minute interval) records of 20 mammal species were obtained (Table 1). The number of records among species varied considerably, with some species being frequently recorded at multiple sites at one extreme, and others being rarely recorded at few sites at the other (Table 1, Suppl. Mat. Fig. S1).

### 3.1. Logged vs unlogged forest

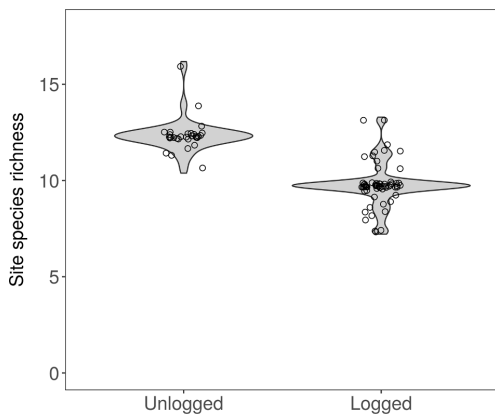
The median estimated size of the metacommunity was 23 species (95% CI: 20–29, Suppl. Mat. Fig. S2). The median estimated site-level richness was 9.8 species (95% CI: 7.6–13.1). Estimated site-level richness was significantly lower at logged compared to unlogged sites ( $R^2 = 0.59$ ,  $t = -11.51$ ,  $P < 0.001$ , Fig. 2).

Logging was negatively related to occupancy rates of most species (Fig. 3, Table 1), but it was only for *Didelphis marsupialis* that the credible interval did not overlap zero (95% CI: -4.7 to -0.3, Fig. 3). There was no significant relationship between detectability of any species and any predictor (Suppl. Mat. Fig. S3).

**Table 1**

Mammalian species recorded by camera traps at Jamari National Forest, total number of photos, number of independent records and mean estimated occupancy rates ( $\psi$ ) at unlogged and logged sites.

Order	Family	Species	Common name	Photos	Records	$\psi$ Unlogged	$\psi$ Logged
Carnivora	Canidae	<i>Atelocynus microtis</i>	Short-eared Dog	96	26	0.65	0.59
		<i>Leopardus pardalis</i>	Ocelot	114	21	0.66	0.58
	Felidae	<i>Leopardus wiedii</i>	Margay	17	2	0.4	0.24
		<i>Panthera onca</i>	Jaguar	21	5	0.51	0.36
		<i>Puma concolor</i>	Puma	84	5	0.49	0.35
		<i>Puma yagouaroundi</i>	Jaguarundi	36	6	0.1	0.07
	Mustelidae	<i>Eira barbara</i>	Tayra	189	30	0.68	0.44
		Procyonidae	<i>Nasua nasua</i>	South American Coati	478	48	0.76
	<i>Procyon cancrivorus</i>		Crab-eating Raccoon	15	4	0.33	0.26
	Cetartiodactyla	Cervidae	<i>Mazama</i> spp	Brocket Deer	2545	308	0.81
<i>Pecari tajacu</i>			Collared Peccary	3271	185	0.7	0.68
Tayassuidae		<i>Tayassu pecari</i>	White-lipped Peccary	1442	34	0.67	0.52
Cingulata	Dasypodidae	<i>Dasybus</i> spp	Armadillo	1592	275	0.78	0.62
		<i>Priodontes maximus</i>	Giant Armadillo	90	14	0.47	0.35
		<i>Didelphis marsupialis</i>	Common Opossum	39	9	0.41	0.16
Didelphimorphia	Didelphidae	<i>Didelphis marsupialis</i>	Common Opossum	39	9	0.41	0.16
Perissodactyla	Tapiridae	<i>Tapirus terrestris</i>	Lowland Tapir	459	46	0.6	0.38
Pilosa	Myrmecophagidae	<i>Myrmecophaga tridactyla</i>	Giant Anteater	105	20	0.44	0.42
	Myrmecophagidae	<i>Tamandua tetradactyla</i>	Southern Tamandua	85	20	0.55	0.46
Rodentia	Cuniculidae	<i>Cuniculus paca</i>	Paca	1209	184	0.56	0.47
	Dasyproctidae	<i>Dasyprocta variegata</i>	Agouti	3902	563	0.72	0.76



**Fig. 2.** Violin plot comparing estimated site-level mammal species richness between unlogged and logged sites at Jamari National Forest.

### 3.2. Effect of logging intensity and road density

Site-level richness was negatively related to logging intensity ( $t = -5.6$ ,  $P < 0.001$ ) and positively related to road density ( $t = 2.6$ ,  $P = 0.01$ ; Fig. 4, Suppl. Mat. Table S3).

Occupancy rates for most species tended to be negatively related to logging intensity and positively related to road density, but in no case was the relationship significant (Fig. 5). There was no overall trend in detection probability across species in their responses to logging intensity, whereas detection for most species tended to be positively related to road density and Julian date (Suppl. Mat. Fig. S4). However, none of these relationships were significant as all credible intervals overlapped zero, apart from the positive relationship between *Dasyprocta variegata* detection and Julian date (95% CI: 0.03–0.68, Suppl. Mat. Fig. S4).

## 4. Discussion

### 4.1. Species richness

We found that logging negatively affected mammal species richness

in the Jamari National Forest logging concessions. As logging changes tree species composition, forest structure (e.g. tree density, basal area) and microclimate (e.g. radiation, temperature and humidity levels), it leads to a myriad of direct and indirect effects (positive and negative) on individual species (e.g., Costantini et al., 2016; Meijaard et al., 2005). For example, herbivores may either suffer from the loss of large fruit-bearing trees (Felton et al. 2010, Granados et al., 2019) or benefit from the influx of browse, flower and fruit in residual forests (Coley and Barone, 1996; Costa and Magnusson, 2003; Putz et al., 2001). Similarly, prey species may either benefit from increased protective cover due to understory regrowth or suffer from facilitated carnivore movement along logging roads (Di Bitetti et al., 2014). For any given species, the final outcome will depend on the relative importance and interactions of a wide range of effects.

Just as individual species responses represent the net outcome of all combined effects of logging on a given species, species richness responses represent the net outcome of all individual species responses combined. Our results show that negative responses predominate at increasing logging intensities, agreeing with a recent meta-analysis that highlighted logging intensity as a major predictor of mammal species richness (Burivalova et al., 2014). Still, the result is surprising given the generally low harvest rates, the adoption of RIL techniques and the fact that concessions are in a federal protected area. Furthermore, it contrasts with a number of studies reporting negligible effects of RIL on medium- to large-sized mammals in tropical forests (Azevedo-Ramos et al., 2006; Laufer et al., 2015; Lhoest et al., 2020; Magintan et al., 2017; Roopsind et al., 2017; Sollmann et al., 2017; Tobler et al., 2018). This disagreement may be related to differences in study design, particularly the fact that most of the aforementioned studies only compared logged and unlogged sites, treating logging as a uniform land use as they lacked spatially accurate data on tree harvest. Furthermore, some studies suffer from spatial and temporal sampling biases that may have limited their ability to detect logging effects (Laufer et al., 2013; Ramage et al., 2013). By using spatially accurate tree harvest data and by sampling sites distributed across a gradient of logging intensities interspersed in the landscape, we detected localized effects of logging that otherwise could have gone unnoticed. This suggests that logging effects are heterogeneous in the landscape and that the scale at which data is aggregated can affect study results.

Road density was positively related to site-level species richness. Roads are a prominent feature of logged landscapes and may have mixed effects on biodiversity. As linear forest clearings, they can be even more damaging than tree harvest, especially at low harvest levels (Asner et al.,

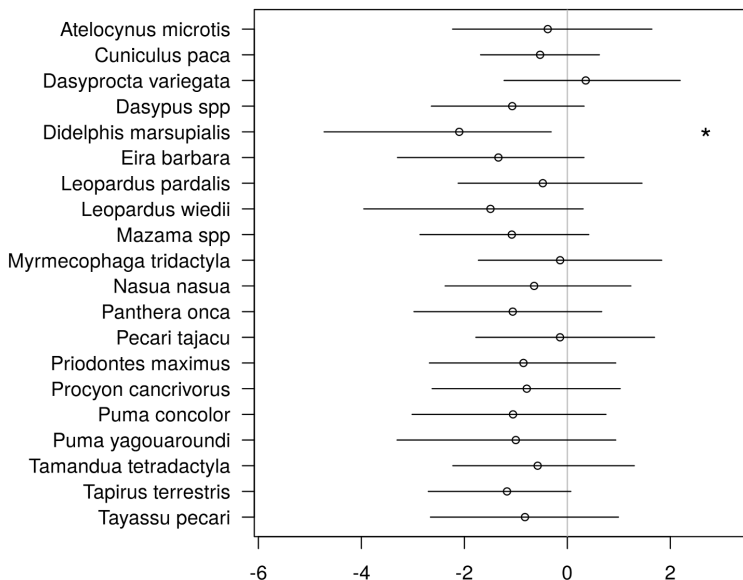


Fig. 3. Means and 95% credible intervals for the posterior distribution of logging status on species occupancies at the logit scale. The asterisk indicate a statistically significant relationship.

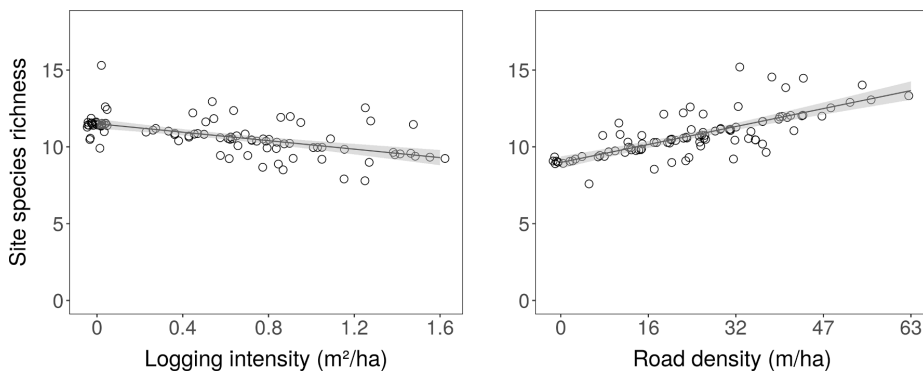


Fig. 4. Partial regressions for predictor variables and estimated site-level species richness at Jamari National Forest.

2004; Kleinschroth and Healey, 2017; Laurance et al., 2009). Furthermore, roads fragment habitat, disrupt soil and hydrology and facilitate secondary impacts, such as increased accessibility to hunters and settlers and invasion by alien species (Lhoest et al., 2020; Poulsen et al., 2011; Van Vliet and Nasi, 2008). However, in some cases species may benefit from roads. Carnivores are prone to use roads as movement corridors (Di Bitetti et al., 2014) and herbivores often benefit from the influx of regrowth, flowers and fruits along roadsides (Kleinschroth and Healey, 2017). The positive effect of road density observed here suggests that the concessions were successful in minimizing the negative effects of roads. The set of adopted measures include pre-harvest road planning, minimizing corridor length and width, deviating from large trees along routes, avoiding the damming of streams and blocking access to roads after harvest (Laurance and Edwards, 2014; Putz et al., 2008).

The increase in species richness at higher road densities did not result from the entry of additional non-forest species to the assemblage – although this may eventually happen. For example, the crab-eating fox

(*Cerdocyon thous*), a habitat generalist that thrives in disturbed forests has already been recorded at Jamari National Forest (Carvalho Jr, unpublished data) and is likely to benefit from the logging road network in the long-term. Similarly, roads may facilitate future invasion by exotic mammals, such as domestic dogs (*Canis lupus familiaris*) (Doherty et al., 2017) and black rats (*Rattus rattus*) (Loveridge et al., 2016).

#### 4.2. Occupancy and detection rates

As species richness was significantly affected by model predictors, it was expected that occupancy of at least some species would also be affected. However, surprisingly, only a single species responded significantly to logging status (logged or unlogged) and no species displayed significant responses to logging intensity and road density. Nevertheless, the direction of occupancy responses was generally consistent with that observed for site-level richness. For example, occupancy for all species was negatively, albeit non-significantly, related to logging status and to

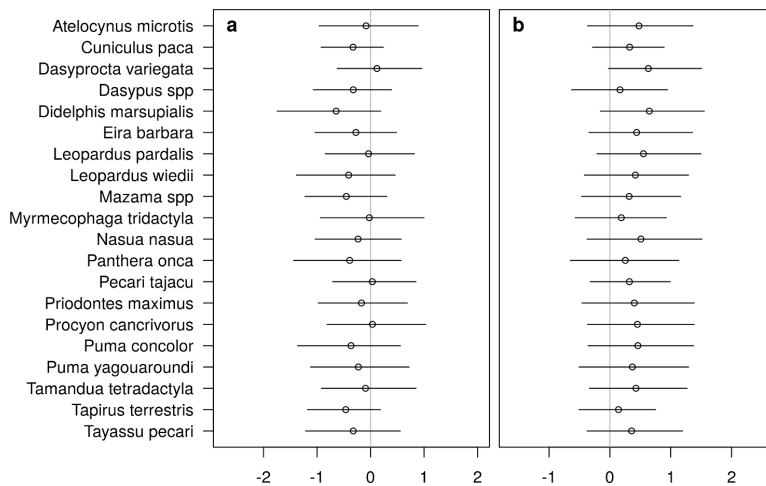


Fig. 5. Means and 95% credible intervals for the posterior distribution of predictor effects on species occupancies at the logit scale for (a) logging intensity and (b) road density.

logging intensity. Lower overall occupancy probabilities could translate to random species loss at logged sites. Alternatively, they could lead to deterministic loss if species respond to effects that are correlated with, but not fully captured by, logging intensity (e.g. changes in thermal environment, habitat structure or resource availability). In this case, the identity of missing species would vary depending on the relative importance of these effects at a given site. A similar reasoning applies to road density, which had a positive, albeit non-significant, effect on the occupancy of most species that was consistent with their positive effect on site-level richness.

As observed for occupancy, detection rates were not significantly related to any predictor (apart from one exception). However, detection for most species tended to be positively, albeit non-significantly, related with road density and Julian date. Since sampling followed a standardized protocol aimed to minimize differences between sites as much as possible, variation in detectability is likely to be related to variation in abundance (McCarthy et al., 2013; Parsons et al., 2017) or activity levels (Neilson et al., 2018). Further studies may help to clarify the relative role of these factors in modulating detection responses in the study area.

#### 4.3. Recommendations

The literature already contains a wealth of recommendations for minimizing logging impacts in tropical forests (Pinard et al., 1995; Putz et al., 2008; Sist, 2000). Our study reaffirms the relevance of commonly proposed measures, such as reducing collateral damage and infrastructure and keeping harvest levels as low as possible (Bicknell et al., 2014; Burivalova et al., 2014; Martin et al., 2015). However, minimizing harvest levels will always be constrained by a trade-off with profitability. At Jamari, logging intensities are already very low so that reducing them even further is unlikely to be feasible. In such cases, the next best alternative is to minimize collateral damage from tree felling and infrastructure.

In terms of infrastructure, roads are a major source of direct and indirect logging impacts (Kleinschroth and Healey, 2017; Laurance et al., 2009). Our results suggest that the concessions at Jamari succeeded in mitigating negative impacts of roads, at least in the short-term. Yet, the situation is liable to change and roads can easily go on to have negative effects in the future. A particular threat is the risk of invasion by hunters, illegal loggers and settlers. We reinforce the need to block access to roads in the long-term (Bicknell et al., 2015a).

There is a debate in the literature about how to best manage forest concessions at the landscape scale. The land-sharing approach advocates low-level exploration throughout the entire concession. Land-sparing argues for sparing a part of the concession from logging activities as a conservation set-aside, while performing higher-intensity logging on the remaining area so that extraction levels are maintained (Edwards et al., 2014b; Montejo-Kovacevich et al., 2018). Our results are insufficient to clarify which of these strategies would be the best, as the study setting corresponds to an intermediate strategy between these two extremes. In some respects, the Jamari concessions resemble a case of land-sparing as APUs are embedded in a continuous forest landscape and they include not only patches destined for logging, but also safe-havens set aside for protection (e.g., areas of permanent protection alongside streams). The higher biodiversity levels observed in unlogged areas points to benefits from a land-sparing approach, where source-sink dynamics can override localized negative effects of logging. Yet, most sites within the concessions at Jamari were harvested at moderate intensities and thus resemble land-sharing. The clear negative relationship observed between logging intensities and biodiversity levels suggests that moderate to low harvest levels throughout the landscape can maintain biodiversity and avoid drastic species loss. However, further investigations are needed to clarify what would be the best logging strategy to maximise overall occupancy and species richness levels in our study region.

#### 4.4. Conclusions

We found that logging negatively affects mammal species richness in Amazonian concessions. However, effects were diffuse as no individual species or set of species were lost and all species were retained in the landscape. Surprisingly, we found a positive effect of logging roads on mammal biodiversity, although this may be a precarious balance as roads are a constant liability, especially in relation to secondary impacts related to human intrusion. We conclude that forest concessions managed under RIL techniques may represent a reasonable compromise between economic and conservation interests.

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### CRediT authorship contribution statement

**Eildo A.R. Carvalho:** Conceptualization, Investigation, Writing - original draft. **Samuel S. Nienow:** Conceptualization, Investigation, Writing - review & editing. **Paulo H. Bonavigo:** Investigation, Writing - review & editing. **Torbjørn Haugaasen:** Supervision, Writing - review & editing.

### Declaration of Competing Interest

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

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### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119401>.

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1 **Supplementary material**

2

3 Table S1. Summary of camera-trap surveys conducted at Jamari National Forest in 2017 and 2018.

4

5 Table S2. Correlation matrix between predictor variables.

6

7 Table S3. Generalized linear model (GLM) results evaluating the relationship between logging  
8 intensity, recovery time and road density on site-level species richness at Jamari National Forest.

9

10 Figure S1. Number of times each mammal species was detected in each of 95 camera-trap sites.

11

12 Figure S2. Bayesian posterior distribution (n = 500 samples) of estimated size of the community of  
13 medium- to large-sized terrestrial mammals at Jamari National Forest. Mean estimated species  
14 richness was 23

15

16 Figure S3. Means and 95% credible intervals for the posterior distribution of predictor effects on  
17 species detection at the logit scale for model 1: (a) treatment (unlogged vs logged), (b) Julian date.

18

19 Figure S4. Means and 95% credible intervals for the posterior distribution of predictor effects on  
20 species detection at the logit scale for model 2: (a) logging intensity, (b) road density, (c) Julian  
21 date. The asterisks indicate a statistically significant relationship.

22

23 Table S1. Summary of camera-trap surveys conducted at Jamari National Forest in 2017 and 2018.

Year	Logged status		Mean effort per site (days)	Effort range (days)
	Unlogged	Logged		
2017	17	30	48.9	34-63
2018	12	36	38.8	13-64

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25

26 Table S2. Correlation matrix between predictor variables.

	Intensity 500 m	Roads 500 m
Intensity 500 m	1	
Roads 500 m	0.39	1

27

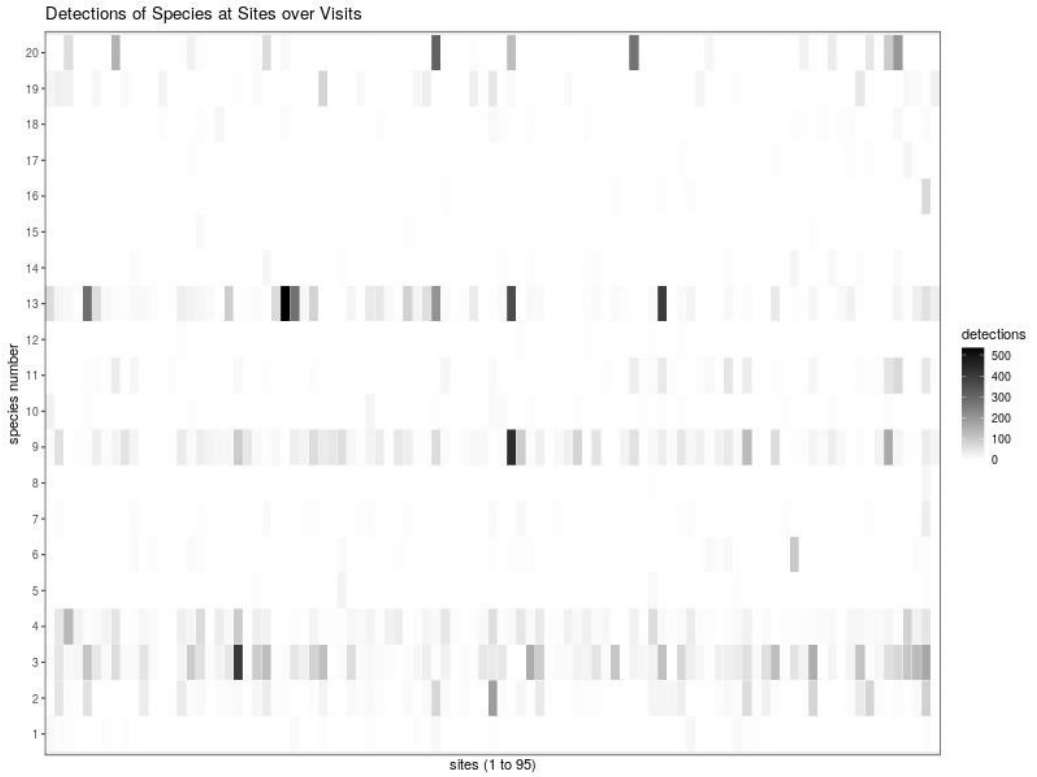
28

29 Table S3. Generalized linear model (GLM) results evaluating the relationship between logging  
30 intensity, recovery time and road density on site-level species richness at Jamari National Forest.

Response/Covariate	Estimate	SE	<i>p</i>	pseudo R <sup>2</sup>
<b>Global</b>				0.54
Intercept	10.7	0.1	<0.01	
Logging intensity	-0.7	0.1	<0.01	
Road length	1.1	0.1	0.01	

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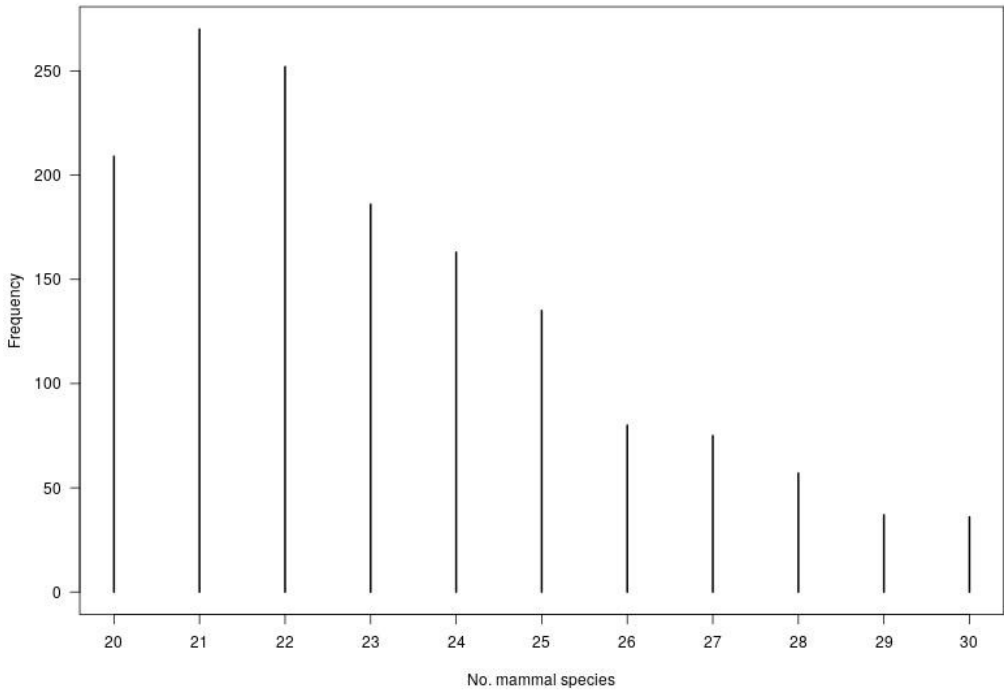


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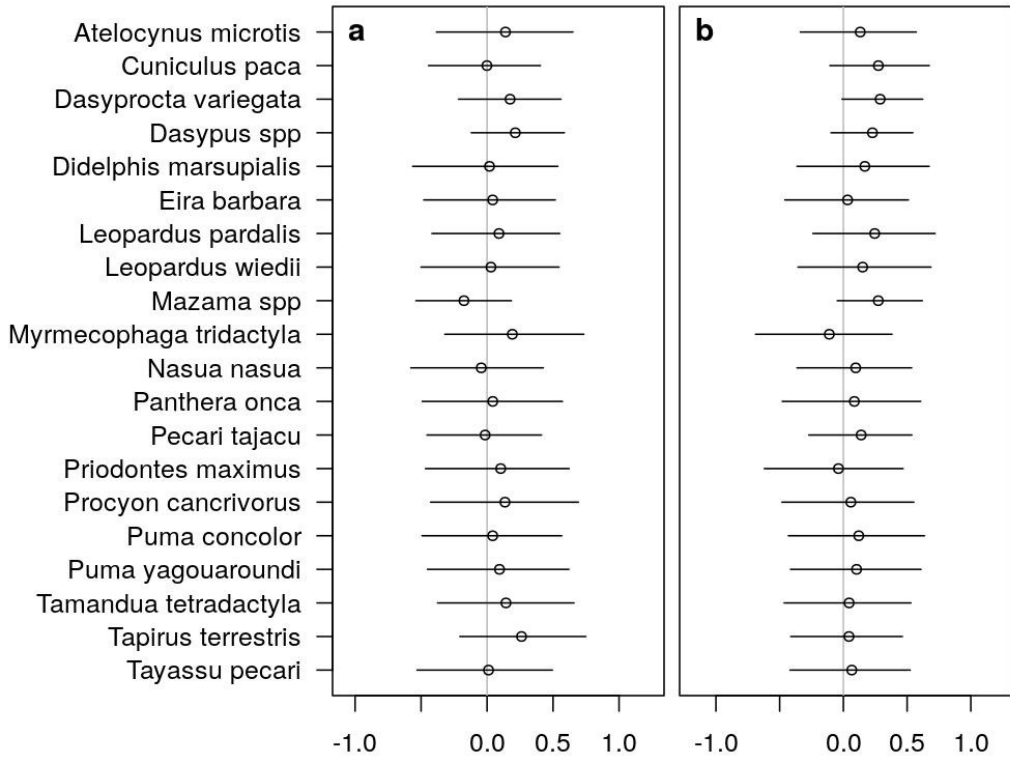


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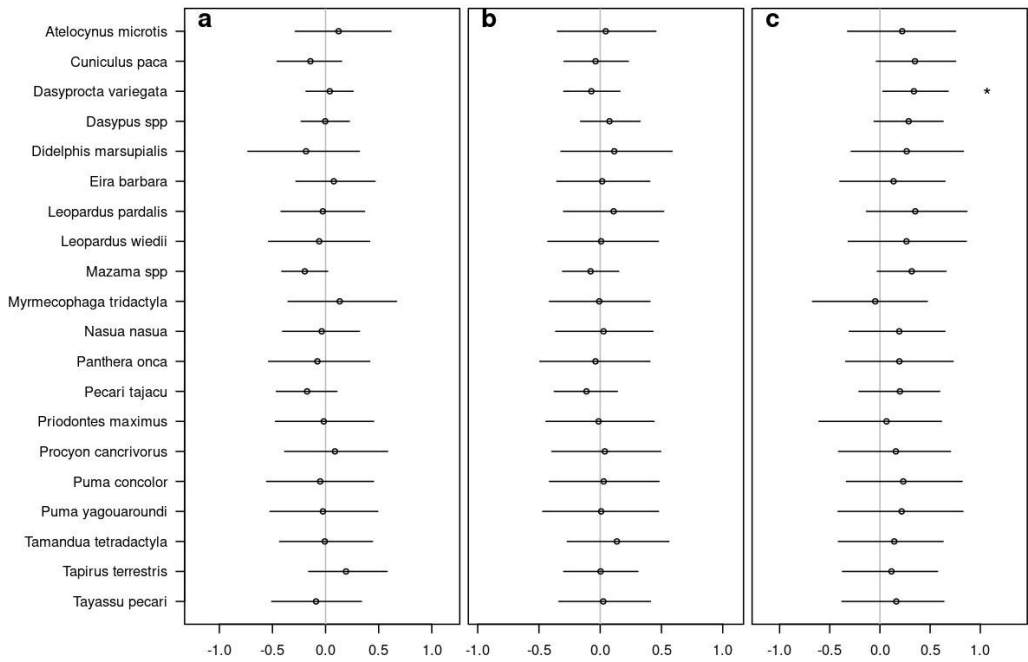


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53 species detection at the logit scale for model 2: (a) logging intensity, (b) road density, (c) Julian

54 date. The asterisks indicate a statistically significant relationship.



# Paper II





## Effects of illegal logging on Amazonian medium and large-sized terrestrial vertebrates

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### ABSTRACT

Selective logging is a major form of land use in tropical rainforests, with more than half of the world's tropical forest already explored. In the Brazilian Amazon, most logging operations are illegal and highly damaging to forests. However, the effects of illegal logging on wildlife are poorly studied. Here we investigate the effects of illegal logging on the assemblage of medium- to large-bodied terrestrial vertebrates at the Gurupi Biological Reserve, a protected area in extreme eastern Amazonia that has been subjected to three decades of illegal logging. We used camera traps to survey the terrestrial vertebrate assemblage and visual interpretation of Landsat time series data (1984–2016) to assess the history of illegal logging (number of logging bouts and recovery time) for each camera trap site. Hierarchical Modelling of Species Communities (HMSC) indicates that logging had a minor effect on both the assemblage composition and individual species abundance. At the local level, the study demonstrates that the reserve effectively safeguards a significant portion of the regional biodiversity even though it suffered degradation by illegal logging. At a wider scale, the results suggest that illegally logged forests can retain much of their conservation value, if they are protected from further anthropogenic impacts such as hunting, fragmentation and fires. However, our study represents a best-case scenario, unlikely to be met in most other illegally logged areas in the tropics, where logging is usually followed by secondary effects that amplify its impacts.

### 1. Introduction

Selective logging is a major form of land use in tropical rainforests. To date, at least half of the world's tropical forests have already been selectively logged or are targeted to be logged in the near future (Asner et al., 2009; Blaser et al., 2011), and the global demand for tropical timber continues on the rise (Sloan and Sayer, 2015). Logging degrades forests, affecting their composition, structure and microclimate, and usually brings in its wake secondary anthropogenic effects, such as colonization, hunting and increased vulnerability to forest fires (Foley et al., 2007; Nepstad et al., 1999). In many regions, logging is a prelude to deforestation (Asner et al., 2006; Shearman et al., 2012). However, logging also generates jobs and revenue and recent evidence suggest that logged forests retain similar ecosystem services and much of the biodiversity found in undisturbed forests (Clark et al., 2009; Edwards et al., 2014; Gaveau et al., 2013; Putz et al., 2012).

In Amazonia, selective logging is a rapidly expanding industry. The area affected by logging in Amazonia is now equivalent in magnitude to the total deforested area (Asner et al., 2006) – at least 20 percent of the region is currently exploited for timber (Asner et al., 2005; Piponi et al., 2019). However, more than half of all logging in the Brazilian Amazon is illegal (Contreras-Hermosilla et al., 2007; Hirschberger, 2008; Smith, 2004). Illegal logging refers to logging that violates laws and regulations concerning the felling of trees (Pacheco et al., 2016). Illegal logging tends to be more damaging than legal operations, as more trees are harvested, are felled with little concern for mitigating collateral damage, and return cycles are often shorter (Putz et al., 2008; Ravenel and Granoff, 2004). As a result, a considerable portion of timber harvest operations in the region are highly damaging to the canopy, leaving forests susceptible to drought and fires (Asner et al., 2006).

There is a rich literature on vertebrate responses to selective logging

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(e.g., Burivalova et al., 2014; Johns, 1992; Meijaard et al., 2005), and studies suggest that medium- and large-bodied vertebrates in general are resilient to its most direct effects (e.g., Barlow et al., 2006; Burivalova et al., 2014; Clark et al., 2009; Johns, 1992; Meijaard et al., 2005; Samejima et al., 2012). However, most studies to date have been conducted in areas subjected to reduced-impact logging (e.g., Azevedo-Ramos et al., 2006; Bicknell and Peres, 2010; Tobler et al., 2018), or in legally logged areas, where at least a minimum of environmental standards are followed. Little is known about wildlife responses in illegally logged areas (Arcilla et al., 2015), perhaps because the activity often occurs in contested, violent areas, where field research is difficult (Asner et al., 2005).

Extreme eastern Amazonia is one of the oldest frontiers in the biome and is home to a major cluster of logging centres (Celentano et al., 2017; Nepstad et al., 1999). The region has been subjected to some of the highest logging intensities observed in the Amazon (Asner et al., 2006), with massive collateral damage (Asner et al., 2004). Loggers often revisit the same forests multiple times, harvesting the most valuable species during their first visit and returning later for the less valuable species as timber markets develop (Holdsworth and Uhl, 1997; Nepstad et al., 1999; Uhl et al., 1991). Repeated logging is highly damaging to forests because the infrastructure created during previous extractions is rarely reused (Gerwing, 2002). When regional forest resources become exhausted, illegal loggers often turn to protected areas and indigenous lands for new sources of timber (Pedlowski et al., 2005). This was the case at Gurupi Biological Reserve, the largest protected area in the region, which has been illegally explored for three decades (Celentano et al., 2017; Martins and Oliveira, 2011). Recently, strategic enforcement succeeded to expel illegal loggers from some sectors of the reserve (Mendonça, 2016), creating an opportunity to investigate the effects of illegal logging on the vertebrate fauna.

In this study, we investigate the effects of illegal logging on the assemblage of medium- to large-sized terrestrial vertebrates at the Gurupi Biological Reserve in extreme eastern Amazonia. Specifically, we evaluate how much variation in the assemblage can be attributed to the effect of illegal logging, after controlling for the potentially confounding effects of edges and fires, and how species respond individually to these variables. We also evaluated if species responses to logging are influenced by taxonomic class, body size and feeding guild.

## 2. Methods

### 2.1. Study area

The Gurupi Biological Reserve is a 270,000 ha protected area located in extreme eastern Amazonia (Fig. 1). Climate is tropical monsoonal with mean annual temperatures > 26 °C and mean annual rainfall of 1800 mm (Alvares et al., 2013; IBAMA, 1999). The terrain is mostly flat to undulated, with elevation ranging from 51 to 340 m a.s.l. The reserve was originally entirely covered by mature evergreen tropical forest, but deforestation for cattle ranching and agriculture in the last three decades led to a 30% loss in forest cover (Celentano et al., 2017; de Hessel and Lisboa, 2015). Furthermore, significant portions of the reserve have been degraded by illegal logging and fires (Martins and Oliveira, 2011). We conducted the study in the northern sector of the reserve, an area dominated by forest, but harbouring some active cattle farms. This sector was illegally explored for timber from 1990 until 2011, when the establishment of a permanent guard post in a strategic location led to the complete cessation of logging and a significant decrease in the movement of unauthorized people. In other parts of the reserve, logging, hunting and other illegal activities still occur (Mendonça, 2016). The reserve is occasionally affected by forest fires, generally localized in extent. However, in the dry season of 2015 the reserve was affected by a massive forest fire that burned approximately half of its area, including significant portions of the northern sector. However, the area where this study was conducted was largely spared

from the fires.

### 2.2. Vertebrate survey

Fieldwork was conducted from August to October 2017 (dry season). We sampled the vertebrate assemblage at Gurupi with camera traps, using the standardized Tropical Ecology Assessment and Monitoring (TEAM) protocol for terrestrial vertebrates (Jansen et al., 2014). We deployed 61 cameras equipped with passive infrared sensors (Bushnell Trophy Cam) in two regular arrays with a density of one camera per 2 km<sup>2</sup> (Fig. 1). The two arrays were located in predominantly unburned forest, although a few camera sites had been burned. We attached cameras to trees at a height of 30–45 cm, perpendicular to the ground and facing either north or south to avoid direct sunlight at sunrise and sunset and we cleared the vegetation directly in front of the cameras. Cameras operated continuously and simultaneously 24 h a day for 62 days, amounting to a total effort of 3782 camera trap days. We processed images in the wild.ID software (Fegraus et al., 2011), following the IUCN Red List as a taxonomic authority. We assumed a 60 min interval for independence between detection events. Since our focus was on medium- to large-sized ground-dwelling birds and mammals amenable to camera trap surveys, we excluded reptiles, passerine birds, primates and species with less than 200 g of adult body mass from the analysis, as well as rare species, defined as the species recorded in less than 5% of the sampling units. Tinamids and species of the genera *Dasyus* and *Penelope* were pooled as single groups for the analysis. The complete list of recorded species is available in the [Supplementary Material](#) (Table A2).

### 2.3. Environmental covariates

We selected two variables to represent the effects of logging (number of logging bouts and recovery time) and two additional covariates for controlling the confounding effects of edges and fires (proportion of deforested area and proportion of burned trees at each camera trap station). We did not include a covariate for hunting pressure, which is often a confounding factor in logging studies (Laufer et al., 2013; Roopsind et al., 2017), because human population density in the study area is low (a few ranch hands), movement of unauthorized people was limited, and the nearest settlement was > 10 km away. A previous study in the Gurupi Biological Reserve reported moderate to low levels of hunting (Lopes and Ferrari, 2000).

We used Landsat time series data (1984–2016) to recover the history of logging in the study area. Evidence of logging, including roads, log decks and large canopy gaps, are detectable in Landsat imagery, often for more than one year after logging, allowing the identification of logged areas through visual interpretation (Asner et al., 2009, 2002; Matricardi et al., 2007; Meijaard et al., 2014; Stone and Lefebvre, 1998). We used the USGS Earth Explorer interface (<http://earthexplorer.usgs.gov>) to download Landsat images from every year of the series, selecting, whenever possible, cloudless images from dry season months (Suppl. Mat. Table A1 and Fig. A1). For each camera trap and for each year in the series, we recorded the presence or absence of visible signs of logging within 500 m buffers centred on camera trap locations. If a logging scar persisted for more than one year, we only considered the first year in which it appeared. If a camera site was obscured by clouds in a given year, we used the spatial context (information from the surrounding area) or images from the preceding and following years to evaluate if logging could have happened in the year of interest. By following this procedure, we estimated the number of different years in which each camera buffer zone was logged (number of logging bouts), and the number of years elapsed since each camera buffer zone was logged for the last time (recovery time). For unlogged sites, we set maximum recovery time as 33 years, corresponding to the start of the time series.

As an index of edge effects, we used the proportion of deforested

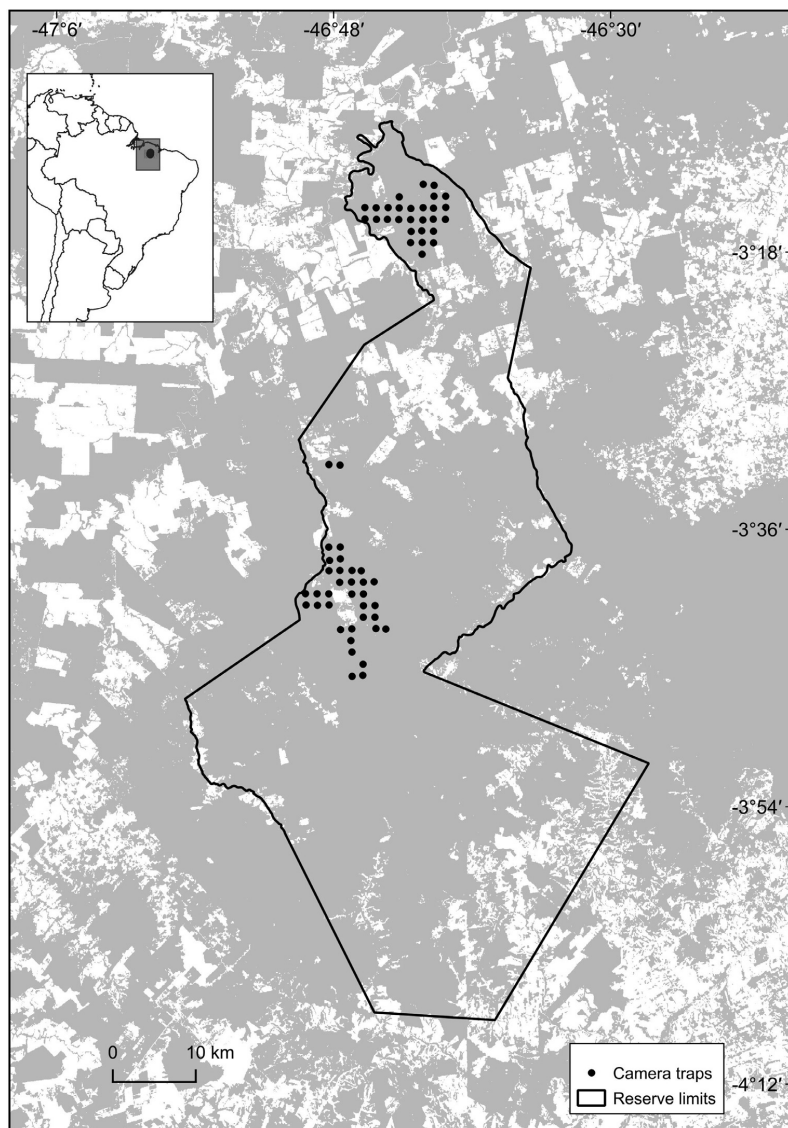


Fig. 1. Map of the Gurupi Biological Reserve, showing the distribution of camera trap stations. Grey colour in the background corresponds to forest cover in 2017 (source: MapBiomias, <http://mapbiomas.org>).

area within 500 m buffers centred on camera locations. We used the 30 m resolution land use and land cover classification of the MapBiomias monitoring system (<http://mapbiomas.org>) for the year 2017. We used the zonal statistics tool of the QGIS software (QGIS Development Team, 2018) to estimate the proportion of non-forest areas in the buffer areas.

As an index of fire effects, we estimated the proportion of burned trees in the vicinity of each camera trap station. Trees were sampled with the point-centred quarter method (Cottam and Curtis, 1956). Starting from each camera location, we ran three 50 m transects, in the direction of 0, 120 and 240 magnetic degrees. Along each transect, we established five sampling points at 10 m intervals. At each sampling

point, we divided the surrounding area into four 90° quarters. For each quarter we recorded if the trunk of the nearest tree with diameter at breast height  $\geq 10$  cm was burned or unburned. In a few cases, the same tree was nearest to quarters from more than one sampling point (1.7% of 3660 quarters). In these cases the tree was tallied only once. The mean number of trees tallied per camera trap station was 58.95.

#### 2.4. Data analysis

We analysed community data using the Hierarchical Modelling of Species Communities (HMSC, (Ovaskainen et al., 2017)). The advantage of this approach is that it allows the simultaneous assessment

of responses at assemblage and species levels, incorporating in a single model the effects of environmental predictors, random factors and spatial distances across a range of taxa. In addition, the model assesses the influence of species traits on their responses to environmental covariates, and by using the residual correlation between species, after controlling for the environmental variables, we can evaluate their association patterns.

HMSC is a hierarchical generalised linear mixed model that views the observed assemblage as the end product of environmental, biotic and neutral filters operating at different scales (Ovaskainen et al., 2017). In our model, the observed assemblage was represented by the number of independent records of each species at each camera-trap station. The filters (predictors) were the logging, edge and fire covariates, and the spatial random effects was the spatial coordinates of sampling sites. To assess if species responses to covariates were affected by their traits, we classified species according to taxonomic class (Aves or Mammalia), log of adult body mass (based on (Haugaasen and Peres, 2008; Paglia et al., 2012)), and feeding niche: herbivore, omnivore or animalivore (based on (Beaudrot et al., 2016 and Voss et al., 2001)).

We fitted the model using Bayesian inference with the package HMSC-R 2.0 (Norberg et al., 2018). We used the Poisson model with default prior distributions, running 150,000 Markov Chain Monte Carlo (MCMC) iterations with a 50,000 burn-in phase and a thinning factor of 100. We evaluated parameter convergence by visual inspection of MCMC trace plots. We assessed the explanatory power of the model with Nakagawa's  $R^2$  (Nakagawa and Schielzeth, 2013), and assessed the relative importance of fixed and random factors by variance partitioning (Ovaskainen et al., 2017). We considered that there was statistical support for a covariate effect when the 95% credible interval of the estimated parameter did not include zero. We assessed the residual correlation between species (after accounting for the covariate effects) to evaluate if species are responding to one another or to unmeasured environmental factors (Warton et al., 2015). Finally, we evaluated the effect of spatial and environmental distance on assemblage similarity (Pearson's correlation coefficient) by decomposing the distance decay in assemblage similarity (Soininen et al., 2007).

### 3. Results

#### 3.1. Species records

We obtained 23,824 animal photos, corresponding to 1702 independent records of 27 bird and mammal species. Twenty-three species met the criteria for inclusion in the analysis (Table 1): 18 mammals (six carnivores, five ungulates, four xenarthrans, two caviomorph rodents and one marsupial) and five birds (two cracids, one psophiid, one odontophorid, and tinamids grouped as a single entity).

#### 3.2. Covariates

Visual interpretation of Landsat imagery revealed that all sites (camera trap buffer zones) except one were logged at least once since the first year of the time series. Apart from two sites logged in 1990, all logging in the study area occurred between 1996 and 2011. The number of different years with evidence of logging per site ranged from one to five (mean = 2.12, SD = 1.16) and recovery time since the last year with logging ranged from six to 21 years (mean = 12.8, SD = 4.6). Only six camera trap locations had deforestation within their 500 m buffers. The mean percentage of deforested area within buffers was 0.6% (SD = 2.33), ranging from zero to 13.3%. Similarly, most camera sites were little affected by fires. Eleven sites (11%) had no burned trees and another 33 (55%) had one to three burned trees, only 16 sites had more than four burned trees. The mean percentage of burned trees for all sites was 4.3% (SD = 4.5), ranging from zero to 21.6%.

**Table 1**

Percent of the explained variance of species occurrence attributable to fixed and random effects, and model  $R^2$  values for each species.

Species	Logging bouts	Recovery time	Edges	Fire	Spatial random effects	$R^2$
Aves						
<i>Odontophorus gujanensis</i>	18	26	17	26	14	6.37
Tinamids	25	16	23	13	22	0.21
<i>Mitu tuberosum</i>	2	38	27	07	08	9.20
<i>Penelope</i> spp.	29	2	27	11	13	6.53
<i>Psophia obscura</i>	2	24	17	22	17	2.18
Mammalia						
<i>Didelphis marsupialis</i>	2	17	17	35	12	6.14
<i>Dasyops</i> spp.	17	15	24	12	33	0.32
<i>Priodontes maximus</i>	18	34	14	21	13	3.61
<i>Myrmecophaga tridactyla</i>	16	13	3	13	28	3.67
<i>Tamandua tetradactyla</i>	16	3	17	23	14	4.48
<i>Cuniculus paca</i>	2	27	21	1	22	2.01
<i>Dasyprocta prymnolopha</i>	13	09	12	11	55	0.19
<i>Mazama americana</i>	25	22	18	18	17	0.22
<i>Mazama nemorivaga</i>	28	28	16	14	15	3.77
<i>Pecari tajacu</i>	15	36	14	14	21	1
<i>Tayassu pecari</i>	33	11	29	16	11	4.48
<i>Tapirus terrestris</i>	18	43	09	05	25	1.09
<i>Nasua nasua</i>	23	2	32	11	13	10.69
<i>Eira barbara</i>	16	14	34	18	18	4.12
<i>Leopardus pardalis</i>	25	24	16	16	19	2.93
<i>Leopardus wiedii</i>	15	25	24	24	12	6.32
<i>Panthera onca</i>	27	18	11	33	12	8.76
<i>Puma concolor</i>	19	28	13	25	16	3.38
Mean for all species	21	23	2	17	19	4.07

#### 3.3. Model results

The explanatory power of the HMSC model at the community level was low ( $R^2$  averaged over species = 4.1%). For individual species, model performance varied widely, with the model explaining between 0.1 and 11 percent of species abundances (Table 1). There was a negative and significant relation between mean species abundances and the explanatory power of the model (GLM,  $p = 0.02$ , Suppl. Mat. Fig. A2).

Considering only the explained variance, variance partitioning revealed that fixed effects captured most (81.4%) of the variance averaged over species (Table 1). Together, the logging covariates captured 44% of the explained variation, followed by edges (20%) and fires (17.3%). Spatially structured random effects accounted for 18.6% of the variance. There was strong statistical support for effects of individual covariates for two species (Fig. 2): the Lowland Tapir (*Tapirus terrestris*) responded positively to recovery time, and the Razor-billed Curassow (*Mitu tuberosum*) responded positively to the proportion of deforested area within the buffer and to recovery time. Traits explained only 15% of species responses to measured covariates, with no individual trait displaying a significant response (Suppl. Mat. Fig. A3).

Community composition was similar across most sites and there was only a slight distance decay in similarity. This was the case considering spatial distances alone and when accompanied by environmental covariates (Suppl. Mat. Fig. A4). The species-to-species association plot shows strong associative patterns between most species after accounting for the effects of covariates (Fig. 3). Most associations were positive, with the majority of species forming a large co-occurring

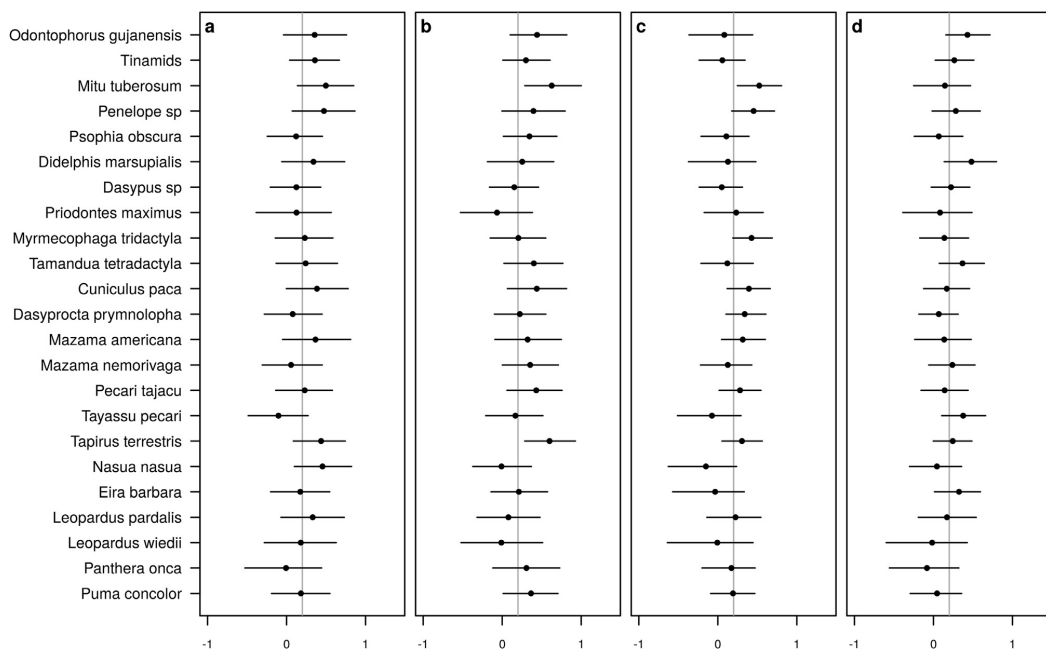


Fig. 2. Posterior distribution of  $\beta$  parameters (responses of species to covariates). Points represent means and lines the 95% credible interval of parameters. (a) Number of logging bouts; (b) Recovery time since last logging bout; (c) Edges (proportion of deforested area within buffer); (d) Fires (proportion of burned trees around camera trap).

group that included most birds, xenarthrans, and small carnivores. A second, smaller group, comprised species that tended to occur together, but not with the first group. This included the two peccaries, the two larger cats and the trumpeter *Psophia obscura*. Finally, a few species such as *Mazama americana* and *Leopardus wiedii* appear to occur independent of the others.

#### 4. Discussion

##### 4.1. Vertebrate responses to logging

Illegal logging appears to have had a minor role in structuring the medium- to large-sized terrestrial vertebrate assemblage at Gurupi Biological Reserve, as the explanatory power of our model was very low. This is consistent with previous studies reporting resilience of terrestrial tropical vertebrates to selective logging, in Amazonia (e.g., Azevedo-Ramos et al., 2006; Bicknell and Peres, 2010; Roopsind et al., 2017; Tobler et al., 2018) and elsewhere (e.g., Edwards et al., 2011; Meijaard and Sheil, 2008; Putz et al., 2012). A possible explanation for this is that several of these tropical forest vertebrates, especially mammals, are ecologically flexible, which could make them resilient to moderate disturbance levels (Gibson et al., 2011). For example, most Neotropical mammals belonging to this guild have wide geographic distributions and occur in different types of natural vegetation (Redford and da Fonseca, 1986), as well as in disturbed sites such as secondary forests and edges (Norris et al., 2008; Parry et al., 2007). Therefore, one would expect them to be resilient to structural habitat changes caused by logging (Arévalo-Sandi et al., 2018; Gibson et al., 2011) that to a certain extent resemble natural disturbances, such as treefall gaps or riparian edges, which cover significant portions of the Amazon basin (Junk, 1993; Uhl and Vieira, 1989).

A growing body of literature suggests that secondary effects of selective logging, such as human colonization and increased hunting

pressure, edge area and fire risk, are more deleterious to biodiversity than the direct effects of logging (Brodie et al., 2015; Pfeifer et al., 2017; Zimmerman and Kormos, 2012). In the present study, however, secondary effects were relatively unimportant. Few camera trap sites were affected by edges and fires, and hunting pressure was likely insignificant (e.g., we never heard gunshots of found shotgun shells during fieldwork). In part, this reflects the fact that the study was conducted in core forest areas of the reserve that were less affected by human impacts. Furthermore, the establishment of a checkpoint on a major access road in 2011 (Mendonça, 2016) led to the complete cessation of logging and reduced the movement of unauthorized people in the northern sector of the reserve, further reducing secondary effects. In other parts of the reserve, however, law enforcement is weaker and secondary effects are likely to be more prevalent.

Species responses to disturbance are influenced by the landscape context (Vetter et al., 2011). At Gurupi, the continuous nature of the forest matrix probably attenuated site-level effects of illegal logging, by providing short-term refuges for wildlife during logging operations, and sources of recolonization after disturbance (Gilroy and Edwards, 2017; Laufer et al., 2015; Samejima et al., 2012). The same would not occur had the forest been fragmented. In isolated forest patches, the effects of logging, edges, fires and hunting are amplified and the recovery potential of small, isolated populations is low (Barlow et al., 2006; Michalski and Peres, 2007; Peres, 2001).

There are other potential explanations for the negligible effect of illegal logging in this study. First, all sampling sites except one have been logged at least once, meaning that there was no unlogged control in this study. It may be that logged sites differ from pristine areas but not from each other, despite differences in the number of logging bouts or recovery time. Furthermore, we did not measure logging intensity, which is an important predictor of logging effect on vertebrates (Burivalova et al., 2014). Unfortunately, this kind of information was unavailable. There were no records of extraction levels, since logging

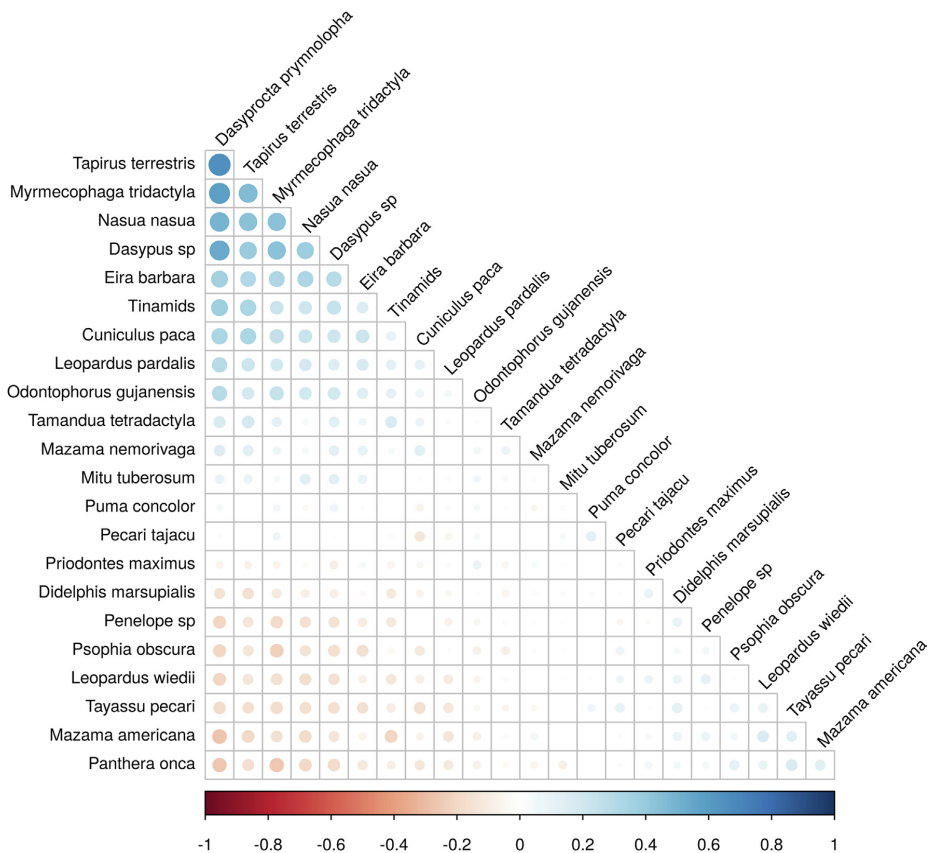


Fig. 3. Species-to-species associations measured by correlation matrix, after accounting for the effect of covariates. Negative associations are displayed in red, and positive ones in blue. Only associations with a posterior probability above 95% are coloured. Species were ordered to optimize visualization of association clusters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was conducted illegally. In addition, visual interpretation of Landsat imagery is useful to identify logged areas, but it has limited value for estimating site-level damage (Asner et al., 2004, 2002).

There was statistical support for effects of covariates for only two species. Lowland Tapir (*Tapirus terrestris*) responded positively to recovery time. This is unexpected, as tapirs can benefit from logging, probably by taking advantage of the increased availability of understorey vegetation in recently disturbed areas (Fragoso, 1991; Roopsind et al., 2017; Tobler et al., 2018). On the other hand, tapirs are sensitive to hunting (Peres and Palacios, 2007), so the positive response to recovery time could be related to recovery from past hunting by loggers during logging operations. However, previous studies in the area reported light hunting pressure (Lopes and Ferrari, 2000) and loggers were also absent in the six years prior to the study, implying that there was enough time for the species to redistribute throughout the area and recolonize zones depleted due to hunting. Yet, the  $R^2$  value for this species was very low (1.1%), meaning that recovery time explains little of the observed distribution of this species. Razor-billed Curassow (*Mitu tuberosum*) responded positively both to recovery time and to edges. The positive response to recovery time is consistent with the reported preference of this species for closed-canopy, mature forests (Michalski and Peres, 2017), although previous studies have reported a neutral or slightly positive response to logging (Azevedo-Ramos et al., 2006; Michalski and Peres, 2017). The positive response to edges appears to

be at odds with a preference for closed forests. However, the species is also frequently found along river margins (Barros et al., 2011), so it may benefit from forest edges in some cases. More detailed studies are needed to elucidate the reasons for the observed responses of this species.

Species responses to environmental disturbances may be mediated by their traits (Edwards et al., 2014). For example, large-bodied species (Costantini et al., 2016), habitat or dietary specialists (Edwards et al., 2013) and members of certain feeding guilds (Gray et al., 2007; Vetter et al., 2011) tend to be more sensitive to disturbance. However, traits measured in this study were relatively unimportant in determining species responses. There are two main potential explanations for this result. Firstly, it may be that the trait measures adopted for the analysis, especially for feeding guilds, were too coarse. Assigning mammals and, to a lesser extent, birds, to precise feeding guilds is notoriously difficult as most species have significant dietary flexibility (Edwards et al., 2013; Voss et al., 2001). Secondly, since virtually no species responded to the covariates, there was not enough variation among species in their responses to allow a robust assessment of trait effects. Additional studies covering stronger gradients of disturbance and species responses may help to elucidate the role of traits in species sensitivity to disturbance.

Most sites were similar in community composition and distance decay in similarity was only slight. The high similarity between sites probably stems from the dominance of a few widespread species (e.g.,



*Dasyprocta prymnolopha*) and from overall community homogenization due to the combination of a highly mobile set of species with a continuous forest landscape that permitted free dispersal. The strong residual correlation found between most species after controlling for the effects of covariates, suggests that there are missing environmental factors and/or species interactions structuring the vertebrate assemblage.

#### 4.2. Considerations about the study setting

This study shows little effect of illegal logging on Amazonian wildlife. However, it represents a best-case scenario, unrepresentative of the conditions prevailing at most sites subjected to illegal logging in the tropics. The study was conducted in a protected area that, although subjected to illegal logging in the recent past, is currently under enforced protection. Mean recovery time at logged sites was more than a decade, longer than in most previous studies (Edwards et al., 2012) and probably enough for the recovery of the vertebrate assemblage (Brodie et al., 2015; Dent and Wright, 2009). Sampling sites were located in continuous forests with low hunting pressure, and most sites were spared from fires, including the severe fire event that burned half of the reserve in 2015. In most other settings conditions are likely to be worse, as logging, whether legal or illegal, is usually followed by increased deforestation and fragmentation, hunting and recurrent fires (Asner et al., 2006; Brodie et al., 2015; Nepstad et al., 1999). This is the situation for the area immediately around the Gurupi Biological Reserve. For example, to date more than 70% of the original forest cover in extreme eastern Amazonia has been lost, and less than 15% of what remains can be considered “core” forest (Vedovato et al., 2016). In addition, 70% of the remaining forests in the region are inside protected areas and indigenous lands, with the rest mostly in small, isolated forest fragments (Celentano et al., 2017). It is unlikely that vertebrate assemblages can cope in the long-term with logging and other sources of forest degradation in such a scenario (Barlow et al., 2016; Michalski and Peres, 2017, 2005).

Furthermore, although the species included in this study were mostly insensitive to logging, other local vertebrates, less amenable to be sampled with camera traps, may be more sensitive. For example, large frugivorous primates are vulnerable to breaks in canopy continuity and loss of key fruiting trees in logged areas (Johns and Skorupa, 1987; Parry et al., 2007). In this regard, Gurupi Biological Reserve is an important stronghold for two species of critically endangered primates, the Ka'apor Capuchin (*Cebus kaapor*) and the Black Bearded Saki (*Chiropotes satanas*) (Buss et al., 2013). Studies evaluating how these species respond to logging and other anthropogenic impacts in the reserve are needed.

#### 4.3. Conclusions

In summary, we found that illegal logging had a minor role in structuring the assemblage of medium- to large-sized terrestrial vertebrates at the Gurupi Biological Reserve. At the local level, this demonstrates that the reserve is effective in safeguarding a significant portion of the regional biodiversity even in the face of degradation by illegal logging. At the wider scale, these results suggest that illegally logged forests can retain much of their conservation value, if they are protected from further anthropogenic impacts such as hunting, fragmentation and fires. However, we recognize that the study setting represents a best-case scenario, unlikely to be met in most cases, at least in the Amazonian deforestation frontier. More studies will be needed to elucidate how wildlife respond to illegal logging at the typically unprotected sites that are usually affected by this activity.

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#### CRedit authorship contribution statement

**Eildo A.R. Carvalho:** Conceptualization, Investigation, Writing - original draft. **Eloisa Neves Mendonça:** Conceptualization, Investigation, Writing - review & editing. **Alexandre Martins:** Investigation, Writing - review & editing. **Torbjørn Haugeaasen:** Supervision, Writing - review & editing.

#### Declaration of Competing Interest

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

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#### Appendix A. Supplementary material

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## Appendix A

### Effect of illegal logging on mid-sized to large terrestrial vertebrates in eastern Brazilian Amazonia

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Logging roads and decks are clearly visible as light green on Landsat TM 5 imagery, as the exploration advances westward over the period. The white circles correspond to 500 m buffers centred on camera locations.

Figure A2. Species-specific  $R^2$  values plotted against mean species abundances.

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Figure A4. Decay in community similarity with spatial and environmental distance.

Table A1. USGS Earth Explorer Landsat datasets used for recovering logging history in the study area.

Year	path/row			
	222/62		222/63	
	Data set	Date	Data set	Date
1984	1-5 MSS C1 Level-1	1984-12-31	4-5 TM C1 Level-1	1984-06-18
1985	1-5 MSS C1 Level-1	1985-06-21	4-5 TM C1 Level-1	1985-06-21
1986	1-5 MSS C1 Level-1	1986-06-10	4-5 TM C1 Level-1	1986-07-10
1987	4-5 TM C1 Level-1	1987-10-17	4-5 TM C1 Level-1	1987-12-20
1988	4-5 TM C1 Level-1	1988-08-16	4-5 TM C1 Level-1	1988-08-16
1989	4-5 TM C1 Level-1	1989-06-16	4-5 TM C1 Level-1	1989-06-18
1990	4-5 TM C1 Level-1	1990-07-14	4-5 TM C1 Level-1	1990-11-10
1991	4-5 TM C1 Level-1	1991-05-21	TM (1984-1997)	1991-07-24
1992	4-5 TM C1 Level-1	1992-12-17	4-5 TM C1 Level-1	1992-12-17
1993	4-5 TM C1 Level-1	1993-05-10	4-5 TM C1 Level-1	1993-05-10
1994	4-5 TM C1 Level-1	1994-09-18	4-5 TM C1 Level-1	1994-04-16
1995	4-5 TM C1 Level-1	1995-06-19	4-5 TM C1 Level-1	1995-07-19
1996	4-5 TM C1 Level-1	1996-07-15	4-5 TM C1 Level-1	1996-07-05
		1997-02-14, 1997-		
1997	4-5 TM C1 Level-1	07-08	4-5 TM C1 Level-1	1997-02-14
		1998-06-25, 1998-		
1998	4-5 TM C1 Level-1	08-28	4-5 TM C1 Level-1	1998-08-28
1999	4-5 TM C1 Level-1	1999-07-14	4-5 TM C1 Level-1	1999-06-28
2000	4-5 TM C1 Level-1	2000-07-20	ETM+	2000-06-06
2001	4-5 TM C1 Level-1	2001-08-04	4-5 TM C1 Level-1	2001-08-04
2002	4-5 TM C1 Level-1	2002-06-28	Sys ETM + L1G	2002-06-28
2003	4-5 TM C1 Level-1	2003-10-05	4-5 TM C1 Level-1	2003-12-16
2004	4-5 TM C1 Level-1	2004-06-25	4-5 TM C1 Level-1	2004-10-15
2005	4-5 TM C1 Level-1	2005-06-14	Global Land Survey	2005-06-14

2006	4-5 TM C1 Level-1	2006-06-15	4-5 TM C1 Level-1	2006-16-15
2007	7 ETM+ C1 Level-1	2007-10-16	4-5 TM C1 Level-1	2007-08-0
2008	4-5 TM C1 Level-1	2008-10-10	4-5 TM C1 Level-1	2008-10-26
2009	4-5 TM C1 Level-1	2009-08-10	4-5 TM C1 Level-1	2009-07-09
2010	4-5 TM C1 Level-1	2010-09-14	4-5 TM C1 Level-1	2010-09-14
2011	7 ETM+ C1 Level-1	2011-09-25	4-5 TM C1 Level-1	2011-09-17
		2012-05-06, 2012-		
2012	7 ETM+ C1 Level-1	08-26	4-5 TM C1 Level-1	2012-10-13
2013	7 ETM+ C1 Level-1	2013-06-26	4-5 TM C1 Level-1	2013-10-16
2014	7 ETM+ C1 Level-1	2014-06-13	4-5 TM C1 Level-1	2014-10-19
2015	7 ETM+ C1 Level-1	2015-08-27	4-5 TM C1 Level-1	2015-06-16
2016	7 ETM+ C1 Level-1	2016-11-25	4-5 TM C1 Level-1	2016-10-07

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Table A2. List of vertebrate species recorded by camera traps at Gurupi Biological Reserve, number of independent records per species and number of sites where each species was recorded.

Class	Order	Family	Species	N records	N sites
Aves	Columbiformes	Columbidae	<i>Leptotila spp.</i>	3	1
Aves	Cuculiformes	Cuculidae	<i>Neomorphus geoffroyi</i>	1	1
Aves	Galliformes	Cracidae	<i>Mitu tuberosum</i>	37	16
Aves	Galliformes	Cracidae	<i>Penelope spp.</i>	19	16
Aves	Galliformes	Odontophoridae	<i>Odontophorus gujanensis</i>	22	15
Aves	Gruiformes	Psophiidae	<i>Psophia obscura</i>	48	19
Aves	Tinamiformes	Tinamidae	<i>Crypturellus</i> and <i>Tinamus</i> spp.	266	55
Mammalia	Carnivora	Canidae	<i>Canis lupus familiaris</i>	1	1
Mammalia	Carnivora	Canidae	<i>Cerdocyon thous</i>	10	1
Mammalia	Carnivora	Canidae	<i>Speothos venaticus</i>	2	2
Mammalia	Carnivora	Felidae	<i>Leopardus pardalis</i>	28	13
Mammalia	Carnivora	Felidae	<i>Leopardus wiedii</i>	4	4
Mammalia	Carnivora	Felidae	<i>Leopardus spp.</i>	11	7
Mammalia	Carnivora	Felidae	<i>Panthera onca</i>	12	9
Mammalia	Carnivora	Felidae	<i>Puma concolor</i>	21	17
Mammalia	Carnivora	Mustelidae	<i>Eira barbara</i>	24	16
Mammalia	Carnivora	Mustelidae	<i>Galictis vittata</i>	3	3
Mammalia	Carnivora	Procyonidae	<i>Nasua nasua</i>	80	32
Mammalia	Cetartiodactyla	Cervidae	<i>Mazama americana</i>	34	13
Mammalia	Cetartiodactyla	Cervidae	<i>Mazama nemorivaga</i>	26	15
Mammalia	Cetartiodactyla	Cervidae	<i>Mazama spp.</i>	268	51
Mammalia	Cetartiodactyla	Tayassuidae	<i>Pecari tajacu</i>	82	24
Mammalia	Cetartiodactyla	Tayassuidae	<i>Tayassu pecari</i>	61	24
Mammalia	Cingulata	Dasypodidae	<i>Cabassous unicinctus</i>	1	1
Mammalia	Cingulata	Dasypodidae	<i>Dasyopus spp.</i>	181	47
Mammalia	Cingulata	Dasypodidae	<i>Priodontes maximus</i>	6	5
Mammalia	Didelphimorphia	Didelphidae	<i>Didelphis marsupialis</i>	9	9
Mammalia	Perissodactyla	Tapiridae	<i>Tapirus terrestris</i>	172	41
Mammalia	Pilosa	Myrmecophagidae	<i>Myrmecophaga tridactyla</i>	49	25
Mammalia	Pilosa	Myrmecophagidae	<i>Tamandua tetradactyla</i>	21	18
Mammalia	Rodentia	Cuniculidae	<i>Cuniculus paca</i>	56	18
Mammalia	Rodentia	Dasyproctidae	<i>Dasyprocta prymnolopha</i>	747	66
Mammalia	Rodentia	Sciuridae	<i>Sciurus aestuans</i>	45	25

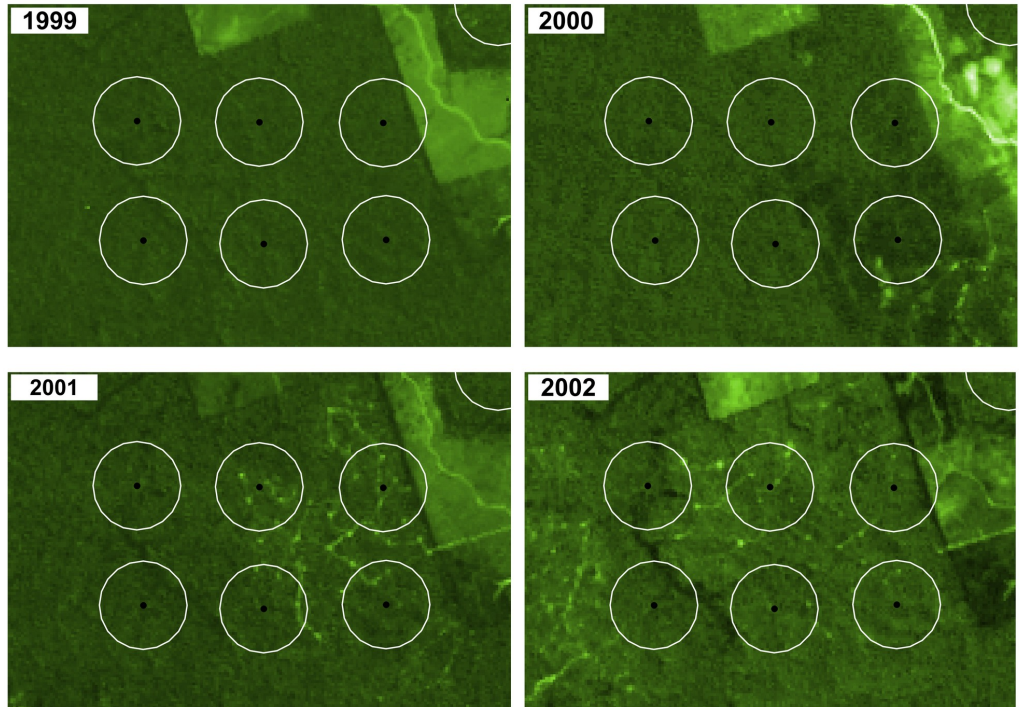


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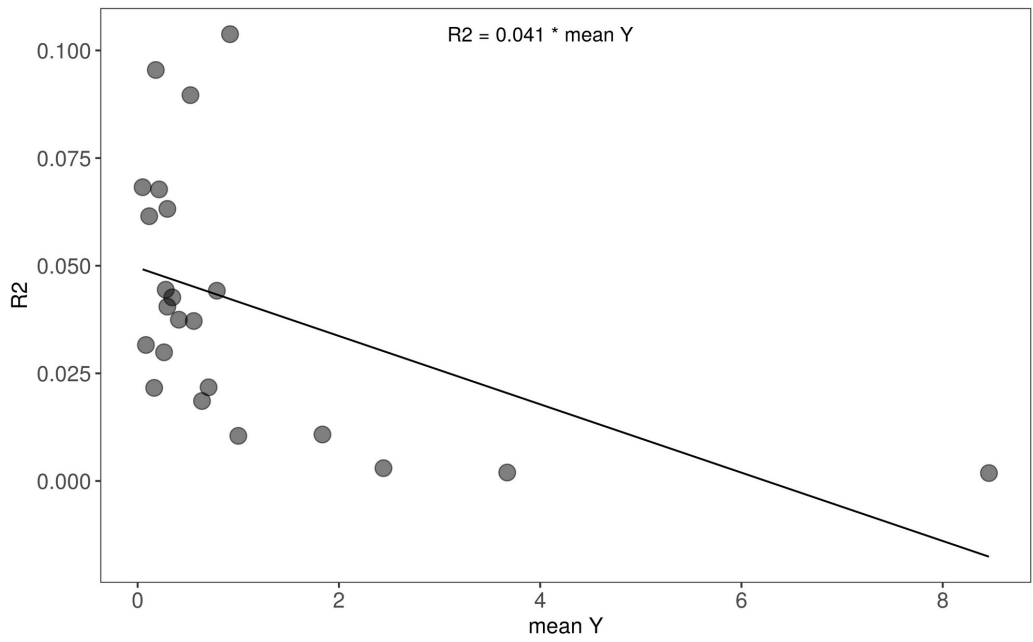


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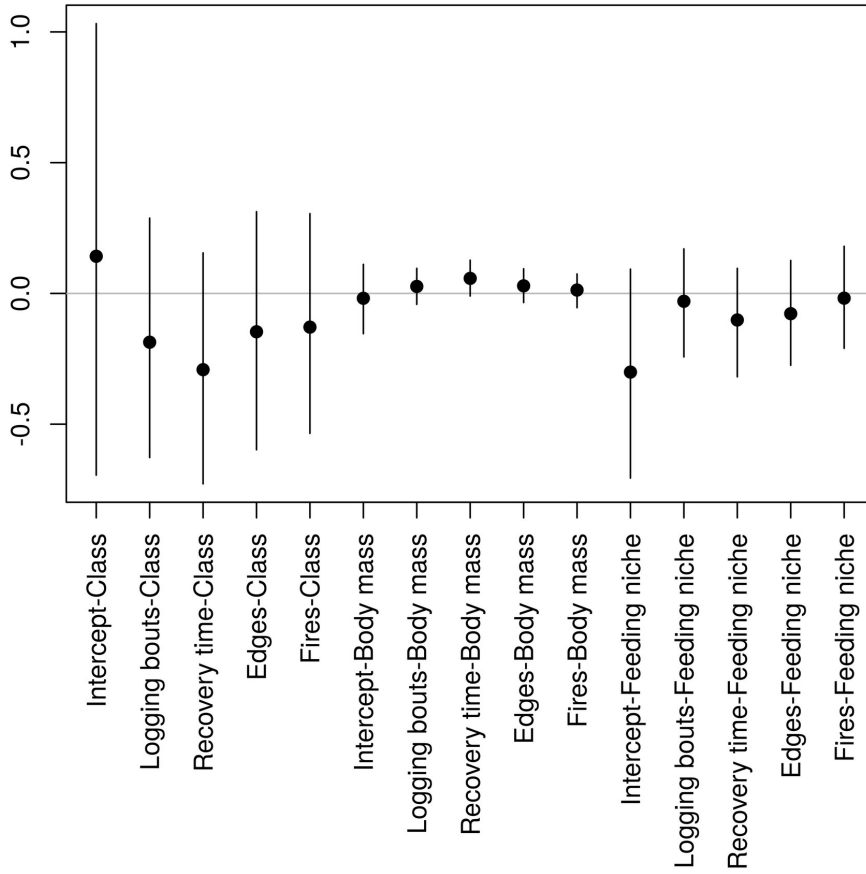


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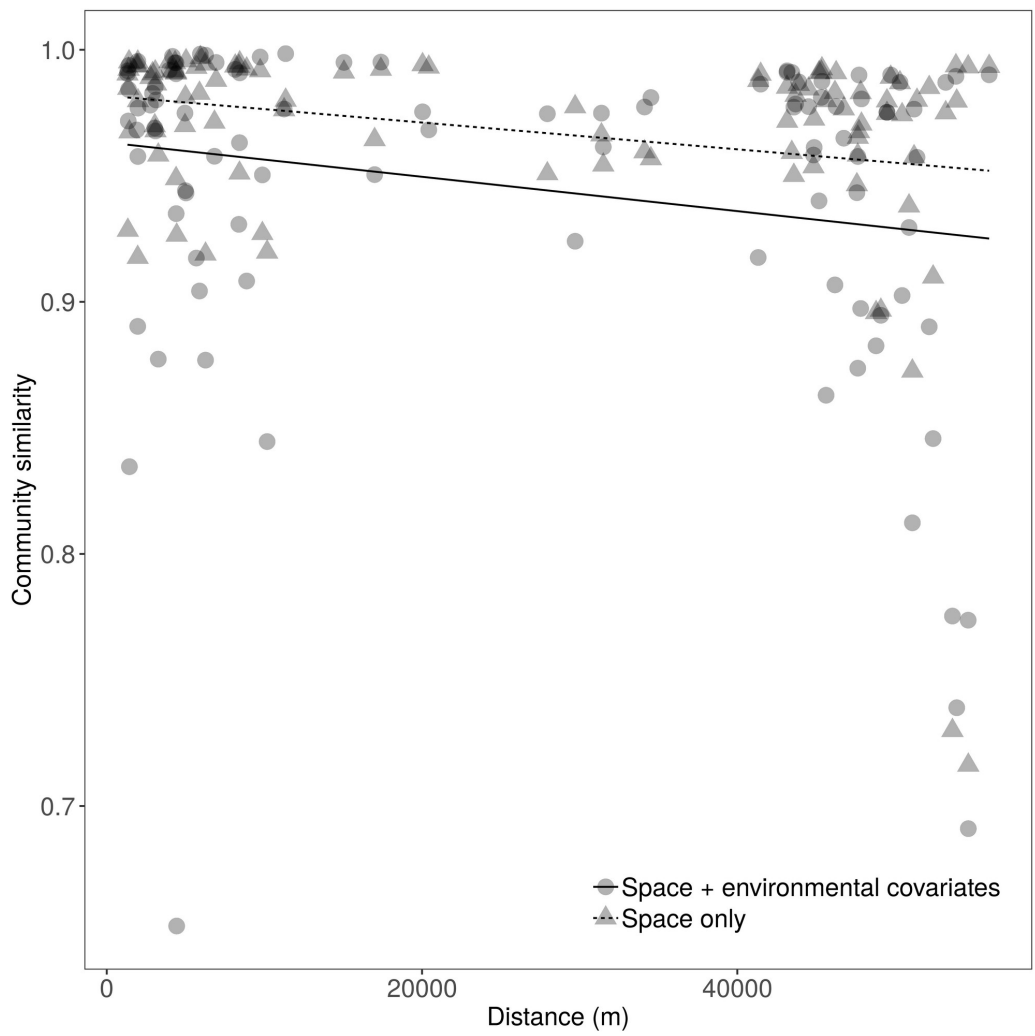


Figure A4. Decay in community similarity with spatial and environmental distance.



# Paper III



# Current status of the Critically Endangered Black-winged Trumpeter *Psophia obscura* in one of its last strongholds

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## Summary

The ‘Critically Endangered’ Black-winged Trumpeter *Psophia obscura* is endemic to the Belém Centre of Endemism in extreme eastern Amazonia and has a declining population and range. Here we report on a five-year (2016–2020) systematic camera-trap ( $n = 61$ ) study of the species in Gurupi Biological Reserve, one of its most important conservation areas. We used a multi-season occupancy model to identify factors affecting occupancy rates and to assess occupancy trends in the reserve. Occupancy was negatively related to elevation and site-level tree density, and was positively related to post-logging recovery times. Average annual occupancy rates remained stable throughout the study period (ranging between 0.57 and 0.67) and this stability was largely driven by high between-year survival rates. Results confirm that the Black-winged Trumpeter is an interior-forest specialist that is highly sensitive to forest disturbance, which underlines the importance of the Gurupi Biological Reserve as a core site for the conservation of the species. However, the species is long-lived, so continuous monitoring is needed to further clarify population trends. We also recommended that the status of the species in other forest remnants, most of which remain unprotected, is assessed.

**Keywords:** Amazonia, Belém Centre of Endemism, Black-winged Trumpeter, *Psophia obscura*

## Introduction

The genus *Psophia* (hereafter, trumpeters) comprises eight species endemic to the Amazon and Guiana regions of northern South America (Ribas *et al.* 2012, Pacheco *et al.* 2021). Trumpeters are large-bodied (> 1 kg), terrestrial, group-living and highly territorial (Sherman 1995b, Sherman

and Eason 1998). They are predominantly frugivorous (Erard *et al.* 1991, 2007, Winkler *et al.* 2020) and play an important role in forest dynamics as they swallow entire fruits and disseminate their intact seeds (Erard *et al.* 2007).

Trumpeters are forest-interior specialists and thus highly sensitive to disturbance (Parry *et al.* 2007, Moura *et al.* 2014, Michalski and Peres 2017, Benchimol and Peres 2021). They tend to be rare or absent from disturbed and secondary forests (Parry *et al.* 2007), and they often disappear from all but the largest fragments in fragmented forest landscapes (Moura *et al.* 2014, Michalski and Peres 2017, Benchimol and Peres 2021). Indeed, they share most of the ecological attributes that make a bird species sensitive to forest disturbance, including large body size, slow breeding rate, and a dependency on forest habitat and its fruit and invertebrate food resources (Newbold *et al.* 2013). In addition, their large body size, conspicuousness and group-living habits makes them vulnerable to hunters (Thiollay 2005). Consequently, three trumpeter species are currently categorized as threatened and two as 'Near Threatened' on the IUCN Red List of Threatened Species (IUCN 2021).

The Black-winged Trumpeter (*Psophia obscura*; Fig. S3 in the online supplementary material) is endemic to the Belém Centre of Endemism in extreme eastern Amazonia (Oppenheimer and Silveira 2009, Ribas *et al.* 2012). The Belém Centre of Endemism coincides with the oldest and most deforested human occupation frontier of the biome and its most threatened region (Moura *et al.* 2014, Vedovato *et al.* 2016, Celentano *et al.* 2017, Silva Junior *et al.* 2020). Due to continued habitat loss and its vulnerability to hunting, the Black-winged Trumpeter is suspected to be declining with possibly <250 individuals left in the wild. It is therefore categorized as 'Critically Endangered' by both IUCN (IUCN criteria A and C; BirdLife International 2018) and the Brazilian Red List of threatened species (IUCN criterion A; Ministério do Meio Ambiente - MMA 2014, Silveira 2018). However, there are no population size estimates for the species, so its categorization, based on the suspected number of mature individuals (criterion C) is questionable.

Despite its threatened status, little is known about the species apart from occasional records in bird inventories throughout its range (Portes *et al.* 2011, Lees *et al.* 2012, Lima and Raices 2012, Moura *et al.* 2014). Current distribution is limited to some of the largest and most undisturbed fragments of the Belém Centre of Endemism (Portes *et al.* 2011, Moura *et al.* 2014) and most of the remaining individuals belong to one of two disjunct populations: a western population at unprotected forest remnants in the municipality of Paragominas and an eastern population at Gurupi Biological Reserve and contiguous Indigenous Lands (Lees *et al.* 2012, Lima and Raices 2012, BirdLife International 2018).

In this study, we investigate site occupancy dynamics of a Black-winged Trumpeter population at Gurupi Biological Reserve, a key stronghold for conservation of the species. More specifically, we use data from five years of camera trap monitoring and a dynamic occupancy modelling approach to investigate potential factors affecting occupancy rates and trends in the reserve as a function of apparent survival and colonization rates.

## Methods

### Study area

Gurupi Biological Reserve is a 270,000-ha protected area located in extreme eastern Amazonia (Fig. 1). Together with contiguous Indigenous Lands, the reserve comprises the last remaining block of continuous Amazonian forests in the Belém Centre of Endemism (Silva Junior *et al.* 2020), and is one of the two most important strongholds for the Black-winged Trumpeter (Lima *et al.* 2014, BirdLife International 2018). The reserve has a tropical monsoonal climate with mean annual temperatures >26 C° and mean annual rainfall of 1,800 mm (Alvares *et al.* 2013). The terrain is flat to undulating with elevation ranging from 50 to 340 m above sea level. The reserve was entirely covered by evergreen tropical forest, but has lost about 30% of its forest cover to illegal deforestation in the last decades (Celentano *et al.* 2017). Much of its remaining forests is degraded by illegal



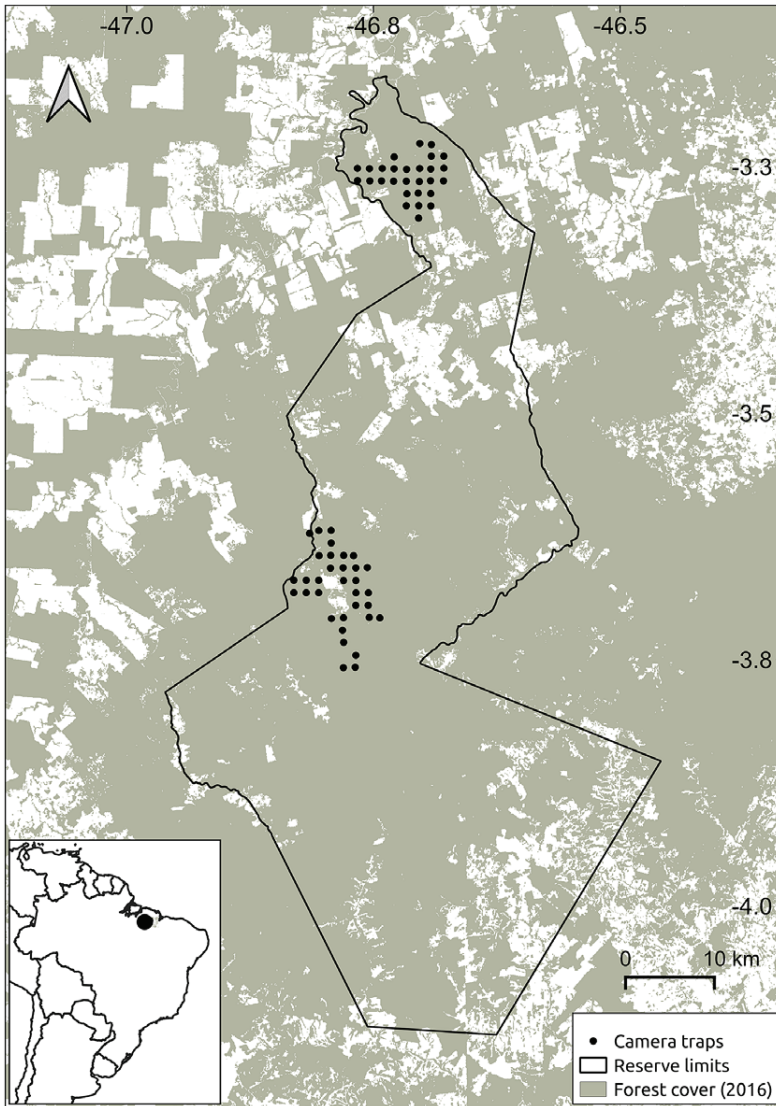


Figure 1. Map of Gurupi Biological Reserve, showing the distribution of camera trap stations. The inset map shows the location of the study area in Northeastern Brazil.

selective logging and fires (Celentano *et al.* 2017, Paiva *et al.* 2020). Still, it safeguards a significant portion of the regional biodiversity, including the full complement of medium- to large-sized terrestrial vertebrates (Lopes and Ferrari 2000, Lima *et al.* 2014, Carvalho *et al.* 2020).

### Camera trapping

Camera trap surveys were conducted between 2016 and 2020 as part of the Brazilian *in situ* monitoring program of Federal Protected Areas (Programa Monitora). Sampling followed the

Tropical Ecology Assessment and Monitoring (TEAM) protocol for vertebrates (Rovero and Ahumada 2017): during every dry season (August to November), we deployed camera-traps (model Bushnell Trophy Cam) at 61 permanent sampling sites distributed in two regular arrays with a density of one sampling site per 2 km<sup>2</sup> (Fig. 1). Cameras were attached to trees at knee height, perpendicular to the ground and facing either north or south to avoid direct sunlight at sunrise and sunset, and the vegetation directly in front of cameras was cleared. Cameras were set to operate continuously for at least 30 days per year. Images were processed in the wild.ID software (Fegraus and MacCarthy 2016). We assumed a 60 min interval for independence between detection events at the same sampling site. Although the same sites were sampled in all years, the number of operational cameras varied between years due to occasional camera malfunctions (Table. S1).

### Occupancy predictors

We quantified seven site-level variables to represent environmental and anthropogenic factors that may plausibly affect Black-winged Trumpeter occupancy and detection rates: (1) Site elevation (mean = 141.7 m, range: 77–270 m) was extracted from the ALOS global digital surface model provided by the Japan Aerospace Exploration Agency (JAXA) (Tadono *et al.* 2014). (2) Distance to water (mean = 1.2 km, range: 0.1–3.8) is the shortest distance between sampling sites and their nearest stream. (3) Distance to edge (mean = 2 km, range: 0.2–5) is the shortest distance between sampling locations and the nearest forest edge, estimated using the 30 m resolution land cover classification of the MapBiomass monitoring system for 2016 (Souza *et al.* 2020). (4) Site-level tree density (mean = 798 trees/ha, range: 523–1569) and (5) basal area (mean = 27.4 m<sup>2</sup>/ha, range: 8.2–45) were estimated using the point-centred quarter method (Cottam and Curtis 1956). Starting from each camera location, we ran three 50-m transects in the direction of 0, 120 and 240 magnetic degrees. Along each transect, we established five sampling points at 10-m intervals. The area around each point was divided into four quarters and the diameter at breast height (dbh) of the nearest tree with dbh  $\geq 10$  cm at each quarter was recorded. Tree density was estimated using the equation:  $D = 1/\bar{r}$ , where  $\bar{r}$  is the mean point-to-tree distance across all quarters (Cottam and Curtis 1956). Basal area was estimated using the equation  $BA = meanBA \cdot D$ , where *meanBA* is the mean basal area of sampled trees across all quarters (Cottam and Curtis 1956), with basal area of individual trees given by the equation  $BA = \pi \cdot (dbh/2)^2$ . To minimize the weight of a few exceptionally large trees, basal area of trees in the top 2.5% quantile ( $n = 9$  trees) were replaced by the quantile threshold value. Finally, we quantified two variables representing site-level impacts of past illegal logging: (6) recovery time (mean = 13, range: 6–21) as the number of years elapsed since any portion of a buffer of 500 m around each sampling site was logged for the last time, and (7) logging bouts (mean = 2, range: 1–5) as the number of different years in which each 500 m buffer zone was logged. To recover the history of illegal logging, we used visual interpretation of 1984–2016 Landsat time series data (Carvalho *et al.* 2020). Evidence of logging, such as roads, log decks and large canopy gaps are detectable in Landsat imagery for one to several years after logging (Stone and Lefebvre 1998, Matricardi *et al.* 2007, Asner *et al.* 2009). We used the USGS Earth Explorer interface (<http://earthexplorer.usgs.gov>) to download Landsat images from every year of the series and selected, whenever possible, cloudless images from dry season months. We then recorded the presence or absence of logging signs within 500-m buffers centred on each camera trap site and for each year in the series. By this procedure we estimated both recovery time and the number of logging bouts. For unlogged sites, we set maximum recovery time as 33 years, corresponding to the start of the time series. More details are provided in Carvalho *et al.* (2020).

All variables were standardized before the analysis. Distance to edges was log-transformed before the analysis. We used Pearson coefficients ( $r$ ) to test for collinearity among predictors, retaining for analysis only one variable from any pair with high ( $|r| > 0.60$ ) correlation. Thus, distance to water and logging bouts were removed from analysis as they were correlated with elevation and recovery time respectively.

### Data analyses

We used multi-season occupancy modelling (MacKenzie *et al.* 2003) to investigate Black-winged Trumpeter occupancy trends. This approach uses detection/non-detection data to estimate occupancy rates (the proportion of sites occupied by the species) and to model temporal changes in occupancy as a function of local survival and colonization processes, while accounting for imperfect detection (Royle and Dorazio 2008, Kéry and Schaub 2012, MacKenzie *et al.* 2017). The model requires sampling at two temporal scales, namely primary and secondary periods. Occupancy at any given sampling site may change between primary periods, but not between secondary periods that are nested within primary periods (MacKenzie *et al.* 2003). In our analysis, primary periods corresponded to years and secondary periods to six-day sampling occasions. To meet the assumption of population closure within primary periods, we only use data from the first 30 days of sampling for any site and year. To increase detection probabilities and facilitate model convergence in data analysis, we collapsed data into six-day sampling occasions.

We modelled occurrence of the species at site  $i$  in year  $k$  ( $z_{i,k}$ ) as a Bernoulli outcome governed by occupancy probability at site  $i$  in year  $k$  ( $\psi_{i,k}$ ):

$$z_{i,k} \sim \text{Bern}(\psi_{i,k})$$

We modelled observations, consisting of detection/non-detection of the species at site  $i$ , sampling occasion  $j$  and year  $k$  ( $y_{i,j,k}$ ) as Bernoulli outcomes governed by the product of  $z_{i,k}$  and detection probability at site  $i$ , sampling occasion  $j$  and year  $k$  ( $p_{i,j,k}$ ):

$$y_{i,j,k} \sim \text{Bern}(z_{i,k} \cdot p_{i,j,k})$$

We used a logit link function to model detection probability as a function of random site and year effects, while assuming constant detection within the same site and year:

$$\text{logit}(p_{i,j,k}) = a_i + \epsilon_k$$

We used a logit link function to model initial occupancy (year  $k=1$ ) as a function of random site effects, elevation, distance to edge, basal area, tree density, and recovery time:

$$\text{logit}(\psi_{i,1}) = a_i + b_1 \cdot \text{elevation}_i + b_2 \cdot \text{distEdge}_i + b_3 \cdot \text{basalArea}_i + b_4 \cdot \text{treeDensity}_i + b_5 \cdot \text{recovery}_i$$

We modelled occupancy in subsequent years as a function of year-specific survival ( $\phi$ ) and colonization ( $\gamma$ ) rates, estimated from the data:

$$\psi_{i,k+1} = \psi_{i,k} \cdot \phi_k + (1 - \psi_{i,k}) \cdot \gamma_k$$

To assess whether year-to-year changes in occupancy were significant, we estimated the derived parameter growth rate ( $\lambda$ ) as follows (Royle and Dorazio 2008):

$$\lambda = \frac{\psi_{k+1}}{\psi_k}$$

We fitted the model in a Bayesian framework, adapting the specifications provided by (Kéry and Schaub 2012). We implemented the model in JAGS (Plummer 2015) using the R2jags package (Su and Yajima 2012). We used non-informative priors for all parameters and ran three chains with

250,000 Markov Chain Monte Carlo (MCMC) iterations, with a burn-in of 100,000 and a thinning rate of 150. We evaluated parameter convergence using the Gelman-Rubin diagnostic (Gelman and Shirley 2011). We considered that there was support for a covariate effect when the 95% posterior credible interval (CI) for the parameter did not include zero. We considered that there was evidence for significant change in occupancy between a given year  $k$  and  $k+1$  if the posterior credible interval of  $\lambda$  did not overlap 1 (Ahumada et al. 2013). Data and R codes for analysis are available at <https://github.com/ICMBio-CENAP/Psophia-obscura>.

## Results

A total effort of 8,674 camera-trap days across five years of sampling yielded 2,876 photos of Black-winged Trumpeter, corresponding to 181 independent detection events (figures refer to data not yet collapsed into six-day occasions; Table S1). In any given year, the species was recorded at 14–22 sites, corresponding to naïve (i.e., uncorrected for imperfect detection) occupancy rates of 0.24–0.39. Table 1 presents posterior summaries for selected model parameters.

Average initial (i.e. for 2016) occupancy probability was 0.57 and average initial detection was 0.14. Initial occupancy probability was negatively related to elevation and tree density, and positively related to recovery time (Table 2, Fig. 2, Fig. S1). Basal area was positively but not significantly related to occupancy, while distance to edges had no relationship with occupancy (Table 2, Fig. S1).

The dynamic occupancy model reveals fluctuating but stable occupancy rates across years, with average annual  $\psi$  fluctuating between 0.57 and 0.67 (Table 1, Fig. 3) and always consistently higher than naïve occupancy rates. Detection rates were low and varied little across years, ranging between 0.09 and 0.15 (Table 1). Between-year growth rates ( $\lambda$ ) ranged between 0.92 and 1.2 over years and

Table 1. Posterior means, standard deviation and 95% credible intervals of selected model parameters. Occupancy ( $\psi$ ) and detection ( $p$ ) rates are estimated by site and year, such that the values shown in the table are averaged across sites. Survival ( $\phi$ ), colonization ( $\gamma$ ) and growth ( $\lambda$ ) rates are estimated on an annual basis for all sites combined.

Parameter	Mean	SD	95% CI
$\Psi_{2016}$	0.57	0.06	0.47–0.7
$\Psi_{2017}$	0.59	0.14	0.33–0.87
$\Psi_{2018}$	0.67	0.12	0.45–0.89
$\Psi_{2019}$	0.6	0.12	0.36–0.86
$\Psi_{2020}$	0.62	0.13	0.38–0.89
$p_{2016}$	0.14	0.02	0.09–0.19
$p_{2017}$	0.09	0.03	0.05–0.15
$p_{2018}$	0.15	0.03	0.1–0.23
$p_{2019}$	0.12	0.03	0.07–0.18
$p_{2020}$	0.1	0.02	0.06–0.15
$\Phi_{2016-2017}$	0.72	0.15	0.42–0.98
$\Phi_{2017-2018}$	0.81	0.13	0.52–0.99
$\Phi_{2018-2019}$	0.72	0.15	0.4–0.97
$\Phi_{2019-2020}$	0.81	0.13	0.52–0.99
$\gamma_{2016-2017}$	0.4	0.23	0.05–0.9
$\gamma_{2017-2018}$	0.47	0.23	0.06–0.94
$\gamma_{2018-2019}$	0.37	0.23	0.03–0.89
$\gamma_{2019-2020}$	0.36	0.23	0.03–0.88
$\lambda_{2016-2017}$	1.03	0.26	0.57–1.58
$\lambda_{2017-2018}$	1.2	0.33	0.71–1.97
$\lambda_{2018-2019}$	0.92	0.22	0.53–1.41
$\lambda_{2019-2020}$	1.07	0.26	0.68–1.7

Table 2. Posterior estimates for the effects of covariates on Black-winged Trumpeter occupancy probabilities.

Parameter	Mean	SD	95% CI
Elevation	-9.08	4.36	-18.7–-2.0
Distance to edge	-0.75	3.83	-8.71–6.47
Basal area	10.3	6	-2.35–22.1
Tree density	-12.0	5.09	-22.8–-2.45
Recovery time	11.9	5.14	3.97–24.0

were never significantly different from unity (Table 1, Fig. S2), which is consistent with the observed stability in occupancy rates. Occupancy dynamics was characterized by high between-year survival probabilities, with  $\phi$  ranging between 0.72 and 0.81 across years, while between-year colonization probabilities were considerably lower, with  $\gamma$  ranging between 0.36 and 0.47 (Table 1).

## Discussion

This study provides the first assessment of factors affecting the distribution and trends of the Black-winged Trumpeter in one of its key conservation areas. Black-winged Trumpeter initial occupancy rate was affected by elevation, tree density and recovery time, a set of variables that represent natural or anthropogenic factors, or a combination of both, while occupancy rates remained stable throughout the study.

The effect of elevation was negative. This is a key determinant of biodiversity distribution in tropical forests as it is correlated to a range of biotic and abiotic variables including water availability, soil and vegetation characteristics, and microclimate (de Castilho *et al.* 2006, de Toledo *et al.* 2011, Norris *et al.* 2014). The negative effect of elevation on trumpeter occupancy may relate to higher humidity and productivity in lower-lying areas; trumpeters prefer the moistest parts of the forest for foraging (Erard *et al.* 2007) and tend to be more abundant at sites closer to water (Michalski *et al.* 2015, Paredes *et al.* 2017, Mere Roncal *et al.* 2019, del Hoyo *et al.* 2020). Such habitat specificity probably increases the species' vulnerability to climate change. Habitat suitability models predict that it might lose more than 70% of suitable areas due to climate change by 2050 (de Moraes *et al.* 2020).

The results confirm that the species is an undisturbed primary forest specialist (Portes *et al.* 2011, Moura *et al.* 2013, Lima *et al.* 2014, del Hoyo *et al.* 2020), even though it can tolerate low levels of disturbance (Lima and Raices 2012). The two variables representing forest structure were strongly related to Black-winged Trumpeter occupancy probability, with tree density having a significantly negative effect and basal area having a positive, albeit non-significant, effect. Both variables are indicators of forest successional stage, with basal area increasing (Lu *et al.* 2003, Myster 2016, Caron *et al.* 2021) and tree density decreasing (Wright 2005) as forests mature. Such a preference for undisturbed forests seems to be universal for the genus (Parry *et al.* 2007, Michalski *et al.* 2015, Michalski and Peres 2017).

The precise mechanism by which forest structure affects the species is unclear and we can only speculate. Perhaps early successional or disturbed forests lack essential resources. For example, disturbed areas have fewer large trees, which provide the bulk of fruit consumed by trumpeters (Erard *et al.* 2007), and may lack trees with appropriate cavities for nesting (Sherman 1995a, Cornelius *et al.* 2008). Dense understorey in disturbed areas may also hinder communication and vigilance. This is detrimental to trumpeters, as they require constant acoustic and visual contact between group members to coordinate their movements and watch for predators (Seddon *et al.* 2002). Whatever the mechanism, the species prefers areas with a structure like mature forests.

Since most logging in the area took place over a decade ago, the positive effect of recovery time implies that logging effects are persistent. The removal of large trees and the increase in understorey density due to logging gaps have similar effects to those discussed above. Even though some

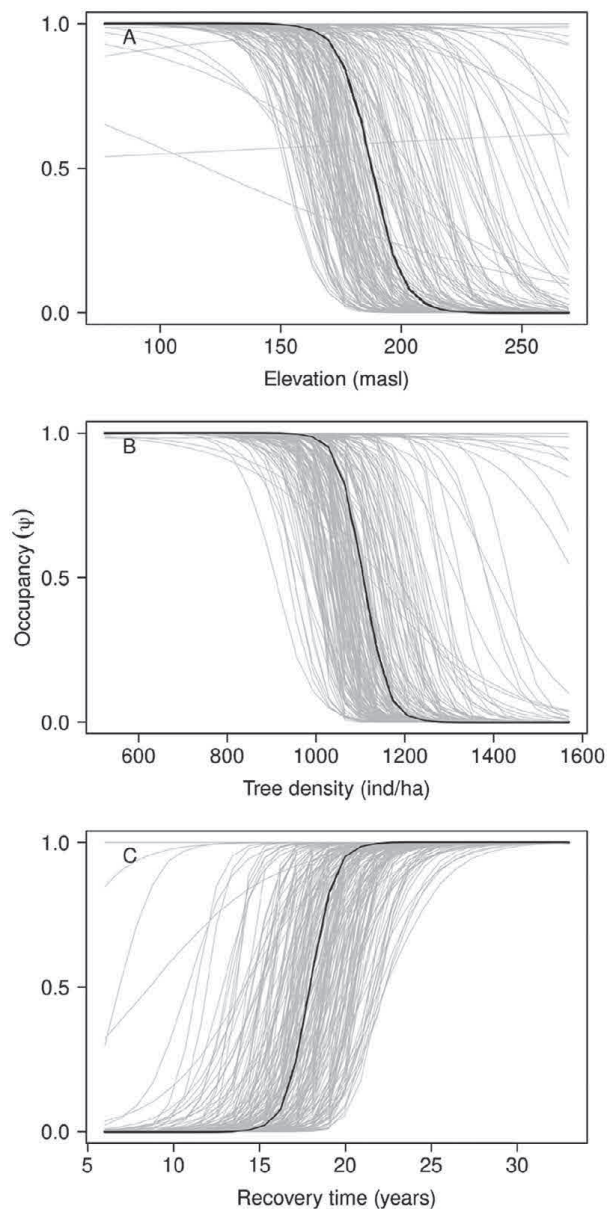


Figure 2. Predicted effect of model covariates on Black-winged Trumpeter initial occupancy probabilities at Gurupi Biological Reserve: (A) elevation (masl); (B) tree density (stems/ha); (C) post-logging recovery time (years). Solid black line represent posterior mean and light grey lines the uncertainty in estimates, based on a random posterior sample of 200 iterations.

parameters such as canopy cover and microclimate recover relatively quickly after logging (Senior *et al.* 2018, Mollinari *et al.* 2019), recovery of forest biomass (Gatti *et al.* 2014), floristic composition (Gauí *et al.* 2019) and availability of large trees (Pinho *et al.* 2020) may take much longer. This is particularly prominent in illegally logged areas, which undergo more severe damage in their

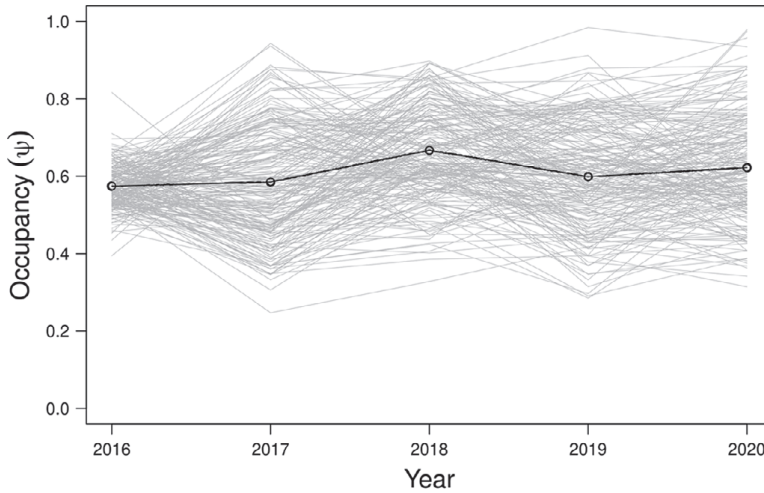


Figure 3. Temporal dynamics in Black-winged Trumpeter occupancy probabilities at Gurupi Biological Reserve, 2016-2020. The solid black line represents the posterior mean, and light grey lines the uncertainty in the estimate, based on a random posterior sample of 200 iterations.

structure and composition (Pacheco *et al.* 2016). Overall, trumpeter responses to logging seem to depend on the amount of damage to the residual forests. Previous studies found variable responses from trumpeters, from negative responses to conventional logging that persist for over a decade (Thiollay 1997) to slightly positive responses to reduced-impact logging in the short-term (Bicknell and Peres 2010). A previous study using a subset of the same data used here did not find a significant response to logging by the Black-winged Trumpeter, although the direction of the response was consistent with what is reported here (Carvalho *et al.* 2020).

The dynamic model revealed fluctuating but stable occupancy rates across years. Given that trumpeters are highly territorial with relatively inflexible home range boundaries (Sherman and Eason 1998) and that camera spacing was large enough to ensure there was no more than one camera per territory (assuming territories of approximately 70 ha; Sherman and Eason 1998), this suggests that the number of occupied territories, and possibly the population, has remained constant throughout the study. This finding underlines the importance of the Gurupi Biological Reserve as a core site for the conservation of the species, whose decline is inferred mostly from the continued loss of habitat (BirdLife International 2018, Silveira 2018), as there are no monitoring data available.

Stable occupancy rates can be interpreted as evidence of territorial saturation, where all suitable sites are occupied, and no vacant territories are available for expansion. Territorial saturation is probably the rule among trumpeters, and has been suggested as a candidate driver for the evolution of cooperative breeding in the genus (Sherman 1995b). This is because trumpeter territory sizes are largely defined by food availability during the lean period (Sherman 1995b, Sherman and Eason 1998), and this limits the number of territories that can fit within a given area. Consistent with this view is the fact that population dynamics was shaped primarily by high survival rates and not colonization, as revealed by the consistently higher estimates for  $\phi$  compared to  $\gamma$ . In fact, this was expected as adult trumpeters have high survival rates (Sherman 1995b) and groups can persist even longer than individuals, leading to continuous occupation of territories by the same group on a multi-year basis.

This view does not rule out the possibility of changes in the occupancy rate in the future. Suitable areas may become vacant if their resident groups collapse and are not replaced. The amount of suitable habitat may decrease if the reserve undergoes additional logging, forest fires or deforestation. The opposite is also possible as the amount of suitable habitat may increase as previously degraded areas recover from disturbance. Continuous monitoring is needed to reveal future trends, while additional studies may indicate the maximum attainable population size in the reserve and what factors may be limiting population growth and expansion.

Observed trends should be interpreted with caution, as the study duration was relatively short. Five years is just a little longer than the average tenure of a dominant individual over a group (Sherman 1995b), and approximately equivalent to the estimated generation length of the Black-winged Trumpeter (Bird *et al.* 2020). For example, the guidelines for using the IUCN Red List categories and criteria require information on population reduction over 10 years or three generations (Rodrigues *et al.* 2006), which for the Black-winged Trumpeter corresponds to 15 years (Bird *et al.* 2020). Therefore, more years of monitoring are needed for robust conclusions on trends for the species.

The apparent stable trumpeter population at Gurupi provides hope for the species within this protected area. However, the conservation prospects for the species remain highly precarious as a large but unknown fraction of its remaining population resides in unprotected forest patches that continue to be lost at alarming rates (Silva Junior *et al.* 2020). Furthermore, even protected areas are prone to habitat degradation from logging, fires, and climate change (de Moraes *et al.* 2020). We reinforce the main recommendations already provided for the conservation of the species, such as expanding the network of protected areas and improving the management of existing ones (BirdLife International 2018, Silveira 2018). We also recommend continued monitoring at Gurupi to further clarify trends in this key area for the species, as well as additional studies to provide reliable estimates of population size in the reserve and in other areas.

## Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270922000077>

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## Supplementary material

### **Current status of the Critically Endangered Black-winged Trumpeter (*Psophia obscura*) in one of its last strongholds**

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Table S1. Summary information about camera-trap sampling at Gurupi Biological Reserve. Mean effort is the mean number of days cameras were operational in a given year. Total effort is the sum of the effort in days of all individual cameras in a given year. Photos is the number of Black-winged Trumpeter photos obtained in a given year. Detection events is the number of independent (>60 minute- interval) detections of Black-winged Trumpeter obtained in a given year.

Figure S1. Posterior distribution of beta coefficients representing the effects of covariates on Black-winged Trumpeter occupancy probabilities.

Figure S2. Mean and 95% posterior credible interval for between-year growth rate ( $\lambda$ ) for Black-winged Trumpeter at Gurupi Biological Reserve, 2016-2020.

Figure S3. A camera-trap record of a *Psophia obscura* group at Gurupi Biological Reserve.

Table S1. Summary information about camera-trap sampling at Gurupi Biological Reserve. Mean effort is the mean number of days cameras were operational in a given year. Total effort is the sum of the effort in days of all individual cameras in a given year. Photos is the number of Black-winged Trumpeter photos obtained in a given year. Detection events is the number of independent (>60 minute- interval) detections of Black-winged Trumpeter obtained in a given year.

Year	N. sites	Mean effort	Total effort	Photos	Detection events
2016	57	30	1710	534	38
2017	59	30	1770	282	20
2018	57	30	1710	927	49
2019	60	30	1727	469	42
2020	59	30	1757	664	32

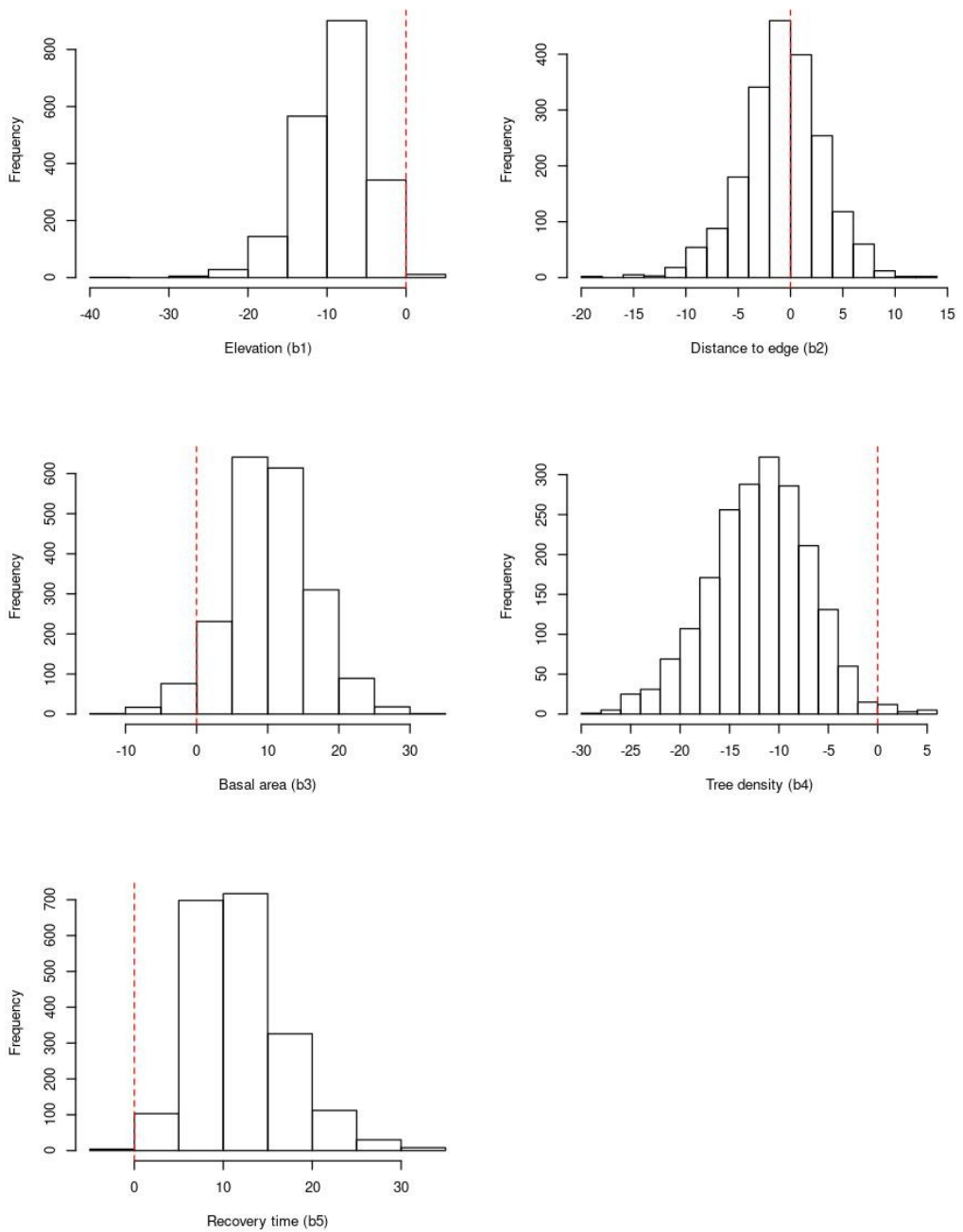


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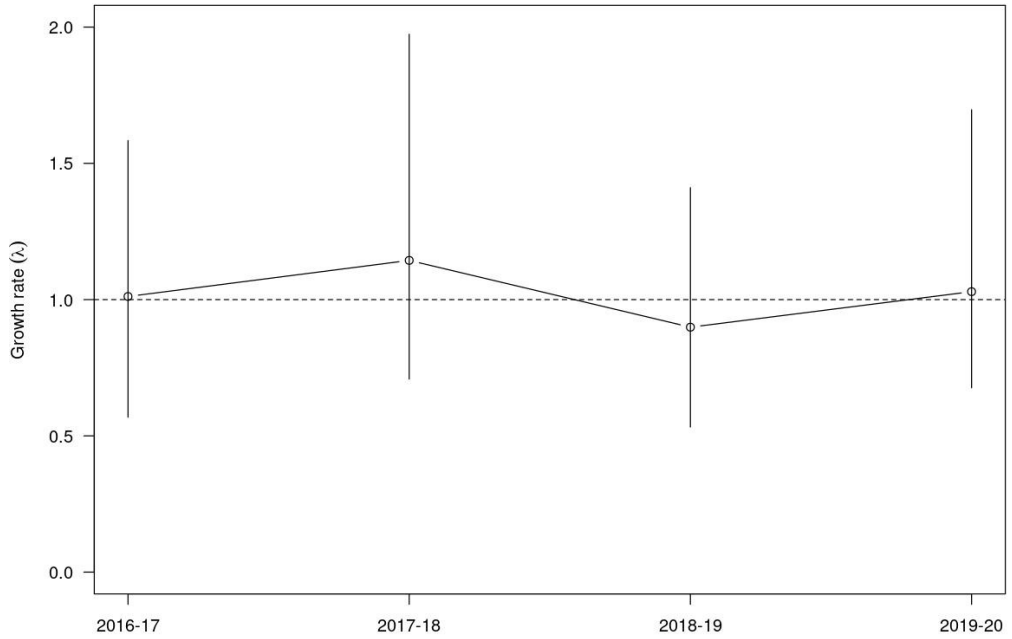


Figure S2. Mean and 95% posterior credible interval for between-year growth rate ( $\lambda$ ) for Black-winged Trumpeter at Gurupi Biological Reserve, 2016-2020.



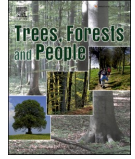


Figure S3. A camera-trap record of a *Psophia obscura* group at Gurupi Biological Reserve.



# Paper IV





## Potential losses of animal-dispersed trees due to selective logging in Amazonian forest concessions

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### ABSTRACT

Fruits and seeds are key food resources for most Amazonian mammals and birds. Selective logging is an increasingly dominant land use in the region that can deplete these resources over large areas. However, this potential impact remains poorly studied. Here we assess potential losses of animal-dispersed (endozoochorous and synzoochorous) trees resulting from reduced-impact logging in Amazonian forest concessions. We use data from forestry surveys conducted by concession companies that include the location, identity and fate (logged or not) of large ( $\geq 40$  cm diameter at breast height) individual trees within concessions to quantify absolute and relative losses of animal-dispersed trees in the landscape. We found that most individual trees (66%) within concessions belong to animal-dispersed genera. However, despite their predominance these trees were significantly less targeted for logging than abiotically-dispersed trees so that their losses were much lower than expected based on overall harvest intensities. However, at least ten percent of all large animal-dispersed trees were lost from the entire landscape, with site-level (50-ha plots) losses sometimes exceeding one third of all animal-dispersed trees. Results suggest that the relatively low level of logging for animal-dispersed trees can still deplete frugivore resources in selectively logged forests.

### Introduction

Fruits and seeds are key food resources for tropical forest vertebrates, with most bird and mammal species depending on them to a large degree (Fleming et al., 1987; Fleming and Kress, 2011; Peres, 1999). Fruit production is a predictor of frugivore diversity, abundance and biomass (Correa et al., 2015; Hanya et al., 2011; Hanya and Aiba, 2010; Jansen and Zuidema, 2001; Stevenson, 2001) and several aspects of frugivore ecology relate to local and regional fruit availability, including population density (Heydon and Bulloh, 1997; Stevenson, 2001), ranging behavior (Mourthé, 2014; Wallace, 2005), body condition (Bush et al., 2020; Peres, 1994) and reproductive success (Goldizen et al., 1988; Thompson et al., 2007).

The converse is also true, with most tropical trees depending on vertebrate frugivores to disperse their seeds (Almeida-Neto et al., 2008; Correa et al., 2015; Forget et al., 2007; Jordano, 1995, 2000). Consequently, vertebrates have major effects on forest structure, composition and dynamics with their loss leading to reduced dispersal and

recruitment (Boissier et al., 2020; Markl et al., 2012; Nasi et al., 1998; Nuñez-Iturri and Howe, 2007; Stoner et al., 2007b), dominance of abiotically dispersed trees (Barlow and Peres, 2008; Gardner et al., 2019; Wright et al., 2007) and depressed carbon stocks in forests (Bello et al., 2015; Peres et al., 2016).

Frugivory is particularly relevant in Neotropical forests, where more than 90% of woody plants are dispersed by birds and mammals (Dugger et al., 2019; Fleming et al., 1987; Gentry, 1982; Howe and Smallwood, 1982; Snow, 1981; Stiles, 1985), with frugivores comprising up to 80% of the biomass (Fleming et al., 1987) and up to two thirds of the diversity in these vertebrate groups at some sites (Moegenburg, 2002). In contrast, frugivory tends to be less prominent in the Paleotropics (Howe and Smallwood, 1982; Stoner et al., 2007a), as African forests are drier and have fewer fleshy fruits (Brugiere et al., 2002; Howe, 1986; Howe and Smallwood, 1982) while Asian tropical forests are dominated by wind-dispersed dipterocarp trees (Brearley et al., 2016; Fleming et al., 1987).

Plant-frugivore interactions are vulnerable to disruption by selective

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logging, one of the prevailing land use types in tropical forests in general (Poker and MacDicken, 2016) and Brazilian Amazonia in particular, where one-fifth of forests is currently being exploited for timber (Asner et al., 2006; Piloniot et al., 2019). By its very definition, selective logging targets a selected subset of trees within forests, typically aiming for large hard-wooded species with commercial potential (Bousfield et al., 2020). Given that hard-wooded trees often produce large, fleshy fruits dispersed by vertebrates (Bello et al., 2015; Forget et al., 2007; Hammond et al., 1996; Rosin, 2014; Yguel et al., 2019), selective logging inevitably depletes at least to some degree the availability of fruit and seed resources to vertebrates. Indeed, several studies have reported food depletion for specialized frugivores in selectively logged forests (Chapman and Chapman, 1997; Davies et al., 2001; Felton et al., 2010; Heydon and Bulloh, 1997; Johns and Skorupa, 1987; Pangau-Adam et al., 2021).

The magnitude of logging impacts on forests and wildlife depends on harvest levels, the amount of collateral damage from tree felling and infrastructure, and the extent to which target trees are important resources to wildlife (Johns, 1992; Rosin, 2014). These impacts can be partially mitigated by the adoption of reduced-impact logging (RIL) techniques (Lima et al., 2018; Putz et al., 2012, 2008). RIL techniques include capacity building, prior planning of harvest activities, best practices in cutting and transporting trees, and post-harvest closure (Pinard et al., 1995; Schulze et al., 2008). RIL harvest usually results in lower damage levels to the residual vegetation, biodiversity and the physical environment (Bicknell et al., 2015; Burivalova et al., 2019; Chaudhary et al., 2016) and better economic and social outcomes (Holmes, 2016; Holmes et al., 2002). However, the effects of RIL on fruit and seed availability in selectively logged forests are still poorly studied.

In this study, we investigate potential effects of logging on frugivore resources in Amazonian forest concessions managed under RIL guidelines. For this, we quantify direct losses of trees belonging to different dispersal modes to assess how much is lost from animal-dispersed trees in absolute and relative terms, and at different spatial scales. We also discuss potential implications for frugivores residing in selectively logged forests.

## Methods

### Study area

Jamari National Forest (-9.21, -62.93, Supplementary material Fig. S1) is a 220,000 ha protected area located in south-western Brazilian Amazonia. The climate is tropical monsoonal with mean annual temperatures  $> 26^{\circ}\text{C}$  and mean annual rainfall ranging between 2200 and 2500 mm (Alvares et al., 2013). The area is covered by dense evergreen tropical forest with patches of open forest; elevation ranges between 100 and 300 m a.s.l. (IBAMA, 2005). Approximately half of Jamari has been allocated as concessions for logging of commercial timber species  $\geq 50$  cm in diameter at breast height (dbh; Kauai et al., 2019; Mollinari et al., 2019). Concessions are divided into annual production units that are logged under RIL techniques in rotation cycles of 25 to 30 years, with harvest levels ranging between 10 and  $15\text{ m}^3\text{ ha}^{-1}$  (Pinagé et al., 2016).

### Tree data

We used data from forestry surveys conducted by two concession companies in 18 annual production units at Jamari (Supplementary material Table S1), to evaluate the composition of logged and unlogged trees. In these surveys, field teams identified, measured and mapped all trees with a dbh  $\geq 40$  cm within production areas (Pinagé et al., 2016), excluding gallery forest strips and non-timber species such as palms and pioneer trees. Trees were identified in the field by parataxonomists, using common names which were later matched as closely as possible to taxonomic binomials by concession technicians (Kauai et al., 2019;

Muhlbauer and Madeflona, 2009; Netto et al., 2017). Surveys were conducted before harvest, with the dataset updated after harvest to indicate the fate (logged or not) of individual trees.

### Data processing and analysis

We base our analysis on tree identification at the genus level to minimize potential identification errors by parataxonomists (Baraloto et al., 2007), as misidentification decreases with lower taxonomic resolution (Baraloto et al., 2007; Guitet et al., 2014). We standardized scientific names following the List of Species of the Brazilian Flora (Brazil Flora Group, 2021). Based on their genera, we assigned individual trees to a one of six fruit-types (berry-like, capsule-like, compound/pseudofruit, drupe-like, pod-like and other) and one of three broad dispersal mode categories: endozoochorous (i.e., gut-dispersed including definite and possible endozoochory), synzoochorous (i.e., scatter-hoarded) and non-zoochorous. Assignment to fruit type and dispersal mode followed the categories used by Hawes et al. (2020), complemented by additional sources (Ferraz et al., 2019; Pontes et al., 2013). We only used data from trees  $\geq 40$  cm dbh as concessions were not always consistent in collecting data from trees below this threshold. In addition, we discarded any trees lacking data on genus, dbh or dispersal mode. This resulted in excluding 7,302 trees (2.24%) for being below the dbh threshold and 2,400 (0.7%) lacking complete data.

We estimated the logging rate for each genus as the proportion of individuals that were logged in relation to all individuals of the same genus within the dataset (Amagnide et al., 2015). We used a t-test to check for differences between the dbh of logged and unlogged trees. We used a chi-squared test of homogeneity (Franke et al., 2012) to check for differences in the proportion of logged trees among the different dispersal modes, and we ran a post hoc analysis with Bonferroni adjustment to test for differences in pairwise comparisons (Beasley and Schumacker, 1995). To evaluate how tree losses vary across the landscape, we generated a regular grid of 50-ha hexagonal cells overlaying the entire concession areas (Supplementary material Fig. S5) and estimated the percentage of basal area loss for each dispersal mode within each cell. We use a 50 ha cell size as this is the standard large tree plot size in tropical forest studies (Condit, 1995; Garzon-Lopez et al., 2014). All analyses were conducted in R version 3.6.3 (R Core Team, 2022), with the spatial analysis conducted using the *sf* package (Pebesma, 2018).

## Results

### The tree community

After data cleaning and processing, the dataset provided information on 291,450 individual trees  $\geq 40$  cm dbh belonging to at least 35 families and 118 genera. Mean landscape-level density of trees  $\geq 40$  cm dbh within concessions was  $12.8\text{ trees ha}^{-1}$  (SD across 50 ha cells = 5.56) and mean basal area was  $5.05\text{ m}^2\text{ ha}^{-1}$  (SD across 50-ha cells = 2.18). The forest was dominated by 13 families which together accounted for more than 95% of the aggregated basal area, with the Fabaceae and Lecythidaceae families alone comprising more than half of all trees and aggregated basal area (Table 1, Supplementary material Fig. S2a). The top five families, ordered by aggregated basal area, were Fabaceae, Lecythidaceae, Moraceae, Vochysiaceae and Anacardiaceae.

Dominance patterns were less prominent at the genus level. Yet, the top 49 genera accounted for more than 95% of the aggregated basal area, while the top 10 genera accounted for more than 50% of the aggregated basal area and nearly half of all trees (Supplementary material Table S2, Fig. S2b). The top five genera, ordered by aggregated basal area, were *Bertholletia*, *Peltogyne*, *Dirinizia*, *Cariniana* and *Astronium*.

The dataset included trees producing nine fruit types, with a predominance of pod, capsule, and drupe-like fruits (Supplementary material Table S3). Two-thirds of all individual trees belonged to animal-

**Table 1**  
Predominant tree families at Jamari National Forest logging concessions, ranked by pre-harvest aggregated basal area.

Family	Basal area (% of total)	Basal area (cumulative %)	No. trees (% of total)	No. trees (cumulative %)
Fabaceae	39.3	39.3	40.2	40.2
Lecythidaceae	21.3	60.6	12.1	52.3
Moraceae	6.6	67.2	8.4	60.7
Vochysiaceae	5	72.2	5.8	66.5
Anacardiaceae	4.7	76.9	5.3	71.8
Burseraceae	4.4	81.3	7.1	78.9
Malvaceae	3.1	84.4	3.2	82.1
Caryocaraceae	2.6	87	2.1	84.2
Sapotaceae	2.5	89.5	3.7	87.9
Myristicaceae	2	91.5	2.6	90.5
Goupiaceae	1.5	93	1.3	91.8
Bignoniaceae	1.3	94.3	1.4	93.2
Combretaceae	1	95.3	0.7	93.9

dispersed genera, with a predominance of endozoochorous (52%) followed by non-zoochorous (35%) and synzoochorous trees (14%, Fig. 1a).

#### Harvested trees

A total of 34,763 trees (11.9% of all trees  $\geq 40$  cm dbh) were harvested for timber. This translates to a mean harvest intensity of 1.53 trees  $\text{ha}^{-1}$ , equivalent to 0.9  $\text{m}^2 \text{ha}^{-1}$  in basal area. A total of 62 different genera were logged, but a subset of 24 genera comprised most (> 95%) of the aggregated basal area logged (Table 2). The top five logged genera, ordered by aggregated basal area, were *Dinizia*, *Couratari*, *Peltogyne*, *Astronium* and *Hymenobium*. Most genera were harvested at low rates (mean = 0.11, SD = 0.12, range: 0.003–0.45), with only 12 genera being logged at rates > 0.25 (Table 2, Supplementary material Fig. S3).

The dbh of logged trees was significantly larger than that of unlogged trees ( $t = 149.43$ ,  $df = 45506$ ,  $p < 0.05$ , Fig. 2). The proportion of logged trees differed between seed dispersal modes (chi-squared = 6022,  $df = 2$ ,  $p < 0.05$ ), with non-zoochorous trees being proportionally more logged than synzoochorous and endozoochorous trees relative to their abundances (Fig. 1b). The post hoc test revealed significant differences for all pairwise comparisons (Supplementary material Table S3).

Basal area losses due to logging were highly variable across the landscape. The mean landscape-level basal area loss for all trees was 18.2%, but site-level losses (i.e., within 50-ha cells) ranged widely from zero to 36% (Fig. 3, Supplementary material Fig. S5). Most site-level basal area losses were due to the harvest of non-zoochorous trees (mean site-level loss = 26%,  $sd = 10.1$ , range: 0–75.6), while losses for endozoochorous (mean = 12.7%,  $sd = 7.33$ , range: 0–36) and synzoochorous trees (mean = 10.2%,  $sd = 6.9$ , range: 0–50.7) were much smaller (Fig. 3).

#### Discussion

We found that most individual trees and most of the basal area within logging concessions at Jamari National Forest belonged to zoochorous (animal-dispersed) tree genera. However, despite their predominance in the community, these trees were logged less than non-zoochorous trees both in absolute and relative terms. Their losses were therefore much lower than would be expected based only on overall harvest intensities. This agrees with data from the global timber market, which indicates a predominance of non-zoochorous trees among species targeted for logging (Jansen and Zuidema, 2001).

However, lower losses of trees with zoochorous compared to non-zoochorous seeds does not necessarily translate to low impacts on resident frugivores. At least ten percent of the large zoochorous trees across the landscape were logged, with site-level losses sometimes exceeding

one third of all zoochorous trees. In addition, collateral damage from tree felling and infrastructure development, which was unaccounted for in our analysis, may further increase losses (Lima et al., 2020; Pinho et al., 2020). These losses may be substantial, as even RIL can result in the incidental mortality or severe damage to non-target large trees (Feldpausch et al., 2005). Fruit production can also be affected by reduced pollination rates due to greater spacing between surviving trees, and by phenological changes in the selectively logged forest (Ghazoul and McLeish, 2001; Johns, 1992).

Disturbed areas such as edges and logging gaps may present enhanced fruit production as light demanding species benefit from increased sunlight and lower competition (Appanah and Manaf, 1990; Costa and Magnusson, 2003; Davies et al., 2001; Peres, 2000; Sheil and Van Heist, 2000). This may benefit small frugivores such as birds and bats in the short term (Burivalova et al., 2015; Clarke et al., 2005). However, it is unlikely to sustain large specialized frugivores, as pioneer trees often produce small and nutrient-poor fruits (Davies et al., 2001; Jordano, 2000; Putz et al., 2001; Velho et al., 2012). Furthermore, production tends to decline as the canopy gradually closes again (Davies et al., 2001; Johns, 1992).

The impact of highly variable losses in animal-dispersed trees across the landscape on resident frugivores will vary depending on the location and size of frugivore home ranges. Fewer zoochorous trees implies a smaller and less predictable resource base as well as increased spacing between food patches and higher travel costs (Aristizabal et al., 2019; Bush et al., 2020; Granados et al., 2019; Suarez, 2014). Depending on the magnitude of local losses, resident frugivores will need to increase the distances travelled for foraging (Johns and Burley, 1997) or shift to alternative food sources (Costa and Magnusson, 2002; Ghazoul and McLeish, 2001; Magioli et al., 2021).

It is common for tropical frugivores to experience seasonal bottlenecks in fruit availability, usually in the dry season (Jordano, 2000; Terborgh, 1986). Further reductions in their resource base may exacerbate these bottlenecks or even lead to extended dry season-like scenarios. For example, areas subject to intensive harvesting of Brazil nuts (*Bertholletia excelsa*) experience a drastic reduction in the availability of seeds available for consumption by agoutis (*Dasyprocta* sp.), and these animals must consequently increase foraging to meet their needs (Haugaasen and Tuck Haugaasen, 2010; Tuck Haugaasen et al., 2010). Similarly, harvest of the açai palm (*Euterpe oleracea*) can depress the abundance and biomass of frugivorous birds (Moegenburg, 2002). A significant loss of resource trees to logging may have a similar effect on frugivores in selectively logged forests.

It is noteworthy that some trees important to frugivores were spared from harvesting. For example, the Brazil nut was the dominant tree genus in the study area but was not harvested since it is protected by law. Palms (Arecaceae), a dominant component of Neotropical forests (Muscarella et al., 2020; ter Steege et al., 2013) and a major resource for frugivores (Dracxler and Kissling, 2022; van der Hoek et al., 2019), are not logging targets so they were not recorded by survey teams. Similarly, gallery forests along streams are also protected from logging and were not surveyed. The sparing of these keystone trees and habitats may provide a lifeline for frugivore species that are highly dependent on them.

Small trees, i.e. stems < 40 cm dbh which were not included in this study, may also provide alternative resources to resident frugivores. Small trees are numerically dominant in tropical forests (Farrion et al., 2016) and include important zoochorous families such as Rubiaceae and Melastomataceae (Bello et al., 2017; Gomes-Westphalen et al., 2012). Nevertheless, the largest trees still represent the major source of fruit for large specialized frugivores as they tend to produce larger fruits and fruit crops (Ali and Wang, 2021; Grogan and Galvão, 2006; Pinho et al., 2020). In some cases, a few individual large trees play a disproportionate role in sustaining local frugivore populations (Ahumada et al., 1998; Muller-Landau and Hardesty, 2005; Peres, 2000). It is therefore unlikely that fruit production by small trees will be able to buffer the loss

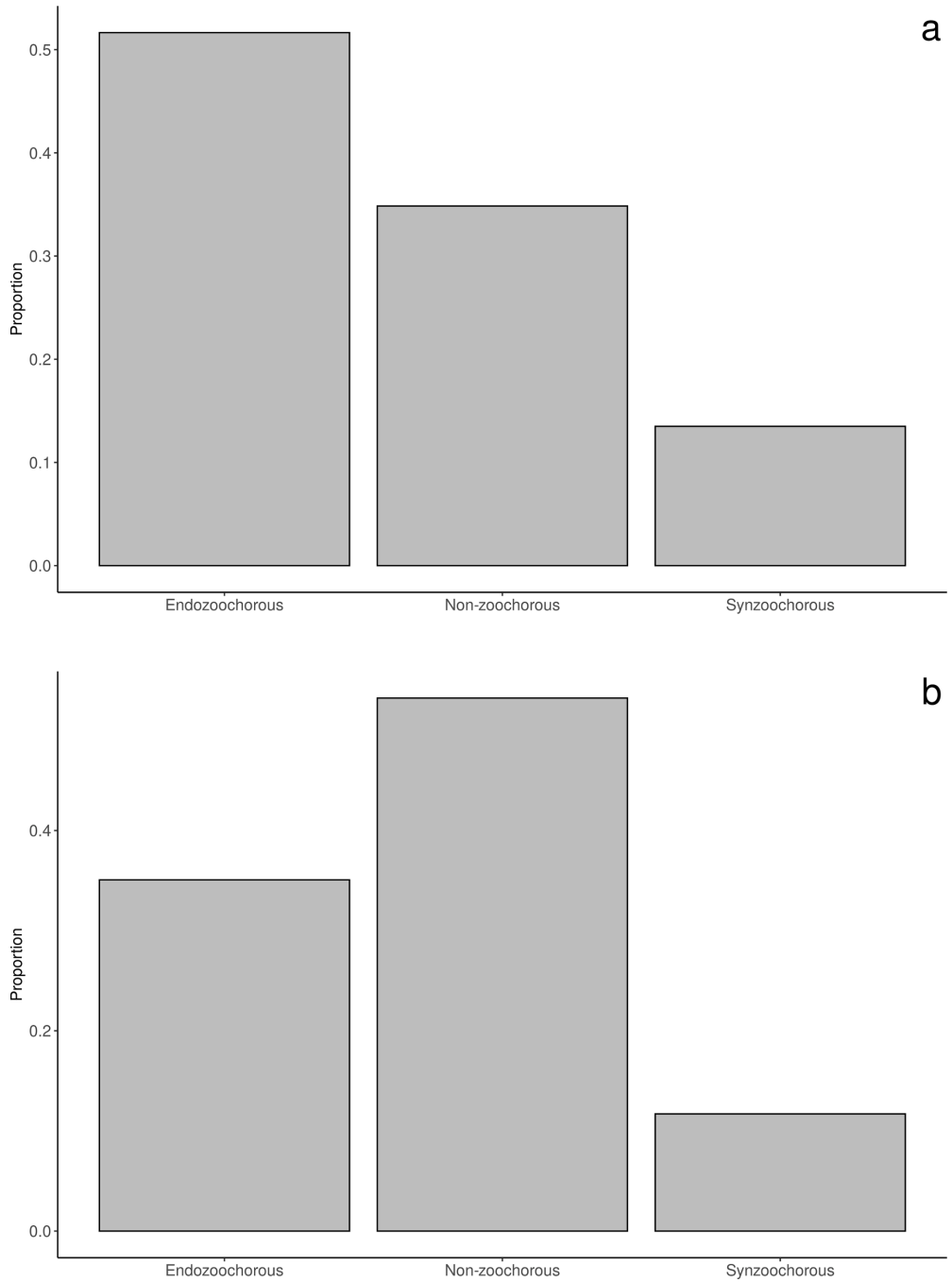


Fig. 1. Proportion of trees belonging to each dispersal mode category for (a) all trees, and (b) logged trees.



Table 2

Top tree genera targeted for timber at Jamari National Forest logging concessions, ranked by aggregated basal area. Only logged trees were included in calculations.

Genus	Family	Basal area (% of total)	Basal area (cumulative %)	No. trees (% of total)	No. trees (cumulative %)	Logging rate	Dispersal mode category
<i>Dinizia</i>	Fabaceae	15.5	15.5	9.5	9.5	0.45	NonZoo
<i>Couratari</i>	Lecythidaceae	11.5	27	10.7	20.2	0.44	NonZoo
<i>Peltogyne</i>	Fabaceae	8.5	35.5	11.8	32	0.12	EndoZoo
<i>Astronium</i>	Anacardiaceae	7.8	43.3	9.2	41.2	0.21	EndoZoo
<i>Hymenobium</i>	Fabaceae	7.5	50.8	6.9	48.1	0.34	NonZoo
<i>Cariniana</i>	Lecythidaceae	6.2	57	3.8	51.9	0.15	NonZoo
<i>Apuleia</i>	Fabaceae	5.6	62.6	4.7	56.6	0.45	NonZoo
<i>Dipteryx</i>	Fabaceae	4.7	67.3	5.9	62.5	0.35	SynZoo
<i>Allantoma</i>	Lecythidaceae	3.4	70.7	3.4	65.9	0.3	NonZoo
<i>Clarisia</i>	Moraceae	3	73.7	4.3	70.2	0.17	EndoZoo
<i>Caryocar</i>	Caryocaraceae	2.8	76.5	2.3	72.5	0.13	SynZoo
<i>Erisma</i>	Vochysiaceae	2.6	79.1	3.3	75.8	0.13	NonZoo
<i>Qualea</i>	Vochysiaceae	2.6	81.7	3.4	79.2	0.18	NonZoo
<i>Handroanthus</i>	Bignoniaceae	2	83.7	2.2	81.4	0.25	NonZoo
<i>Goupia</i>	Goupiaceae	1.8	85.5	1.8	83.2	0.17	EndoZoo
<i>Brosimum</i>	Moraceae	1.7	87.2	1.8	85	0.07	EndoZoo
<i>Cedrelinga</i>	Fabaceae	1.4	88.6	0.8	85.8	0.1	SynZoo
<i>Hymenaea</i>	Fabaceae	1.2	89.8	1.6	87.4	0.13	SynZoo
<i>Bagassa</i>	Moraceae	1.1	90.9	1	88.4	0.28	EndoZoo
<i>Andira</i>	Fabaceae	1	91.9	0.7	89.1	0.29	SynZoo
<i>Bowdichia</i>	Fabaceae	0.8	92.7	1.4	90.5	0.25	NonZoo
<i>Pouteria</i>	Sapotaceae	0.8	93.5	1.5	92	0.05	EndoZoo
<i>Mezilaurus</i>	Lauraceae	0.6	94.1	0.9	92.9	0.28	EndoZoo
<i>Diptotropis</i>	Fabaceae	0.6	94.7	1.1	94	0.19	NonZoo

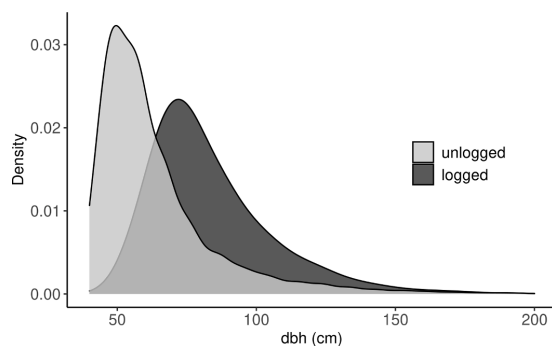


Fig. 2. Density plot of diameter at breast height (dbh) of unlogged and logged trees at Jamari National Forest logging concessions.

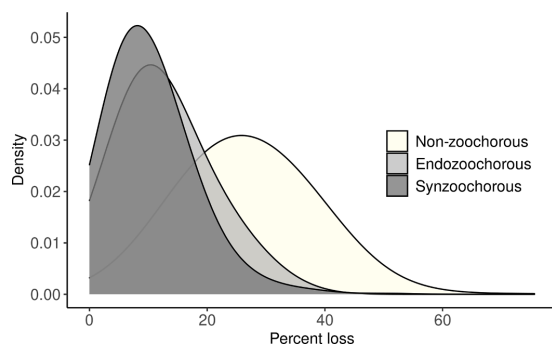


Fig. 3. Density plot of percent basal area loss for non-zoochorous, endozoochorous and synzoochorous trees within 50-ha cells ( $n = 492$ ) at Jamari National Forest logging concessions.

of large fruiting trees.

In summary, zoochorous tree losses from logging were lower than expectations based on overall harvest intensities alone. However, at least ten percent of all large zoochorous trees across the landscape were lost, with site-level losses sometimes exceeding a third of all zoochorous trees. These are conservative estimates as other factors may also reduce fruit production in residual trees within selectively logged forests. Our results therefore suggest that logging can deplete frugivore resources, even though abiotically dispersed trees are more heavily targeted. However, our analyses are based on indirect measures of potential fruit availability and further studies are needed to assess how the observed patterns may directly affect frugivore populations in selectively logged forests.

#### Declaration of Competing Interest

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

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.tfp.2022.100316](https://doi.org/10.1016/j.tfp.2022.100316).

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## Supplementary material

### Potential losses of animal-dispersed trees due to selective logging in Amazonian forest concessions

Elildo A.R. Carvalho Jr, Joseph E. Hawes, Torbjørn Haugaasen

Table S1. Summary information on forest concessions at Jamari National Forest and their annual production units included in the analysis. Values may differ from official records\* due to data processing and cleaning. UMF = Unidade de Manejo Florestal [Forest Management Unity, i.e., concession ID]; UPA = Unidade de Produção Anual [Annual Production Unit].

Table S2. Predominant tree genera at Jamari National Forest logging concessions, ranked by pre-harvest aggregated basal area.

Table S3. Summary information on fruit type produced by the sample of trees at Jamari National Forest logging concessions.

Table S4. Results of post-hoc Chi-square tests with Bonferroni adjustment for the proportion of logged and unlogged trees for three broad dispersal mode categories at Jamari National Forest logging concessions.

Figure S1. Map of Jamari National Forest in south-western Brazilian Amazonia, showing the Annual Production Units within concession areas (forest cover from MapBiomas, <http://mapbiomas.org>). Inset shows the location of the study area in South America.

Figure S2. Rank-abundance curves of (a) tree families and (b) tree genera at Jamari National Forest logging concessions.

Figure S3. Frequency of fruit types across all individual trees at Jamari National Forest logging concessions.

Figure S4. Frequency histogram showing logging rates for 62 tree genera at Jamari National Forest logging concessions.

Figure S5. Hexagonal grid map displaying percent tree basal loss (all trees combined) at Jamari National Forest logging concessions. Each cell has an area of 50 ha.

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UMF	UPA	Year logged	Area (ha)	No. trees	No. logged trees	Basal area	
						Basal area (m <sup>2</sup> /ha)	logged (m <sup>2</sup> /ha)
UMF-1	UPA-02	2011	564	6,503	1,106	2,527	664
UMF-1	UPA-03	2012	584	6,827	1,309	2,597	706
UMF-1	UPA-04	2013	591	9,080	1,082	3,394	684
UMF-1	UPA-05	2014	598	10,837	1,646	4,019	982
UMF-1	UPA-06	2016	525	9,205	653	3,284	461
UMF-1	UPA-08	2019	512	7,878	1,131	3,041	695
UMF-1	UPA-09	2018	507	5,886	972	2,254	574
UMF-1	UPA-10	2017	512	8,405	912	2,990	553
UMF-1	UPA-11	2015	520	7,452	1,096	2,858	684
UMF-3	UPA-01	2010	1587	26,430	2,958	10,456	1,507
UMF-3	UPA-02	2012	1946	31,284	3,095	13,399	2,026
UMF-3	UPA-03	2013	1944	25,910	1,784	10,268	1,230
UMF-3	UPA-04	2014	1780	29,219	2,360	10,673	1,377
UMF-3	UPA-05	2015	1927	17,579	3,064	8,650	1,653
UMF-3	UPA-06	2016	1827	22,926	2,074	9,027	1,269
UMF-3	UPA-11	2018	2474	26,090	3,188	9,554	1,701
UMF-3	UPA-12	2018	2433	22,783	3,734	8,538	2,082
UMF-3	UPA-14	2017	1847	17,156	2,599	6,991	1,544

\*official records are available on the website <https://www.florestal.gov.br/documentos/concessoes-florestais/concessoes-florestais-florestas-sob-concessao/flona-do-jamari>

Table S2. Predominant tree genera at Jamari National Forest logging concessions, ranked by pre-harvest aggregated basal area.

Genus	Family	Basal area (% of total)	Basal area (cumulative %)	No. trees (% of total)	No. trees (cumulative %)
<i>Bertholletia</i>	Lecythidaceae	8.7	8.7	3.8	3.8
<i>Peltogyne</i>	Fabaceae	7.9	16.6	11.5	15.3
<i>Dinizia</i>	Fabaceae	6.8	23.4	2.5	17.8
<i>Cariniana</i>	Lecythidaceae	6.5	29.9	3	20.8
<i>Astronium</i>	Anacardiaceae	4.6	34.5	5.2	26
<i>Protium</i>	Burseraceae	4.3	38.8	6.9	32.9
<i>Couratari</i>	Lecythidaceae	3.9	42.7	2.9	35.8
<i>Tachigali</i>	Fabaceae	3.9	46.6	5.3	41.1
<i>Hymenobium</i>	Fabaceae	2.8	49.4	2.4	43.5
<i>Brosimum</i>	Moraceae	2.8	52.2	3.1	46.6
<i>Erisma</i>	Vochysiaceae	2.6	54.8	3	49.6
<i>Caryocar</i>	Caryocaraceae	2.6	57.4	2.1	51.7
<i>Parkia</i>	Fabaceae	2.6	60	2.4	54.1
<i>Pouteria</i>	Sapotaceae	2.2	62.2	3.3	57.4
<i>Clarisia</i>	Moraceae	2.1	64.3	3	60.4
<i>Huberodendron</i>	Malvaceae	2	66.3	1.9	62.3
<i>Cedrelinga</i>	Fabaceae	2	68.3	0.9	63.2
<i>Apuleia</i>	Fabaceae	2	70.3	1.2	64.4
<i>Dipteryx</i>	Fabaceae	1.9	72.2	2	66.4
<i>Qualea</i>	Vochysiaceae	1.9	74.1	2.2	68.6
<i>Copaifera</i>	Fabaceae	1.6	75.7	2.6	71.2
<i>Allantoma</i>	Lecythidaceae	1.5	77.2	1.3	72.5
<i>Goupia</i>	Goupiaceae	1.5	78.7	1.3	73.8
<i>Iryanthera</i>	Myristicaceae	1.3	80	1.6	75.4
<i>Hymenaea</i>	Fabaceae	1.2	81.2	1.4	76.8
<i>Schizolobium</i>	Fabaceae	1	82.2	1	77.8
<i>Terminalia</i>	Combretaceae	1	83.2	0.7	78.5
<i>Handroanthus</i>	Bignoniaceae	1	84.2	1	79.5
<i>Vatairea</i>	Fabaceae	1	85.2	1.3	80.8
<i>Enterolobium</i>	Fabaceae	0.9	86.1	0.9	81.7
<i>Eschweilera</i>	Lecythidaceae	0.7	86.8	1.1	82.8
<i>Martiodendron</i>	Fabaceae	0.7	87.5	0.8	83.6
<i>Aspidosperma</i>	Apocynaceae	0.6	88.1	0.6	84.2
<i>Castilla</i>	Moraceae	0.6	88.7	0.8	85
<i>Vochysia</i>	Vochysiaceae	0.5	89.2	0.6	85.6
<i>Bagassa</i>	Moraceae	0.5	89.7	0.4	86
<i>Osteophloeum</i>	Myristicaceae	0.5	90.2	0.6	86.6
<i>Bowdichia</i>	Fabaceae	0.5	90.7	0.7	87.3
<i>Cedrela</i>	Meliaceae	0.5	91.2	0.5	87.8

<i>Andira</i>	Fabaceae	0.5	91.7	0.3	88.1
<i>Simarouba</i>	Simaroubaceae	0.5	92.2	0.6	88.7
<i>Diplotropis</i>	Fabaceae	0.4	92.6	0.7	89.4
<i>Pseudolmedia</i>	Moraceae	0.4	93	0.7	90.1
<i>Minquartia</i>	Olacaceae	0.4	93.4	0.6	90.7
<i>Cordia</i>	Boraginaceae	0.4	93.8	0.5	91.2
<i>Vataireopsis</i>	Fabaceae	0.3	94.1	0.5	91.7
<i>Mezilaurus</i>	Lauraceae	0.3	94.4	0.4	92.1
<i>Manilkara</i>	Sapotaceae	0.3	94.7	0.4	92.5
<i>Annona</i>	Annonaceae	0.3	95	0.3	92.8

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Table S3. Summary information on fruit type produced by the sample of trees at Jamari National Forest logging concessions.

<b>Fruit type</b>	<b>No. trees</b>	<b>No. trees (% of total)</b>	<b>No. trees (cumulative %)</b>
Pod-like	107,851	37	37
Capsule-like	75,191	25.8	62.8
Drupe-like	60,158	20.64	83.4
Compound/pseudofruit	22,490	7.72	91.12
Berry-like	18,809	6.45	97.57
Follicle-like	3,027	1.04	98.61
Samara	2,383	0.82	99.43
Nut-like	430	0.38	99.81
Syncarpium	1,111	0.15	100

Table S4. Results of post-hoc Chi-square tests with Bonferroni adjustment for the proportion of logged and unlogged trees for three broad dispersal mode categories at Jamari National Forest logging concessions.

<b>Group1</b>	<b>Group2</b>	<b>p</b>	<b>p.adj</b>
EndoZoo	NonZoo	0	0
EndoZoo	SynZoo	< 0.001	< 0.001
NonZoo	SynZoo	< 0.001	< 0.001

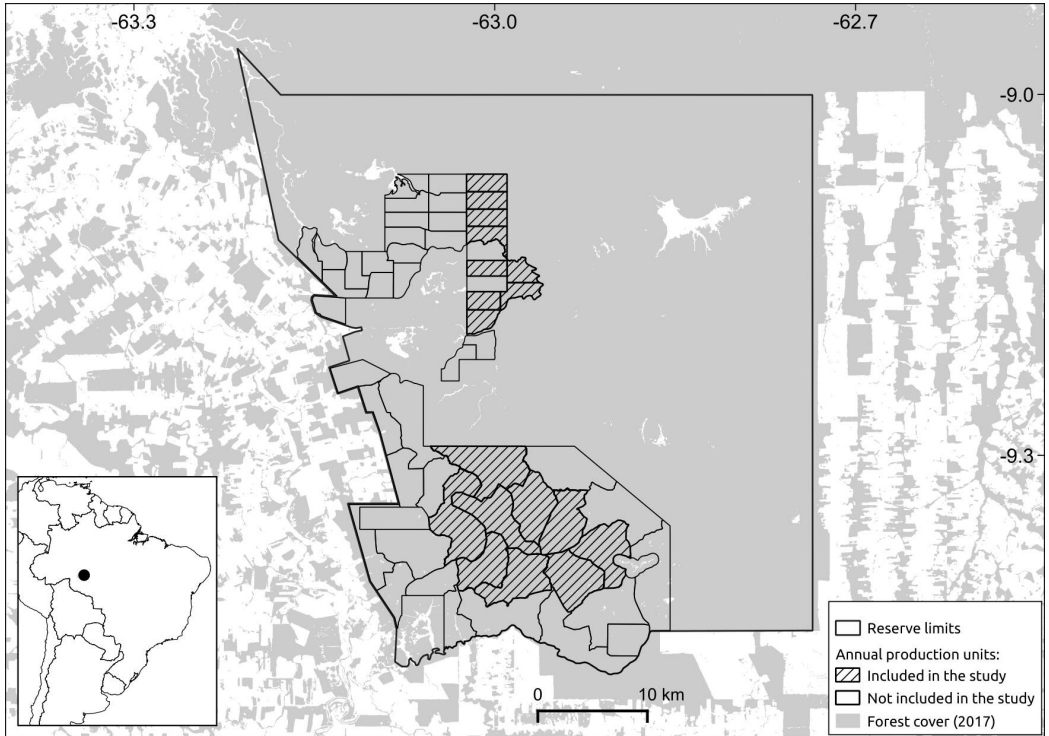


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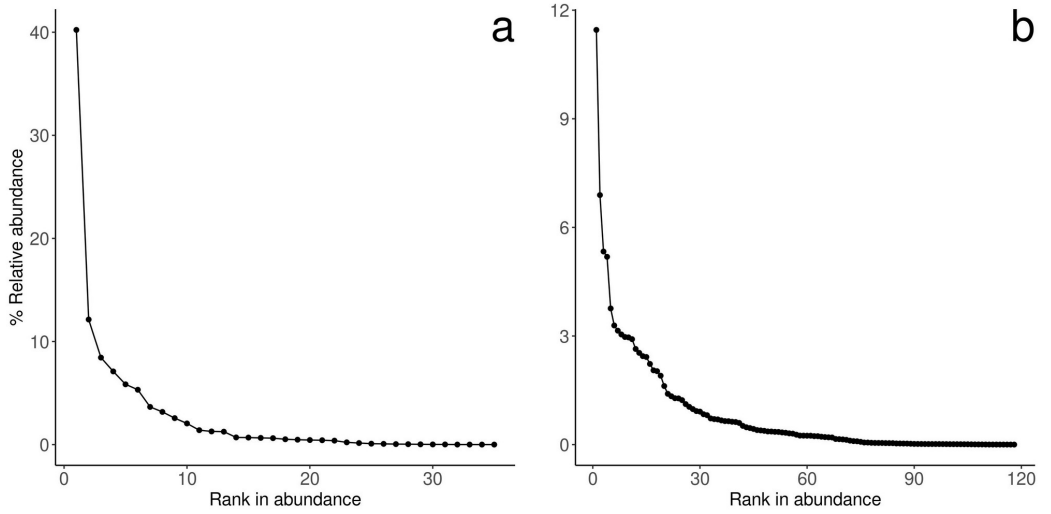


Figure S2. Rank-abundance curves of (a) tree families and (b) tree genera at Jamari National Forest logging concessions.

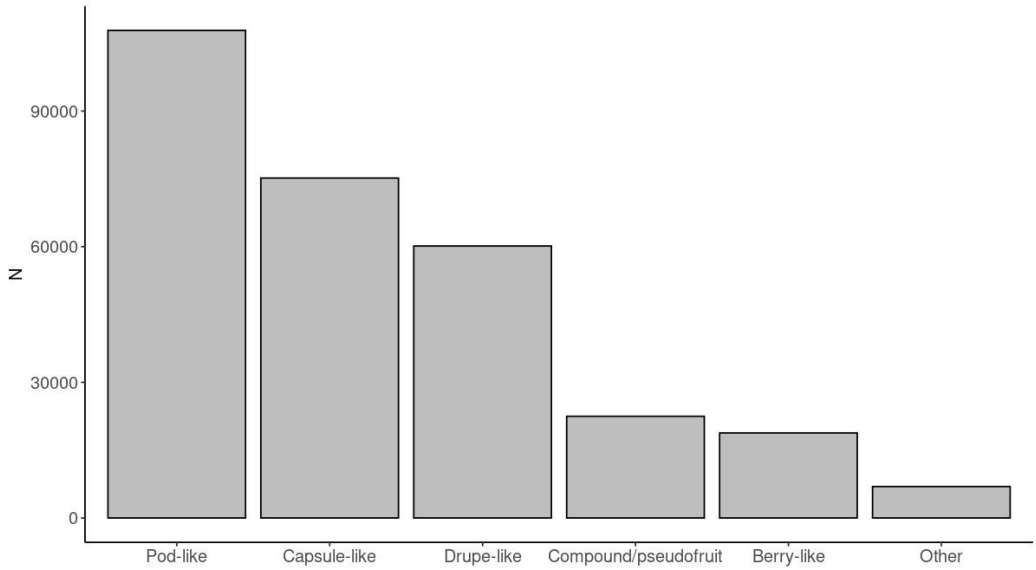


Figure S3. Frequency of fruit types across all individual trees at Jamari National Forest logging concessions.

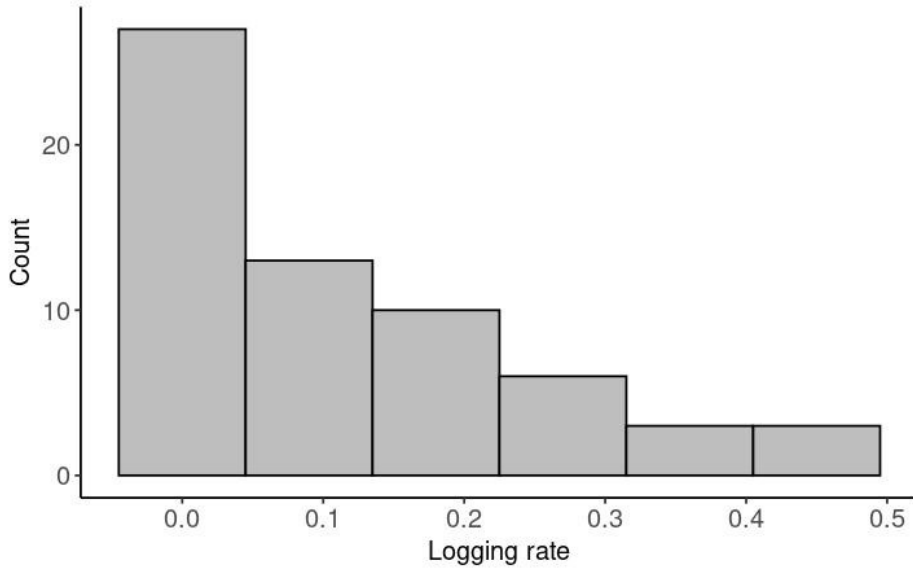


Figure S4. Frequency histogram showing logging rates for 62 tree genera at Jamari National Forest logging concessions.

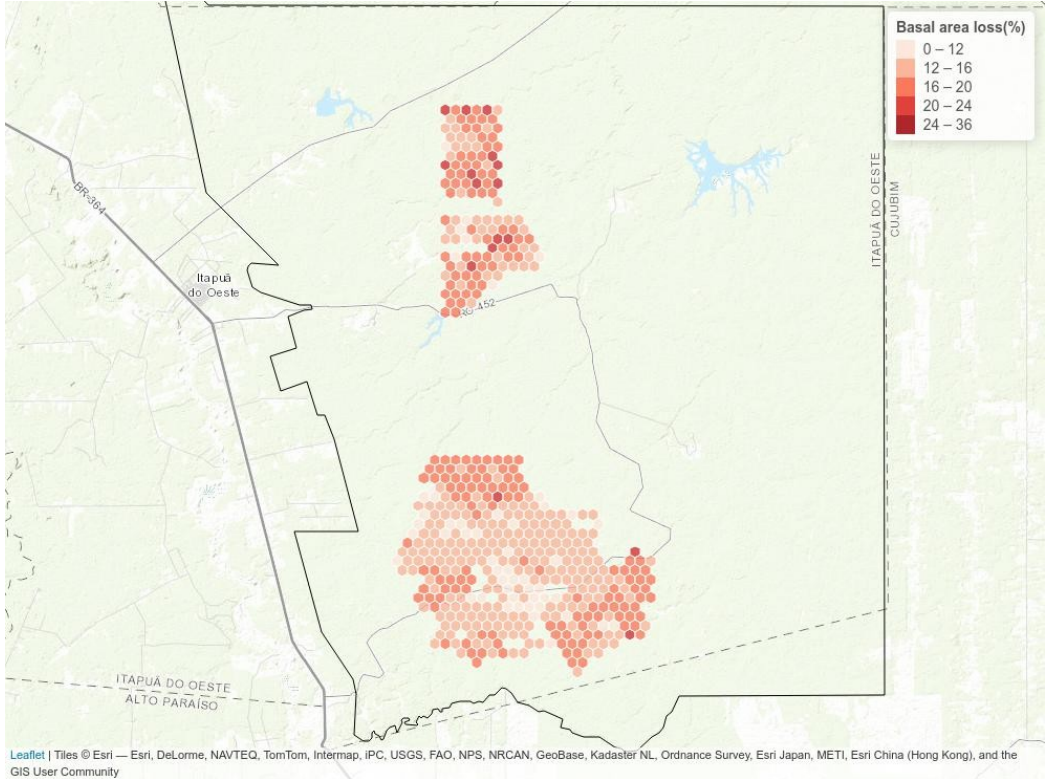


Figure S5. Hexagonal grid map displaying percent tree basal loss (all trees combined) at Jamari National Forest logging concessions. Each cell has an area of 50 ha.

## 7 Other publications

1. **Carvalho Jr. E. A. R.** (2019) Jaguar hunting in Amazonian extractive reserves: Acceptance and prevalence. *Environmental Conservation* 46: 334–339. <https://doi.org/10.1017/S0376892919000274>
2. **Carvalho Jr. E. A. R.**, Gonçalves H., Pinha P., Coutinho I. & Haugaasen T. (2021) Distribution and abundance of water buffalo populations in eastern Amazonian floodplains. *Management of Biological Invasions* 12: 408–419. <https://doi.org/10.3391/mbi.2021.12.2.13>
3. Mendonça E. N., Martins A., K.M Albernaz A. L. & **Carvalho Jr. E. A. R.** (2021) Avaliação da Efetividade da Reserva Biológica do Gurupi na Conservação de Vertebrados Terrestres de Médio e Grande Porte. *Biodiversidade Brasileira - BioBrasil* 11: 1–16. <https://doi.org/10.37002/biobrasil.v11i3.1769>
4. de Paula M. J., **Carvalho E. A. R.**, Lopes C. K. M., Sousa R. de A., Maciel E. L. P., Wariss M., Barboza R. S. L., Braga F. C. de A., Félix-Silva D., Peres C. A. & Pezzuti J. C. (2022) Hunting sustainability within two eastern Amazon Extractive Reserves. *Environmental Conservation* 49: 90–98. <https://doi.org/10.1017/S0376892922000145>
5. Ponce-Martins M., Lopes C. K. M., **Carvalho-Jr E. A. R.**, Castro F. M. R., de Paula M. J. & Pezzuti J. C. B. (2022) Assessing the contribution of local experts in monitoring Neotropical vertebrates with camera traps, linear transects and track and sign surveys in the Amazon. *Perspectives in Ecology and Conservation*. <https://doi.org/10.1016/j.pecon.2022.08.007>
6. Wang B., Rocha D. G., Abrahams M. I., Antunes A. P., Costa H. C. M., Gonçalves A. L. S., Spironello W. R., Paula M. J. de, Peres C. A., Pezzuti J. C. B., Ramalho E., Reis M. L., **Carvalho Jr. E. A. R.**, Rohe F., Macdonald D. W. & Tan C. K. W. (2019) Habitat use of the ocelot ( *Leopardus pardalis* ) in Brazilian Amazon. *Ecology and Evolution* 9: 5049–5062. <https://doi.org/10.1002/ece3.5005>





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