



**How to best manage selective logging for carbon and biodiversity retention in the Brazilian Amazon**

**By:**

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AS YOU SET OUT FOR ITHAKA  
HOPE YOUR ROAD IS A LONG ONE

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## General summary

Tropical forests are currently under incredible pressure by land-use change, putting in risk global sources of carbon stocks and biodiversity. Selective logging is one of the most extensive land uses and is currently expanding under a sustainable activity label. However, the damage caused by logging depends greatly on how forests are managed. In this manuscript I ask how logging intensity affects above-ground carbon stocks (Chapter 2), soil organic carbon stocks (Chapter 3) and tree diversity (Chapter 4) after logging in the Brazilian Amazon. Additionally, I explore whether implementing extensive logging with low intensity (land-sharing logging) or sparing a continuous piece of land coupled with intensified logging (land-sparing logging), retain more carbon stocks and tree diversity. To explore the disturbance effects of logging I set 0.5 ha plots in unlogged and logged forests in Brazil. I measured local intensity by  $\text{m}^3$  of wood removed inside each plot. I simulate equivalent land-sharing and land-sparing harvests on spatially explicit emulated forests. Then, I predicted for above-ground carbon stocks (Chapter 2), soil organic carbon stocks (Chapter 3) and tree abundance (Chapter 4) in function of logging intensity. I found that above-ground carbon stocks and abundance decreased with logging intensity (Chapters 2 and 4). Logging intensity did not affect soil carbon stocks and diversity values (Chapters 3 and 4). However, in Chapter 3, unlogged forest was higher in soil carbon stocks than logged forest. Land-sparing logging retained in general more above-ground carbon, soil carbon stocks and tree abundance. In chapter 4, spared lands contributed significantly to species number in land-sparing scenarios. These findings illustrate the capacity of land sparing to retain more carbon and tree diversity than land sharing with equivalent yield and the benefits of primary forest in allocated lands.



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## Statement of contribution

I declare that the work presented here is my own, with the guidance and intellectual contribution of my supervisors David P. Edwards and Carlos A. Peres.

Chapter 2 is currently in review as: Ileana A Acosta, Zuzana Burivalova, Carlos A Peres, David P Edwards. In review. Does land-sharing or land-sparing logging best retain tropical carbon stocks?

I did all the writing, fieldwork, data preparation and analyses. D.P.E., Z.B. and C.A.P reviewed the manuscript. D.P.E., conceived the idea for the project and guided the fieldwork. C.A.P. conducted the partnership with AMATA enterprise. Z.B. gave intellectual input for the analyses and reviewed and tested the code. AMATA provided with the maps and timber trees spatial data. Alexandre E. Santos identified the tree species on the field. D. Edwards, supervised the fieldwork methods, reviewed the manuscript and gave important intellectual and input.

Chapter 3 is in preparation to be submitted. I did all the writing, fieldwork and analyses. Plinio Barbosa Camargo guided the fieldwork methodology, soil sampling materials and performed the soil carbon laboratory analysis. D. Edwards reviewed the manuscript and gave important intellectual input.

Chapter 4 is in preparation to be submitted. I did all the writing, fieldwork and analyses. AMATA provided with the maps and timber trees spatial data. Alexandre E. Santos identified the tree species on the field. D. Edwards, supervised the fieldwork methods, reviewed the manuscript and gave important intellectual contribution and input.

All typos found in this manuscript are attributed to Titivillus, patron demon of scribes.



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# Chapter 1

## General Introduction

### 1 Introduction

#### 1.1 Forests, global change, and biodiversity loss

Forests ecosystems inhabit around of 40% of global terrestrial area and their impact is crucial on regional and global economy, ecosystem processes and climate regulation. Forests provide resources to humans and wildlife (e.g. food security, wood and medicine) and regulate vectors and diseases that have a direct impact on human well-being (Keesing et al., 2006). Forests ecosystems regulate climate by light interception and reducing albedo surfaces (Thom et al., 2017), by the water cycle via evapotranspiration (Schlesinger and Jasechko, 2014) and by absorbing atmospheric carbon (sink) and storing it as biomass (Lal, 2008). They also house the vast majority of global terrestrial biodiversity. These capacities for carbon retention and the services provided to biodiversity makes forests a key element in buffering and reducing the effects of the current global crisis on climate change produced by greenhouse gases and global biodiversity loss.

##### 1.1.1 Forests and climate change

Current global temperature changes represent a particular risk to biodiversity and forest cover in the tropics, where species have smaller thermal tolerances (Buckley and Huey, 2016). Fossil fuel emissions are the main driver of climate change by contributing to 9 Gigatonnes of carbon (Gt C) per year to the atmosphere, followed by land-use change that releases 0.9 Gt C year<sup>-1</sup> (Le Quéré et al., 2015). However, beyond carbon emissions, land-use change contributes greatly to carbon sink loss as forests capacity to absorb these emissions from the atmosphere is close to 3 Gt per year. The carbon cost for converting 93,000 ha of forest to farmland in Brazil, represented an 86% carbon loss with only 6% of plant species remaining (Fujisaka et al., 1998). Converting forest to biofuel production lands is also highly detrimental to carbon stocks, (Danielsen et al., 2009) and estimations of recovering the emissions from deforestation would take 75–93 years in avoided fossil fuel emissions by using biofuels in a dry dipterocarp forest and about



400 years in a peatland forest. By reducing deforestation, we can maintain the living carbon sink and prevent further carbon emissions related to disturbance (Canadell and Raupach, 2008; Kindermann et al., 2008).

### **1.1.2 Forests and biodiversity loss**

Globally, biodiversity is in decline (Butchart et al., 2010), again with the tropics the epicentre of loss (Barlow et al., 2016). Biodiversity loss impacts multiple ecosystem functions, as species loss influence on plant biomass production (Díaz et al., 2006), nutrient cycling and decomposition, soil formation and retention (Harris, 2009; Lavelle et al., 2006). Drivers of biodiversity loss are varied, and present multiple interactions currently not very well understood (Mazor et al., 2018). Invasive species are one of the main drivers of extinction for species of birds, promoting taxonomical homogenization (Clavero et al., 2009). Defaunation by hunting and illegal trade have negative consequences for population dynamics in tree species, large-bodied vertebrates and cage birds, leading to a gradual decline in biodiversity (Symes et al., 2018; Harrison et al., 2013; Kurten, 2013). However, land-use change is considered as the main cause of species loss (Sala et al., 2000), especially in continental hyper-diverse ecosystems like tropical forests, which are the most threatened by the expansion of agriculture (Laurance et al., 2014).

Forest cover is crucial to retain biodiversity. A recent study of four taxa in an Amazonian forest that was cleared and subsequently converted to cropland showed that >40 % of tree cover area can prevent biodiversity loss (Decaëns et al., 2018). Agriculture by itself accounts for nearly three-quarters of deforestation in the tropics (Hosonuma et al., 2012), from this, commercial agriculture is the most prevalent type, driven by the market of cattle products and industrialized plantations (i.e. oil palm and soybean) (Faminow, 1998). In the Amazonas, cattle ranching is a very common and profitable land-use practice and it requires the conversion of forest for cattle pasturelands, implemented by both large and small producers (Walker et al., 2000; Fearnside, 2005). In the case of plantations for biodiesel or other products, forest conversion for oil palm lands predominates in SE Asia, soybean plantations are expanding in Brazil (also used as animal feed; Achten and Verchot (2011)), and rubber is an increasing risk in SE and E Asia (Warren-Thomas et al., 2015). Although soybean plantations do not impact directly on forests (with clearance normally focused in the Cerrado), it represents a constant threat to forest fringes due the growing infrastructure and area used.

## 1.2 Selective logging in the tropics

Selective logging is one of the most widespread land-uses and continues to expand globally. More than half of tropical forests worldwide are managed for selective logging and from 2005 to 2010 there was an increase of 24% (Blaser et al. 2011). South-East Asia dominates global production: these forests are dominated by dipterocarp trees, presenting high densities of marketable species and allowing high yields (Shearman et al., 2012). In central Africa, managed forest extends to 60 million hectares, with Republic of Congo expanding logging activities to occupy 63% of forests (Laporte et al., 2007). Logging extents across Africa will likely increase further with future global demands, as timber exports from SE Asia decline (Henders et al., 2015) and the population in Africa increases rapidly (Gerland et al., 2014). Across the Brazilian Amazon, a large-scale remote-sensing analysis reported twice the area expected for logged forests, equating to between 10 and 15 million Mt of carbon of harvested volume (Asner, 2005).

Selective logging operates by targeting only marketable species. In legalised systems, there are minimum limits for trees harvested diameter at breast height, which are usually from above 50 cm diameter at breast height (Shearman et al., 2012) and minimum cycles between harvests to allow recovery, ranging from ~25 to 70-years. Impacts of selective logging on forest structure start with construction of the road network, which is the first step of forest fragmentation (Arima et al., 2005). Log decks are used as storage areas next to the roads, usually created by clearing the local vegetation with tractors or skidders. The gap fraction in log decks measured in a logged forest in Eastern Amazon was close to 100% (Asner et al., 2004b). Harvest tree felling also damages nearby trees, increasing tree mortality rates after logging (Chambers et al., 2004) where crown canopy height is related to gap size (Feldpausch et al., 2005).

Damages to the forest structure caused by logging translates into carbon stock loss and leftover deadwood. The removal of big trees can represent a significant forest loss. For example, in Eastern Amazon, trees bigger than 60 cm DBH represented up to 40% of biomass loss in the first years after logging (Sist et al., 2014). Large canopies can also influence the amount of deadwood produced after felling, with forests in Gabon presenting an additional 38 Mg ha<sup>-1</sup> of necromass after logging (Carlson et al., 2017) and in a Malaysian forest constituting half of above-ground biomass (Pfeifer et al., 2015). This switch from living biomass to deadwood represents a change in carbon flux, whereby carbon stocks becomes sources of carbon emissions (Saner et al., 2012).

Species responses to logging are induced by canopy gap opening, loss of canopy cover, and access of hunters by roads (Barlow et al., 2006; Barlow and Peres, 2006).

Gaps and roads allow more light exposure and drier microclimates (Felton et al., 2008), reduce climbing surfaces availability (Wells et al., 2006), as well as foraging areas or refuge spots (Bernard, 2004). As wildlife responds to an increase in environment heterogeneity, species will be redistributed according to their adaptations to logged forest characteristics or their sensitivity to changes in primary forest (Clarke et al., 2005; Summerville, 2013). Timber harvest can also contribute to species loss when sensitive or endemic species are affected, with logging associated with the reduction in the abundance of larger-bodied birds in Borneo (Costantini et al., 2016). Changes in community composition can determine future community structure in tropical trees, when population densities of harvested species decline (Jalonen et al., 2014). This reduction in vulnerable species combined with the increase in light demanding species that thrive in gaps (Terborgh et al., 2017; Hall et al., 2003), will likely shape future community composition (Slik et al., 2002).

### **1.2.1 Vulnerability of logged forests**

The post-logging period puts forest at further risk. The creation of highways to open up large areas of forest for logging (e.g. Kleinschroth et al., 2016) facilitate human population expansion (Laurance et al., 2009) and illegal logging if concessions are not closed. In addition, if the remaining timber does not recover initial abundance or volume for another logging cycle within a suitable (or suitably short) timeframe, then land rent uncertainty combined with infrastructure make logged forest vulnerable to further land-use change (Edwards et al. 2014 TREE). Within 4 years after harvest, 34% of selectively logged areas studied in the Amazon were cleared (Asner et al., 2006). Logging roads also promote fire incidence, soil erosion, landslides and access to hunters (Kleinschroth and Healey, 2017). In Malaysia, hunting is not directly correlated with logging, but when it occurs it was linked to a reduction of 37% of mammalian species (Brodie et al., 2015). In Africa, the abundances of guilds of vertebrates changed after logging and hunting, with primates and monkeys reducing in numbers (61% and 44 % lower, respectively) but insectivorous and frugivorous birds increasing (90% and 77% higher, respectively) (Poulsen et al., 2011).

### **1.2.2 How does management affect outcomes of selective logging?**

The variety of techniques, machinery and intensity used in selective logging, as well as the time since logging sampled within the survey, generates a gradient of outcomes on forest stand damage and biodiversity disturbance. Reduced impact logging (RIL) includes applications to logging guidelines, designed to prevent unnecessary damage to the soil and the forest stand, and thus to facilitate recovery processes (Putz et al., 2000). In tropical forests, RIL generally involves: 1) pre-harvest inventory and mapping of

timber trees; 2) Infrastructure planning (i.e. roads and skid trails); 3) pre-harvest cutting of canopy connecting vines; 4) restrictions on cutting trees; and 5) directional felling techniques and optimal cutting to avoid waste (Sist, 2001). RIL techniques often result in consistently less damage to the forest canopy than conventional logging practices (Asner et al., 2004a) and in half of tree-fall rates of unharvested trees compared to conventional logging (Schulze and Zweede, 2006). In Sabah, Malaysia, implementing RIL permitted to reduce forest stand damage from 50% to 28% (Pinard et al., 2000).

Even though the evidence of RIL in reducing damage to vegetation, impacts on wildlife may vary. In a meta-analysis by (Bicknell et al., 2014) on publications reporting the impact of logging on wildlife comparing between conventional logging and RIL in a first rotation of logging, showed that there is less detrimental effect on biodiversity in general, especially on birds, mammals and arthropods with implementation of RIL techniques. For instance, in the Amazon, within 6 months of RIL during a first logging rotation, invertebrates and bird richness increased after logging and mammal species richness did not change (Azevedo-Ramos et al., 2006). However, using a second rotation of RIL after a first rotation of conventional logging may not offer biodiversity benefits. In Borneo, there was no major differences in the richness or composition of birds, ants and dung beetles between RIL and conventional logging (Edwards et al., 2012). Thus, the benefits of RIL are obtained in the first cut.

The economic potential of RIL is, however, debatable. Training workers, upgrading machinery and changing management operations may come at a high initial economic cost, that dissuade loggers to adopt these practices (Putz, 2000). In Malaysia, although RIL was proven efficient in retaining carbon against conventional logging, discounts in carbon payments can elevate the cost of per m<sup>3</sup> of timber logged (Healey et al., 2000). In Amazonas, it has been demonstrated that RIL is not enough to ensure yield sustainability in a 30-year cycle (Sist and Ferreira, 2007), and a silvicultural system needed be added to allow timber production recovery (Valle et al., 2007) which can represent further costs. However, RIL can represent an investment in the long run, by increasing operational efficiency and avoiding costs by wasted wood (Holmes et al., 2002; Boltz et al., 2003).

### **1.3 Logging intensity – resilience and thresholds**

Martin et al. (2015) demonstrated in their pantropical meta-analysis that above-ground biomass has a negative relation to logging intensity. Forests with low intensity logging using RIL have showed a comparable damage with natural tree falls in several studies or very rapid recover of carbon stocks to primary forest levels in just a few years (Longo et al., 2016; West et al., 2014). The removal of several and/or large trees, caused by high

logging intensities, results in higher tree damage, broken canopies, tree mortality rates and overall carbon stock loss (Pereira et al., 2002; Sist et al., 2014).

In forests where low-intensity logging produces mild disturbance, species recruitment by canopy opening and light can maintain or boost richness in trees (Hill and Curran, 2003; Hamer et al., 2003). Furthermore, species richness and abundance were not affected in SE Asian butterflies (Hill, 1999), in bats in Trinidad (Clarke et al., 2005), small mammals in Borneo and Bolivia (Fredericksen and Fredericksen, 2002; Bernard, 2004) and in Amazonian ants (Vasconcelos et al., 2000). Abundance increases after logging have been reported across different taxa, in SE Asian ants, African monkeys, elephants and frugivorous birds (Gunawardene et al., 2010; Poulsen et al., 2011). However, at higher intensities, butterfly abundance and diversity declined in Thailand, as well as some species of African primates (Plumptre and Reynolds, 1994). Indeed, in a pan-tropical meta-analysis of the impacts of logging intensity of species richness, Burivalova et al. (2014) found that at invertebrates, mammals and amphibians decreased as intensity increased, although their analysis lacked higher logging intensity studies from SE Asia.

#### **1.4 Land sharing versus land sparing**

To balance land production and biodiversity conservation, two strategies were developed initially to most effectively manage agricultural production and expansion, by balancing crop yields with conservation either within the farmland system or within undisturbed lands (Green et al., 2005). Land sparing corresponds to a more traditional conservation practice by setting aside well preserved natural areas combined with high-intensity yields in production zones. Under land sharing or ‘wildlife-friendly’ farming, the entire area is designated for production while having patches with lower intensities (e.g. organic farming) or conserved set-asides (e.g. hedgerows, isolated trees, etc.) that reduce yield but allow the incorporation of biodiversity preservation within production lands (Fischer et al., 2008). However, both approaches can be contemplated as endpoints on a continuum (Fischer et al., 2008) and, therefore, mixed strategies can be also evaluated.

In terms of agriculture, land sharing strategies have gained popularity under the assumption that conservation is locally compatible, particularly within locally diversified traditional uses (Grau et al., 2013), because lower intensity farmland favours diversity over intensive agriculture (Hodgson et al., 2010). However, empirical studies from across the tropics suggest that the richness of different taxa measured (including trees, birds, and dung beetles) would be higher under land sparing, mostly because of a subsequent loss of species after extensive agriculture was implemented (Phalan et al., 2011; Gilroy et al., 2014; Hulme et al., 2013). Furthermore, since production lands are not isolated,

location from primary forest plays an important role in species richness continuity (Gilroy and Edwards, 2017). For example, in the Colombian Andes, while land sharing retained as many species of dung beetles and birds than land sparing at 500 m distance from primary forests, as the separation between farmland and primary forest increased, land sparing offered increasingly higher biodiversity retention (Gilroy et al., 2014). Furthermore, a recent review of 78 studies reveals that there are biases in studies based in site region, study scope and methods; where most tropical studies advocated for sparing, non-biodiversity focused studies and opinion pieces favoured sharing (Luskin et al., 2018). These findings open the discussion on how individual perspectives and priorities can shape results.

#### **1.4.1 Land sharing versus land sparing framework in timber harvest**

Only recently, the sharing-sparing framework started to be tested for timber harvest. In land-sharing logging the wood harvest extends throughout the available extraction area, logging at lower to medium intensities, which means to cut less or smaller trees. On the other hand, land-sparing logging involves allocating area of primary forest for preservation, and harvesting the rest using higher intensities (cut more or higher in diameter trees) to meet wood volume goals. A study in Borneo presented predictions of higher abundance and richness in birds, ants and dung beetle communities in forests logged via land sparing (Edwards et al., 2014a). More recently, prediction models using pan-tropical data of carbon stocks and biodiversity, testing for intensity, land tenure and RIL implementation, showed that low intensities combined with RIL offers the best outcomes for biodiversity, but the worst if the low intensity logged land had insecure tenure and used conventional logging methods (Griscom et al., 2018). Thus, sparing land was more beneficial when deforestation was absent. This study also found that carbon loss was higher in low intensity logged forest compared to medium and high intensities. The authors also highlight the importance of RIL and land tenure to reduce carbon and biodiversity loss for any logging intensity range.

#### **1.4.2 Current debate**

The agricultural framework for conservation with land sharing and land sparing has been based on economic models (yield) and classification of species as winners or losers depending on their survival post disturbance (Phalan et al., 2011). Yield models focus on crop efficiency, and advocate for food security (Ewers et al. 2009) and food production, but some argue that this perspective undervalues the benefits of ecosystem services and the real limiting factor between production and conservation is scarcity of land (Fischer et al., 2014). Others argue that food security relies not only on production, but in demand changes and reduction of food waste (Bajželj et al., 2014; Tilman et al., 2011).

Another of the critiques of the sharing-sparing framework is that, in terms of scale, management is contained in farmland areas, risking spared lands to be of insufficient dimensions causing landscape fragmentation and disrupting meta-population dynamics (Laurance et al., 2014). If conservation is the goal, Law et al. (2015) proposed that prospective land-use plans are more beneficial to biodiversity by strategically allocating land for stake-holders and biodiversity needs. When applied at large scale, a study in the Brazilian Cerrado revealed significant benefits for biodiversity and water when planned for specific goals at larger scale (Kennedy et al., 2016). This, of course, would need effective policies and good law regulation at the same scale level of the managed landscape.

Selective logging compares to agriculture in the scale of designated managed lands and the dependence of land tenure and effective policies. However, most logged forests are able to either maintain or recover carbon and biodiversity, they are very likely to represent a porous environment for dispersing individuals maintaining connectivity between primary patches and meta-population dynamics (Edwards et al., 2014b), and recovery potential can be boosted by applying RIL and/or silviculture (Cerullo and Edwards, 2018). This establishes logged forests in a better position for conservation value than agriculture even at the highest intensities (and largest blocks of spared primary forest).

Logging relies upon roads, which as noted above, can cause multiple negative outcomes, making land sharing a riskier option for biodiversity. Nevertheless, valuable timber in spared lands can attract illegal logging or corrupted policies. Additionally, in areas very heavily logged, tree composition might be altered so severely that timber species will never recover there. As selective logging is an extraction-based land use, intensities will depend upon the spatial distribution and density of timber species as well as forest heterogeneity. Therefore, land-use strategies in logging must adapt to this heterogeneity and extrapolate with caution methods used for agriculture.

## **2 Thesis rationale and overview**

The central aim of this research was to evaluate the effects by selective logging in above-ground and soil carbon stocks (Chapters 2 and 3) and tree diversity (Chapter 4) in the Brazilian Amazon, and to evaluate whether land-sharing logging or land-sparing logging would best for conservation. The field survey for this research was conducted in two field seasons (2015-2016) in a logging concession located in FLONA do Jamari, in Rondônia, Brazil.

The Brazilian forest service established a forest concession system for production and services (mainly timber harvest and other forest products) focused in reduced environmental impact and social benefit. The concessions are granted by a bidding process to the enterprises that offer the best prices and logging practices. These forests are operated under a sustainable forest management plan and the logging companies are subject to independent auditing.



Figure 1.1: Selective logging in Jamarí National Forest, under AMATA enterprise management. A) Chainsaw operators cut attached lianas and make preliminary cuts to direct tree felling. B) Harvest aftermath, tree stump and log. C) Main logging road in the concession. D) Main log deck for storage and transport.

Rondônia state was one of the first areas with National Forest areas for logging and historically, went through an extensive deforestation by multiple human activities. By 2003 cumulative forest loss was estimated in 67,764 km<sup>2</sup>. FLONA Jamarí in Rondônia, has an extension of around 46,000 ha and was divided to support three logging concessions for a cycle of 40 years. The surveys were conducted inside the forest management unit number III, coordinated by AMATA enterprise. RIL practices conducted by AMATA include road planning, vine cutting, and directional felling performed by highly trained crews. Prior to logging, they record each tree species ID, diameter at breast height (DBH) and geographic coordinates.



Selective logging can have diverse outcomes for carbon and biodiversity due to the varied techniques used. Logging intensity can be independent from RIL and can vary widely in among regions, countries and policies. In all data chapters, I set half hectare plots in unlogged forest and logged forest with a diverse range of logging intensity. I considered logging intensity at Annual Production Unit (~1500 ha) scale of 20 m<sup>3</sup> and at plot level (0.5 ha) determined by the sum of volume extracted in that area. Then, I calculated carbon stocks from living trees, liana and deadwood pools (Chapter 2); calculated soil carbon stocks from soil samples of bulk density and soil carbon concentration analysis (Chapter 3), and assessed tree species richness, diversity and stem density (Chapter 4). I modelled the effects of logging intensity for each explanatory variable in Chapters 2,3 and 4 and then calculated the predicted outcomes for land-sharing and land-sparing logging scenarios.

The land sharing-sparing debate is oriented toward agriculture and it is argued that is not fitted well for conservation because is a yield-oriented system. Little has been debated in terms of this strategies regarding selective logging. In contrast to plantations and croplands, selective logging system fits better as an extraction model, where loggers seek and select the available timber trees to harvest. Therefore, yield is dependent of the heterogeneity of the forest, as well as the access, availability and density of timber species. Under the land sharing versus land sparing context, intensification in logging can be achieved by selecting bigger trees and/or cutting more trees and by broadening the variety of selected species. To capture the tree availability and variation in logging intensity, I simulated forests of 1500 ha containing spatially explicit trees with volume values in m<sup>3</sup>, randomly drawn from the tree data base provided by AMATA (see Chapter 2). For each forest, I laid over a grid layer of one-hectare resolution, to generate a data base with each tree, their volume and grid location. To simulate land-sharing logging a tree was removed on each hectare through the whole area. Land-sparing logging was emulated by removing all trees per ha, sequentially taking the nearest grid until reaching the yield set with land sharing scenario. In Chapter 3, I used the simulated forests developed in Chapter 2 and adapted the harvest scenarios to fit the effect of logging intensity in soil carbon stocks. In Chapter 4 I assess the outcome for trees >15 cm DBH and trees <15 cm DBH separately, using simulated forests and harvests as in Chapter 2.

In Chapter 5 I summarise the main findings and discuss the performance of the harvest simulations. I also address the practicality of land sharing-sparing on a conservation context, as well with current forest management policies.

## Chapter 2

# Does land-sharing or land-sparing logging best retain tropical carbon stocks?

### Abstract

Selective timber extraction is increasing across the tropics with direct consequences to forest carbon stocks. A key question is how to best manage logging to maximise carbon retention in forest stands. Here we explore whether yield-equivalent alternatives between low intensity harvest strategies applied throughout the stand (land sharing) or higher intensity logging that ensures protection of some primary forests (land sparing) would best protect landscape-level carbon stocks. We first modelled the effects of logging intensity on carbon stocks using direct measurements from 28.5 ha of logged and unlogged forest plots within a logging concession in the Brazilian Amazon that practices reduced-impact logging (RIL). We then simulated land sharing and land sparing outcomes, distinguishing the latter between two methods based on prioritizing either sparing contiguous land (spatially-dependent sparing) or harvesting only highest-yield areas (intensity-dependent sparing). Logging intensity had a negative effect on carbon stocks but positive impact on collateral deadwood biomass. Spatially-dependent sparing on average retained more carbon than did land sharing whilst protecting ~56% of the overall concession area as contiguous unlogged primary forest. Intensity-dependent sparing was most detrimental to carbon stocks despite sparing ~75% of the concession, albeit interspersed by logged patches. Our findings suggest that, considering the range of available timber yields, logging a single forest block; is most effective in retaining carbon within selectively logged concessions, and this provides a practical approach to minimize carbon loss across the tropics. We suggest that mechanisms should be developed to encourage spatially concentrated higher-intensity logging, to minimize carbon loss, with the added benefit of less extensive road networks.

# 1 Introduction

Tropical forests contain the largest above-ground biomass carbon stocks, representing 30.8% of the global forest carbon sink (Pan et al., 2011), thereby having a vital role in precluding severe climate change. Carbon emissions from rapid deforestation and forest degradation, which is centred in the tropics, are second only to the burning of fossil fuels (Le Quéré et al., 2015). Within tropical forests, selective logging—the targeted harvesting of commercially valuable trees (Edwards et al., 2014b)—is the most widespread driver of degradation. About one fifth of all tropical forests worldwide have been allocated to selective logging, covering 4 million km<sup>2</sup> (Asner et al., 2009).

Following one cycle of selective logging, tropical forest loses on average 24% of carbon stocks, but this amount can vary greatly (from 3 to 53%) across the tropics depending on harvestable timber stocks, logging intensity and extraction techniques (Putz et al., 2012). While carbon stocks are lost from harvested timber and associated deadwood in crowns, most carbon emissions result from residual damage to surrounding vegetation and the creation of logging infrastructure (Pearson et al., 2014). Poor practices and highly intensive logging therefore result in a high volume of damaged or lost biomass, which leads to carbon emissions comparable to those from deforestation, given that selectively logged forest are substantially more extensive than deforested area (Asner, 2005; Huang and Asner, 2010).

To meet timber demands, while minimizing adverse impacts on the forests, two logging strategies have been suggested: land sparing (LSP) and land sharing (LSH), which aim to reach a specific target yield (timber volume and/or net profit) by adjusting harvest intensity and area (Edwards et al., 2014a). Under land sparing, logged areas are intensively harvested allowing a portion of unlogged land to be set aside for conservation, whereas under land sharing, all available land is designated to low intensity harvest. There also exists a continuum between these two extremes of intermediate intensities and/or mixed strategies (Fischer et al., 2008; Lin and Fuller, 2013). Either of these strategies could be applied when using improved logging methods aimed to reduce the detrimental environmental impacts but not timber yields (i.e., reduced-impact logging, RIL; Putz et al., 2008), and thus enhance longer-term sustainability.

This framework has been used to understand how to best protect biodiversity in selectively logged landscapes (Edwards et al., 2014a; Griscom et al., 2018). For example, land-sparing logging in Borneo showed a higher abundance and species richness of birds, dung beetles and ants. Additionally, focusing on Amazonian dung beetles, there are non-linear declines in species richness and biomass with increasing yield, such that

even low yields can cause substantial biodiversity losses, suggesting that land sparing would be the optimal solution (França et al., 2017).

How land-sparing and land-sharing logging impacts carbon stocks is less well understood. A meta-analysis showed a clear negative effect of logging intensity on aboveground tree biomass (Martin et al., 2015). Most recently, a modelling study using pan-tropical data predicted higher carbon loss with land sharing after two logging events within 60 years, practicing RIL and assuming no deforestation risk (Griscom et al., 2018). However, to date there has not been an empirical test of whether land-sparing or land-sharing logging would best protect carbon stocks in a natural tropical forest system.

In this study, we focused on the Brazilian Amazon, where 460,000 ha of national forests have been granted as governmental logging concessions over the last decade (Azevedo-Ramos et al., 2015), with over 30 million hectares of additional national and state forests slated for logging. We investigate the impact of local logging intensities on above-ground forest biomass and then using these data, we simulate the effects of both land sparing and land sharing strategies on carbon stocks.

## 2 Methods

### 2.1 Study site

This study was conducted in the Jamarí National Forest or FLONA do Jamarí, which encompasses the municipal counties of Candeias do Jamarí, Itapuã do Oeste and Cujubim in the State of Rondônia State, Brazil. Dry season spans from May to September/October, when less than 10% of the annual precipitation of 2200-2600 mm/year occurs (IBAMA, 2005). The prevailing vegetation is described as “Floresta Tropical Ombrófila Densa” (Veloso et al., 1991), where large canopy trees of ~40 m in height occur within a mosaic of palm trees *Athalea* and *Astrocaryum* sp.

At FLONA Jamarí, 90,000 ha of forest were designated for timber harvest by the Brazilian Environment Institute (IBAMA) in 2008. This area was divided into three “Forestry Management Units” (UMF), with our sampling sites located on UMF3, where a forest management enterprise (AMATA S/A) was granted access to extract up to 21.5 m<sup>3</sup> of timber per hectare. UMF3 was subdivided into 25 Annual Production Units (UPAs) of varying sizes between 1,600 and 2,050 ha, with timber offtake occurring at a single UPA each year, effectively amounting to a 25-year cutting cycle. In the year prior to harvesting, AMATA deploys an exhaustive pre-harvest census of all stems  $\geq 40$  cm

diameter at breast height (DBH) of the 65 commercially exploited timber species and three protected species, with all stems georeferenced and barcode tagged. Selective logging of target canopy trees ( $\geq 50$  cm DBH) is then carried out during the following dry season, with consecutive logging seasons 2011 to date. AMATA applies Reduced Impact Logging (RIL) practices by trained crews, including vine-cutting of trees to be harvested, directional felling to minimize collateral damage, and sparing of some large individuals of each species as seed producers.

## 2.2 Field survey

We surveyed a total of 57 half-hectare (100 m $\times$ 50 m) plots (28.5 ha in total), including 16 plots in unlogged, old-growth forest that were close ( $\sim 900$  m) to 41 plots in logged forest that had been harvested between 2011 and 2015 (2011=12 plots; 2012=6; 2013=7; 2014=10; 2015=7) (Fig. 2.1). Logged sites were selected according to the number of trees harvested, using spatially explicit, individual tree harvest data provided by AMATA and a GIS-generated harvest density map created using the Arcmap 10.1 software. We selected sites spanning the entire range of tree density and timber volume harvested per 0.5 ha (range: 1 to 9 trees; and 1.9 to 80.3 m<sup>3</sup> timber) observed within this concession.

Plot position was determined by a semi-stratified method, selecting areas that were at least 500 m apart, 60 m from any perennial stream (along which a width of 25 m of un-logged riparian forest was retained) and, to reduce any potential edge effects or influence from illegal logging, 200 m from the main (mining) road and 150 m from any secondary logging roads. Additionally, we consider having the highest range of number of cut trees inside the plots. We mapped all possible sites that fitted best these characteristics and designated a cardinal direction a priori on map to lay the center line on the field. Sites that failed to match cut tree coordinates or were inaccessible were discarded. We measured all live trees and palms, deadwood, and woody lianas inside each plot and estimated their carbon pools. Within the entire 0.5 ha plot, we sampled live trees and arborescent palms  $\geq 15$  cm DBH, and all live small trees and palms  $\geq 10$ – $< 15$  cm DBH, live woody lianas, and deadwood within a nested subplot of 100 m $\times$ 5 m along the plot centre line. Stumps inside the plot were counted and cross-referenced with AMATA's database to measure intensity of logging.

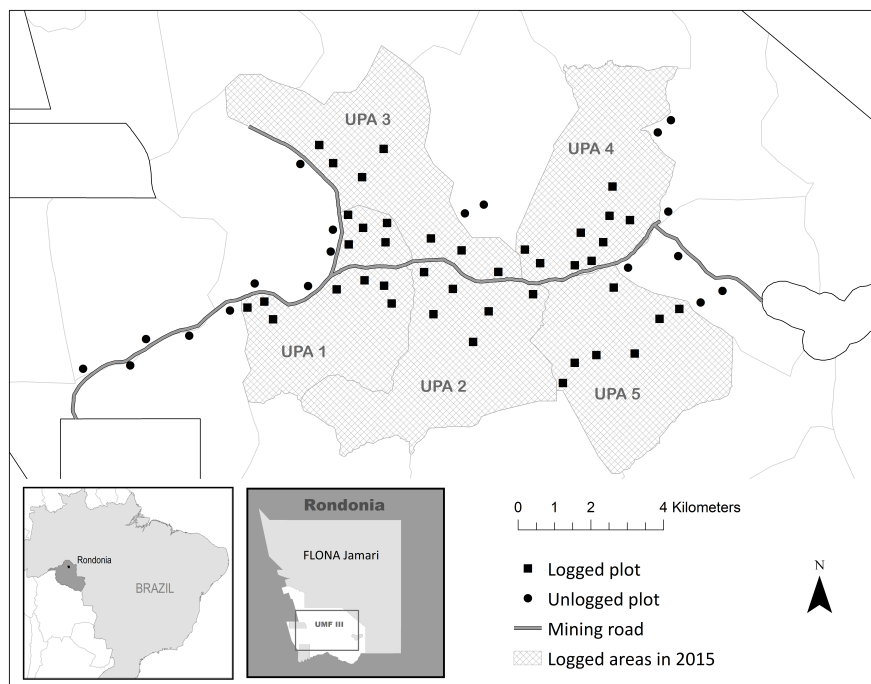


Figure 2.1: Location of study plots across the logging concession at the Jamarí National Forest, Rondônia, southwestern Brazilian Amazon. Numbers of Annual production units (UPA) correspond to each year along a harvest sequence of five UPAs (amounting to a total area of 91,837 ha) beginning with UPA1 (from 2011 to 2015).

### 2.3 Aboveground biomass of live trees, palms and woody lianas

All trees  $\geq 15$  cm DBH within each plot and all small trees  $\geq 10$ – $< 15$  cm DBH, were tagged and their DBH measured. Whenever a tree forked below 1.30 m ( $n = 3$ ), it was recorded as two individuals. Non-palms and palm trees were identified to species level in the field by an expert parobotanist (Alexandre E. Santos) with 25 years of experience in the central-southwestern Amazon. For biomass estimations, species wood density values were taken from the Global Wood Density Database (Chave et al., 2009) and the supporting information in Fauset et al. (2015). Biomass was estimated using the diameter-height allometric equation described in Chave et al. (2014), which was extended and enhanced from Chave et al. (2005). The equation is location-specific, using temperature and precipitation seasonality from the Worldclim and climatic water deficit databases (Fick and Hijmans, 2017).

For palms  $\geq 15$  cm DBH in plots and  $\geq 10$  – $< 15$  cm DBH in the nested subplot, we measured DBH and height using a clinometer. We then used the genus specific equations defined by Goodman et al. (2013) that were derived from direct measures based on an extensive data set of the most common Amazonian palm species. All woody lianas inside

the nested subplots were recorded at 130 cm above ground and otherwise measured as described in the protocol by Gerwing (2006) and using a diameter-based equation for Amazonian forests for biomass conversion (Gehring et al., 2004). Aggregate live phytomass was converted to carbon using the 45.35% proportion (Martin and Thomas, 2011).

## 2.4 Deadwood

All ground or standing deadwood logs and branches  $\geq 10$  cm diameter and  $\geq 1$  m in length were measured. Only the fraction of any deadwood piece that was inside the plot was measured, and logs that were more than half buried on the ground or that were completely hollow were not recorded. Stump volume was estimated by measuring height and surface diameters, assuming a cylinder shape with elliptical base area. All stumps were considered as deadwood for carbon calculations, since all recent stumps died within a year. For fallen woody debris, we measured the length and diameter at both ends (D1, D2); fallen tree crowns and tree branches were measured using branches as separate units. In the case of standing deadwood, we measured the base diameter, DBH and height using a digital clinometer, and then estimated the top diameter using the taper function of Chambers et al. (2000). Volume of each deadwood segment was calculated using the frustum of a cone formula (Baker et al., 2007). Biomass was then estimated by applying a pre-defined deadwood density for tropical forests of  $0.33 \text{ g/cm}^3$  (Chambers et al., 2000), which was then transformed into carbon content at 47.35% (Martin and Thomas, 2011).

To determine if deadwood pieces were a product of natural tree falls or damage from logging (i.e. tree cut, residual crushing, or skidder trail), we carefully evaluated the context of each felled tree in terms of direction, crown position, forest gap and residual damage from felling. In addition, we mapped all cut stumps of known identity (barcode tags had been nailed to each post-cut stump) and the crowns of logged trees that fell inside the plot, including those whose stumps were outside of the plot. These data acquisition steps were conservative in defining a deadwood segment as resulting from logging damage, and any item that did not show obvious signs of resulting from logging was classified as natural tree-falls.

## 2.5 Plot-level carbon stocks and damage by logging

Total carbon per plot was computed by adding the carbon stocks of living non-palm and palm trees, lianas and deadwood, extrapolating from sub-plots to scale to 0.5 ha. Total deadwood stocks per plot that resulted from logging were estimated from the deadwood (crown and stump) from felled trees and deadwood from secondary damage following:

$$C_{\text{damage by logging}} = C_{\text{crown}} + C_{\text{stump}} + C_{\text{secondary damage}}$$

## 2.6 Data analysis

### 2.6.1 Effects of logging intensity on carbon stocks

All statistical analyses were conducted using the R platform version 1.0.136. To evaluate the continuous effect of logging intensity on carbon stocks, we fitted a linear regression model and included years from logging and proportion of trees <per plot as fixed effects. To address the influence of large trees on carbon measurements (Sist et al., 2014), we set three DBH classes from 15 cm to 60 cm, 60 cm to 100 and above 100 cm DBH. Trees above 60 cm has been used as limit to delimit large trees class (Sist et al., 2014; Feldpausch et al., 2005). Trees bigger than 60cm represented close to half of the above ground biomass (46.9%) and trees above 100 cm DBH represented around a fourth of the above ground biomass (23.6%) . We then calculated the proportion of individuals in plot for each class and included them as an explanatory variable on the linear model. Only the proportion of trees >100 cm had significative influence ( $p > 0.05$ ,  $R^2 = 0.61$ ) on the changes in carbon inside the plots. To assess collinearity between possible variables, we used pairwise tests, correlation coefficients, and variance inflation factors (VIF). We found strong collinearity between logging intensity and number of trees, and logging intensity determined by wood volume ( $r = 0.79$ ). We thus decided to use logging intensity by volume values, since these define amounts of timber sold to market, which we sqrt-transformed to reduce spread caused by large values. We also evaluated how logging intensity affects deadwood volumes by fitting a linear regression model, and testing carbon values from deadwood produced by logging as a function of logging intensity and years since logging. Additionally, to asses if there was no selection bias from the loggers by choosing areas in advance with higher timber density, we added bole and residual volume carbon values to logged areas to compare it with unlogged plots. We did not find indication for any systematic variation between logged and unlogged plots (Fig. A.2).

### 2.6.2 Simulating land sparing vs land sharing scenarios

**UPAs simulation—** To examine the remaining carbon after timber extraction under both land sparing and land sharing scenarios, we first simulated spatially explicit UPAs using tree coordinates and volume data provided by AMATA, which included the concession areas, ID and coordinates of all 53376 surveyed trees, harvest status and estimated timber volume. From this data base, we selected trees larger than 50 cm DBH and those which had not been classified as protected or in areas excluded from logging (Fig. A.1). We determined a clumped spatial distribution



using the nearest neighbour statistic and Ripley's K (Haase, 1995). We then fitted a cluster model on the point data occurring only in logged areas, using the *kkpm* function from the *spatstat* package (Baddeley and Turner, 2004), and used the intensity of the Poisson process of cluster centres, the radius of the clusters and the mean number of points per cluster to generate a simulated point process. These represented trees within a 1,500 ha UPA, which is the average operational logging area per UPA at Jamarí, and then overlaid a 30×50 ha grid (resulting in a total of 1,500 grid cells) (Fig. A.3). This spatial simulation assumes potential variation in terms of local logging intensity at the grid cell scale by including a wide range of both canopy timber tree densities (range = 0 –34) and potential volumetric offtakes (range = 0 –231.9 m<sup>3</sup>) within 1-ha cells. We did not account differences between the 65 commercial species in terms of ID, DBH or other metric.

**Simulating land-sharing and land-sparing harvests—** Under both land-sharing and land-sparing scenarios, we simulated harvests that reached an average timber yield of 20 m<sup>3</sup> ha<sup>-1</sup>, the currently maximum harvest quota set for National Forests in Brazil and specifically for FLONA Jamarí (Azevedo-Ramos et al., 2015). To simulate land-sharing logging, we built a function that randomly selects one tree per grid cell (1 ha), from which extract a volume value in m<sup>3</sup> that represents intensity. The harvest continues through the entire area and repeats the cycle if necessary, until an average intensity of 20 m<sup>3</sup> ha<sup>-1</sup> (i.e., 37,500 mm<sup>3</sup> harvested in total across the UPA) is reached. The sum of volumes in each grid represents the local intensity in a determined cell (ha). To address the variation in maximum local logging intensities, provided by the forest simulations, we set a maximum of 70 m<sup>3</sup> under the land-sharing scenario. To address the variation in maximum local logging intensities, provided by the forest simulations, we set a maximum of 70 m<sup>3</sup> under the land sharing scenario. To simulate land-sparing logging, we selected every available timber tree within a grid cell and repeating this process across grid cells until the same average volume per ha was reached as under the land-sharing scenario. We approached the spatial variation in local maximum intensities under land-sparing harvest by either (1) prioritizing contiguous spared land (spatially-dependent sparing) or (2) logging the highest intensities available (intensity-dependent sparing). Spatially-dependent sparing thus, simulates logging the maximum potential harvest in each consecutive grid cell until attaining the land-sharing scenario limit and, in doing so, sparing the remaining contiguous area as an entire intact block. Intensity-dependent sparing simulates logging in the cell with the highest local volume regardless of spatial location, and so on, until attaining the land-sharing scenario limit. Therefore, spared land is spread across the concession and is interspersed with patches of

intensively logged forest (Fig. 2.2).

**Predicting carbon values**— To calculate the aggregate UPA-scale carbon stocks for both land sharing and land sparing simulations, we used our linear regression model (described above) to predict carbon stocks one year after logging. We used the mean proportions of large emergent trees (>100 cm DBH) across the simulated UPAs in our predictions. For each grid cell that had been logged, we used the volume of harvested trees as our intensity value, and for unlogged grid cells we used the model intercept as 0 intensity. We then calculated the total remaining carbon stocks per hectare for each of our 100 simulated UPAs, compared between our two harvest strategies.

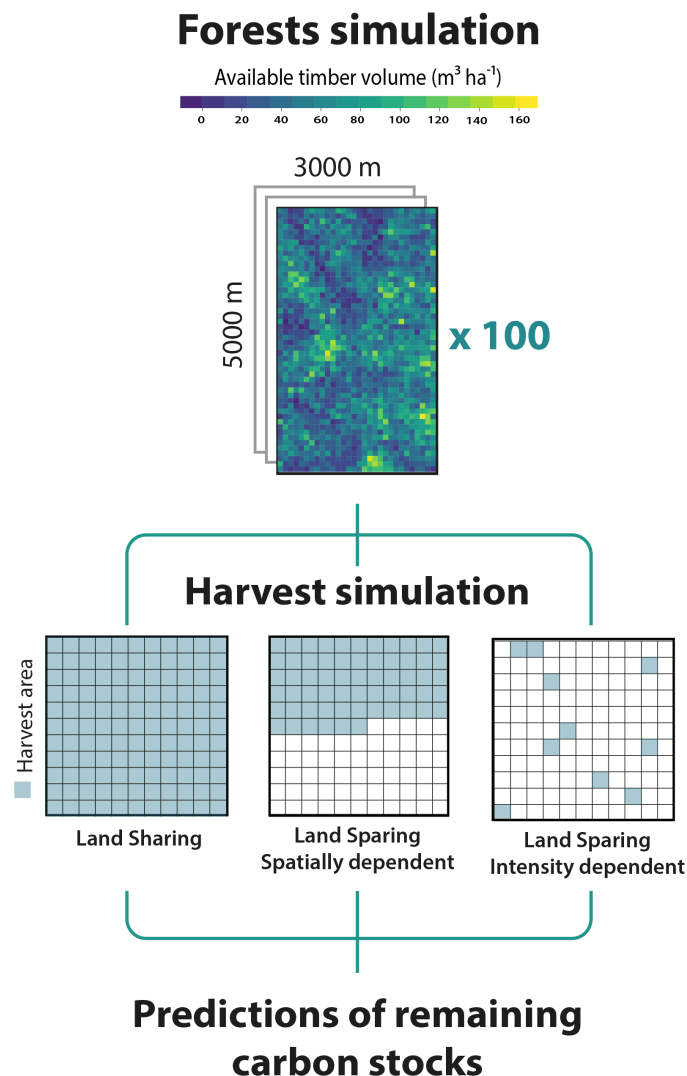


Figure 2.2: Schematic representation of land sharing and land sparing scenarios of harvest strategy

## 3 Results

### 3.1 Carbon stocks in unlogged and logged forest

We recorded a total of 2,743 trees and 1,270 deadwood pieces from 16 unlogged forest plots, and 5,145 trees and 5,895 deadwood pieces from 41 logged forest plots. Live trees above 15 cm DBH contributed most to overall carbon stocks, representing 86.5% and 85.2% of above-ground biomass in unlogged and logged forest, respectively (Fig. 2.3). Carbon stocks in unlogged forest plots ( $92.8 \pm 30.02 \text{ Mg } 0.5 \text{ ha}^{-1}$ ) were marginally higher than those in logged forest plots ( $85.7 \pm 25.13 \text{ Mg } 0.5 \text{ ha}^{-1}$ ), but this difference was not significant when a linear regression was fitted ( $p = 0.48$ ).

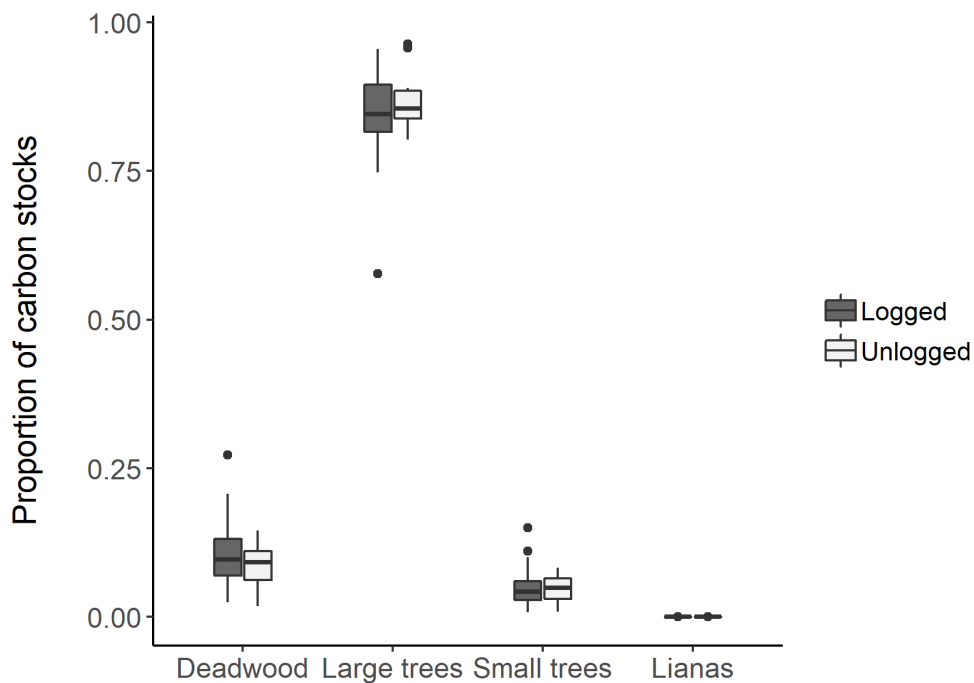


Figure 2.3: Proportion of carbon stocks ( $\text{Mg } 0.5 \text{ ha}^{-1}$ ) present in logged and unlogged forest plots by carbon pool source.

### 3.2 Effects of logging intensity in carbon stocks and deadwood

Carbon stocks decreased significantly with higher logging intensity (estimate =  $-4.206$ ,  $p < 0.003$ ,  $R^2 = 0.62$ ) (Fig 2.4A), and the proportion of large trees was also important in explaining the change in carbon stocks across levels of logging intensity. As expected, deadwood production induced by logging increased with logging intensity (estimate =  $0.955$ ,  $p < 0.001$ ,  $R^2 = 0.46$ ) (Fig 2.4B). Effects on remaining carbon stocks estimates from years after logging were proven non-significant ( $p > 0.1$ ).

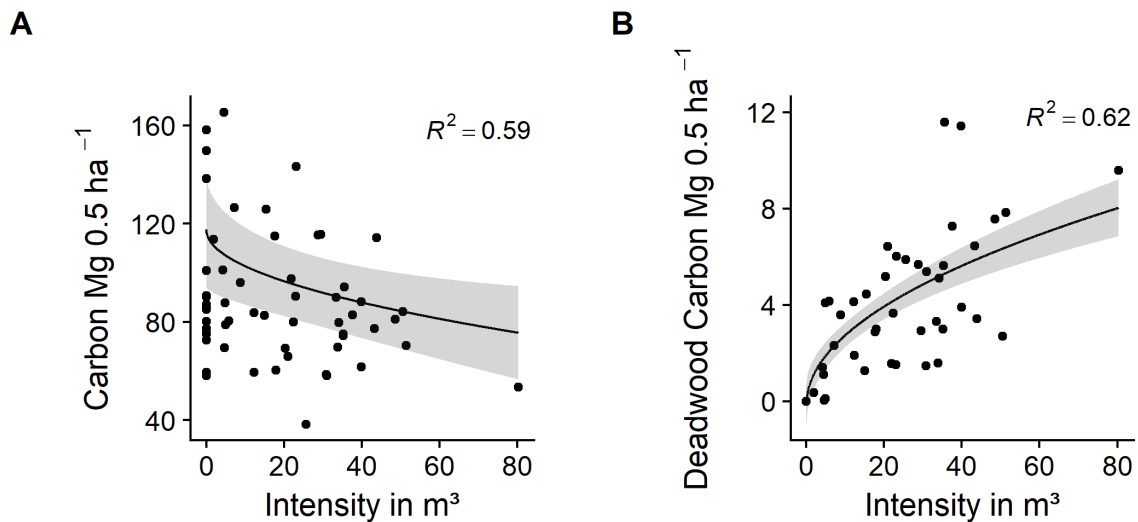


Figure 2.4: Effects of logging intensity (timber offtake in  $\text{m}^3$ ). (A) On total carbon pools per plot (B) On deadwood resulting from logging damage. Grey areas indicate 95% confidence intervals.

### 3.3 Land sparing vs land sharing scenarios

Spatially-dependent sparing resulted in the logging of  $636.4 \pm 51.7$  ha per 1,500 ha, leaving an average of 57.6% of the area set aside as unlogged primary forest. This is twice the harvested area when compared with intensity-dependent sparing ( $369.4 \pm 50.7$  ha logged, 75.4% of spared forest). However, spatially-dependent land sparing scenarios on average retained  $26.5 \text{ Mg ha}^{-1}$  more carbon per hectare than land sharing, and  $36.6 \text{ Mg ha}^{-1}$  more carbon than intensity-dependent sparing (Fig. 2.5). Intensity-dependent sparing performed marginally worse ( $9.9 \text{ Mg ha}^{-1}$  lower) than did land sharing.

Local intensities from all 100 simulated UPAs ranged from  $0.9$  to  $70 \text{ m}^3 \text{ ha}^{-1}$  in land sharing with a mean of  $22.7 \pm 8.8 \text{ m}^3 \text{ ha}^{-1}$ . By contrast, local mean intensity within the intensity-dependent sparing scenario was  $91.8 \pm 20 \text{ m}^3 \text{ ha}^{-1}$ , ranging from  $56.4$  to  $231.9 \text{ m}^3 \text{ ha}^{-1}$ . Spatially-dependent sparing intensities were intermediate between the other two strategies (from  $1.03$  to  $231.9 \text{ m}^3 \text{ ha}^{-1}$ ) with a mean of  $53.3 \pm 28.1 \text{ m}^3 \text{ ha}^{-1}$  (Fig. A.4). The relationship between strategies did not show differences across lower ( $15 \text{ m}^3 \text{ ha}^{-1}$ ) or higher ( $40 \text{ m}^3 \text{ ha}^{-1}$ ) timber extraction quotas in terms of harvest strategy performance (Fig. A.5).

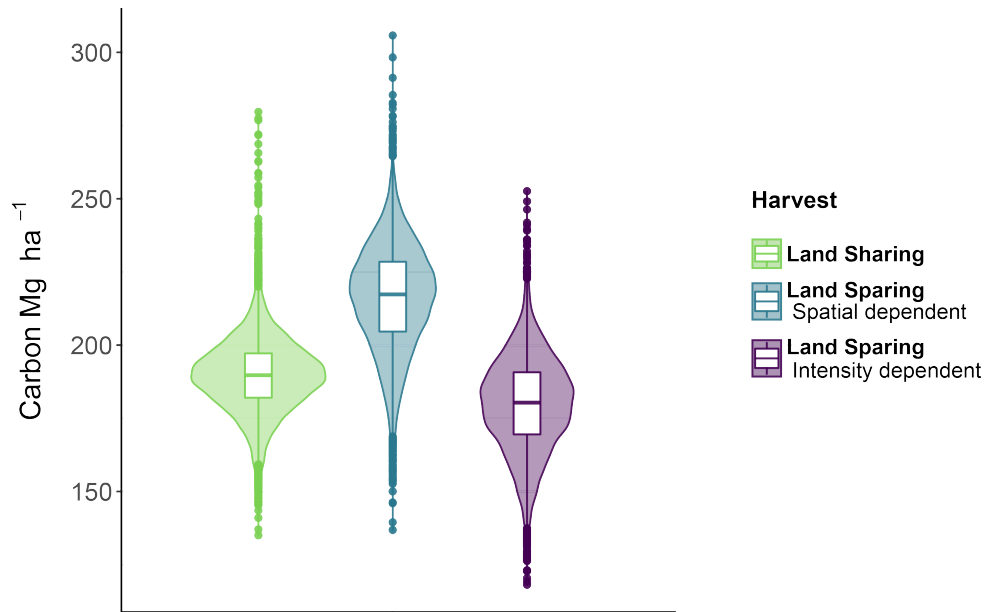


Figure 2.5: Differences in predicted forest carbon stocks within selectively logged forest following three different timber harvest strategies—(1) land sharing, (2) spatially-dependent sparing, and (3) intensity-dependent sparing—based on 100 simulated Annual Production Units (UPAs).

## 4 Discussion

We explored how to best retain aboveground carbon stocks in selectively logged Amazonian forest by implementing potentially competing timber harvest strategies based on either land sparing or land sharing. Using field estimates of carbon stocks and logging intensities, we predicted remaining carbon stocks under different simulated harvest strategies. Scenarios using spatially-dependent sparing retained the highest amount of forest carbon, leaving intact as unlogged primary forest more than half of any given ~1500-ha UPA.

Mean carbon values in our study fell within the range of reported western Amazonian carbon stock estimates (Gibbs et al., 2007; Houghton et al., 2008). However, in contrast with many findings elsewhere (Putz et al., 2012; West et al., 2014) and against our expectations, there were no differences in carbon stocks between logged and unlogged forests. The RIL timber extraction methods used by AMATA at our study landscape (including directional felling, liana cutting and road planning) combined with low logging intensities likely reduces structural forest disturbance in logged areas. Recent studies on low-intensity logging combined with RIL practices suggest that this can often prevent high rates of carbon loss, resulting in selectively logged forests with similar post-harvest carbon stocks compared to neighbouring unlogged areas (Longo et al., 2016).

The occurrence and density of very large trees in both logged and unlogged UPAs can also explain these similarities. Brazilian logging companies are legally required to set-aside protected tree species and non-timber forest resources, as well as 10% of all canopy trees of any given species as seeders, which are usually mature trees. Studies across the tropics have documented that large trees make an overwhelmingly important contribution to carbon stocks estimates (Carlson et al., 2017; Sist et al., 2014; Slik et al., 2013; Feldpausch et al., 2005). This framework, however, solely pertains to data collected after harvest and the variation in logging intensity may be confounded with any pre-existing site variables that influence above ground biomass. The similarity in carbon stocks between logged and unlogged forests may also suggest that unlogged UPAs have been bypassed by loggers in favour of allocating their initial harvests to UPAs with higher tree densities and therefore carbon, such that there is no discernible differences in carbon stocks after logging in relation to primary forests. However, we did not find any differences in variation between unlogged forest and logged plots with added lost carbon from harvest. Our results may be improved with before and after comparisons, however, space for time substitution is more convenient for time-budgeted research and allows to take more samples (Buyantuyev et al., 2012)

The reduction of carbon stocks at sites that were heavily disturbed by logging supports a recent meta-analysis (Martin et al., 2015). High logging intensities result from the extraction of larger and/or more trees, resulting in higher tree damage, broken canopies and tree mortality rates (Pereira et al., 2002; Sist et al., 2014). Deadwood biomass generated by logging represented only 10% of the total carbon stocks in our low-intensity RIL forest, contrasting with over 50% of necromass that could be produced at higher intensities under conventional logging practices (Pfeifer et al., 2015). Thus, our study provides further support for the notion that low-intensity logging combined with stringent RIL practices often reduce tree mortality and carbon loss (Dionisio et al., 2017; Medjibe et al., 2011; Miller et al., 2011). However, timber yields at lower harvest intensities are reduced, thereby inducing the potential need to expand the overall logging area to meet revenue targets and/or market demand.

Our simulations allowed us to treat selective logging as an extraction model with local variation in naturally occurring yields. This provided the option to implement land-sparing logging under two different scenarios, either sparing an extensive contiguous area of primary forest (spatially-dependent land sparing) or prioritizing the highest yielding areas (intensity-dependent land sparing). We found that intensity-dependent sparing, despite requiring only a quarter of the area, was the least efficient at retaining forest carbon, which reinforces the argument that extremely high intensities

can be strongly detrimental to carbon retention (Rozak et al., 2018; Gerwing, 2006). Alternatively, spatially-dependent sparing resulted in the greatest amount of carbon retention, with 26.5 Mg C ha<sup>-1</sup> (12.03% higher) over land sharing whilst sparing over half of any given UPA area as unlogged primary forest. This suggests that prioritizing area over intensity allows logging enterprises to spare land while meeting timber quotas, supporting intensive logging as a form of preserving primary forest (França et al., 2017; Griscom et al., 2018).

The ability to spare large blocks of forest would enable retention of many seed trees and natural seedling abundances, with potential benefits for seed dispersal from unlogged areas into adjacent logging disturbed stands. Across the entire concession, this would also likely benefit species diversity, with previous studies from Borneo and the Amazon suggesting that such spared forests are critical to minimize overall biodiversity losses to logging (França et al., 2017; Edwards et al., 2014a). However, a spatially-dependent land sparing scenario can still induce high logging intensities, which would likely result in local forest structure and composition of uncertain recovery potential (Roopsind et al., 2018; Bonnell et al., 2011; Mazzei et al., 2010). This can include large canopy gaps that are particularly prone to desiccation and subsequent wildfires (Cochrane and Laurance, 2008), and over-logged patches would likely have substantially altered biological communities (Burivalova et al., 2014).

We estimated local structural impacts from logging on forest carbon without including logging roads and patios (cleared patches where logs are stored temporarily) as potential sources of carbon emissions from timber harvest. The need for more extensive road networks across all forest areas under land sharing (and to a lesser degree intensity-dependent sparing) is a potentially large disadvantage to both loggers (in terms of operational costs including planning, clearing and creation of log storage decks) and residual forest ecosystem services (in terms of carbon stocks). Beyond carbon loss, logging roads may contribute greatly to the vulnerability of forests to fires by inducing severe desiccation (Kleinschroth and Healey, 2017), with logging road infrastructure development often promoting further land use change (Laurance et al., 2009). In terms of future logging (whether legal or not), spared lands are vulnerable because they represent a source of high-quality timber, while under land sharing, forests remain susceptible to illegal loggers using the extensive road network or further degradation of forest quality following successive rotations as companies may target smaller trees or expand the number of target species.

Even in logged forests that avoid further habitat disturbance, logging roads can erode biodiversity via habitat edge effects that reduce the core area of interior forest

remaining. Such edge effects resulted in altered dung beetles communities in Borneo up to 170 m into the forest (Edwards et al., 2017). They may also prevent movements of some understorey species that prefer the forest interior (Laurance et al., 2004) and enable easy access to the majority of the forest estate by illegal hunters who can rapidly overexploit large-bodied vertebrates if wildlife protection is not enforced properly (Brodie et al., 2015; Poulsen et al., 2011; Laurance et al., 2012).

Avoiding degradation via an early second logging rotation or illegal entry depends strongly on law enforcement and long-term conservation plans. It may also depend upon applying silvicultural (forest restoration) techniques via climber cutting and even planting of timber seedlings to facilitate timber recovery (Cerullo and Edwards, in press). Nevertheless, as long as National and State Forests remain protected in the Amazon, whether by loggers, law enforcement, or both, sparing areas adjacent to more intensively logged patches, appears to offer the most optimal solution for retaining the highest forest carbon stocks following selective logging.





## Chapter 3

# Effects of logging intensity on soil carbon stocks and the benefits of land sparing

### Abstract

The current expansion of selective logging in the tropics, can compromise the capacity of these forests to maintain their carbon stocks. However, the effect from logging disturbance on soil carbon pools is poorly documented in the tropics, compared to temperate forests or other land uses. In this study, we surveyed soil carbon pools in logged forests in the Brazilian Amazon. We evaluated if forests maintained their soil organic carbon pools after logging and in turn, how logging intensity affects soil carbon stocks. Additionally, we explored which of two harvest strategies were best at retaining soil organic carbon: whether using high logging intensities while allocating primary forest (land-sparing logging) or logging extensively using lower intensities (land-sharing logging). We sampled for organic carbon and bulk density in a Brazilian logging concession with areas from one to five years since logging. We estimated logging intensity by the volume extracted in each 0.5 ha plot. Soil organic carbon was compared between unlogged and logged forests and across logging intensities. To test whether land sharing or land sparing retained more soil carbon stocks, we used hypothetical 1500 ha forests. We then simulate harvest emulating land sharing (by using all available land with low intensity) and land sparing (by saving part of the land and using higher intensities) while obtaining equivalent yield. Soil carbon was higher in unlogged forests, but we did not find differences between logging intensities and across years in logged forests. Land sparing scenarios retained 1.5 Mg ha<sup>-1</sup> of more soil carbon stocks when allocating 10% of the area. These results show land-sparing logging benefited from the presence of unlogged forest since logging intensity did not have a significant effect on SOC from one to five years since logging.

# 1 Introduction

Selective logging is rapidly expanding in the tropics under a framework of quasi-sustainable land use. The selective harvest of large, valuable timber trees fragments the closed canopy and causes substantial residual damage to non-harvest trees as timber trees fall and are extracted. Despite this damage, logged forests retain much biodiversity (Edwards et al., 2014b, Chapter 4), although some forest interior species decline, and some edge species increase in abundance (Griscom et al., 2018; Putz et al., 2012), especially at higher logging intensities (Burivalova et al., 2014, Chapter 2) and with poorer logging techniques (Bicknell et al., 2015). With the present massive extent (over 400 million hectares of tropical forest are in the permanent timber estate; Blaser et al. 2011) and future expansion of logging, selective logging raises a particular concern for carbon emissions and subsequent carbon recovery and stocking under the current climate change crisis.

Changes in carbon dynamics caused by selective logging are result mainly from the direct removal of wood and secondary damage of above-ground biomass, leading to increase in tree mortality rates (Pereira et al., 2002; Pearson et al., 2014; Sist et al., 2014) and deadwood (Carlson et al., 2017; Pfeifer et al., 2015). A meta-analysis of 59 studies in selectively logged forests, showed on average a ~24% decline in carbon stocks one year after logging, and a recent pantropical analysis confirmed that logging carbon emissions can vary from 6.8 to 50.7 Mg ha<sup>-1</sup> per harvest. Logging in Eastern Brazilian Amazon resulted in ~20 to 50 Mg ha<sup>-1</sup> more deadwood than undisturbed forest (Keller et al., 2004), while in Malaysia, within twice-logged forests 7–10 years post-harvest, tree necro-mass constituted from a fifth to half of the total above-ground biomass, shifting the carbon flux from sequestration to carbon emissions (Pfeifer et al., 2015). Over time, decomposition takes place, releasing up to 1.2 Mg ha<sup>-1</sup> a year in Central Amazon forests (Chambers et al., 2000). However, despite initial carbon losses, post-logging recovery of above-ground biomass can be rapid, especially when reduced-impact harvest techniques are used, and the volumes extracted are low. Indeed, after just 51 years in a reduced-impact logged forest, above-ground carbon stocks can reach primary forest levels (Huang and Asner, 2010).

As selective logging is increasing in the tropics, there is urgency to examine whether well-managed logged forests can prevent soil organic carbon (SOC) loss, as has been demonstrated for above-ground biomass stocks (Huang and Asner, 2010; Miller et al., 2011). Changes in soil carbon stocks have been extensively documented following conversion from forest to cropland, with declines for decades post clearance (Guillaume et al., 2015; Don et al., 2011; Murty et al., 2002). Forest clearance and near clear-cutting

intensities are much more common in temperate forest, where previous research showed that the effects of logging on SOC impacted negatively on all soil layers (Dean et al., 2017; Achat et al., 2015), while others did not find overall change in soil carbon after harvest (Nave et al., 2010).

Carbon stocks in soil can be influenced by soil type, nutrients, microorganisms and soil biota dynamics, and the synergy between these (Averill et al., 2014; Barbhuiya et al., 2004; Hu et al., 2017; Macdonald et al., 2018; Negrete-Yankelevich et al., 2007). Selective logging causes direct physical disturbance by soil compaction as result of road building, skidders trails and tree fall impacts (Olander et al., 2005; Pinard et al., 2000), which may result in higher bulk density, soil temperature changes and reduction in soil moisture, often followed by erosion (Olander et al., 2005; de Mello-Ivo and Ross, 2006; Guillaume et al., 2015). Logging also alters litterfall volume and increases deadwood mass (Chapter 2, (Pfeifer et al., 2015)), increasing soil organic carbon nutrient release by decomposition; hence, shifting the labile carbon pool which is the first and faster pool to integrate carbon to the soil by microorganisms (Guillaume et al., 2015; Leff et al., 2012; Laurance et al., 2009). Shifts tree community composition by selective logging could indirectly affect soil carbon stocks, as the plant community is strongly involved in C cycling and storage (Fry et al., 2018). Edge effects produced by roads, broad gaps and logging decks can affect the pH and fertility on soil (Magnago et al., 2017). Accordingly, management practices have a direct influence on the soil carbon storage dynamics and logging management should be optimized to enable sustainability on production forests (Jandl et al., 2007). However, key knowledge gaps remain, including how logging intensity and time since logging impact soil carbon, and in turn, whether logging via land sparing (high intensity and saving more primary forest) or land sharing (low intensity over larger scales) would best protect soil carbon at landscape levels.

In this study, we focus on the Brazilian Amazonia, where National and State Forests can be designated for logging, giving concessions to certified companies in exchange for preventing illegal timber harvest and wildlife poaching in extensive and remote areas. We specifically ask (i) how selective logging intensities and time since logging affect soil carbon stocks, and (ii) whether land-sharing or land-sparing logging will stock most soil carbon.

## 2 Methods

### 2.1 Field site

This study was conducted in July and August of 2016 in the Jamarí National Forest or FLONA do Jamarí, which is located between the municipal counties of Candeias do Jamarí, Itapuã do Oeste and Cujubim in the State of Rondônia, Brazil. Dry season spans from May to September/October, when less than 10% of the annual precipitation of 2200-2600  $\text{mm}/\text{year}$  occurs (IBAMA, 2005). Soil types present in the area are classified as “Latossolo Amarelo” and “Latosolo Vermelho-Amarelo” in Brazilian soil classification. Latossols are equivalent to Oxisols in the American denomination, they are described by homogenous yellow/red colour and a uniform distribution of clay content along the soil profile (Ker, 1997). The prevailing vegetation is described as “Floresta Tropical Ombrófila Densa” (Velooso et al., 1991), where large canopy trees of ~40 m in height occur within a mosaic of palm trees *Athalea* and *Astrocaryum* sp.

Jamarí is one of the two National Forests in Rondônia designated for timber harvest in 2008 by the Brazilian Environment Institute (IBAMA). Within Jamarí, the survey was conducted in Forest Management Unit (FMU) number three, encompassing around 46,000 hectares, managed by AMATA SA enterprise, and one of the three concessions inside the 90,000 ha of the FLONA designated for timber extraction. This FMU is divided into 25-year production units (UPA) of ~1800 ha each intended for around 20 cubic meters of wood extraction per year.

### 2.2 Soil survey and analysis

We set 52 survey plots of half hectare (50×100 m), 41 in logged forest and 11 in unlogged. To avoid edge effects, we situated the survey plots at least 500 m from each other, 60 m from rivers, 200 m from the main road and 150 m from secondary roads. We based the survey plot locations on a point density map created from spatial data of all the logged trees across the concession, enabling us to sample across the gradient from low to high intensity logging within the concession. We measured logging intensity by number of harvested trees inside the plot. After verifying the stump presence and serial number in the field, we then obtained the wood volume in cubic meters reported by AMATA.

Inside the plots, we set three sampling points along the 100 m centre line at 25 m, 50 m and 75 m, with a three-meter distance from the line. We decided the direction from the centre line, right or left randomly. We recorded if samples landed in a range of five m radius of proximity to a tree, a stump or under impact area. For the SOC samples we used an auger to take surface samples (0–15 cm) after leaf litter removal and

sub-surface samples (15–30 cm). Bulk density samples were collected from a pit between depth intervals of 0–15 cm and 15–30 cm using a volumetric cylinder Fig. B.1. For every sample point, we recorded the qualitative damage as “no visible damage” “under tree-fall impact zone” and “under natural impact zone” We discarded the variable of soil type, since the soil type “Latossolo amarelo-vermelho” is predominant in the concession, and only two plots were classified with “Latossolo amarelo” soil type.

Samples were analysed for analysis for the percent of total carbon concentration by dry combustion in a CN analyser (Isotopic Ecology Laboratory, Agriculture Nuclear Energy Centre (CENA), Sao Paulo University, Brazil). Soil carbon stocks were calculated following (Ellert et al., 2007):

$$\text{SOC} = \frac{BD \times D \times Cc}{0.001},$$

where  $BD$  is bulk density measured in  $\text{g cm}^{-3}$ ,  $D$  is the depth in centimetres and  $Cc$  is the carbon concentration (%), divided by 0.001 which converts the output to  $\text{Mg ha}^{-1}$ .

## 2.3 Data analysis

In addition to logging intensity in  $\text{m}^3$  and years since logging, we included site spatial location (UPA), elevation and deadwood values (Chapter 2). To describe changes in soil carbon between logged and unlogged forest, we compared the SOC between habitats with a linear model ( $\log(y) = \text{Habitat} + \text{UPA}$ ).

To study the effects of logging intensity on SOC we selected the best performing following the methodology by Zuur et al. (2010). Spatial distance and deadwood were dropped for all models as they did not improve the model fit. Therefore, all models used have the formula for soil carbon:  $\log(y) = \text{intensity} + \text{years} + \text{elevation}$ .

### 2.3.1 Land sparing and land sharing scenarios

To explore the differences between land sparing and land sharing management effects on SOC after logging, we built a hypothetical landscape of 10,000 ha. For land sharing scenarios, we assigned an intensity of  $21 \text{ m}^3 \text{ ha}^{-1}$  for the entire area. For land sparing scenarios, we spared harvest of 10% and 30% of the concession area and adjusted the logging intensity to  $23.33 \text{ m}^3$  and  $30 \text{ m}^3$  respectively to maintain the same yield from the land sparing scenarios. We then predicted the SOC for each management type and each year by fitting a model for 1000 random field plot samples.

### 3 Results

#### 3.1 Soil carbon concentrations and bulk density in unlogged and logged forests

Soil carbon concentration showed an increase from the first 15 cm to the 15–30 cm soil layer (Fig. 3.1B), but there was no significant difference between habitats ( $p > 0.5$ ). We found a marginally, but not significantly, higher bulk density in logged versus primary forest at the first 15 cm depth and at 15–30 cm depth. (Fig. 3.1A). Differences in bulk density between intervals were also marginally higher but not significantly so.

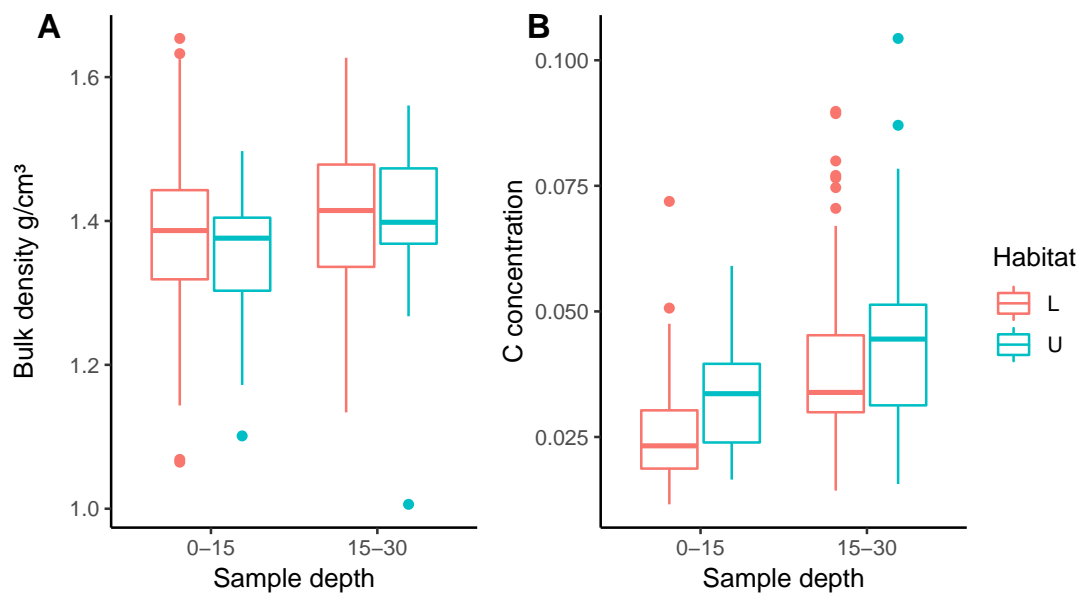


Figure 3.1: Bulk density (A) and soil organic carbon concentrations (B) between logged (L) and unlogged forest (U).

#### 3.2 Impacts of logging intensity on SOC stocks

SOC ranged from 15.63 to 104.4 Mg ha<sup>-1</sup> in unlogged and from 11.59 to 89.8 Mg ha<sup>-1</sup> in logged forest. We found significantly higher soil carbon in unlogged versus logged forest at 0–15 cm depth ( $p < 0.001$ ,  $R^2 = 0.09$ ), and marginally significantly higher at 15–30 cm depth ( $p > 0.07$ ,  $R^2 = 0.01$ ) (Fig. 3.1A). There was significantly higher soil carbon at 15–30 cm than 0–15 cm depth in both unlogged ( $p = 0.002$ ,  $R^2 = 0.12$ ) and logged forest ( $p < 0.001$ ,  $R^2 = 0.31$ ).

Logging intensity was not a good predictor of soil carbon at both 0–15 cm ( $p > 0.8$ ,  $R^2 = 0.28$ ; Fig. 3.2B) and 15–30 cm ( $p > 0.5$ ,  $R^2 = 0.18$ ; Fig. 3.2D) depths. Time since logging was a significant predictor of soil carbon (0–15 depth  $p < 0.5$ ,  $R^2 = 0.21$ ,

15-30 depth  $p > 0.5$ ,  $R^2 = 0.12$ ), with a significant reduction at years three to four at 0–15 cm depth (Fig. 3.2C) and 15–30 cm depth intervals, with high variation at year five (Fig. 3.2F).

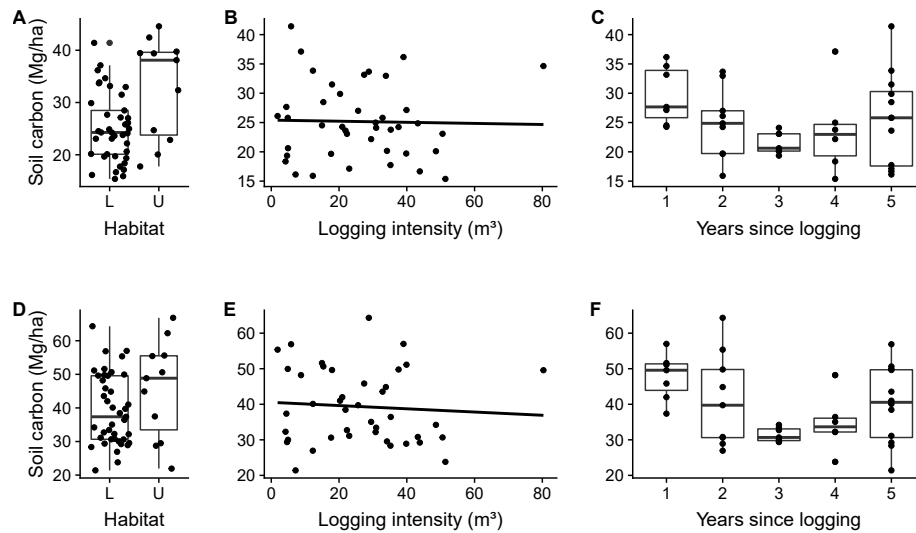


Figure 3.2: Comparison of soil carbon ( $\text{Mg ha}^{-1}$ ) between Habitats (L = Logged, U = unlogged) (A, D), logging intensity in  $\text{m}^3$  (B, E) and years since logging (C, F). Soil carbon values from sample intervals of 0-15 cm (A-C), and 15-30 cm depth (B-F).

### 3.3 Impacts of land-sparing versus land-sharing logging on SOC

Soil carbon stocks did not change with logging intensity, therefore, we did not apply the intensity dependent scenarios in land sparing described in Chapter 2, otherwise predictions on SOC would result in null or non-significant differences compared with other scenarios. Predicted SOC  $\text{Mg ha}^{-1}$  in logged forest was consistently lower under land sharing per year compared to land sparing. SOC  $\text{Mg ha}^{-1}$  values increased as more forest area was spared. Sparing 10% of forest had 1.56 of SOC  $\text{Mg ha}^{-1}$  more than sharing, likewise, sparing 30% of the area showed a mean additional 0.64 SOC  $\text{Mg ha}^{-1}$  per year (Fig. 3.3).

## 4 Discussion

In this study, we compared the carbon pools between unlogged and logged forest, and across a gradient of logging intensities and times since logging in a managed forest using Reduced Impact Logging (RIL). We found a reduction in soil carbon in logged forest, especially after 3–4 years since logging, but that there was no impact of logging intensity. Given the huge scale of selective logging, this underscores that logging represents a



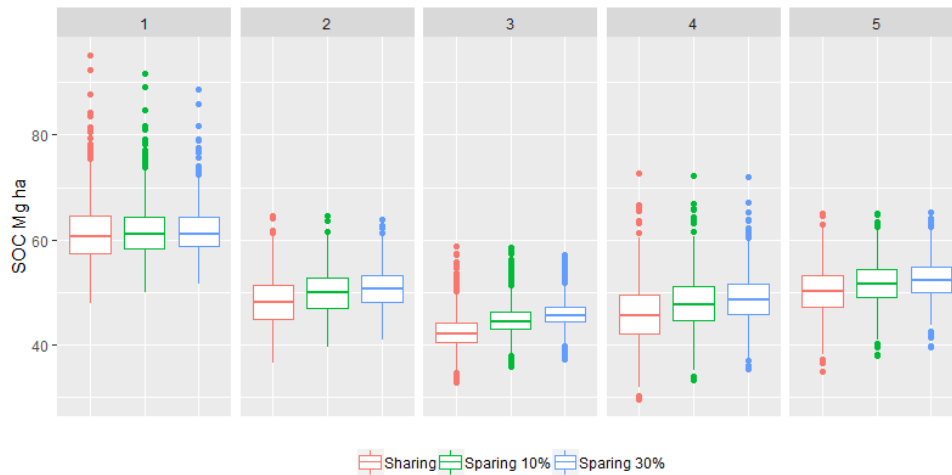


Figure 3.3: SOC in Mg ha<sup>-1</sup> predictions per year for land sharing, land sparing with 10% of unlogged forest retained and land sparing with 30% of unlogged forest retained.

significant source of carbon emissions shortly after harvesting, but that over time there is strong potential for soil carbon recovery as woody debris breaks down into the soil and canopy cover is restored. We found higher SOC level in the 15-30 cm layer in logged forests, which might suggest that the first layer may be more susceptible to bulk density changes caused by logging (Amanuel et al., 2018; Fredericksen and Pariona, 2002). Logging can also lead to the decrease of litterfall which is associated with topsoil carbon contents (Leff et al., 2012).

#### 4.1 Logging effects on soil structure and carbon pool

We found higher bulk density on logged plots, which is a common outcome of disturbance from selective logging (Olander et al., 2005; McNabb et al., 1997). Fredericksen and Pariona (2002) found that soil compaction levels doubled as a result of scarification by skidders in logged Bolivian rain forests. Research in Brazilian latosol showed that skidder trails presented higher levels of bulk density and penetration resistance coupled with lower moisture levels (de Mello-Ivo and Ross, 2006). Consequently, higher logging activity is linked with higher bulk density (McNabb et al., 1997); therefore land-sparing logging high intensities might result in increased soil compaction levels, that can affect carbon sequestration potential and alter regeneration rates for timber trees (Fredericksen and Pariona, 2002; Pinard et al., 2000). Conversely, land-sharing logging extended road network can multiply the exposure to the subsoil after scarification (Kleinschroth and Healey, 2017). A previous study on logging infrastructure in the amazon, showed that logging decks and roads can leave up to 70% of their area as bare soil (Olander et al., 2005), exposing it to further erosion, aggravated by precipitation and the constant machinery and transportation traffic, as roads are often built before the rain season (Macdonald et al., 2018; Holmes et al., 2000). However, in this study we only considered

bulk density and carbon concentration.

Soil carbon stock values in unlogged forest within our south-western Amazonian study area are  $\sim 10 \text{ Mg ha}^{-1}$  higher for the 0–15 cm interval and inside the range for the 15–30 cm depth as reported in De Camargo et al. (1999) for primary forest in eastern Amazonia. The higher value of soil carbon in unlogged than logged forest in the 0–15 cm depth contradicts results found by Berenguer et al. (2014), where there was no difference between logged and primary forest across the entire 0–30 cm depth intervals. However, in their study they used remote-sensing to determine logging intensity, which could suggest that direct sampling is necessary to detect minor changes. Logging directly affects the physical characteristics of the soil via soil compaction altering water infiltration rates, porosity, and, in the case of bulk density, would directly influence the soil carbon pools (Don et al., 2011; Malmer and Grip, 1990).

Differences in logging intensity did not affect soil carbon. This finding contrasts with a global meta-analysis of logging where the highest intensities were related to lower soil carbon stocks (Achat et al., 2015). However, Achat et al. did not have sufficient tropical forest data to address the differences between temperate and tropical forests. Our findings lend support to a study in Malaysian Borneo, which showed no differences in soil disturbance between intensities (volume harvested) for forests under RIL (Pinard et al., 2000).

Soil carbon stocks for both depth intervals declined through years one and three after logging and had a slight recovery in years four and five. Physical alterations can disturb the soil microclimate, and the microbial activity and communities of macro-invertebrates that directly participate in the C cycling (Zummo and Friedland, 2011; Negrete-Yankelevich et al., 2007). The indication of recovery after five years, particularly for the top soil, is likely related to decomposition of the extra litterfall plus deadwood from slash and residual damage (Leff et al., 2012). However, in a review of long-term predictions of soil carbon after logging, forests that suffer a  $\sim 40\%$  loss in above-ground biomass and are continuously logged show a subsequent long-term loss by  $>300$  years (Dean et al., 2017).

## **4.2 Consequences of management on logging effects in SOC**

The predicted values in SOC under the land sparing/land sharing simulation showed a small but favourable effect of sparing, with up to 2.9 of SOC Mg per ha saved by allocating retaining 10% of the land as primary forest. While logged forest still retain much of their carbon, our findings evidence the importance of undisturbed forest (Gibson

et al., 2011). They underline that sparing land from logging would, at landscape scales, reduce overall losses in both the soil (this study) and above-ground (Chapter 2) carbon pools. Thus, avoiding the extensive footprint even of low-intensity logging appears to be critical. Such a land sparing approach would very likely generate benefits for animal (Montejo-Kovacevich et al., 2018; Edwards et al., 2014a) and plant diversity (Chapter 4), potentially benefitting species that rely on rich carbon habitats for their survival (Silva Pedro et al., 2015) and for sensitive litter invertebrate communities that take long time to recover from logging disturbance (Negrete-Yankelevich et al., 2007).

## Chapter 4

# Land-sparing logging best protects tree abundance and diversity in the Amazon

### Abstract

Biodiversity loss is a global issue that leads to loss of ecosystem functions and services, as well as impacting on general human well-being. Compared to other biomes, tropical forests are simultaneously high in biodiversity and exceptionally susceptible to species loss rate under land use change. Timber harvest activities are one of the most extended and prevalent activities in the tropics, leading to further degradation and subsequent land conversion of logged forests. Forest management can play a key role preventing irreparable damage from logging and securing the conservation potential of logged forests for biodiversity. Here, we explored how logging intensity affected tree biodiversity and tested two management strategies to retain more biodiversity: (1) extensive logging with low/moderate intensity (land sharing) and (2) logging more intensively but allocating non-harvest areas (land sparing). We studied the impacts of logging intensity on tree species abundance, richness and diversity and predicting the outcomes of land-sharing and land-sparing logging. We set 0.5 ha plots in unlogged and logged forest in the Brazilian Amazon. We measured logging intensity by wood removed per plot, the surveyed all trees >15 cm DBH and trees >2cm <15 cm DBH in a 0.05 subplot. We modelled the effects of logging intensity on abundance, species richness and diversity and then simulated forest and harvest to determine the outcomes of land-sharing and land-sparing logging. We predicted stem density (abundance ha<sup>-1</sup>) for both tree size classes and species abundance for trees <15 cm. Logging intensity did not explained changes in richness or diversity. Stem density decreased as logging intensity increased in both tree size categories. Land sparing had ~15 more trees >15cm DBH than forests treated with land sharing. With trees <15 cm land sparing and land sharing scenarios had similar stem density, however land-sparing logging benefited from species only present in unlogged forest, predicting three times more tree abundance than land-sharing logging.

# 1 Introduction

Neotropical forests are one of the most hyper-diverse tropical globally, with ~18,000 tree species (Slik et al., 2015), but unfortunately, they are also one of the most vulnerable to anthropogenic land use change. They are currently losing 38.87 million ha per year through deforestation for agriculture and plantations (FAO,2010), while remaining forests are being rapidly degraded by fires and selective logging. Within the Brazilian Amazon—the most important tropical forest globally—the allocation of timber harvest in public forests has been implemented as a sustainable solution to combat deforestation and help regulate vast expanses of forest from illegal logging.

This allocation appears an intuitive decision, since selective logging has less detrimental effects to various taxa when compared with other activities (Gibson et al., 2011), and several studies support that with good management practices a forest can retain most of its biodiversity (Bicknell et al., 2015; Edwards et al., 2014b). However, this allocation has further boosted the expansion of selective logging, which was already very widespread in the Amazon, with 20% harvested between 2000 and 2005 (Asner, 2005).

While Reduced impact logging (RIL) practices cause relatively minor disturbance in carbon and diversity across taxa, especially when contrasted to Conventional Logging (CL), the direct removal of target tree species threatens inbreeding and long-term population viability (Biscaia de la Cerda and Nimmo, 2010). Their harvest also generates substantial physical disturbance in the environment, fragmenting the closed forest canopy, changing the growth and recovery rates of many species (Burivalova et al., 2014). For instance, in a study comparing unlogged and logged forests in Central Africa, target species recruitment in selective logged forest was compromised and there was a shift in dominance of canopy trees from shade tolerant to light tolerant species (Hall et al., 2003).

Within RIL and CL systems, two key variables affect the degree of disturbance recorded: the logging intensity (i.e. the number and size of trees cut) and the time since logging when a study is conducted. Results from a meta-analysis of 23 studies across the tropics showed that tree species richness had an inverse relationship with logging intensity (Martin et al., 2015), although the result was less clear for studies with RIL. Similarly, in a modeling study, Griscom et al. (2018) found higher species loss at higher logging intensities. In eastern Amazonia, tree mortality rates between shade-tolerant and light-demanding species were similar regardless of logging intensity and stabilized after eleven years (Dionisio et al., 2017). However, there remains little consensus of the

impacts of logging intensity on tree communities within the Amazon, and particularly in the southern region where much logging is ongoing.

Since logging affects multiple age stages within the tree community and post-logging recruitment of dispersed seeds, the outcome of logging disturbance extends over time. Initially there is mortality of communities from residual damage caused by falling lumber and log extraction, followed by enhanced growth for surviving trees and generation of conditions suitable for recruitment of light-loving pioneer species. These processes influence the results of biodiversity studies, given that they tend to vary in the time of survey since logging and rarely sample across multiple years (Medjibe et al., 2013; Carreño-Rocabado et al., 2012; Villela et al., 2006; but see Baraloto et al., 2012; Berry et al., 2008). Furthermore, how the influence of time since logging on tree community outcomes intersect with logging intensity is a frontier.

Although RIL can reduce significantly the impacts of logging at a local scale, logging management should be considered at the landscape level. At bigger scales, by modifying logging intensity and harvested area, we can opt for logging extensively with intermediate to low logging intensities (land sharing), or to conduct a more intensive harvest reaching the desired timber yield on less land and allowing the remainder to be protected as primary forest (land sparing) (Edwards et al., 2014b). These strategies for land production have recently been proposed as a form of meeting yield and conservation goals on timber harvest concessions. In Borneo, land sparing promoted higher richness in ant, dung beetle and bird communities (Edwards et al., 2014a); in the Brazilian Amazon land sparing was marginally better for butterflies due to several species retaining much higher abundances than under land sharing (Montejo-Kovacevich et al., 2018); and a recent study using modelled data showed a similar species loss under land sharing and intensified logging scenarios, but with the requirement that the former had secure land tenure (Griscom et al., 2018). However, we still do not know whether land-sparing or land-sharing logging would be the optimal strategy for plant diversity.

In this study we focus on the southern Brazilian Amazon and on trees. Under the current picture of land tenure uncertainty for protected areas in Brazil (Silveira et al., 2018), well-managed forests can be a sustainable option. However, this management requires that we can predict biodiversity responses to logging intensity. Here, we investigate the impact of local logging intensities and recovery through the five years after harvest on tree diversity and composition. We then compare which logging strategy (land sharing or land sparing) better protects tree diversity.

## 2 Methods

### 2.1 Study site

Our study was conducted in the Jamarí National Forest or FLONA do Jamarí, located between the municipal counties of Candeias do Jamarí, Itapuã do Oeste and Cujubim in the State of Rondônia State, Brazil. Dry season spans from May to September/October, when less than 10% of the annual precipitation of 2200–2600 mm/year occurs (IBAMA, 2005). The prevailing vegetation is described as “Floresta Tropical Ombrófila Densa” (Veloso et al., 1991), where large canopy trees of ~40 m in height occur within a mosaic of palm trees *Athalea* and *Astrocaryum* sp. Jamarí is one out of the two National Parks in Rondônia designated for timber harvest in 2008 by the Brazilian Environment Institute (IBAMA), with an extension of 90,000 ha of forest. The survey was conducted in the Forest Management unit number three, one of the three concessions inside, encompassing around 46,000 hectares and managed by AMATA SA enterprise. This is divided in 25-year production units (UPA) of ~1800 ha each intended for around 20 cubic meters of wood extraction per year. They are also allowed to harvest deadwood and other forest products, e.g. fruits and oil.

### 2.2 Tree survey and local logging intensity

We carried out the tree survey over the months of May to July of 2015 and 2016. We set 58 survey plots of half hectare (50 m×100 m), 41 in logged forest and 17 unlogged. Logged areas spanned from 1 to 5 years since logging. To avoid edge effects, we situated the survey plots at least 500 m from each other, 60 m from rivers, 200 m from the main road and 150 m from secondary roads. We based the sampling plots locations on a point density map created from spatial data of all the logged trees across the concession. We recorded all trees inside the plot with 15 cm or more of diameter at breast height (DBH). We also added a nested central subplot situated along the centre line of 100 m long and 5 m wide, where we surveyed trees from 1 cm to less than 15 cm DBH. Trees were identified to species level in the field by an expert parobotanist (Alexandre E. Santos) with 25 years of experience in the central-southwestern Amazon. Species nomenclature status was verified and updated with the `ThePlantList` database (The Plant List, 2013). We measured logging intensity by number of harvested trees inside the plot. After verifying the stump presence and serial number in the field, we then obtained the wood volume in cubic meters reported by AMATA.

## 2.3 Analysis

To compare species richness and diversity between unlogged and logged forest we used rarefaction and prediction curve models that standardize samples by sample size and sample completeness proposed by Chao et al. (2014). These rarefaction/extrapolation models are based on the first three Hill numbers: species richness, the exponential of Shannon's entropy index and the inverse of Simpson's concentration index (Hill, 1973). The 95% confidence intervals were calculated with a bootstrap method based on 100 iterations. To maintain the extrapolated estimator with minimum bias on species richness, we used the double of the sample size.

We fitted generalized linear models to examine the effects of logging intensity and years after logging on species richness and diversity. We used the estimates from the rarefaction and extrapolation analysis to avoid biases caused by plot size and abundance. We also examined the effects of logging intensity on tree density (abundance per ha) we fitted a Poisson generalized linear model and square root transformed logging intensity, as well as the interaction between these. To test for collinearity between variables, we calculated pairwise Pearson correlation coefficients among all metrics within each model.

We used the Importance Value Index (IVI) as data overview for tree species species turnover after logging and for visualization purposes. IVI summarizes relative abundance, frequencies and dominance (basal areas) of each species in each plot and habitat (Curtis and McIntosh, 1951). To calculate species dissimilarity between unlogged and logged forest, we used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017). Non-metric multidimensional scaling (NMDS; Kruskal, 1964) was used to explore the variability in species composition between plots using the Bray-Curtis dissimilarity as distance matrix (Krebs, 1989) with log-transformed abundance data.

### 2.3.1 Land sparing versus land sharing simulations

We explored the differences in stem density between land-sparing and land-sharing logging using the simulated forests and harvests described in Chapter 2. Each of the 100 simulated forests of 1500 ha, has a paired harvest for a land sharing scenario, defined as having at least one logged tree per ha before surpassing the  $20 \text{ m}^3 \text{ ha}^{-1}$  quota for logged timber wood volume. Land sparing scenarios were defined by harvesting all available trees one hectare at a time, until the same yield reached in the land sharing scenario was met. The generated intensity values in  $\text{m}^3$  were used as a predictor, along with the explanatory variables of years since logging from one to five and keeping elevation



constant at mean values. Areas without available trees on both scenarios and spared areas in land-sparing logging were considered as unlogged forest. Number of individuals that occurred in unlogged forest were randomly sampled from the unlogged plots data pool for each species.

We examined how total stem density varied across land sharing versus land sparing scenarios across forests for the 0.5 ha plots using a generalized linear mixed model with Poisson family to predict stem density from logging intensity/volume of timber extracted for each scenario. We then calculated total abundance per hectare for each scenario. We refrained from conducting species-level analyses for large trees >15 cm DBH, since we cannot directly explain impacts of logging intensity on large tree abundances at the individual species level within five years.

Individual species – We also explored how abundances of individual tree species are affected by logging intensity and how they differ between scenarios, focusing on small trees (i.e., with DBH between 2 and 15 cm). We fitted generalized additive models (GAMs) with a Poisson error distribution rather than linear models to allow for non-linear relationships between logging intensity and species abundance. We restricted species-level analyses to species with sufficient samples, selected as those that have at least 0.05% of the total number of individuals for both unlogged and logged forests and that occurred in at least three plots in logged areas.

The species subset represented 25% ( $n = 59$ ) of total species number in 0.05 ha plots (236) for logged forest and 37.3% ( $n = 98$ ) for unlogged forest. This proportion of discarded species is represented by the highly skewed species distribution with most species present at very low occurrence. From the subset species used in the scenarios, 47 species occurred only in unlogged forest in contrast to eight species that were exclusively found within logged forest. The abundance of each species in spared (primary) areas was taken from random samples of the unlogged plots subset. We summed the total predicted abundances across all 100 simulated forests and compared species stem density between the land sparing and land sharing scenarios. Abundance per hectare was calculated by the sum of the prediction values and unlogged areas per hectare for each forest. We then calculated the differences in abundance between land sharing and land sparing to flag the optimal strategy for each modelled species.

### 3 Results

#### 3.1 Tree survey

We recorded a total of 16,775 live trees across 29 ha, belonging to 367 species, 212 genera and 66 families (Table D). Numbers of individuals per 0.5 ha plot ranged from 104 to 153 in unlogged forest and from 74 to 168 in logged. In the 0.05 ha subplots number of individuals ranged from 115 to 204 in unlogged forest and from 67 to 234 in logged. Timber species represented 18.2% of surveyed species and 3.13% of recorded individuals above 15 cm DBH (165 stumps in 20.5 ha). Across UPAs, AMATA cut between 8.1 to 21.1% of individuals censused above 40 cm DBH.

#### 3.2 Diversity

The rarefaction/prediction curves showed no significant differences between habitats (Fig. 4.1). In the 0.5 ha plots (trees >15 cm DBH), confidence intervals overlapped in richness and Simpson estimates. Both had very high predicted sample completeness (0.98 for logged and 0.97 for unlogged). Again, in the 0.05 ha plots (trees >1cm <15cm DBH) confidence intervals overlapped in richness and Simpson estimates. In the case of species richness estimates, logged forest might become higher than unlogged, but beyond double the sample size predictions become biased in this method (Chao et al 2014). The sampling completeness in sub-plots was again very close to completeness (0.99 for logged and 0.97 for unlogged).

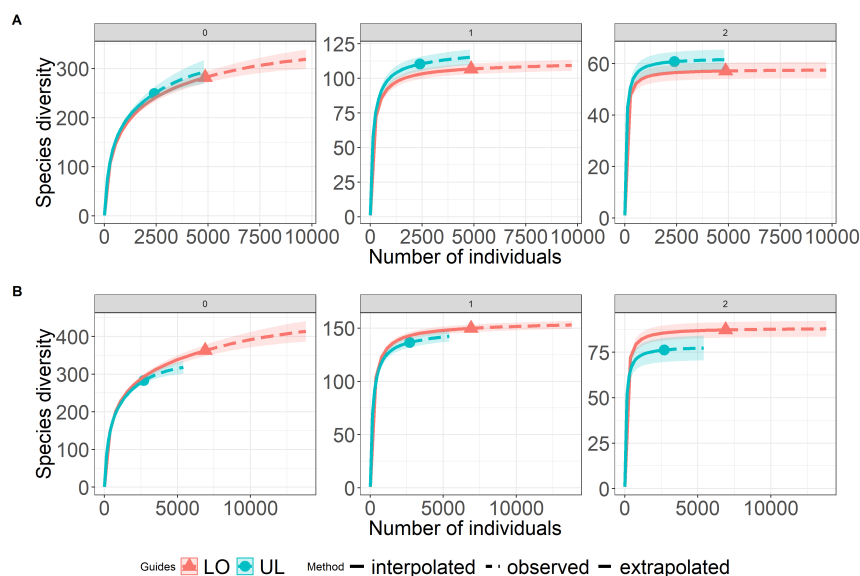


Figure 4.1: Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) of tree diversity based on Hill numbers (0=Richness, 1=Shannon and 2=Simpson) for unlogged and logged forests. A) 0.5 ha plots tree DBH  $\geq 15$ cm, B) 0.05 plots trees >1cm DBH <15 cm. Shaded regions depict the 95% confidence intervals.

When focusing on the impacts of logging intensity on species richness and diversity estimates across time after logging, logging intensity had little effect on species richness in both plot sizes (bigstemsestimate = 0.006,  $SE = 0.01$ ,  $p \gg 0.05$ ; smallstemsestimate = 0.029,  $SE = 0.2$ ,  $p = 0.14$ ). Species richness, however, was higher in the third year (bigstemsestimate = 0.006,  $SE = 0.01$ ,  $p = 0.012$ ; smallstemsestimate = 0.22,  $SE = 0.11$ ,  $p = 0.05$ ). There was no clear effect of either logging intensity or time since logging on Shannon diversity in both 0.5ha plots (estimate  $\ll 0$ ,  $p \gg 0.05$ ) and 0.05 ha plots plot sizes (estimate = 0.005,  $p \gg 0.05$ ).

There was a strong negative effect of logging intensity on stem density for both large trees (estimate = 0.02,  $SE = 0.009$ ,  $p < 0.00$ ) and small class sizes (estimate = -0.05,  $SE = 0.004$ ,  $p \ll 0.00$ ). Time since logging was not a good predictor for either small or big size class trees, the first two years in trees  $\geq 15$  cm showed higher variation but there was no visible change through the five years (bigsetmestimate = 0.015,  $p > 0.5$ ) (Fig. 4.2B). However, Only stem density in both tree size classes  $>15$  cm DBH and  $<15$  cm DBH showed a significant interaction between logging intensity and each year since logging ( $p \gg 0.05$ ) from the Poisson generalized linear model:  $\text{stemdensity} = \text{intensity} * \text{years} + \text{elevation}$ .

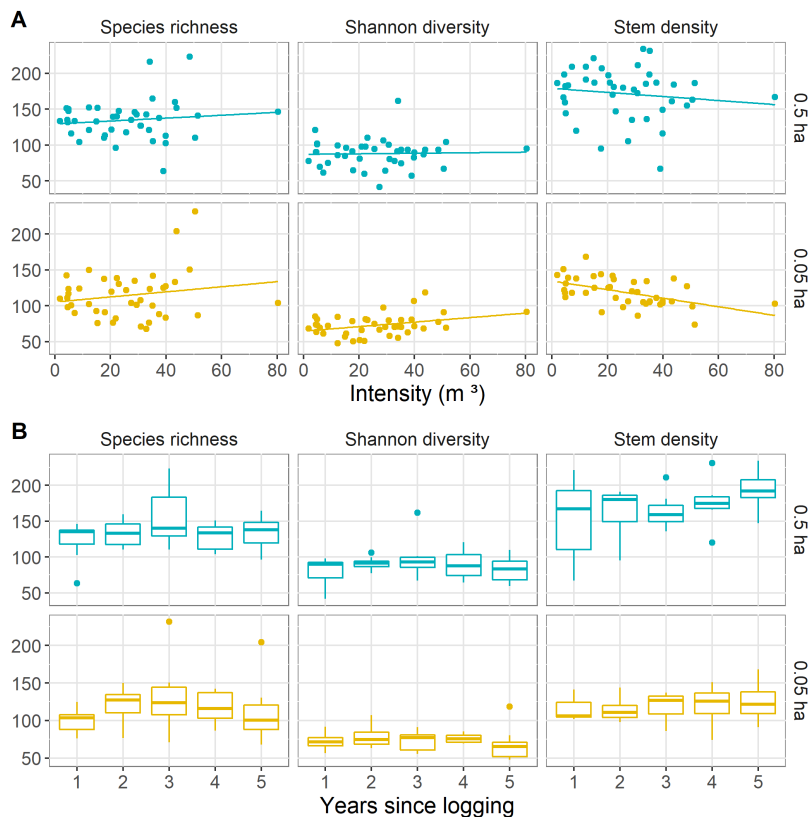


Figure 4.2: Estimates of species richness, Shannon Diversity and Stem Density versus A) Logging intensity and B) Years since logging. Logged plots of 0.5 ha (blue) and 0.05 ha (yellow). Lines represent predicted estimates from the linear models.

Overall species importance values were similar between habitats for both plot sizes. In the 0.5 ha plot, scores were almost identical for the first three ranked species. *Tetragrastis altissima* had the highest species importance value regardless of habitat, surpassing by two times the second ranked species. The biggest difference within species between habitats was found in the target species *Dinizia excelsa* with 3.3 score difference. In 0.05 ha subplots *Hirtela racemosa* and *Sorocea muriculata* had the highest important values (Fig. 4.3).

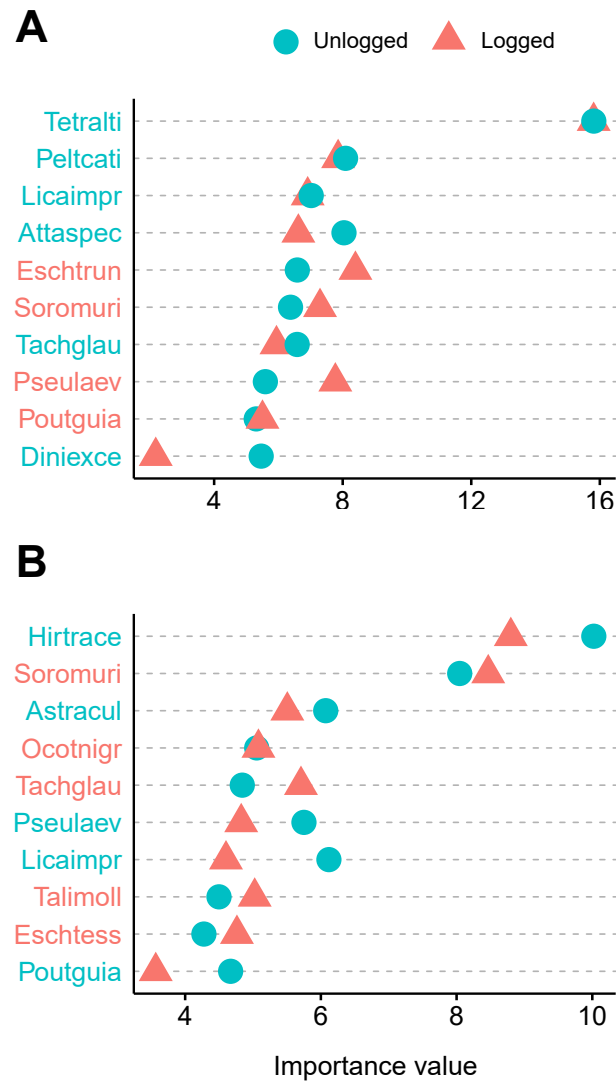


Figure 4.3: Comparative plot between habitats showing species importance value taking unlogged highest ranked species as reference, in A) 0.5 h plots and B) 0.05 ha subplots. Species codes can be matched with scientific names in Appendix D.

### 3.3 Community composition

There was little difference in community composition between unlogged and logged forest at both plot sizes (PERMANOVA,  $p > 0.05$ ). Plotted scores of unlogged and logged plots across NMDS axis 1 and 2 showed similar composition of unlogged forest with the first two years since logging for both plot sizes (Fig. C.1). Intensity and Years after logging were plotted along the NMDS axis 1 as community similarity (Fig. 4.4), Axis 1 which explained a third of the variance for both plot sizes (see Fig. C.1).

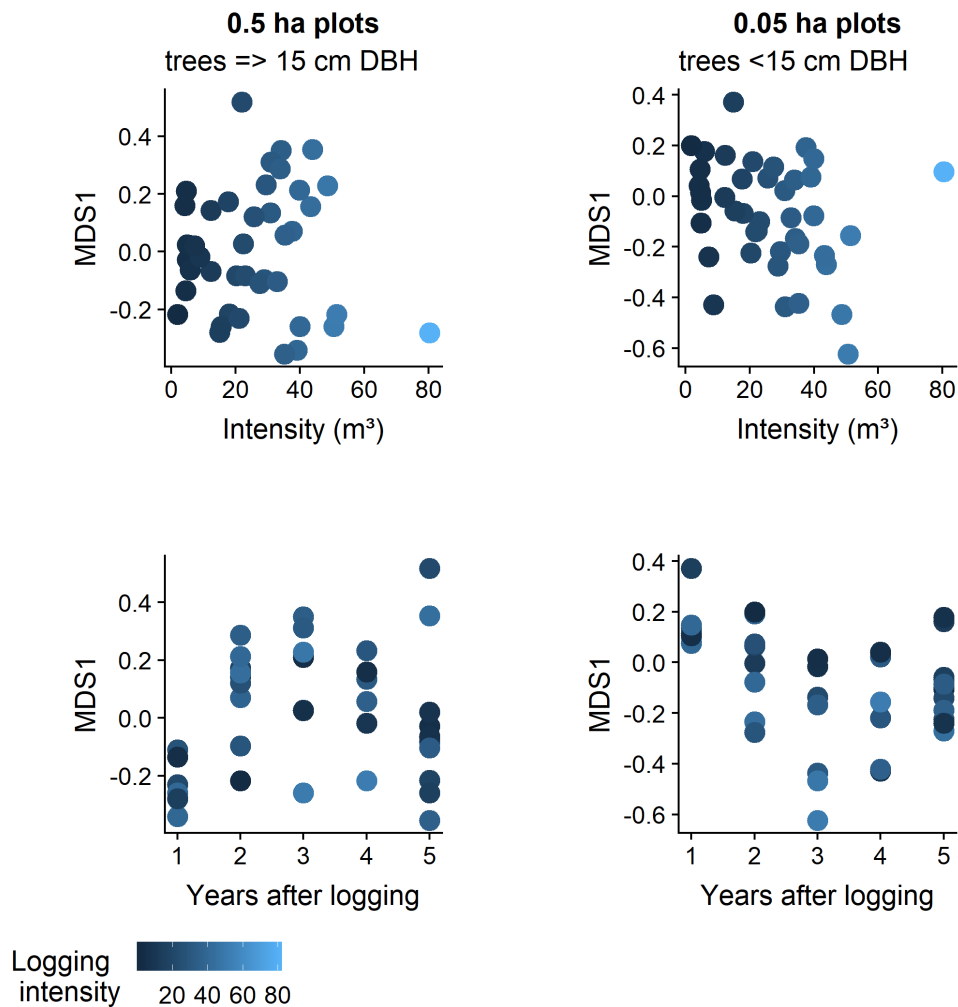


Figure 4.4: Relationship between years and logging intensity with NMDS axis 1 scores. Logging intensity per plot is represented by shades of blue.

### 3.4 Land sparing –land sharing simulations

The scenarios predicted an overall mean of 261.7 ( $SE = 16$ ) large stems ha<sup>-1</sup> for land sparing and a mean of 277 ( $SE = 19.5$ ) stems ha<sup>-1</sup>. When comparing both scenarios, land sparing consistently had ~15 individuals ha<sup>-1</sup> more than the forests with the land sharing scenarios through each year since logging (Fig. 4.5).

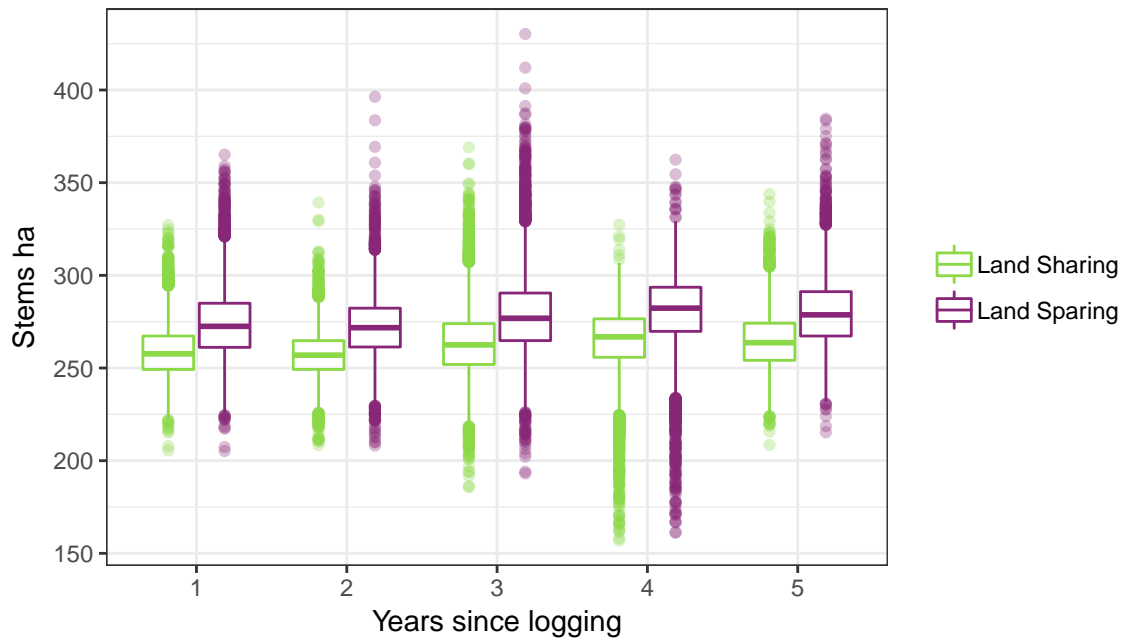


Figure 4.5: Comparison between land sharing and land sparing predicted stem density (individuals ha<sup>-1</sup>) by years since logging in trees  $\geq 15$  cm DBH.

Individual species — Tree species in logged forest presented diverse responses across logging intensities: 10 had a clear decline (Fig. 4.8. F1-F6,G1-G4) and 12 had a clear increase in individuals across intensity (Fig. 4.7. A1-A6, B1-B6), while 9 (Fig. 4.7, 4.8. D1-D6, E1-E3) had higher abundance at medium intensities. Species in Figs. 4.7, 4.8, and 4.9 showed gradual increases or decreases across the years since harvest. Overall predicted stem density highly overlapped between land sharing and land sparing for each year since logging (Fig. C.2), showing no difference in overall predicted abundance.

Focusing on the impact of time since logging on stem density per species, for species that occurred within logged forests, land sharing retained higher abundances of 17 species within four or five of the five modelled years. 27 species had mixed outcomes and 15 species had predominantly higher abundances within land sparing scenarios (Fig. C.3). However, when including the species found only in unlogged areas, the number of species benefitting from land sparing increases from 17 to 64, making land sparing optimal for 70-75% of species within a year (Fig. 4.6).

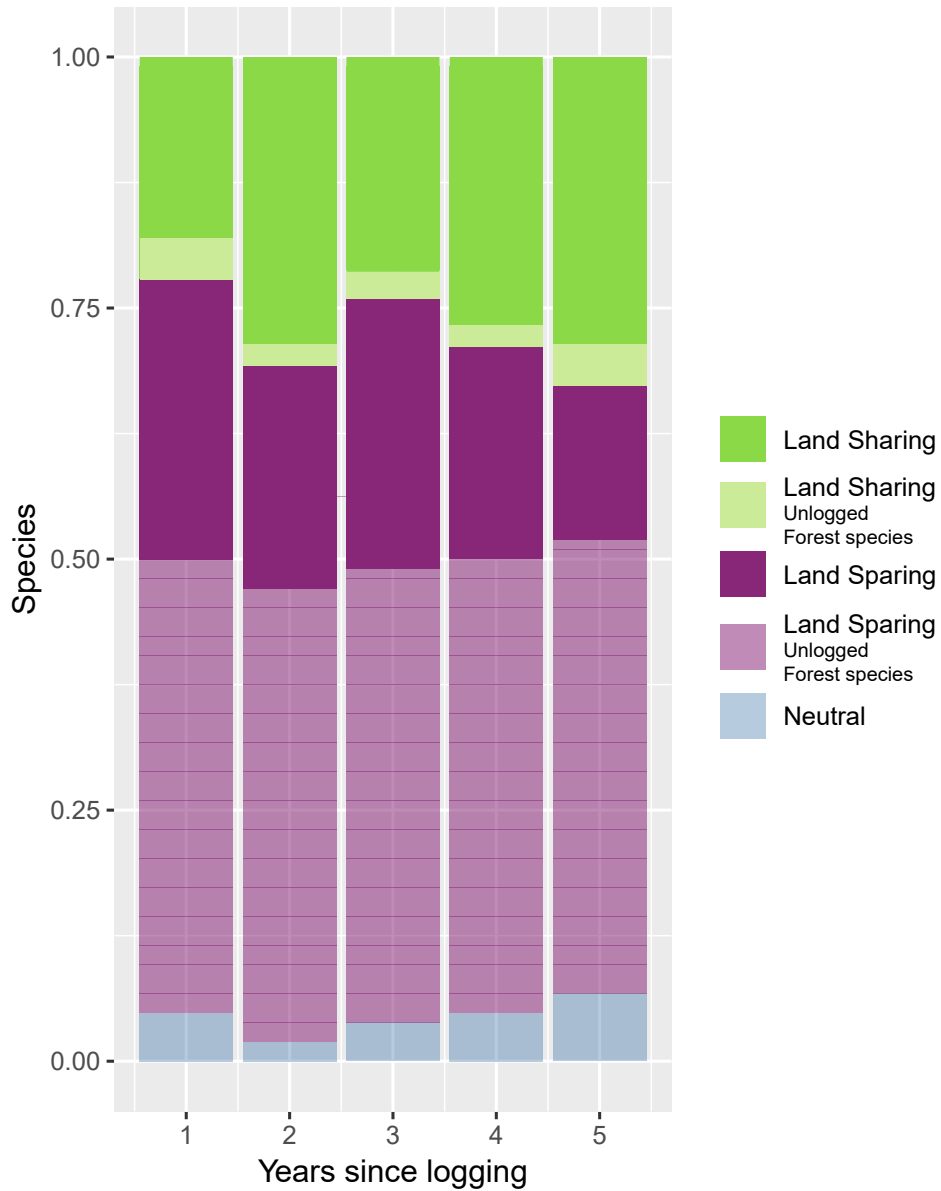


Figure 4.6: Proportion of all species (i.e. including those from primary and logged forest) classified according to the strategy with higher predicted abundance by years since logging. Class was assigned as neutral if the difference between land sharing and land sparring was between -1 and 1. The contribution of species specific to unlogged forest is highlighted in light purple.

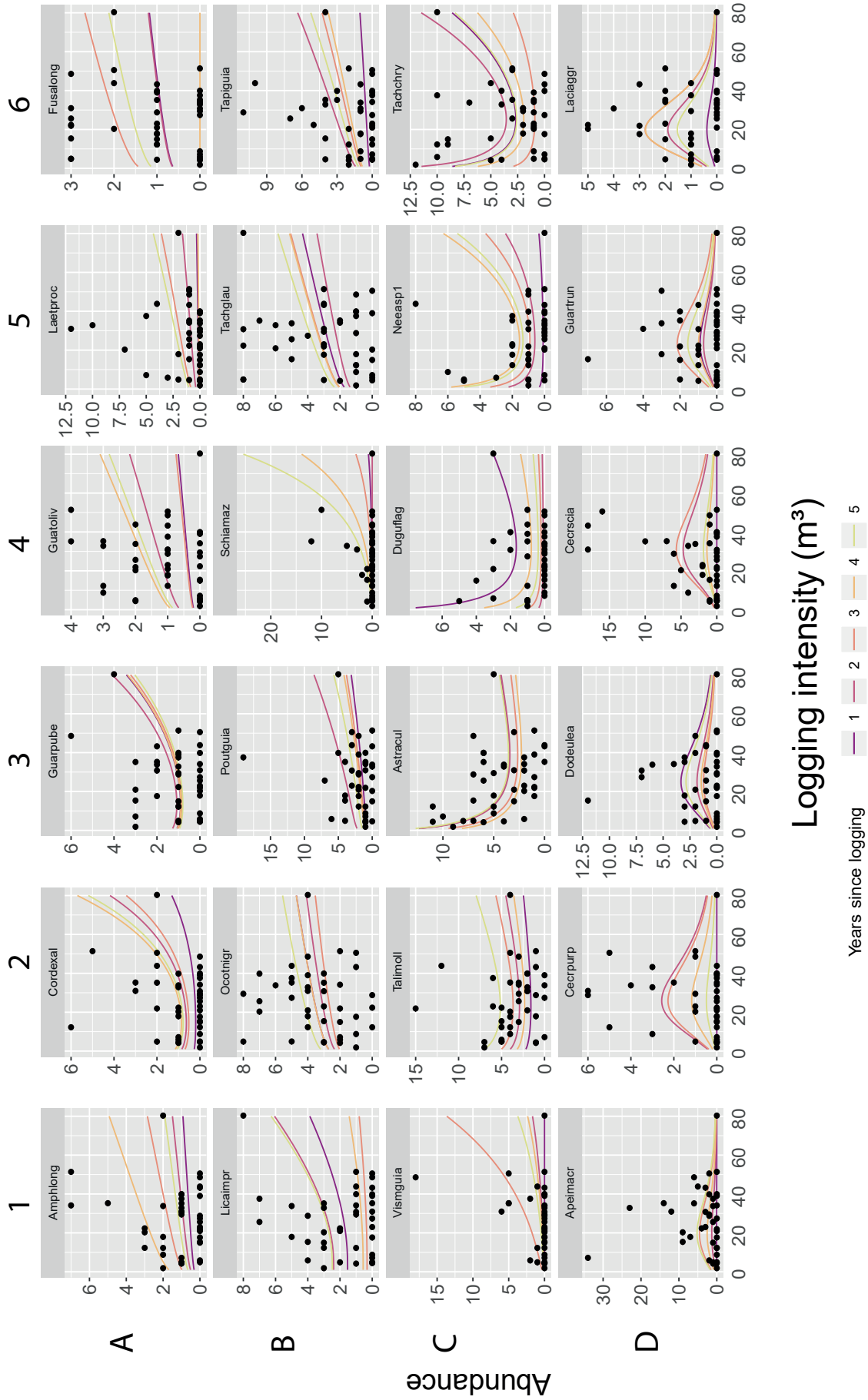


Figure 4.7: Visualization of the relationship between logging intensity and the 59 species in the 0.05 ha plots. Each line represents a fitted generalized additive model per year since logging. Black points are real abundances per plot.



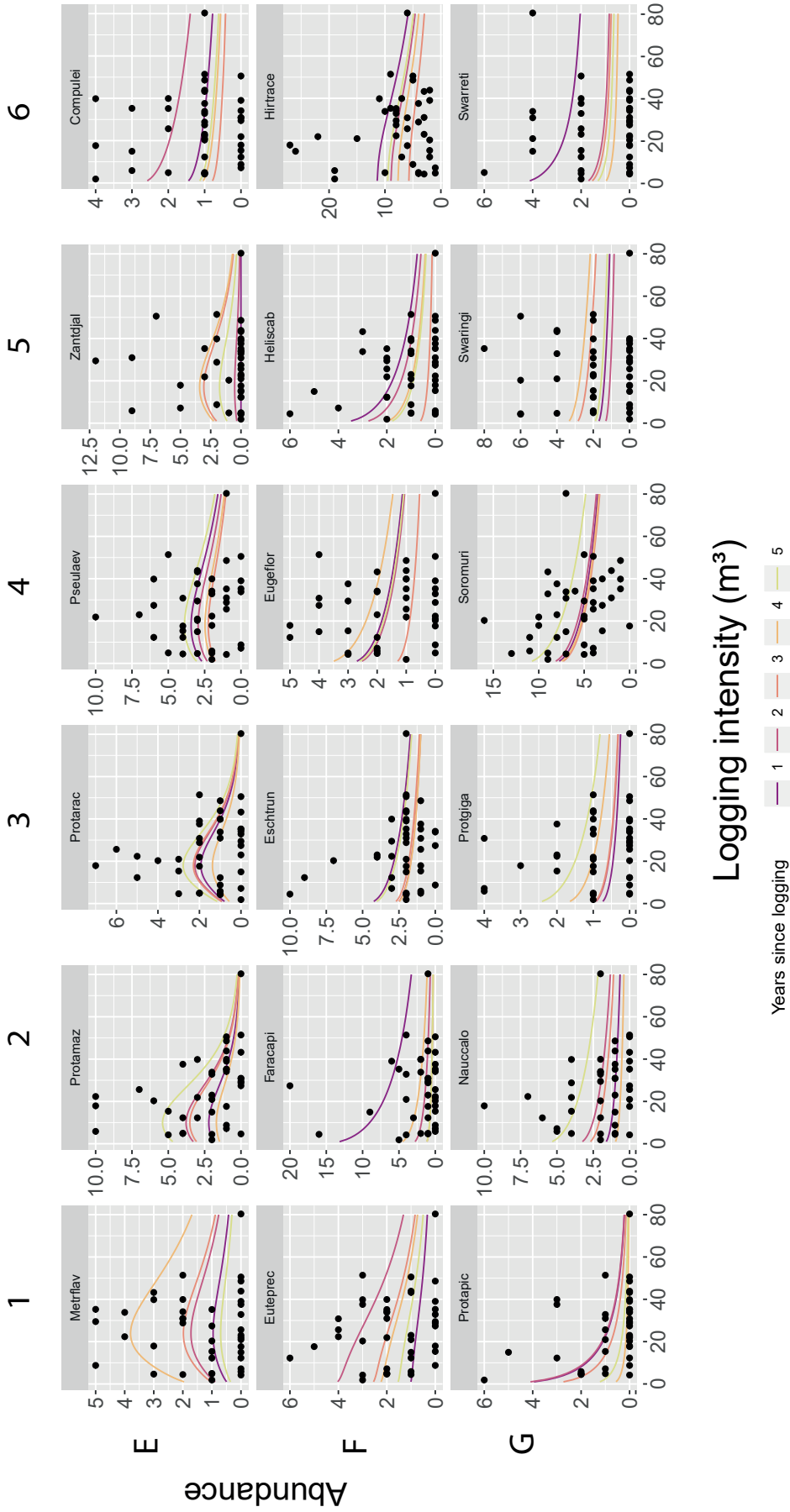
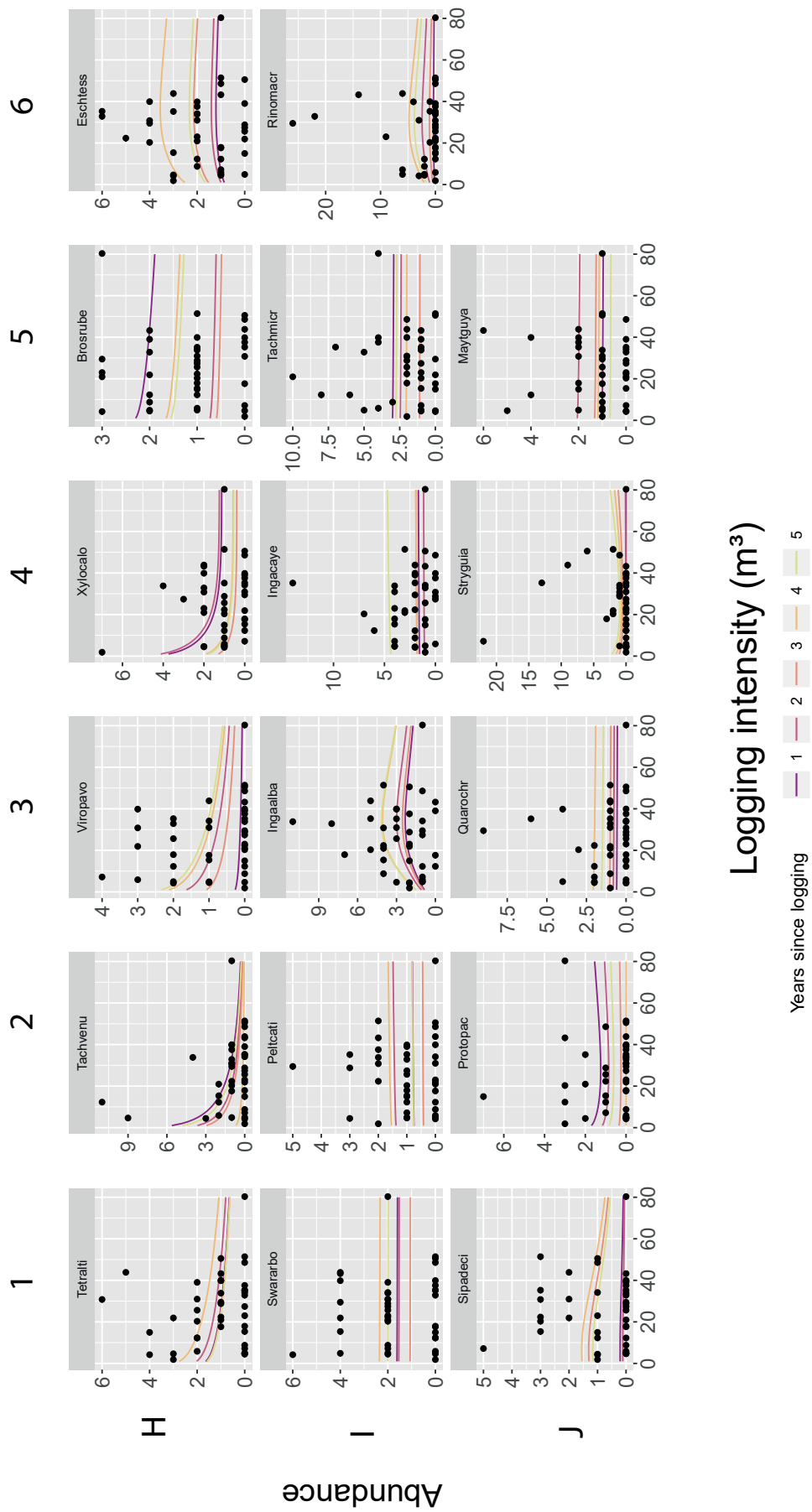


Figure 4.8: Continued from fig. 4.7



## Logging intensity ( $m^3$ )

Years since logging 1 2 3 4 5

Figure 4.9: Continued from fig. 4.8

## 4 Discussion

We studied the effects of logging intensity and time since logging on tree diversity and composition, using plot-specific local intensities and surveys from each of five years since logging. We found no overall differences in species richness between unlogged and logged forest in both plot sizes (0.5 ha and subplot of 0.05 ha). Similar results are found in recent studies that compare unlogged and logged forest in Borneo (Berry et al., 2010; Cleary, 2017; Verburg and van Eijk-Bos, 2003), in South-east Brazil (Villela et al., 2006) and West and Central Africa (Cazzolla Gatti et al., 2015). Both Shannon diversity and Simpson diversity showed similar estimates between habitats. Low and medium logging intensities can behave very similar to natural forest under RIL (Cazzolla Gatti et al., 2015; Imai et al., 2012). This suggests that RIL practices can effectively buffer disturbance changes on diversity.

### 4.1 Diversity and forest structure

We found that logging intensity did not alter species richness. This contrasts with a pantropic meta-analysis (Martin et al., 2015) that reported an initial richness increase at low logging intensities. As richness is a presence-absence metric, changes are only seen if logging intensity is damaging enough to cause species loss or gain, or when growth means that new species enter a size category. For the five years after logging, only the third year revealed a significant increase in richness for both plot sizes. After a couple years of pioneer species growth, young trees experience a peak in mortality rates (Dionisio et al., 2017; Silva Pedro et al., 2015) as the canopy starts to close, reducing light exposure (Montgomery and Chazdon, 2002).

Changes in tree densities in both tree size classes ( $\geq 15$  cm DBH and  $< 15$  cm DBH) were explained by an interaction between logging intensity and time since logging. As expected, logging intensity had a negative effect on tree density, as tree mortality is directly linked with crown and gap size (Jackson et al., 2002), which confirms previous observations for stem density increases after logging (Villela et al., 2006; Hall et al., 2003). In trees  $> 15$  cm DBH, time since logging had a negative effect on density. Larger trees are more vulnerable to damage (Uhl and Vieira, 1989), increasing the probabilities of death during the years after logging.

Diversity was not affected by logging intensity or across years post-harvest in both tree size classes. These results match the finding with Hall et al. (2003); Imai et al. (2012); Cazzolla Gatti et al. (2015). It is well known that gaps promote the growth of light-demanding species (Hubbell et al., 1999), but they can also harbor lower diversity than their undisturbed counterparts (Terborgh et al., 2017; Baker et al., 2016). Our framework,

however, solely pertains for logging intensity measured as volume extracted, without accounting for the size of gap openness.

## **4.2 Community composition**

Tree assemblage in both tree size classes showed during the first two years since harvest, logged plots had a close composition to unlogged plots, especially for trees <15 cm DBH. Damage caused by logging may not be enough to differ from primary forest (Imai et al., 2012), until saplings reach a sufficient size to fall into a sampled size category. The species importance index showed that unlogged and logged forest share dominant species, especially for trees  $\geq 15$  cm DBH. Prior research on Amazonian logged forests support that some species can maintain their dominance after logging (Valverde-Barrantes and Rocha, 2014), suggesting that composition post-disturbance is influenced by the former floristic composition (Chazdon et al., 2007). Timber species can be eventually replaced by non-timber species that share functional traits (e.g. seed mass, wood density). Predictions based on a simulation of growth and yield in an Amazonian logged forest, showed a shift in dominance from emergent species of high value to low-value pioneers Valle et al. (2007). Although logged timber species only represented a 3.13% of individuals above 15 cm DBH and 18% of the recorded species in this study, species with low densities of fertile adults could be at risk of temporary depletion and susceptible to be replaced for the next cycle.

## **4.3 Land sparing versus land sharing logging**

We found that abundance trees above 15 cm DBH is higher in forests harvested with land sparing for every year since logging. This is consistent with multiple studies reporting the secondary damage logging can cause and the increase in adult tree mortality rates (Mazzei et al., 2010; Roopsind et al., 2018) and its negative relationship with logging intensity (Martin et al., 2015). This study shows a limitation of time for space substitution in adult tree predictions as changes through time could be driven by masked variables.

In the abundance predictions for trees <15 cm DBH, the filtered species represented 62.7% for unlogged forests and 75% for logged forests. This reflects the hyper-dominance of some families and species recorded in the Amazon (Fauset et al., 2015) that accentuates the number of rare species, which can be also in a clustered pattern making it hard to sample (Condit et al., 2000). This can influence our simulations since they rely on the available species in logged forests and sample frequency to fit the models. The predictions for overall abundance of small trees did not show differences between land sparing and land sharing, which may be caused by the wide range of species responses to logging intensity. Decline in abundance by logging intensity can suggest sensitive

and shade tolerant species, while an increase in individuals can be reflect of pioneers and light tolerant species (Terborgh et al., 2017; Richardson and Peres, 2016). Our projections assumed that tree species absence is due to logging or secondary damage, however, the data base used for the land sparing-sharing scenarios was delimited by a subset of species that occurred at least on three plots and had at least the 0.05% of individuals. It is common in tropical forests that a few species encompass most of the individuals (Fauset et al., 2015), therefore, by restricting the simulation to the 25% most abundant species the probability of recording species stochastic occurrence decreases. These findings mirror suggestions that land sparing logging would retain more biodiversity in Borneo (Edwards et al., 2014a), and much higher abundance of some butterfly species in the Amazon (Montejo-Kovacevich et al., 2018).

This study again underscores the high conservation value of logged tropical forests, indicating that their protection remains a core goal for conservation. The finding that higher intensity logging has some negative impacts on tree diversity indicates the importance of managing logging effectively. One option, therefore, is to reduce the maximum logging intensity across entire landscapes. However, this 'land sharing' strategy would require more land to be logged to meet a particular yield. Thus, critical is investigating whether higher intensity logging, if coupled with protected areas of primary forest (i.e. land sparing), would protect a higher diversity and abundance of trees at the landscape scale. Findings suggest that land sparing logging will protect more carbon (Chapter 2), while there are modeled suggestions that it will also protect more or similar diversity Griscom et al. (2018).

## Chapter 5

### General discussion

Selective logging in the tropics is becoming more and more relevant under a global change context. The capacity of logged forests to retain carbon and biodiversity will play a crucial role mitigating climate change (Edwards et al., 2014b; Putz et al., 2012), however this can only be achieved under responsible management and effective policies. Differences in logging practices makes challenging the development of a standardized solution. However, the land sharing-sparing approach can help evaluate trade-offs and better direct our conservation goals (Phalan, 2018).

In Chapters 2, 3 and 4, I measured intensity at plot scale, which permitted to discern the effects of logging intensity that may go undetected at bigger scales with RIL practices. Higher logging intensities affected negatively above-ground carbon stocks (Chapter 2) and tree abundances (Chapter 4). The direct and localized damage of tree felling and skid trails is correlated with higher tree mortality rates during and after the disturbance (Mazzei et al., 2010; Asner et al., 2006). This is reflected in both above-ground carbon stocks and tree abundances after logging, underlining the importance of scale when studying the effects of logging. Conversely, soil carbon pools (Chapter 3) and tree richness and diversity (Chapter 4) did not showed significant changes through different logging intensities. Both soil and tree species diversity involve more complex processes that could be reflected best at larger spatial and time scales.

Studies in agriculture based on that compare the retention of biodiversity of land sharing and land sparing have approached simulations based on one single yield metric (Hulme et al., 2013; Phalan et al., 2011). The simplicity of this models can work under an agricultural context where yield is directly controlled. Other studies had used blocks of land built by randomly selecting the survey sites (Williams et al., 2017). Land sharing-sparing studies using logging systems had followed before a similar framework for birds (Edwards et al., 2014a), and butterflies (Montejo-Kovacevich et al., 2018), with successful results as this taxa work better with at large spatial scale surveys. The methods proposed in this study can work at both large and fine scales. In chapter 3 the scenarios were

fitted to lower resolutions, as soil only presented changes between logged and unlogged forests. In Chapters 2 and 4, the methods allowed to detect local intensity changes in above-ground carbon stocks and tree abundance (Chapter 2 and 4), suggesting that might be useful for other static or low range and microhabitats.

With these simulations (introduced in Chapter 2) I showed that natural forest heterogeneity (at least in terms of timber trees availability) can buffer the effects of intensification, making feasible allocating large blocks of primary forest. Additionally, I demonstrated on Chapters 3 and 4 that the spared areas make a relevant contribution to the overall above-ground and soil carbon pools as well as tree abundance retention, positioning land sparing as the preferred strategy. In Chapter 4 I show that of species that occurred unlogged forest benefits highly to land-sparing logging, underlying once again, the importance of primary forests, particularly for aggregated and/or rare species (Condit et al., 2000). The outcomes from land-sharing and land-sparing logging on forests with higher densities timber trees and therefore higher possible wood removal, are yet to be tested with the approach of this study.

## **1 Research limitations**

This research was carried out in one Brazilian logging concession, subjected to a specific government and regulations. Data and results came directly from their logging practices in their first 5 years. Many of other concessions may not share the same sustainable goals, RIL practices, specialized training or precise mapping techniques. Researchers should proceed with caution when comparing these results with data from conventional logging managed forests, which can produce contrasting outcomes for above-ground biomass and biodiversity (Pfeifer et al., 2015; Slade et al., 2011). Conventional logging practices are still prevalent in the timber industry, however, there is increasing evidence that RIL reduces the impacts on biodiversity and carbon loss which is becoming part of logging policy (Bicknell et al., 2014, 2015; Zimmerman and Kormos, 2012; Putz et al., 2008). Since the objective is a practical conservation strategy, any concession or policy that seeks to implement land sparing should apply RIL practices and align their goals with a sustainable logging perspective.

An important limitation throughout this research was the available quality and quantity of the field samples, with a delimited range of logging intensity values for each plot. The availability of sites with a wide range of logging intensities was influenced by spatial restrictions (avoiding getting closer than 500 m from each other) and the accessibility to the sites in the field. The results based on these intensity measures must

be extrapolated with caution. It is known that Amazonian forests have less timber tree density than SE Asia dipterocarp forests, which may produce different outcomes by using land-sparing logging in this highly dense timber forests.

In chapters 2,3 and four, I simulated forests from spatial explicit data, which are delimited by the design of hypothetical concessions without restricted and inaccessible areas, meaning all surface area was considered logging area. With this, edge effect from the fringe with other UPAs, roads and riparian areas were discarded; mainly because the study focuses on direct impacts of selective logging on carbon and biodiversity. Nevertheless, the importance of edge effects must be acknowledged in practice. An important assumption is that each hectare had the same initial values of each explanatory variable (carbon, soil carbon and diversity) that are affected later with logging impacts. These values were taken from bootstrapping unlogged values, therefore limited by the sampling of the unlogged areas.

The concession managed by AMATA enterprise only had 5 years of harvest activities by the time the field survey was carried out. This represents an important limitation, especially when assessing the logging effects in soil carbon and tree diversity which their dynamics involve long-term processes. After disturbance, soil properties can present shifts in nutrient dynamics for the first 16 years (McNabb et al., 1997), nevertheless, drops in plant biomass could result in long-term reduction of soil organic carbon pool (Dean et al., 2017). Moreover, diversity dynamics change constantly over the years operated by different factors caused from disturbance from opening and closing gaps, local variation in light, temperature and humidity, species presence and the functional groups of timber species (Baraloto et al., 2012; Oliveira Filho et al., 2004). This shows the importance of long-term studies for measuring logging effects on soil carbon and diversity; nevertheless, the concession program in Brazil is quite young, along with the policies advocating for a sustainable timber harvest (Azevedo-Ramos et al., 2006). Further studies must be made and can be compared with concessions in Africa, which have longer time operating with a concession scheme (Karsenty et al., 2008). This, however, reveals the novelty and relevance of this research by offering an initial insight of logging effects on highly monitored concessions.

In this study I used space for time (SFT) substitution for my sampling design, which consists in building a chronosequence from the sampled sites at different time stages and has been used to assess anthropogenic impacts in the environment when previous data of the undisturbed area is non-existent (Pickett, 1989). Therefore, studies must assume that pre-disturbance conditions are equivalent in the sampled sites. A study in the Brazilian Amazon assessing the impact of logging on the dung beetle community (França et al.,



2017), reported that before and after surveys showed higher detail in alpha and beta diversity changes than those tested with space for time substitution. However, before and after studies require planning ahead in collaboration with the logging companies, contrary to SFT substitution, which enables to increase the sample size (Buyantuyev et al., 2012). In this study, SFT substitution allowed to survey all logged area at the time, which otherwise would be limited to only two UPAs, forcing to reduce the number of samples or risking sample pseudoreplication. Further studies will be required to address the effects of logging long-term on ecological processes in soil carbon and tree diversity.

## **2 Impacts on ecological mechanisms**

Historically, the timber industry has relied on the over-exploitation of a few timber species halting their reproduction and subsequent local depletion (Pinedo-Vasquez et al., 2001; Martini et al., 1994). This “boom and boost” approach has been common across the tropics; in SE Asia the highly dense dipterocarp forests have been almost depleted with disturbances compared to deforestation (Shearman et al., 2012; Saner et al., 2012), in Amazonian countries is common practice to skew the extraction to a few set of high-value timber species (Veríssimo et al., 1998; Uhl et al., 1991; Schulze et al., 2008a) jeopardizing their recovery for the next harvest cycles (Richardson and Peres, 2016). A similar trend follows the accelerating logging expansion in Africa, as international timber demands increases due the shortage in SE Asian forests (Terheggen, 2010; Laporte et al., 2007). Once the high value species are depleted or inaccessible, loggers often refocus on less valuable species (Barany et al., 2003). Species abundance reduction or loss can erode ecological interactions risking future ecosystem services and sustainability (Valiente-Banuet et al., 2015), however, if managed well, second harvest can retain high levels of biodiversity and maintain a relevant conservation status (Borah et al., 2018; Struebig et al., 2013; Edwards et al., 2011).

The land sparing strategy proposed in this research aims for a sustainable selective logging that will require a long-term planning. Therefore ensuring timber availability for the next cycles is essential to avoid stepping back to conventional or non-sustainable logging practices. Nevertheless, managing timber for industrial profit is a challenging task that impact on an array of ecological factors and processes that often remain largely unexplored (Schulze et al., 2008a). The selective pressure on specific timber species, can drive compositional shifts in the community, that in turn, can influence close related taxa. A study in Indonesian logged forests found that changes in tree community composition influences on mammal species assemblages, suggesting that food availability is a strong determinant for wildlife presence (Jati et al., 2018). In turn, the change in wildlife species as a result of habitat degradation or other pressures, can represent a threat for

tree diversity by the loss of crucial animal dispersers coupled with an increase in seed predators (Markl et al., 2012; Guariguata et al., 2000). At population levels, the decrease in abundance of timber species affects population density and increases the distance between individuals, diminishing the effectiveness of pollen dispersal and facilitating inbreeding (Soliani et al., 2016; Vinson et al., 2015).

Land sparing allows to preserve large blocks of forests while meeting logging volume demands. It is imperative, however, to identify thresholds for vulnerable species (França et al., 2017; Burivalova et al., 2014) and designate logging areas carefully to avoid fragmentation and spatial disruption of species (Magnago et al., 2017). Responses and resilience to logging from timber species are diverse and will depend on specific life traits. Susceptible species will have trouble to regenerate if they are light intolerant or have short lived seeds and saplings (Snook, 1996). Growth rate may be promoted by different factors causing mismatching on timing for minimum cutting size (da Cunha et al., 2016; Sasaki et al., 2016). Some species like *Manilkara huberi* could require around 100 years to recover pre-logging features, making it susceptible to depletion (Castro et al. 2014). Although biomass recovery can be boosted by RIL, functional traits groups (e. g. pioneers, light demanding, shade-tolerant) may also determine species resistance to disturbance (Vidal et al. 2016); additionally, this could influence wood density potential which will determine timber quality (Macpherson et al., 2012). Likewise, species ecological traits might affect silviculture effectiveness and recovery. The endemic dipterocarp *Dryobalanops lanceolata*, maintained seedling recruitment in logged forest compared with those in primary forest, using reducing-damage silviculture (Pillay et al., 2018). Enrichment planting in logging gaps boosted growth in volume of *Schizolobium parahyba var. amazonicum* and shortened the harvest cycle by 13 years (Schwartz et al., 2017). Finally, loggers must take advantage of effective silviculture practices for resilient species and fast growing, giving more time for logging-susceptible species to recover.

### **3 Forest management, conservation and policy**

The land sharing versus land sparing debate can push management in a practical direction for conservation by exploring the trade-offs in each strategy. However, the debate between land sharing and land sparing should be treated different under a selective logging context, which diverges from the land scarcity scope for food production in agriculture (Fischer et al., 2014). First of all, timber is a non-vital commodity and in terms of conservation, logged forests still offer additional environmental services compared to croplands and plantations (Gibson et al., 2011; Edwards et al., 2014b). Therefore, management methods should be specifically developed to address selective

logging characteristics.

Land sparing in the tropics is favoured by conservationists because of the key value of undisturbed old-growth forests (Luskin et al., 2018; Watson et al., 2018; Gibson et al., 2011), however, there is a growing concern whether allocating land can properly fulfil its conservation aims (Balmford et al., 2019). The spatial characteristics of the spared land may vary across countries and landscapes, which can influence yields and the retention of carbon and biodiversity. Hence, area size, shape, location and other characteristics will concern to both loggers and conservationists (De Pellegrin Llorente et al., 2017). The logging industry benefits from the spatial information of resources and transport logistics. Likewise, biodiversity conservation efforts often rely on spatial dynamics of species and landscape (Teixeira et al., 2009; Verheyen et al., 2004). Spatial relationships between forest stands are complex and multifaceted, they are affected by diverse disturbances and processes i.e. fragmentation, edge effects, connectivity, shape and size of allocated areas that will take part of a land-sparing model outcomes (Magnago et al., 2017; Matos et al., 2017; Benchimol and Peres, 2015; Das et al., 2017).

Selective logging can cause small scale fragmentation from large gaps, roads and patios (Broadbent et al., 2008). Additionally, abiotic conditions can be affected by fragmentation and edge effects; a study in Brazilian forest stand, showed that smaller fragments and edge areas presented higher air temperature and reduced humidity (Magnago et al., 2017). Therefore, a highly fragmented land-sparing-logging, meaning a matrix of small fragments, could be counterproductive for conservation purposes. Large blocks of forest (around 1000 ha) retained more bird species than the land-sharing and land-sparing with small fragments scenarios in tropical forests and croplands in Ghana (Lamb et al., 2016). However, the area required for populations will depend of specific demographics and reproduction traits.

Selectively logged forests are less likely to lose environmental functions and connectivity by keeping overlapping canopies. This is fundamental for species to move across the landscape allowing access to food and promoting seed dispersal (Wilson et al., 2007; Grass et al., 2019). However, there is the risk that broad roads, clearings and gaps disrupt connectivity and deter the crossing of bird and mammal potential dispersers (Yguel et al., 2016; Laurance et al., 2009). Additionally, the intensive harvest of timber species with highly aggregated distributions can isolate groups and reduce a big proportion of individuals, causing genetic erosion (Sork and Smouse, 2006). Therefore, to maximize conservation benefits of land-sparing logging, blocks of unlogged forests should be either connected with corridors or placed contiguously, therefore planning is priority to prevent adverse outcomes.

The current concession system in Brazil can help securing land tenure, which is one of the main vulnerabilities of any conservation strategy. Without land tenure, a land-sparing logging would leave areas with valuable timber trees exposed to further logging or illegal trade. Concessions are easier to regulate than small holders, and as the land keeps its protected forests status, land-use change is less likely to happen (Karsenty et al., 2008). The Brazilian government is currently relying on private investors to manage and monitor these forests (Azevedo-Ramos et al., 2015) with additional 7 million hectares planned to be designated for logging activities by 2020 (Serviço Florestal Brasileiro, [www.florestal.gov.br](http://www.florestal.gov.br)). Nevertheless, the potential to diversify selective logging outside National forests can bring social, economic and environmental benefits to private landowners and community managed production forests (Merry et al., 2009; Bray et al., 2003). The landscape allocation proposed by Law (Law et al., 2015) could be a good alternative to prevent further degradation in a long term, by working at regional level with predetermined targets from different stakeholder goals. Under a regional scale, vulnerable and degraded habitats can be prioritized for restoration and long-term use (Rappaport et al., 2015). The multifunctional landscape approach developed by Santika et al. (2015) allows to evaluate the relationship between land-uses and their vulnerability for further conversion. However, implementing large scale plans will require further modification in policies and long-term land-use planning.

## **4 Economic implications of selective logging**

Results in Chapters 2,3 and 4 showed that land sparing can meet timber volume demands while retaining aboveground carbon stocks, soil carbon and tree diversity. Timber harvest is a highly profitable activity; thus, if we want to apply a conservation strategy, we must address the economic implications for implementing practical and viable conservation goals (Boltz et al., 2003). By implementing land-sparing logging, allocating land and harvest intensification must fit in the economic perspective of the logging concession. To make this possible, the benefits of land-sparing logging must be higher than the overall costs that come from intensifying the harvest (e.g. extensive secondary damage, requirement of RIL and intensified silviculture to diminish disturbance). First, the trade-off from allocating land will be contrasted by the cost of holding from cutting valuable and large timber trees with the decrease in operational costs from harvest in a reduced logging area.

Main costs in a logging concession that corresponds to the harvest area besides administration and equipment, entails pre-harvest costs (e.g. inventory, vine cutting, map-making), harvest planning (tree marking, road and log deck planning) and

infrastructure (road and log deck building) (Holmes et al., 2000); which involves the overall transport costs (fuel, maintenance and drivers) and training crews for census and cutting. Choosing the best area for harvest, considering species, prices and abundance by using land-sparing logging, could require a sophisticated planning that will translate in additional required pre-harvest investment. Sparing land also means taking timber trees out of the market, making it harder for certified logging companies to fulfil the growing demand for cheap timber and to compete against uncertified or illegal logging cheaper prices (Bisschop, 2012). However, the reduction in logging area represents a direct reduction of said costs, as a direct result of shrinking the distance of roads and number of logging decks and shortening labour times. Managing a smaller area can also be easier and more efficient to handle, allowing to invest in staff and machinery, making the harvesting process more precise and efficient.

Nevertheless, one of the major challenges for land-sparing logging will be avoiding the counterproductive outcomes that high intensity harvests may produce, which would compromise both economic and conservation goals (Pfeifer et al., 2015; Fisher et al., 2011). Logging can reduce the nutrient availability of the soils (Olander et al., 2005), making silviculture practice less efficient and more expensive, it can also enable the risk of fire, that could represent a long-term disturbance disabling the area for the next harvest (Nepstad et al., 1999). Therefore, reducing logging impacts will be crucial for the implementation of land sparing as a conservation strategy, as we must ensure timber trees availability for the next cycle to keep the spared area un-logged. Despite that RIL practices are being disregarded by loggers due to opportunity costs from additional training, labour and planning (Putz et al., 2000), some studies had demonstrated that by avoiding unnecessary damage in marketable timber, preventing disturbance and maintaining timber production can avoid opportunity costs (Sasaki et al., 2016; Holmes et al., 2000), showing that RIL can be profitable in the long-term.

Expanding DBH cutting thresholds can be another method for intensification. It would allow to cut more trees per hectare and will benefit from bigger trees. However, this method is dangerously close to treat timber as a non-renewable resource (Mæstad, 2001), very common in conventional logging practices by taking all possible timber in one harvest which could be a counterproductive practice for both conservation and economic goals. Higher thresholds will increase cutting cycles time and may reduce growth rates and timber volume (Schulze et al., 2008b)(Schulze et al. 2008). Additionally, they could compromise tree reproduction by logging fertile individuals and have a higher impact on less dense populations (Richardson and Peres, 2016). Intensification by expanding the species timber lists is a practice already implemented by concessions, timber prices depend on species and is often sorted in a class system regarding wood

prices (IBAMA, 2005; Schaafsma et al., 2014). Including more species would affect the profit balance between commodity wood and high-quality timber, higher number of less profitable timber trees will have to be cut to make up for the high profitable timber. Silviculture treatments might be challenging and costly to implement, as the responses vary among tree functional groups (Peña-Claros et al., 2008). Selecting more species can reduce the pressure on the most marketable ones; this, however, can cause greater secondary damage and generating greater gaps putting in risk the recovery of species for the next cycle.

The preserved blocks of intact forests have the potential of benefiting from monetizing ecosystem services and carbon offset payments (Kremen et al., 2000; Edwards et al., 2010). The modified program “Reducing Emissions for Deforestation and Degradation” (REDD+) is an international offset carbon scheme based on economic compensation for the losses caused by avoiding deforestation and degradation (Gibbs et al., 2007). The additional income from these subsidies could promote a sustainable land-sparing logging and prevent land use change by providing short term benefits. However, these programs must balance opportunity, implementation and transaction costs with monetary benefits translated in payments, incentives or subsidies (Rakatama et al., 2017). REDD+ projects are widely varied depending on conservation goals (e.g. involving restoration, improving connectivity and preventing habitat degradation) and consequently with varied outcomes (Panfil and Harvey, 2016)(Panfil and Harvey 2016). Nonetheless, with defined goals, RIL practices and allocated areas for preservation, land-sparing logging has a good opportunity for a successful carbon payment project (West et al., 2014; Sasaki et al., 2016).

## **5 Recommendations for future research**

The land sharing versus land sparing debate has been useful to explore effects of disturbance on several taxa throughout the tropics, however, as the debate is moving forward in agriculture (Fischer et al., 2014). It is desirable to consider production forest as a disturbance with widely different characteristics and management options. There is an increasing volume of research advocating for the conservation potential of selectively logged forest, which is directly influenced by management decisions (Edwards et al., 2014b; Macpherson et al., 2012).

Long term studies on the effect of logging intensities on soil carbon and tree community shifts are vital to build a chronosequence that allows solid predictions (Dean et al., 2017). Furthermore, a knowledge gap still exists in the synergies of carbon stocks, tree assemblages and soil nutrient dynamics. In this regard, before and after studies will

be highly valuable to address succession after disturbance and will reduce uncertainty of species with stochastic occurrence.

In order to achieve conservation goals, it is crucial to find land-sparing logging thresholds for sensitive species and carbon retention for higher intensities as those found in SE Asian forests (Banin et al., 2014). The shape and size of allocated lands need more attention in future research involving land-sparing logging. Future work should address the goals for long-term tenure of spared lands, coupled with service and carbon offset payment schemes to prevent land-conversion.

## Literature cited

- Achat, D. L., Fortin, M., Landmann, G., Ringeval, B., and Augusto, L. (2015). Forest soil carbon is threatened by intensive biomass harvesting. *Scientific Reports*, 5(1):15991.
- Achten, W. M. J. and Verchot, L. V. (2011). Implications of Biodiesel-Induced Land-Use Changes for CO<sub>2</sub> Emissions: Case Studies in Tropical America, Africa, and Southeast Asia. *Ecology and Society*, 16(4):art14.
- Amanuel, W., Yimer, F., and Karlun, E. (2018). Soil organic carbon variation in relation to land use changes: the case of Birr watershed, upper Blue Nile River Basin, Ethiopia. *J. Ecol. Environ.*, 42(1):16.
- Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). In *Wiley StatsRef: Statistics Reference Online*, pages 1–15. John Wiley & Sons, Ltd, Chichester, UK.
- Arima, E. Y., Walker, R. T., Perz, S. G., and Caldas, M. (2005). Loggers and Forest Fragmentation: Behavioral Models of Road Building in the Amazon Basin. *Annals of the Association of American Geographers*, 95(3):525–541.
- Asner, G. P. (2005). Selective Logging in the Brazilian Amazon. *Science*, 310(5747):480–482.
- Asner, G. P., Broadbent, E. N., Oliveira, P. J. C., Keller, M., Knapp, D. E., and Silva, J. N. M. (2006). Condition and fate of logged forests in the Brazilian Amazon. *Proceedings of the National Academy of Sciences*, 103(34):12947–12950.
- Asner, G. P., Keller, M., Pereira, Jr, R., Zweede, J. C., and Silva, J. N. M. (2004a). Canopy damage and recovery after selective logging in Amazonia: field and satellite studies. *Ecological Applications*, 14(sp4):280–298.
- Asner, G. P., Keller, M., and Silva, J. N. M. (2004b). Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology*, 10(5):765–783.



- Asner, G. P., Rudel, T. K., Aide, T. M., DeFries, R. S., and Emerson, R. (2009). A Contemporary Assessment of Change in Humid Tropical Forests. *Conservation Biology*, 23(6):1386–1395.
- Averill, C., Turner, B. L., and Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, 505(7484):543–545.
- Azevedo-Ramos, C., de Carvalho, O., and do Amaral, B. D. (2006). Short-term effects of reduced-impact logging on eastern Amazon fauna. *Forest Ecology and Management*, 232(1-3):26–35.
- Azevedo-Ramos, C., Silva, J. N. M., and Merry, F. (2015). The evolution of Brazilian forest concessions. *Elementa: Science of the Anthropocene*, 3(0):000048.
- Baddeley, A. J. and Turner, R. (2004). Spatstat: An R package for analyzing spatial point patterns.
- Bajželj, B., Richards, K. S., Allwood, J. M., Smith, P., Dennis, J. S., Curmi, E., and Gilligan, C. A. (2014). Importance of food-demand management for climate mitigation. *Nature Climate Change*, 4(10):924–929.
- Baker, T. R., Honorio Coronado, E. N., Phillips, O. L., Martin, J., van der Heijden, G. M. F., Garcia, M., and Silva Espejo, J. (2007). Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia*, 152(3):495–504.
- Baker, T. R., Vela Díaz, D. M., Chama Moscoso, V., Navarro, G., Monteagudo, A., Pinto, R., Cangani, K., Fyllas, N. M., Lopez Gonzalez, G., Laurance, W. F., Lewis, S. L., Lloyd, J., ter Steege, H., Terborgh, J. W., and Phillips, O. L. (2016). Consistent, small effects of treefall disturbances on the composition and diversity of four Amazonian forests. *Journal of Ecology*, 104(2):497–506.
- Balmford, B., Green, R. E., Onial, M., Phalan, B., and Balmford, A. (2019). How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology*, 56(1):73–84.
- Banin, L., Lewis, S. L., Lopez-Gonzalez, G., Baker, T. R., Quesada, C. A., Chao, K.-J., Burslem, D. F. R. P., Nilus, R., Salim, K. A., Keeling, H. C., Tan, S., Davies, S. J., Mendoza, A. M., Vásquez, R., Lloyd, J., Neill, D. A., Pitman, N., and Phillips, O. L. (2014). Tropical forest wood production: a cross-continental comparison. *Journal of Ecology*, 102(4):1025–1037.
- Baraloto, C., Hérault, B., Paine, C. E. T., Massot, H., Blanc, L., Bonal, D., Molino, J.-F., Nicolini, E. A., and Sabatier, D. (2012). Contrasting taxonomic and functional

- responses of a tropical tree community to selective logging. *Journal of Applied Ecology*, 49(4):861–870.
- Barany, M., Hammett, A. L., and Araman, P. (2003). Lesser used wood species of Bolivia and their relevance to sustainable forest management. 53(7):6.
- Barbhuiya, A. R., Arunachalam, A., Pandey, H. N., Arunachalam, K., Khan, M. L., and Nath, P. C. (2004). Dynamics of soil microbial biomass C, N and P in disturbed and undisturbed stands of a tropical wet-evergreen forest. *Eur. J. Soil Biol.*, 40:113–121.
- Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., Thomson, J. R., Ferraz, S. F. d. B., Louzada, J., Oliveira, V. H. F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., Jr, R. C. d. O., Souza Jr, C. M., Moura, N. G., Nunes, S. S., Siqueira, J. V., Pardini, R., Silveira, J. M., Vaz-de Mello, F. Z., Veiga, R. C. S., Venturieri, A., and Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535(7610):144–147.
- Barlow, J., Peres, C., Henriques, L., Stouffer, P., and Wunderle, J. (2006). The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biological Conservation*, 128(2):182–192.
- Barlow, J. and Peres, C. A. (2006). Effects of Single and Recurrent Wildfires on Fruit Production and Large Vertebrate Abundance in a Central Amazonian Forest. *Biodiversity and Conservation*, 15(3):985–1012.
- Benchimol, M. and Peres, C. A. (2015). Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *J. Ecol.*, 103(2):408–420.
- Berenguer, E., Ferreira, J., Gardner, T. A., Aragão, L. E. O. C., Camargo, P. B. D., Cerri, C. E., Durigan, M., Oliveira, R. C. D., Vieira, I. C. G., Barlow, J., De Camargo, P. B., Cerri, C. E., Durigan, M., Oliveira, R. C. D., Vieira, I. C. G., and Barlow, J. (2014). A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, 20(12):3713–3726.
- Bernard, H. (2004). Effects of selective logging on the microhabitat-use patterns of non-volant small mammals in a Bornean tropical lowland mixed-dipterocarp forest. *Nature and Human Activities*, 8:1–11.
- Berry, N. J., Phillips, O. L., Lewis, S. L., Hill, J. K., Edwards, D. P., Tawatao, N. B., Ahmad, N., Magintan, D., Khen, C. V., Maryati, M., Ong, R. C., and Hamer, K. C. (2010). The high value of logged tropical forests: lessons from northern Borneo. *Biodiversity and Conservation*, 19(4):985–997.

- Berry, N. J., Phillips, O. L., Ong, R. C., and Hamer, K. C. (2008). Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape Ecology*, 23(8):915–929.
- Bicknell, J. E., Struebig, M. J., and Davies, Z. G. (2015). Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *Journal of Applied Ecology*, 52(2):379–388.
- Bicknell, J. E., Struebig, M. J., Edwards, D. P., and Davies, Z. G. (2014). Improved timber harvest techniques maintain biodiversity in tropical forests. *Current Biology*, 24(23):R1119–R1120.
- Biscaia de la Cerda, A. E. and Nimmo, E. R. (2010). Can we really manage tropical forests without knowing the species within? Getting back to the basics of forest management through taxonomy. *Forest Ecology and Management*, 259(5):995–1002.
- Bisschop, L. (2012). Out of the woods: the illegal trade in tropical timber and a European trade hub. *Glob. Crime*, 13(3):191–212.
- Boltz, F., Holmes, T. P., and Carter, D. R. (2003). Economic and environmental impacts of conventional and reduced-impact logging in Tropical South America: a comparative review. *Forest Policy and Economics*, 5(1):69–81.
- Bonnell, T. R., Reyna-Hurtado, R., and Chapman, C. A. (2011). Post-logging recovery time is longer than expected in an East African tropical forest. *Forest Ecology and Management*, 261(4):855–864.
- Borah, B., Quader, S., and Srinivasan, U. (2018). Responses of interspecific associations in mixed-species bird flocks to selective logging. *Journal of Applied Ecology*, 55(4):1637–1646.
- Bray, D. B., Merino-Pérez, L., Negreros-Castillo, P., Segura-Warnholtz, G., Torres-Rojo, J. M., and Vester, H. F. M. (2003). Mexico's Community-Managed Forests as a Global Model for Sustainable Landscapes. *Conserv. Biol.*, 17(3):672–677.
- Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., and Silva, J. N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.*, 141:1745–1757.
- Brodie, J. F., Giordano, A. J., Zipkin, E. F., Bernard, H., Mohd-Azlan, J., and Ambu, L. (2015). Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conservation Biology*, 29(1):110–121.

- Buckley, L. B. and Huey, R. B. (2016). How Extreme Temperatures Impact Organisms and the Evolution of their Thermal Tolerance. *Integrative and Comparative Biology*, 56(1):98–109.
- Burivalova, Z., Şekercioğlu, Ç. H., and Koh, L. P. (2014). Thresholds of Logging Intensity to Maintain Tropical Forest Biodiversity. *Current Biology*, 24(16):1893–1898.
- Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vie, J.-C., and Watson, R. (2010). Global Biodiversity: Indicators of Recent Declines. *Science*, 328(5982):1164–1168.
- Buyantuyev, A., Xu, P., Wu, J., Piao, S., and Wang, D. (2012). A Space-For-Time (SFT) Substitution Approach to Studying Historical Phenological Changes in Urban Environment. *PLoS One*, 7(12):e51260.
- Canadell, J. G. and Raupach, M. R. (2008). Managing Forests for Climate Change Mitigation. *Science*, 320(5882):1456–1457.
- Carlson, B. S., Koerner, S. E., Medjibe, V. P., White, L. J. T., and Poulsen, J. R. (2017). Deadwood stocks increase with selective logging and large tree frequency in Gabon. *Global Change Biology*, 23(4):1648–1660.
- Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J.-C., and Poorter, L. (2012). Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology*, 100(6):1453–1463.
- Cazzolla Gatti, R., Castaldi, S., Lindsell, J. A., Coomes, D. A., Marchetti, M., Maesano, M., Di Paola, A., Paparella, F., and Valentini, R. (2015). The impact of selective logging and clearcutting on forest structure, tree diversity and above-ground biomass of African tropical forests. *Ecological Research*, 30(1):119–132.
- Cerullo, G. R. and Edwards, D. P. (2018). Actively restoring resilience in selectively logged tropical forests. *Journal of Applied Ecology*, 0(0).
- Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V., and Melack, J. M. (2000). Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, 122(3):380–388.

- Chambers, J. Q., Higuchi, N., Teixeira, L. M., dos Santos, J., Laurance, S. G., and Trumbore, S. E. (2004). Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia*, 141(4):596–611.
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., and Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1):45–67.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., and Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145(1):87–99.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4):351–366.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20(10):3177–3190.
- Chazdon, R. L., Letcher, S. G., van Breugel, M., Martínez-Ramos, M., Bongers, F., and Finegan, B. (2007). Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 362(1478):273–89.
- Clarke, F. M., Pio, D. V., and Racey, P. A. (2005). A Comparison of Logging Systems and Bat Diversity in the Neotropics. *Conservation Biology*, 19(4):1194–1204.
- Clavero, M., Brotons, L., Pons, P., and Sol, D. (2009). Prominent role of invasive species in avian biodiversity loss. *Biological Conservation*, 142(10):2043–2049.
- Cleary, D. F. R. (2017). Impact of logging on tree, liana and herb assemblages in a Bornean forest. *Journal of Sustainable Forestry*, 36(8):806–817.
- Cochrane, M. A. and Laurance, W. F. (2008). Synergisms among Fire, Land Use, and Climate Change in the Amazon. *AMBIO: A Journal of the Human Environment*, 37(7):522–527.

- Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S. P., Foster, R. B., Itoh, A., LaFrankie, J. V., Lee, H. S., Losos, E., Manokaran, N., Sukumar, R., and Yamakura, T. (2000). Spatial patterns in the distribution of tropical tree species. *Science*, 288(5470):1414–8.
- Costantini, D., Edwards, D. P., and Simons, M. J. (2016). Life after logging in tropical forests of Borneo: A meta-analysis. *Biological Conservation*, 196:182–188.
- Curtis, J. T. and McIntosh, R. P. (1951). An Upland Forest Continuum in the Prairie-Forest Border Region of Wisconsin. *Ecology*, 32(3):476–496.
- da Cunha, T. A., Finger, C. A. G., and Hasenauer, H. (2016). Tree basal area increment models for *Cedrela*, *Amburana*, *Copaifera* and *Swietenia* growing in the Amazon rain forests. *Forest Ecology and Management*, 365:174–183.
- Danielsen, F., Beukema, H., Burgess, N. D., Parish, F., Brühl, C. A., Donald, P. F., Murdiyarso, D., Phalan, B., Reijnders, L., Struebig, M., and Fitzherbert, E. B. (2009). Biofuel Plantations on Forested Lands: Double Jeopardy for Biodiversity and Climate. *Conservation Biology*, 23(2):348–358.
- Das, A. A., John, R., and Anand, M. (2017). Does structural connectivity influence tree species distributions and abundance in a naturally discontinuous tropical forest formation? *Journal of Vegetation Science*, 28(1):7–18.
- De Camargo, P. B., Trumbore, S. E., Martinelli, L. A., Davidson, E. A., Nepstad, D. C., and Victoria, R. L. (1999). Soil carbon dynamics in regrowing forest of eastern Amazonia. *Global Change Biology*, 5(6):693–702.
- de Mello-Ivo, W. M. P. and Ross, S. (2006). Effect of selective logging on some physical characteristics of a yellow latosol under rainforest in Central Amazonia State. *Rev. Bras. Ciência do Solo*, 30(5):769–776.
- De Pellegrin Llorente, I., Hoganson, H. M., Carson, M. T., and Windmuller-Campione, M. (2017). Recognizing Spatial Considerations in Forest Management Planning. *Curr. For. Reports*, 3(4):308–316.
- Dean, C., Kirkpatrick, J. B., and Friedland, A. J. (2017). Conventional intensive logging promotes loss of organic carbon from the mineral soil. *Global Change Biology*, 23(1):1–11.
- Decaëns, T., Martins, M. B., Feijoo, A., Oszwald, J., Dolédec, S., Mathieu, J., Arnaud de Sartre, X., Bonilla, D., Brown, G. G., Cuellar Criollo, Y. A., Dubs, F., Furtado, I. S., Gond, V., Gordillo, E., Le Clec'h, S., Marichal, R., Mitja, D., de Souza, I. M., Praxedes, C., Rougerie, R., Ruiz, D. H., Otero, J. T., Sanabria, C., Velasquez, A., Zararte, L. E. M., and

- Lavelle, P. (2018). Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. *Conservation Biology*, 32(6):1380–1391.
- Díaz, S., Fargione, J., Chapin, F. S., and Tilman, D. (2006). Biodiversity Loss Threatens Human Well-Being. *PLoS Biology*, 4(8):e277.
- Dionisio, L. F. S., Schwartz, G., Mazzei, L., Lopes, J. d. C., dos Santos, G. G. A., and Oliveira, F. d. A. (2017). Mortality of stocking commercial trees after reduced impact logging in eastern Amazonia. *Forest Ecology and Management*, 401:1–7.
- Don, A., Schumacher, J., and Freibauer, A. (2011). Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Global Change Biology*, 17(4):1658–1670.
- Edwards, D. P., Backhouse, A. R., Wheeler, C., Khen, C. V., and Hamer, K. C. (2012). Impacts of logging and rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *Journal of Insect Conservation*, 16(4):591–599.
- Edwards, D. P., Fisher, B., and Boyd, E. (2010). Protecting degraded rainforests: enhancement of forest carbon stocks under REDD. *Conserv. Lett.*, 3:313–316.
- Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J. R., Derhé, M. A., Docherty, T. D. S., Hsu, W. W., Mitchell, S. L., Ota, T., Williams, L. J., Laurance, W. F., Hamer, K. C., and Wilcove, D. S. (2014a). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Global Change Biology*, 20(1):183–191.
- Edwards, D. P., Larsen, T. H., Docherty, T. D. S., Ansell, F. A., Hsu, W. W., Derhé, M. A., Hamer, K. C., and Wilcove, D. S. (2011). Degraded lands worth protecting: the biological importance of Southeast Asia’s repeatedly logged forests. *Proc. R. Soc. B Biol. Sci.*, 278(1702):82–90.
- Edwards, D. P., Tobias, J. A., Sheil, D., Meijaard, E., and Laurance, W. F. (2014b). Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology & Evolution*, 29(9):511–520.
- Edwards, F. A., Finan, J., Graham, L. K., Larsen, T. H., Wilcove, D. S., Hsu, W. W., Chey, V., and Hamer, K. C. (2017). The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. *Biological Conservation*, 205:85–92.
- Ellert, B. H., Janzen, H. H., VandenBygaart, A. J., and Bremer, E. (2007). Measuring change in soil organic carbon storage. *Soil sampling and methods of analysis*, pages 25–38.
- Faminow, M. D. (1998). *Cattle, deforestation, and development in the Amazon: an economic, agronomic, and environmental perspective*. CAB international.

- Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo M., A., Brienen, R. J., Feldpausch, T. R., Lopez-Gonzalez, G., Malhi, Y., ter Steege, H., Pitman, N. C., Baraloto, C., Engel, J., Pétronelli, P., Andrade, A., Camargo, J. L. C., Laurance, S. G., Laurance, W. F., Chave, J., Allie, E., Vargas, P. N., Terborgh, J. W., Ruokolainen, K., Silveira, M., Aymard C., G. A., Arroyo, L., Bonal, D., Ramirez-Angulo, H., Araujo-Murakami, A., Neill, D., Hérault, B., Dourdain, A., Torres-Lezama, A., Marimon, B. S., Salomão, R. P., Comiskey, J. A., Réjou-Méchain, M., Toledo, M., Licona, J. C., Alarcón, A., Prieto, A., Rudas, A., van der Meer, P. J., Killeen, T. J., Marimon Junior, B.-H., Poorter, L., Boot, R. G., Stergios, B., Torre, E. V., Costa, F. R., Levis, C., Schiatti, J., Souza, P., Groot, N., Arets, E., Moscoso, V. C., Castro, W., Coronado, E. N. H., Peña-Claros, M., Stahl, C., Barroso, J., Talbot, J., Vieira, I. C. G., van der Heijden, G., Thomas, R., Vos, V. A., Almeida, E. C., Davila, E. Á., Aragão, L. E., Erwin, T. L., Morandi, P. S., de Oliveira, E. A., Valadão, M. B., Zagt, R. J., van der Hout, P., Loayza, P. A., Pipoly, J. J., Wang, O., Alexiades, M., Cerón, C. E., Huamantupa-Chuquimaco, I., Di Fiore, A., Peacock, J., Camacho, N. C. P., Umetsu, R. K., de Camargo, P. B., Burnham, R. J., Herrera, R., Quesada, C. A., Stropp, J., Vieira, S. A., Steininger, M., Rodríguez, C. R., Restrepo, Z., Muelbert, A. E., Lewis, S. L., Pickavance, G. C., and Phillips, O. L. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, 6(1):6857.
- Fearnside, P. M. (2005). Deforestation in Brazilian Amazonia: History, Rates, and Consequences. *Conservation Biology*, 19(3):680–688.
- Feldpausch, T. R., Jirka, S., Passos, C. A., Jasper, F., and Riha, S. J. (2005). When big trees fall: Damage and carbon export by reduced impact logging in southern Amazonia. *Forest Ecology and Management*, 219(2-3):199–215.
- Felton, A., Wood, J. T., Felton, A. M., Lindenmayer, D. B., and Hennessey, B. A. (2008). A comparison of bird communities in the anthropogenic and natural-tree fall gaps of a reduced-impact logged subtropical forest in Bolivia. *Bird Conservation International*, 18(02):129–143.
- Fick, S. E. and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12):4302–4315.
- Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G., and von Wehrden, H. (2014). Land Sparing Versus Land Sharing: Moving Forward. *Conservation Letters*, 7(3):149–157.
- Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., Lindenmayer, D. B., Manning, A. D., Mooney, H. A., Pejchar, L., Ranganathan, J., and Tallis, H. (2008).



- Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, 6(7):380–385.
- Fisher, B., Edwards, D., Larsen, T. H., Ansell, F. a., Hsu, W. W., Roberts, C. S., and Wilcove, D. S. (2011). Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. *Conserv. Lett.*, 4(6):443–450.
- França, F. M., Frazão, F. S., Korasaki, V., Louzada, J., and Barlow, J. (2017). Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. *Biological Conservation*, 216:115–122.
- Fredericksen, N. J. and Fredericksen, T. S. (2002). Terrestrial wildlife responses to logging and fire in a Bolivian tropical humid forest. *Biodiversity and Conservation*, 11(1):27–38.
- Fredericksen, T. S. and Pariona, W. (2002). Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest. *Forest Ecology and Management*, 171(3):223–230.
- Fry, E. L., De Long, J. R., and Bardgett, R. D. (2018). Plant Communities as Modulators of Soil Carbon Storage. In *Soil Carbon Storage*, pages 29–71. Elsevier.
- Fujisaka, S., Castilla, C., Escobar, G., Rodrigues, V., Veneklaas, E., Thomas, R., and Fisher, M. (1998). The effects of forest conversion on annual crops and pastures:. *Agriculture, Ecosystems & Environment*, 69(1):17–26.
- Gehring, C., Park, S., and Denich, M. (2004). Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management*, 195(1-2):69–83.
- Gerland, P., Raftery, A. E., Ev ikova, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B. K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G. K., and Wilmoth, J. (2014). World population stabilization unlikely this century. *Science*, 346(6206):234–237.
- Gerwing, J. J. (2006). The influence of reproductive traits on liana abundance 10 years after conventional and reduced-impacts logging in the eastern Brazilian Amazon. *Forest Ecology and Management*, 221(1-3):83–90.
- Gibbs, H. K., Brown, S., Niles, J. O., and Foley, J. A. (2007). Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, 2(4):045023.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., and Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369):378–81.

- Gilroy, J. J. and Edwards, D. P. (2017). Source-Sink Dynamics: a Neglected Problem for Landscape-Scale Biodiversity Conservation in the Tropics. *Current Landscape Ecology Reports*, 2(1):51–60.
- Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Medina Uribe, C. A., Hugaasen, T., and Edwards, D. P. (2014). Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes. *Global Change Biology*, 20(7):2162–2172.
- Goodman, R. C., Phillips, O. L., del Castillo Torres, D., Freitas, L., Cortese, S. T., Monteagudo, A., and Baker, T. R. (2013). Amazon palm biomass and allometry. *Forest Ecology and Management*, 310:994–1004.
- Grass, I., Loos, J., Baensch, S., Batary, P., Libran-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., and Tscharncke, T. (2019). Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, 1(2):262–272.
- Grau, R., Kuemmerle, T., and Macchi, L. (2013). Beyond ‘land sparing versus land sharing’: environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. *Current Opinion in Environmental Sustainability*, 5(5):477–483.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W., and Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307(5709):550–5.
- Griscom, B. W., Goodman, R. C., Burivalova, Z., and Putz, F. E. (2018). Carbon and Biodiversity Impacts of Intensive Versus Extensive Tropical Forestry. *Conservation Letters*, 11(1):e12362.
- Guariguata, M. R., Adame, J. J. R., and Finegan, B. (2000). Seed Removal and Fate in Two Selectively Logged Lowland Forests with Constrasting Protection Levels. *Conserv. Biol.*, 14(4):1046–1054.
- Guillaume, T., Damris, M., and Kuzyakov, Y. (2015). Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by  $\delta^{13}C$ . *Global Change Biology*, 21(9):3548–3560.
- Gunawardene, N., Majer, J., and Edirisinghe, J. (2010). Investigating residual effects of selective logging on ant species assemblages in Sinharaja Forest Reserve, Sri Lanka. *Forest Ecology and Management*, 259(3):555–562.
- Haase, P. (1995). Spatial pattern analysis in ecology based on Ripley’s K-function: Introduction and methods of edge correction. *Journal of Vegetation Science*, 6(4):575–582.

- Hall, J. S., Harris, D. J., Medjibe, V., and Ashton, P. S. (2003). The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. *Forest Ecology and Management*, 183(1-3):249–264.
- Hamer, K. C., Hill, J. K., Benedick, S., Mustaffa, N., Sherratt, T. N., Maryati, M., and K., C. V. (2003). Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, 40(1):150–162.
- Harris, J. (2009). Soil Microbial Communities and Restoration Ecology: Facilitators or Followers? *Science*, 325(5940):573–574.
- Harrison, R. D., Tan, S., Plotkin, J. B., Slik, F., Detto, M., Brenes, T., Itoh, A., and Davies, S. J. (2013). Consequences of defaunation for a tropical tree community. *Ecology Letters*, 16(5):687–694.
- Healey, J. R., Price, C., and Tay, J. (2000). The cost of carbon retention by reduced impact logging. *Forest Ecology and Management*, 139(1-3):237–255.
- Henders, S., Persson, U. M., and Kastner, T. (2015). Trading forests: land-use change and carbon emissions embodied in production and exports of forest-risk commodities. *Environmental Research Letters*, 10(12):125012.
- Hill, J. K. (1999). Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology*, 36(4):564–572.
- Hill, J. L. and Curran, P. J. (2003). Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography*, 30(9):1391–1403.
- Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, 54(2):427–432.
- Hodgson, J. A., Kunin, W. E., Thomas, C. D., Benton, T. G., and Gabriel, D. (2010). Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecology Letters*, 13(11):1358–1367.
- Holmes, T. P., Blate, G. M., Zweede, J. C., Barreto, P., Boltz, F., and Bauch, R. (2000). Financial costs and benefits of reduced impact logging relative to conventional logging in the Eastern Amazon. Technical report.
- Holmes, T. P., Blate, G. M., Zweede, J. C., Pereira, R., Barreto, P., Boltz, F., and Bauch, R. (2002). Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. *Forest Ecology and Management*, 163(1-3):93–110.

- Hosonuma, N., Herold, M., De Sy, V., De Fries, R. S., Brockhaus, M., Verchot, L., Angelsen, A., and Romijn, E. (2012). An assessment of deforestation and forest degradation drivers in developing countries. *Environmental Research Letters*, 7(4):044009.
- Houghton, R. A., Lawrence, K. T., Hackler, J. L., and Brown, S. (2008). The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, 7(7):731–746.
- Hu, Z., Xu, C., McDowell, N. G., Johnson, D. J., Wang, M., Luo, Y., Zhou, X., and Huang, Z. (2017). Linking microbial community composition to C loss rates during wood decomposition. *Soil Biology and Biochemistry*, 104:108–116.
- Huang, M. and Asner, G. P. (2010). Long-term carbon loss and recovery following selective logging in Amazon forests. *Global Biogeochemical Cycles*, 24(3).
- Hubbell, S. P., Foster, R. B., Condit, R., Wechsler, B., and Wright, S. J. (1999). Light-Gap Disturbances , Recruitment Limitation , and Tree Diversity in a. *Science*, 283(January):554–557.
- Hulme, M. F., Vickery, J. A., Green, R. E., Phalan, B., Chamberlain, D. E., Pomeroy, D. E., Nalwanga, D., Mushabe, D., Katebaka, R., Bolwig, S., and Atkinson, P. W. (2013). Conserving the Birds of Uganda’s Banana-Coffee Arc: Land Sparing and Land Sharing Compared. *PLoS ONE*, 8(2):e54597.
- IBAMA (2005). Plano de Manejo da Floresta Nacional do Jamari, RO.
- Imai, N., Seino, T., Aiba, S.-i., Takyu, M., Titin, J., and Kitayama, K. (2012). Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales. *Plant Ecology*, 213(9):1413–1424.
- Jackson, S. M., Fredericksen, T. S., and Malcolm, J. R. (2002). Area disturbed and residual stand damage following logging in a Bolivian tropical forest. *Forest Ecology and Management*, 166(1-3):271–283.
- Jalonen, R., Hong, L. T., Lee, S. L., Loo, J., and Snook, L. (2014). Integrating genetic factors into management of tropical Asian production forests: A review of current knowledge. *Forest Ecology and Management*, 315:191–201.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkinen, K., and Byrne, K. A. (2007). How strongly can forest management influence soil carbon sequestration? *Geoderma*, 137(3):253–268.
- Jati, A. S., Samejima, H., Fujiki, S., Kurniawan, Y., Aoyagi, R., and Kitayama, K. (2018). Effects of logging on wildlife communities in certified tropical rainforests in East Kalimantan, Indonesia. *For. Ecol. Manage.*, 427:124–134.

- Karsenty, A., Drigo, I. G., Piketty, M.-G., and Singer, B. (2008). Regulating industrial forest concessions in Central Africa and South America. *For. Ecol. Manage.*, 256(7):1498–1508.
- Keesing, F., Holt, R. D., and Ostfeld, R. S. (2006). Effects of species diversity on disease risk. *Ecology Letters*, 9(4):485–498.
- Keller, M., Palace, M., Asner, G. P., Pereira, R., and Silva, J. N. M. (2004). Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology*, 10(5):784–795.
- Kennedy, C. M., Hawthorne, P. L., Miteva, D. A., Baumgarten, L., Sochi, K., Matsumoto, M., Evans, J. S., Polasky, S., Hamel, P., Vieira, E. M., Develey, P. F., Sekercioglu, C. H., Davidson, A. D., Uhlhorn, E. M., and Kiesecker, J. (2016). Optimizing land use decision-making to sustain Brazilian agricultural profits, biodiversity and ecosystem services. *Biological Conservation*, 204:221–230.
- Kindermann, G., Obersteiner, M., Sohngen, B., Sathaye, J., Andrasko, K., Rametsteiner, E., Schlamadinger, B., Wunder, S., and Beach, R. (2008). Global cost estimates of reducing carbon emissions through avoided deforestation. *Proceedings of the National Academy of Sciences*, 105(30):10302–10307.
- Kleinschroth, F. and Healey, J. R. (2017). Impacts of logging roads on tropical forests. *Biotropica*, 49(5):620–635.
- Kleinschroth, F., Healey, J. R., Sist, P., Mortier, F., and Gourlet-Fleury, S. (2016). How persistent are the impacts of logging roads on Central African forest vegetation? *Journal of Applied Ecology*, 53(4):1127–1137.
- Krebs, C. J. (1989). *Ecological Methodology*. Harper and Row Publishers, New York, 1 edition.
- Kremen, C., Niles, J. O., Dalton, M. G., Daily, G. C., Ehrlich, P. R., Fay, J. P., Grewal, D., and Guillery, R. P. (2000). Economic incentives for rain forest conservation across scales. *Science*, 288(5472):1828–1832.
- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, 29(2):115–129.
- Kurten, E. L. (2013). Cascading effects of contemporaneous defaunation on tropical forest communities. *Biological Conservation*, 163:22–32.
- Lal, R. (2008). Sequestration of atmospheric CO<sub>2</sub> in global carbon pools. *Energy & Environmental Science*, 1(1):86.

- Lamb, A., Balmford, A., Green, R. E., and Phalan, B. (2016). To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing? *Biological Conservation*, 195(Supplement C):264–271.
- Laporte, N. T., Stabach, J. A., Grosch, R., Lin, T. S., and Goetz, S. J. (2007). Expansion of Industrial Logging in Central Africa. *Science (80-. )*, 316(5830):1451.
- Laurance, S. G., Stouffer, P. C., and Laurance, W. F. (2004). Effects of Road Clearings on Movement Patterns of Understory Rainforest Birds in Central Amazonia. *Conservation Biology*, 18(4):1099–1109.
- Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J. A., Sloan, S. P., Laurance, S. G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K. S., Cannon, C. H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M. A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A. R., McClearn, D., Mudappa, D., Nielsen, M. R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C. A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C. J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H. S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J. C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H.-b., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A. L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M. R., Smith, T. B., de Almeida, S. S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K. E., Sukumar, R., Surbeck,

- M., Tobler, M., Tschardtke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Vereza, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D. D., Wright, P., Xiankai, L., Yonzon, P., and Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489(7415):290–294.
- Laurance, W. F., Goosem, M., and Laurance, S. G. W. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24(12):659–669.
- Laurance, W. F., Sayer, J., and Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, 29(2):107–116.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., and Rossi, J.-P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, 42(SUPPL. 1):S3–S15.
- Law, E. A., Meijaard, E., Bryan, B. A., Mallawaarachchi, T., Koh, L. P., and Wilson, K. A. (2015). Better land-use allocation outperforms land sparing and land sharing approaches to conservation in Central Kalimantan, Indonesia. *Biological Conservation*, 186:276–286.
- Le Quéré, C., Moriarty, R., Andrew, R. M., Canadell, J. G., Sitch, S., Korsbakken, J. I., Friedlingstein, P., Peters, G. P., Andres, R. J., Boden, T. A., Houghton, R. A., House, J. I., Keeling, R. F., Tans, P., Arneeth, A., Bakker, D. C. E., Barbero, L., Bopp, L., Chang, J., Chevallier, F., Chini, L. P., Ciais, P., Fader, M., Feely, R. A., Gkritzalis, T., Harris, I., Hauck, J., Ilyina, T., Jain, A. K., Kato, E., Kitidis, V., Klein Goldewijk, K., Koven, C., Landschützer, P., Lauvset, S. K., Lefèvre, N., Lenton, A., Lima, I. D., Metzl, N., Millero, F., Munro, D. R., Murata, A., Nabel, J. E. M. S., Nakaoka, S., Nojiri, Y., O'Brien, K., Olsen, A., Ono, T., Pérez, F. F., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., Rödenbeck, C., Saito, S., Schuster, U., Schwinger, J., Séférian, R., Steinhoff, T., Stocker, B. D., Sutton, A. J., Takahashi, T., Tilbrook, B., van der Laan-Luijkx, I. T., van der Werf, G. R., van Heuven, S., Vandemark, D., Viovy, N., Wiltshire, A., Zaehle, S., and Zeng, N. (2015). Global Carbon Budget 2015. *Earth System Science Data*, 7(2):349–396.
- Leff, J. W., Wieder, W. R., Taylor, P. G., Townsend, A. R., Nemergut, D. R., Grandy, A. S., and Cleveland, C. C. (2012). Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. *Global Change Biology*, 18(9):2969–2979.
- Lin, B. B. and Fuller, R. A. (2013). FORUM: Sharing or sparing? How should we grow the world's cities? *Journal of Applied Ecology*, 50(5):n/a–n/a.

- Longo, M., Keller, M., Dos-Santos, M. N., Leitold, V., Pinagé, E. R., Baccini, A., Saatchi, S., Nogueira, E. M., Batistella, M., and Morton, D. C. (2016). Aboveground biomass variability across intact and degraded forests in the Brazilian Amazon. *Global Biogeochemical Cycles*, 30(11):1639–1660.
- Luskin, M. S., Lee, J. S., Edwards, D. P., Gibson, L., and Potts, M. D. (2018). Study context shapes recommendations of land-sparing and sharing; a quantitative review. *Global Food Security*, 16:29–35.
- Macdonald, C. A., Delgado-Baquerizo, M., Reay, D. S., Hicks, L. C., and Singh, B. K. (2018). Chapter 6 - Soil Nutrients and Soil Carbon Storage: Modulators and Mechanisms. In Singh, B. K., editor, *Soil Carbon Storage*, pages 167–205. Academic Press.
- Macpherson, A. J., Carter, D. R., Schulze, M. D., Vidal, E., and Lentini, M. W. (2012). The sustainability of timber production from Eastern Amazonian forests. *Land use policy*, 29(2):339–350.
- Mæstad, O. (2001). Timber trade restrictions and tropical deforestation: a forest mining approach. *Resource and Energy Economics*, 23(2):111–132.
- Magnago, L. F. S., Magrach, A., Barlow, J., Schaefer, C. E. G. R., Laurance, W. F., Martins, S. V., and Edwards, D. P. (2017). Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? *Functional Ecology*, 31(2):542–552.
- Malmer, A. and Grip, H. (1990). Soil disturbance and loss of infiltrability caused by mechanized and manual extraction of tropical rainforest in Sabah, Malaysia. *Forest Ecology and Management*, 38(1-2):1–12.
- Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., Wright, S. J., and Boehning-Gaese, K. (2012). Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. *Conserv. Biol.*, 26:1072–1081.
- Martin, A. R. and Thomas, S. C. (2011). A Reassessment of Carbon Content in Tropical Trees. *PLoS ONE*, 6(8):e23533.
- Martin, P. A., Newton, A. C., Pfeifer, M., Khoo, M., and Bullock, J. M. (2015). Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *Forest Ecology and Management*, 356:224–233.
- Martini, A. M. Z., Rosa, N. d. A., and Uhl, C. (1994). An Attempt to Predict Which Amazonian Tree Species May be Threatened by Logging Activities. *Environ. Conserv.*, 21(2):152–162.



- Matos, F. A. R., Magnago, L. F. S., Gastauer, M., Carreiras, J. M. B., Simonelli, M., Meira-Neto, J. A. A., and Edwards, D. P. (2017). Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. *Journal of Ecology*, 105(1):265–276.
- Mazor, T., Doropoulos, C., Schwarzmüller, F., Gladish, D. W., Kumaran, N., Merkel, K., Marco, M. D., and Gagic, V. (2018). Global mismatch of policy and research on drivers of biodiversity loss. *Nature Ecology & Evolution*, 2(7):1071.
- Mazzei, L., Sist, P., Ruschel, A., Putz, F. E., Marco, P., Pena, W., and Ferreira, J. E. R. (2010). Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management*, 259(3):367–373.
- McNabb, K. L., Miller, M. S., Lockaby, B. G., Stokes, B. J., Clawson, R. G., Stanturf, J. A., and Silva, J. N. M. (1997). Selection harvests in Amazonian rainforests: long-term impacts on soil properties. *For. Ecol. Manage.*, 93(1):153–160.
- Medjibe, V. P., Putz, F. E., and Romero, C. (2013). Certified and Uncertified Logging Concessions Compared in Gabon: Changes in Stand Structure, Tree Species, and Biomass. *Environmental Management*, 51(3):524–540.
- Medjibe, V. P., Putz, F. E., Starkey, M. P., Ndouna, A. A., and Memiaghe, H. R. (2011). Impacts of selective logging on above-ground forest biomass in the Monts de Cristal in Gabon. *Forest Ecology and Management*, 262(9):1799–1806.
- Merry, F., Soares-Filho, B., Nepstad, D., Amacher, G., and Rodrigues, H. (2009). Balancing Conservation and Economic Sustainability: The Future of the Amazon Timber Industry. *Environ. Manage.*, 44(3):395–407.
- Miller, S. D., Goulden, M. L., Hutyra, L. R., Keller, M., Saleska, S. R., Wofsy, S. C., Silva Figueira, A. M., da Rocha, H. R., and de Camargo, P. B. (2011). Reduced impact logging minimally alters tropical rainforest carbon and energy exchange. *Proceedings of the National Academy of Sciences of the United States of America*, 108(48):19431–19435.
- Montejo-Kovacevich, G., Hethcoat, M. G., Lim, F. K., Marsh, C. J., Bonfanti, D., Peres, C. A., and Edwards, D. P. (2018). Impacts of selective logging management on butterflies in the Amazon. *Biological Conservation*, 225:1–9.
- Montgomery, R. and Chazdon, R. (2002). Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, 131(2):165–174.
- Murty, D., Kirschbaum, M. U. F., Mcmurtrie, R. E., and MCGilvray, H. (2002). Does conversion of forest to agricultural land change soil carbon and nitrogen? a review of the literature. *Global Change Biology*, 8(2):105–123.

- Nave, L. E., Vance, E. D., Swanston, C. W., and Curtis, P. S. (2010). Harvest impacts on soil carbon storage in temperate forests. *Forest Ecology and Management*, 259(5):857–866.
- Negrete-Yankelevich, S., Fragoso, C., Newton, A. C., and Heal, O. W. (2007). Successional changes in soil, litter and macroinvertebrate parameters following selective logging in a Mexican Cloud Forest. *Appl. Soil Ecol.*, 35(2):340–355.
- Nepstad, D. C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., and Brooks, V. (1999). Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398:505–508.
- Olander, L. P., Bustamante, M. M., Asner, G. P., Telles, E., Prado, Z., and Camargo, P. B. (2005). Surface Soil Changes Following Selective Logging in an Eastern Amazon Forest. *Earth Interactions*, 9(4):1–19.
- Oliveira Filho, A., Carvalho, D. A., Vilela, E. A., Curi, N., and Fontes, M. A. L. (2004). Diversity and structure of the tree community of a fragment of tropical secondary forest of the Brazilian Atlantic Forest domain 15 and 40 years after logging. *Brazilian J. ...*, 27(4):685–701.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., and Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, 333(6045):988–993.
- Panfil, S. N. and Harvey, C. A. (2016). REDD+ and Biodiversity Conservation: A Review of the Biodiversity Goals, Monitoring Methods, and Impacts of 80 REDD+ Projects. *Conserv. Lett.*, 9(2):143–150.
- Pearson, T. R. H., Brown, S., and Casarim, F. M. (2014). Carbon emissions from tropical forest degradation caused by logging. *Environmental Research Letters*, 9(3):034017.
- Peña-Claros, M., Fredericksen, T. S., Alarcón, A., Blate, G. M., Choque, U., Leño, C., Licona, J. C., Mostacedo, B., Pariona, W., Villegas, Z., and Putz, F. E. (2008). Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *For. Ecol. Manage.*, 256(7):1458–1467.
- Pereira, R., Zweede, J., Asner, G. P., and Keller, M. (2002). Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management*, 168(1-3):77–89.
- Pfeifer, M., Lefebvre, V., Turner, E., Cusack, J., Khoo, M., Chey, V. K., Peni, M., and Ewers, R. M. (2015). Deadwood biomass: an underestimated carbon stock in degraded tropical forests? *Environmental Research Letters*, 10(4):044019.

- Phalan, B. (2018). What Have We Learned from the Land Sparing-sharing Model? *Sustainability*, 10(6):1760.
- Phalan, B., Onial, M., Balmford, A., and Green, R. E. (2011). Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, 333(6047):1289–91.
- Pickett, S. T. A. (1989). Space-for-Time Substitution as an Alternative to Long-Term Studies. In *Long-Term Stud. Ecol.*, pages 110–135. Springer New York, New York, NY.
- Pillay, R., Hua, F., Loiselle, B. A., Bernard, H., and Fletcher Jr, R. J. (2018). Multiple stages of tree seedling recruitment are altered in tropical forests degraded by selective logging. *Ecology and Evolution*, 8(16):8231–8242.
- Pinard, M., Barker, M., and Tay, J. (2000). Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. *Forest Ecology and Management*, 130(1-3):213–225.
- Pinedo-Vasquez, M., Zarin, D. J., Coffey, K., Padoch, C., and Rabelo, F. (2001). Post-Boom Logging in Amazonia. *Hum. Ecol.*, 29(2):219–239.
- Plumptre, A. J. and Reynolds, V. (1994). The Effect of Selective Logging on the Primate Populations in the Budongo Forest Reserve, Uganda. *The Journal of Applied Ecology*, 31(4):631.
- Poulsen, J. R., Clark, C. J., and Bolker, B. M. (2011). Decoupling the effects of logging and hunting on an Afrotropical animal community. *Ecological Applications*, 21(5):1819–1836.
- Putz, F., Sist, P., Fredericksen, T., and Dykstra, D. (2008). Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management*, 256(7):1427–1433.
- Putz, F. E. (2000). Economics of home grown forestry. *Ecological Economics*, 32(1):9–14.
- Putz, F. E., Dykstra, D. P., and Heinrich, R. (2000). Why Poor Logging Practices Persist in the Tropics. *Conservation Biology*, 14(4):951–956.
- Putz, F. E., Zuidema, P. A., Synnott, T., Peña-Claros, M., Pinard, M. A., Sheil, D., Vanclay, J. K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., and Zagt, R. (2012). Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters*, 5(4):296–303.
- Rakatama, A., Pandit, R., Ma, C., and Iftekhhar, S. (2017). The costs and benefits of REDD+: A review of the literature. *For. Policy Econ.*, 75:103–111.

- Rappaport, D. I., Tambosi, L. R., and Metzger, J. P. (2015). A landscape triage approach: combining spatial and temporal dynamics to prioritize restoration and conservation. *Journal of Applied Ecology*, 52(3):590–601.
- Richardson, V. A. and Peres, C. A. (2016). Temporal Decay in Timber Species Composition and Value in Amazonian Logging Concessions. *PLOS ONE*, 11(7):e0159035.
- Roopsind, A., Caughlin, T. T., van der Hout, P., Arets, E., and Putz, F. E. (2018). Trade-offs between carbon stocks and timber recovery in tropical forests are mediated by logging intensity. *Global Change Biology*, 24(7):2862–2874.
- Rozak, A. H., Rutishauser, E., Raulund-Rasmussen, K., and Sist, P. (2018). The imprint of logging on tropical forest carbon stocks: A Bornean case-study. *Forest Ecology and Management*, 417:154–166.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459):1770–4.
- Saner, P., Loh, Y. Y., Ong, R. C., and Hector, A. (2012). Carbon Stocks and Fluxes in Tropical Lowland Dipterocarp Rainforests in Sabah, Malaysian Borneo. *PLoS ONE*, 7(1):e29642.
- Santika, T., Meijaard, E., and Wilson, K. A. (2015). Designing multifunctional landscapes for forest conservation. *Environmental Research Letters*, 10(11):114012.
- Sasaki, N., Asner, G. P., Pan, Y., Knorr, W., Durst, P. B., Ma, H. O., Abe, I., Lowe, A. J., Koh, L. P., and Putz, F. E. (2016). Sustainable Management of Tropical Forests Can Reduce Carbon Emissions and Stabilize Timber Production. *Front. Environ. Sci.*, 4.
- Schaafsma, M., Burgess, N. D., Swetnam, R. D., Ngaga, Y. M., Kerry Turner, R., and Treue, T. (2014). Market Signals of Unsustainable and Inequitable Forest Extraction: Assessing the Value of Illegal Timber Trade in the Eastern Arc Mountains of Tanzania. *World Dev.*, 62:155–168.
- Schlesinger, W. H. and Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, 189-190:115–117.
- Schulze, M., Grogan, J., Landis, R. M., and Vidal, E. (2008a). How rare is too rare to harvest? *For. Ecol. Manage.*, 256(7):1443–1457.

- Schulze, M., Grogan, J., Uhl, C., Lentini, M., and Vidal, E. (2008b). Evaluating ipê (Tabebuia, Bignoniaceae) logging in Amazonia: Sustainable management or catalyst for forest degradation? *Biol. Conserv.*, 141(8):2071–2085.
- Schulze, M. and Zweede, J. (2006). Canopy dynamics in unlogged and logged forest stands in the eastern Amazon. *Forest Ecology and Management*, 236(1):56–64.
- Schwartz, G., Pereira, P. C. G., Siviero, M. A., Pereira, J. F., Ruschel, A. R., and Yared, J. A. G. (2017). Enrichment planting in logging gaps with *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby: A financially profitable alternative for degraded tropical forests in the Amazon. *For. Ecol. Manage.*, 390:166–172.
- Shearman, P., Bryan, J., and Laurance, W. F. (2012). Are we approaching ‘peak timber’ in the tropics? *Biological Conservation*, 151(1):17–21.
- Silva Pedro, M., Rammer, W., and Seidl, R. (2015). Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia*, 177(3):619–630.
- Silveira, F. a. O., Ferreira, M. C., Perillo, L. N., Carmo, F. F., and Neves, F. S. (2018). Brazil’s protected areas under threat. *Science (New York, N.Y.)*, 361(6401):459.
- Sist, P. and Ferreira, F. N. (2007). Sustainability of reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management*, 243(2-3):199–209.
- Sist, P., Mazzei, L., Blanc, L., and Rutishauser, E. (2014). Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. *Forest Ecology and Management*, 318:103–109.
- Slade, E. M., Mann, D. J., and Lewis, O. T. (2011). Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biol. Conserv.*, 144(1):166–174.
- Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M. L., Bellingham, P. J., van den Berg, E., Bernacci, L., da Conceição Bispo, P., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., Breuer-Ndoundou Hockemba, M., Bunyavejchewin, S., Calderado Leal Matos, D., Castillo-Santiago, M., Catharino, E. L. M., Chai, S.-L., Chen, Y., Colwell, R. K., Chazdon, R. L., Clark, C., Clark, D. B., Clark, D. A., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., DeWalt, S. J., Doucet, J.-L., Duque, A., Durigan, G., Eichhorn, K. A. O., Eisenlohr, P. V., Eler, E., Ewango, C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., de Oliveira Filho, A. T., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J.-F., Amarnath, G., Griffith, D. M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai,

N., Itoh, A., Jansen, P. A., Joly, C. A., de Jong, B. H. J., Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F., Lawes, M. J., do Amaral, I. L., Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E. H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Metzger, J. P., Millet, J., Mohandass, D., Montero, J. C., de Morisson Valeriano, M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Onrizal, Page, N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M. T. F., Pitman, N. C. A., Poorter, L., Poulsen, A. D., Poulsen, J., Powers, J., Prasad, R. C., Puyravaud, J.-P., Razafimahaimodison, J.-C., Reitsma, J., dos Santos, J. R., Roberto Spironello, W., Romero-Saltos, H., Rovero, F., Rozak, A. H., Ruokolainen, K., Rutishauser, E., Saiter, F., Saner, P., Santos, B. A., Santos, F., Sarker, S. K., Sattichanh, M., Schmitt, C. B., Schöngart, J., Schulze, M., Suganuma, M. S., Sheil, D., da Silva Pinheiro, E., Sist, P., Stevart, T., Sukumar, R., Sun, I.-F., Sunderland, T., Suresh, H. S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D. W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J. L. C. H., Van Do, T., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S. A., Webb, C. O., Whitfeld, T., Wich, S. A., Williams, J., Wittmann, F., Wöll, H., Yang, X., Adou Yao, C. Y., Yap, S. L., Yoneda, T., Zahawi, R. A., Zakaria, R., Zang, R., de Assis, R. L., Garcia Luize, B., and Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences*, 112(24):7472–7477.

Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G. E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G., and Zweifel, N. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, 22(12):1261–1271.

Slik, J. W. F., Verburg, R. W., and Kessler, P. J. A. (2002). Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodiversity and Conservation*, 11(1):85–98.

Snook, L. K. (1996). Catastrophic disturbance, logging and the ecology of mahogany (*Swietenia macrophylla* King): grounds for listing a major tropical timber species in CITES. *Bot. J. Linn. Soc.*, 122(1):35–46.

- Soliani, C., Vendramin, G. G., Gallo, L. A., and Marchelli, P. (2016). Logging by selective extraction of best trees: Does it change patterns of genetic diversity? The case of *Nothofagus pumilio*. *For. Ecol. Manage.*, 373:81–92.
- Sork, V. L. and Smouse, P. E. (2006). Genetic analysis of landscape connectivity in tree populations. *Landscape Ecology*, 21(6):821–836.
- Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., and Bell, D. (2013). Chapter Three - Quantifying the Biodiversity Value of Repeatedly Logged Rainforests: Gradient and Comparative Approaches from Borneo. In Woodward, G. and O’Gorman, E. J., editors, *Adv. Ecological Research*, volume 48 of *Global Change in Multispecies Systems: Part 3*, pages 183–224. Academic Press.
- Summerville, K. S. (2013). Forest lepidopteran communities are more resilient to shelterwood harvests compared to more intensive logging regimes. *Ecological Applications*, 23(5):1101–1112.
- Symes, W. S., Edwards, D. P., Miettinen, J., Rheindt, F. E., and Carrasco, L. R. (2018). Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. *Nature Communications*, 9(1):4052.
- Teixeira, A. M. G., Soares-Filho, B. S., Freitas, S. R., and Metzger, J. P. (2009). Modeling landscape dynamics in an Atlantic Rainforest region: Implications for conservation. *Forest Ecology and Management*, 257(4):1219–1230.
- Terborgh, J., Huanca Nuñez, N., Alvarez Loayza, P., and Cornejo Valverde, F. (2017). Gaps contribute tree diversity to a tropical floodplain forest. *Ecology*, 98(11):2895–2903.
- Terheggen, A. (2010). The new kid in the forest: the impact of China’s resource demand on Gabon’s tropical timber value chain.
- The Plant List (2013). Version 1.1; <http://www.theplantlist.org/> (accessed 15 September 2018).
- Thom, D., Rammer, W., and Seidl, R. (2017). The impact of future forest dynamics on climate: interactive effects of changing vegetation and disturbance regimes. *Ecological Monographs*, 87(4):665–684.
- Tilman, D., Balzer, C., Hill, J., and Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, 108(50):20260–20264.
- Uhl, C., Veríssimo, A., Mattos, M. M., Brandino, Z., and Guimarães Vieira, I. C. (1991). Social, economic, and ecological consequences of selective logging in an Amazon frontier: the case of Tailândia.

- Uhl, C. and Vieira, I. C. G. (1989). Ecological Impacts of Selective Logging in the Brazilian Amazon: A Case Study from the Paragominas Region of the State of Para. *Biotropica*, 21(2):98.
- Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., and Zamora, R. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3):299–307.
- Valle, D., Phillips, P., Vidal, E., Schulze, M., Grogan, J., Sales, M., and van Gardingen, P. (2007). Adaptation of a spatially explicit individual tree-based growth and yield model and long-term comparison between reduced-impact and conventional logging in eastern Amazonia, Brazil. *Forest Ecology and Management*, 243(2-3):187–198.
- Valverde-Barrantes, O. J. and Rocha, O. J. (2014). Logging impacts on forest structure and seedling dynamics in a *Prioria copaifera* (Fabaceae) dominated tropical rain forest (Talamanca, Costa Rica). *Revista de Biología Tropical*, 62(1):308–318.
- Vasconcelos, H., Vilhena, J., and Caliri, G. (2000). Responses of ants to selective logging of a central Amazonian forest. *Journal of Applied Ecology*, 37(3):508–514.
- Veloso, H. P., Rangel Filho, A. L. R., and Lima, J. C. A. (1991). *Classificação da vegetação brasileira, adaptada a um sistema universal*. Ministério da Economia, Fazenda e Planejamento, Fundação Instituto Brasileiro de Geografia e Estatística, Diretoria de Geociências, Departamento de Recursos Naturais e Estudos Ambientais.
- Verburg, R. and van Eijk-Bos, C. (2003). Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *Journal of Vegetation Science*, 14(1):99–110.
- Verheyen, K., Vellend, M., Calster, H. V., Peterken, G., and Hermy, M. (2004). Metapopulation Dynamics in Changing Landscapes: A New Spatially Realistic Model for Forest Plants. *Ecology*, 85(12):3302–3312.
- Veríssimo, A., Júnior, C. S., Stone, S., and Uhl, C. (1998). Zoning of Timber Extraction in the Brazilian Amazon. *Conserv. Biol.*, 12(1):128–136.
- Villela, D. M., Nascimento, M. T., Aragao, L. E. O. C., and da Gama, D. M. (2006). Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest. *Journal of Biogeography*, 33(3):506–516.
- Vinson, C. C., Kanashiro, M., Harris, S. A., and Boshier, D. H. (2015). Impacts of selective logging on inbreeding and gene flow in two Amazonian timber species with contrasting ecological and reproductive characteristics. *Molecular Ecology*, 24(1):38–53.



- Walker, R., Moran, E., and Anselin, L. (2000). Deforestation and Cattle Ranching in the Brazilian Amazon: External Capital and Household Processes. *World Development*, 28(4):683–699.
- Warren-Thomas, E., Dolman, P. M., and Edwards, D. P. (2015). Increasing Demand for Natural Rubber Necessitates a Robust Sustainability Initiative to Mitigate Impacts on Tropical Biodiversity. *Conservation Letters*, 8(4):230–241.
- Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J. C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J. G., Painter, M., Wilkie, D., Filardi, C., Laurance, W. F., Houghton, R. A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R. K., Silva-Chávez, G. A., Ervin, J., and Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.*, 2(4):599–610.
- Wells, K., Pfeiffer, M., Lakim, M. B., and Kalko, E. K. V. (2006). Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo. *Journal of Animal Ecology*, 75(5):1212–1223.
- West, T. A. P., Vidal, E., and Putz, F. E. (2014). Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. *Forest Ecology and Management*, 314(Supplement C):59–63.
- Williams, D. R., Alvarado, F., Green, R. E., Manica, A., Phalan, B., and Balmford, A. (2017). Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico. *Global Change Biology*, 23(12):5260–5272.
- Wilson, R. F., Marsh, H., and Winter, J. (2007). Importance of canopy connectivity for home range and movements of the rainforest arboreal ringtail possum (*Hemibelideus lemuroides*). *Wildl. Res.*, 34(3):177–184.
- Yguel, B., Hérault, B., Gourlet-Fleury, S., Dourdain, A., Fontaine, C., and Forget, P.-M. (2016). Disrupted dispersal in logged tropical forest.
- Zimmerman, B. L. and Kormos, C. F. (2012). Prospects for Sustainable Logging in Tropical Forests. *Bioscience*, 62(5):479–487.
- Zummo, L. M. and Friedland, A. J. (2011). Soil carbon release along a gradient of physical disturbance in a harvested northern hardwood forest. *Forest Ecology and Management*, 261(6):1016–1026.
- Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1):3–14.

# Appendices



## Appendix A

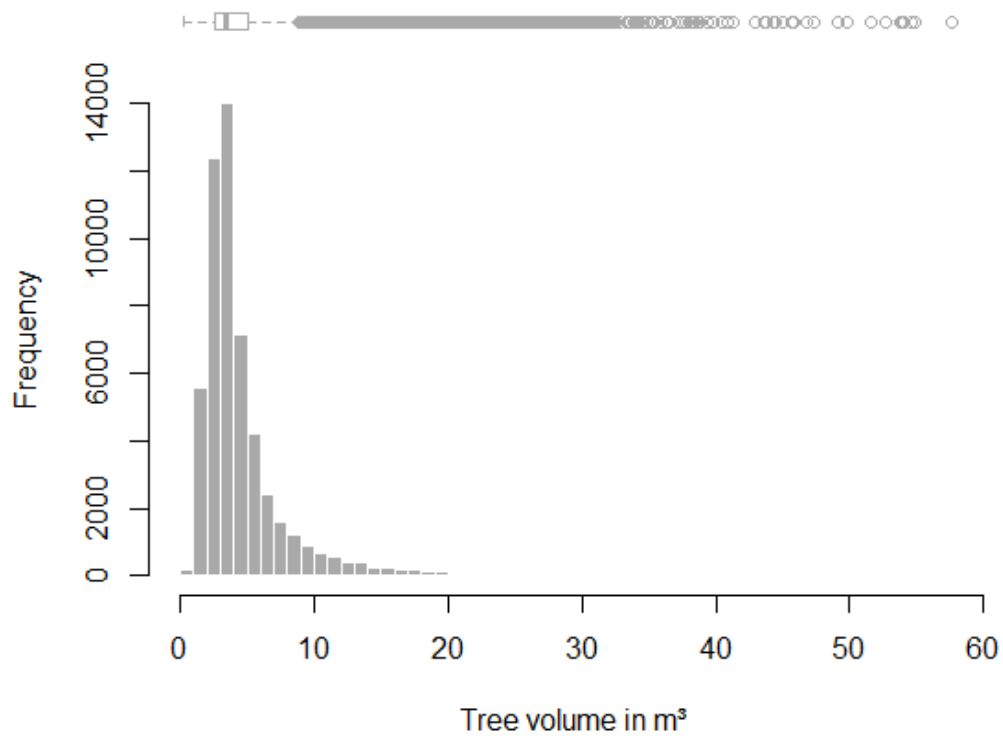


Figure A.1: Frequency distribution of individual tree volume values present in UPAs 2, 3 and 4 with DBH less than 50 cm. Data taken from AMATA's database.

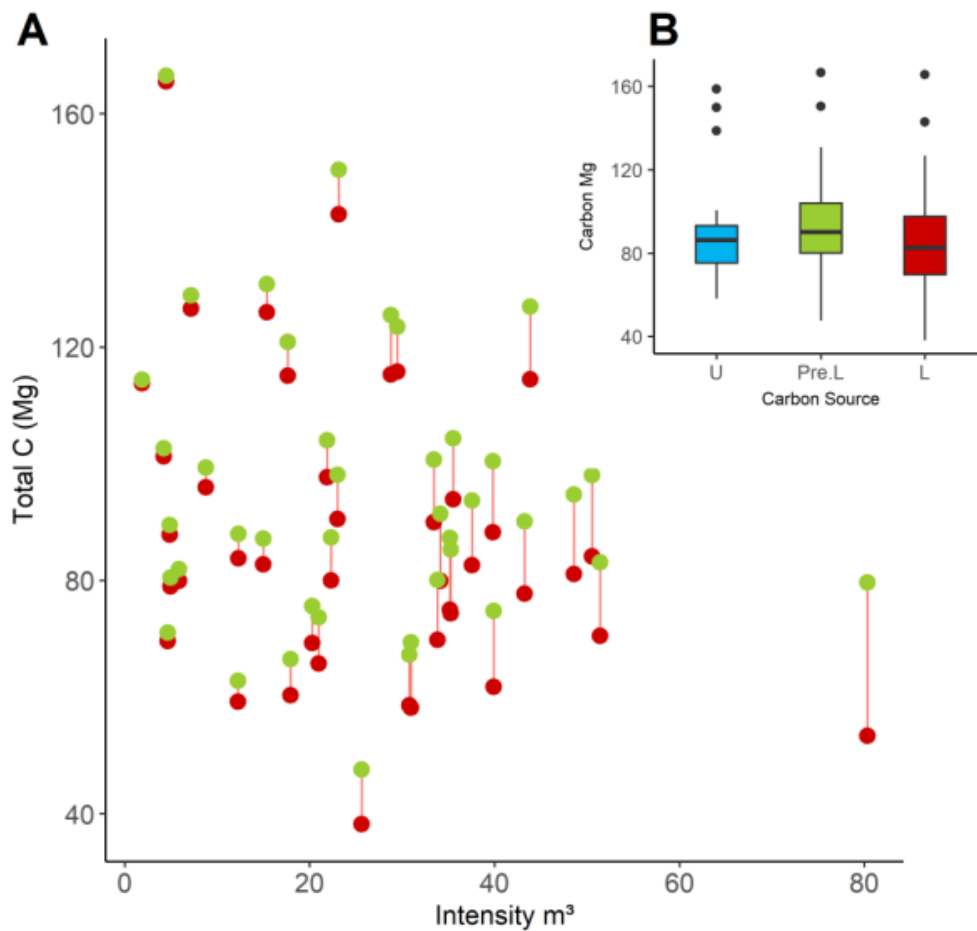


Figure A.2: Carbon stocks per plot after adding back bole and deadwood as a result from logging. A) Pairs of points represent each plot, with carbon values for logged forest (red) and after the bole and deadwood carbon is added (green). Red lines indicate the difference between pre-logged and logged per plot carbon values. B) Total carbon values per carbon source: Pre-L., pre-logged plots in colour green, L., for logged plots in red and U, unlogged plots in blue.

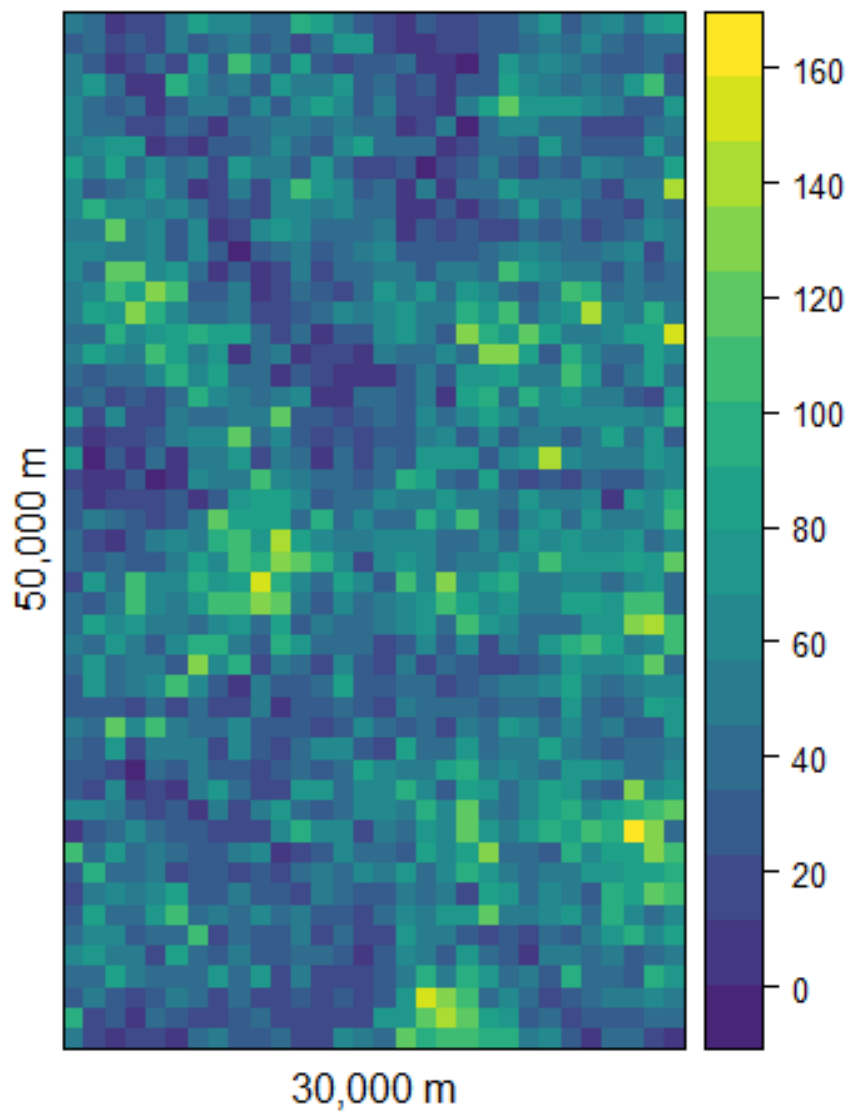


Figure A.3: Example of a simulated UPA with one ha resolution. Colour range represents the sum of volume ( $\text{m}^3$ ) values from the simulated trees that occur inside each grid cell.

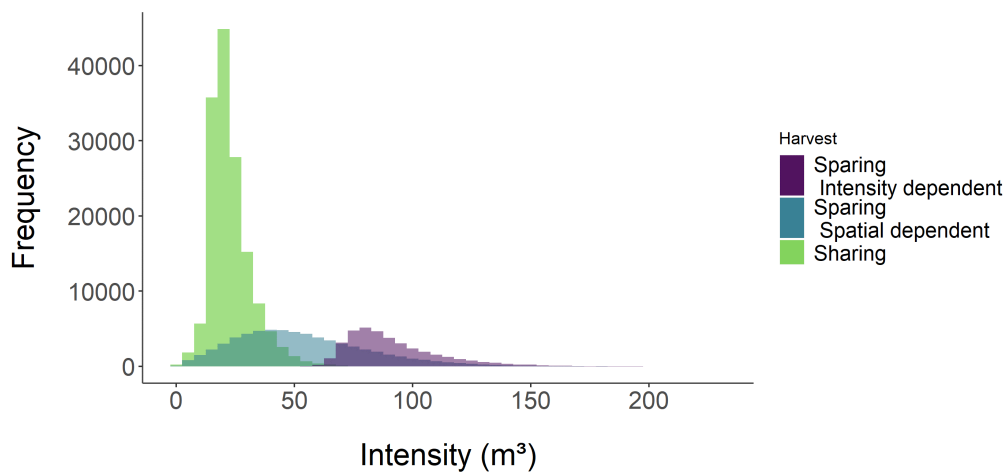


Figure A.4: Histogram of intensity values of every ha from the 100 forest simulations, sorted by harvest strategy.

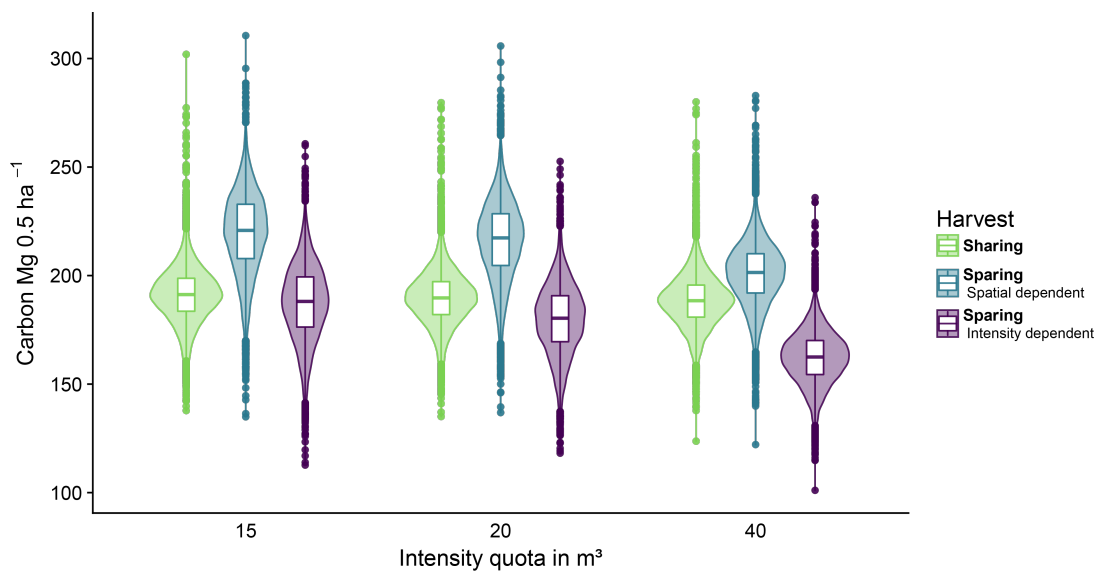


Figure A.5: Differences in predicted Carbon stocks per hectare on harvest strategies across different logging intensity quotas.

## Appendix B



Figure B.1: Bulk density sampling at 0-15 cm depth example picture in a logged forest plot.





Figure B.2: Soil physical impacts observed in the field. Main road with visible soil compaction(left) and road borders with evident scarification by tractors (right)

## Appendix C

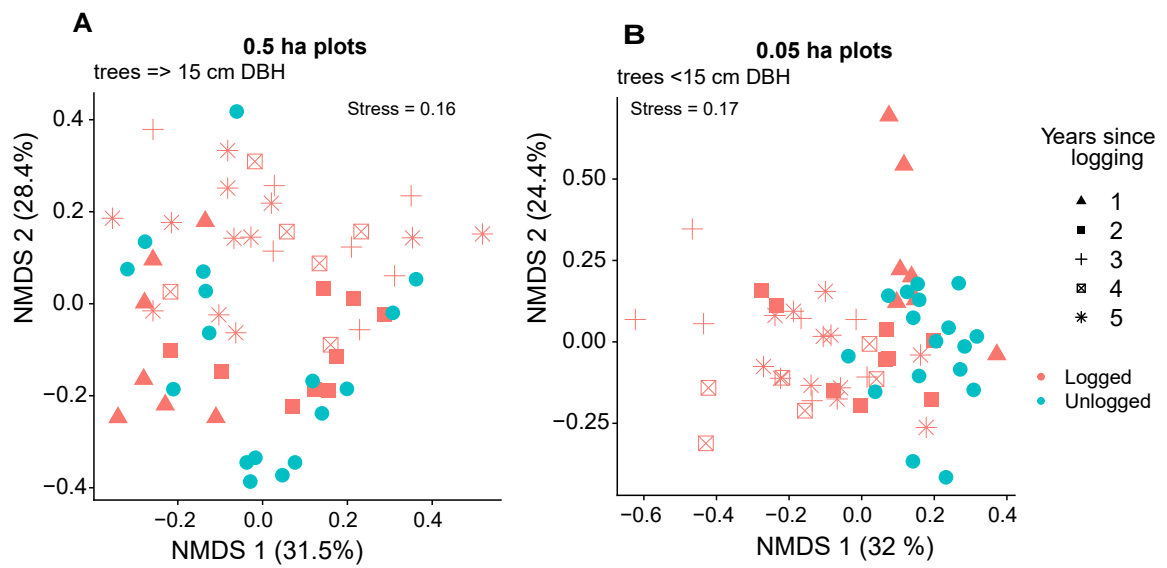


Figure C.1: Ordination of tree community similarities (Bray-Curtis distances) of unlogged and logged forests. NMDS analysis axis 1 and 2 in (A) 0.5 ha plots with trees  $\geq$  15 cm and (B) 0.05 ha plots with trees < 15 cm DBH. Proportion of variance (loadings) for each axis and stress values are shown.

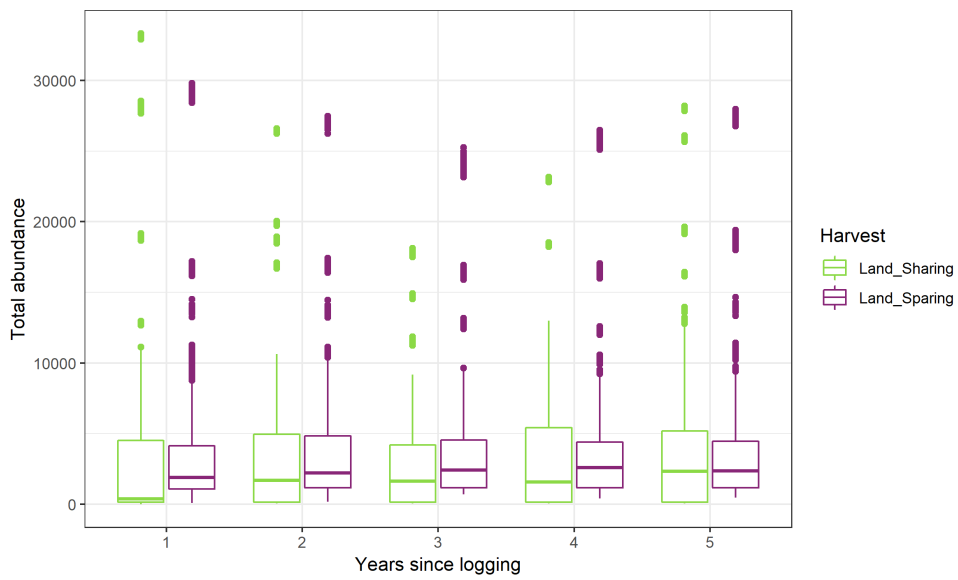


Figure C.2: Comparison of overall predicted stem density (individuals ha<sup>-1</sup>) of trees <15 cm DBH between land sharing and land sparing across five years since logging.

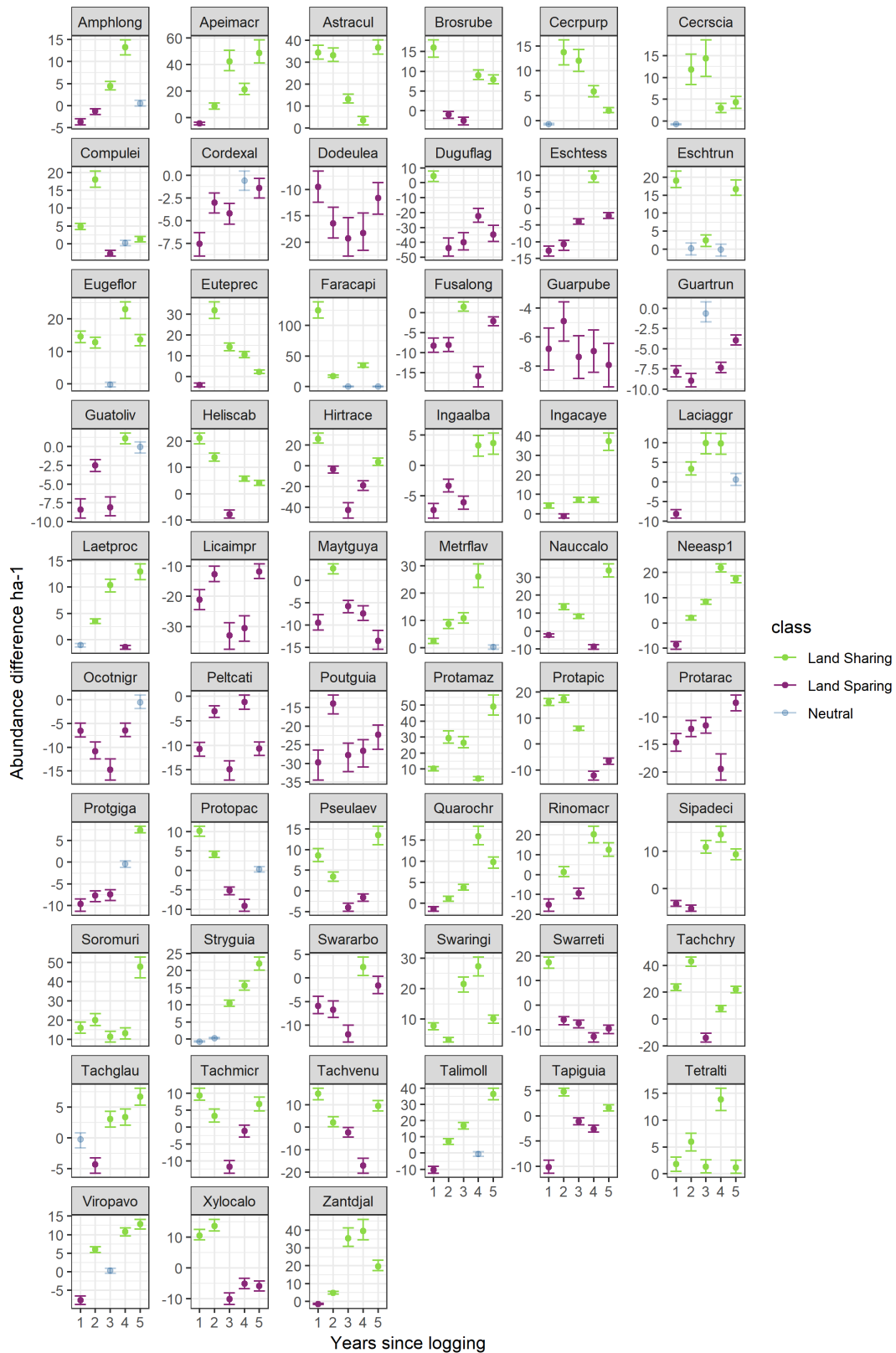


Figure C.3: Prediction values grouped by species and years since logging and classified according to the strategy with higher predicted stem density for species found in logged forest. Class was assigned as neutral if the difference in predicted stem density between land sharing and land sparing was between -1 and 1.



## Appendix D

Table D.1: List of code-named tree species.

Code	Scientific Name	Family
Abarjupu	<i>Abarema jupunba</i>	Leguminosae
Agonsilv	<i>Agonandra silvatica</i>	Opiliaceae
Alchflor	<i>Alchorneopsis floribunda</i>	Euphorbiaceae
Alexgran	<i>Alexa grandiflora</i>	Leguminosae
Allolati	<i>Allophylus latifolius</i>	Sapindaceae
Ampeeden	<i>Ampelocera edentula</i>	Ulmaceae
Amphlong	<i>Amphirrhox longifolia</i>	Violaceae
Anacgiga	<i>Anacardium giganteum</i>	Anacardiaceae
Andimicr	<i>Andira micrantha</i>	Leguminosae
Andiunif	<i>Andira unifoliolata</i>	Leguminosae
Anibcane	<i>Aniba canellila</i>	Lauraceae
Anibmega	<i>Aniba megaphylla</i>	Lauraceae
Anibrosa	<i>Aniba rosaeodora</i>	Lauraceae
Anismana	<i>Anisophyllea manausensis</i>	Anisophylleaceae
Annofoet	<i>Annona foetida</i>	Annonaceae
Annoneoi	<i>Annona neoinsignis</i>	Annonaceae
Aparcord	<i>Aparisthmium cordatum</i>	Euphorbiaceae
Apeimacr	<i>Apeiba macropetala</i>	Malvaceae
Apeitibo	<i>Apeiba tibourbou</i>	Malvaceae
Apulleio	<i>Apuleia leiocarpa</i>	Leguminosae
Aspiarar	<i>Aspidosperma araracanga</i>	Apocynaceae
Aspiniti	<i>Aspidosperma nitidum</i>	Apocynaceae
Astracul	<i>Astrocaryum aculeatum</i>	Arecaceae
Astrleco	<i>Astronium lecointei</i>	Anacardiaceae
Attaspec	<i>Attalea speciosa</i>	Arecaceae
Bactacan	<i>Bactris acanthocarpa</i>	Arecaceae
Bactsimp	<i>Bactris simplicifrons</i>	Arecaceae
Bagaguaia	<i>Bagassa guianensis</i>	Moraceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Balieleg	<i>Balizia elegans</i>	Leguminosae
Bateflor	<i>Batesia floribunda</i>	Leguminosae
Bauhrufa	<i>Bauhinia rufa</i>	Leguminosae
Bellegen	<i>Bellucia egensis</i>	Melastomataceae
Bellimpe	<i>Bellucia imperialis</i>	Melastomataceae
Bertexce	<i>Bertholletia excelsa</i>	Lecythidaceae
Bixaarbo	<i>Bixa arborea</i>	Bixaceae
Bocamult	<i>Bocageopsis multiflora</i>	Annonaceae
Bowdniti	<i>Bowdichia nitida</i>	Leguminosae
Brosguia	<i>Brosimum guianense</i>	Moraceae
Brospari	<i>Brosimum parinarioides</i>	Moraceae
Brosputa	<i>Brosimum potabile</i>	Moraceae
Brosrube	<i>Brosimum rubescens</i>	Moraceae
Buchgran	<i>Buchenavia grandis</i>	Combretaceae
Byrscris	<i>Byrsonima crispa</i>	Malpighiaceae
Byrspic	<i>Byrsonima spicata</i>	Malpighiaceae
Calobras	<i>Calophyllum brasiliense</i>	Calophyllaceae
Calobras	<i>Calophyllum brasiliense</i>	Clusiaceae
Calycoch	<i>Calycolpus cochleatus</i>	Myrtaceae
Calygoet	<i>Calycolpus goetheanus</i>	Myrtaceae
Capideco	<i>Capirona decorticans</i>	Rubiaceae
Carapunc	<i>Caraipa punctulata</i>	Calophyllaceae
Carimicr	<i>Cariniana micrantha</i>	Lecythidaceae
Cariparv	<i>Cariniana parvifolia</i>	Lecythidaceae
Caryglab	<i>Caryocar glabrum</i>	Caryocaraceae
Caryvill	<i>Caryocar villosum</i>	Caryocaraceae
Casejavi	<i>Casearia javitensis</i>	Salicaceae
Caselong	<i>Casearia longifolia</i>	Salicaceae
Casepitu	<i>Casearia pitumba</i>	Salicaceae
Cecrdist	<i>Cecropia distachya</i>	Urticaceae
Cecrpurp	<i>Cecropia purpurascens</i>	Urticaceae
Cecrscia	<i>Cecropia sciadophylla</i>	Urticaceae
Cedrcate	<i>Cedrelinga cateniformis</i>	Leguminosae
Cedrodor	<i>Cedrela odorata</i>	Meliaceae
Cespspat	<i>Cespedesia spathulata</i>	Ochnaceae
Chaukapp	<i>Chaunochiton kappleri</i>	Olacaceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Chimbarb	<i>Chimarrhis barbata</i>	Rubiaceae
Chimtur	<i>Chimarrhis turbinata</i>	Rubiaceae
Chryamaz	<i>Chrysophyllum amazonicum</i>	Sapotaceae
Chrysang	<i>Chrysophyllum sanguinolentum</i>	Sapotaceae
Clarmoll	<i>Clarisia mollis</i>	Moraceae
Clarrace	<i>Clarisia racemosa</i>	Moraceae
Coccmoll	<i>Coccoloba mollis</i>	Polygonaceae
Coccp1	<i>Coccoloba</i> sp. 1	Polygonaceae
Cochorin	<i>Cochlospermum orinocense</i>	Bixaceae
Compulei	<i>Compsonera ulei</i>	Myristicaceae
Concguia	<i>Conceveiba guianensis</i>	Euphorbiaceae
Conneria	<i>Connarus erianthus</i>	Connaraceae
Copamult	<i>Copaifera multijuga</i>	Leguminosae
Copaoblo	<i>Copaifera oblongifolia</i>	Leguminosae
Cordexal	<i>Cordia exaltata</i>	Boraginaceae
Cordfall	<i>Cordia fallax</i>	Boraginaceae
Cordnodo	<i>Cordia nodosa</i>	Boraginaceae
Coryalta	<i>Corythophora alta</i>	Lecythidaceae
Coryrimo	<i>Corythophora rimosa</i>	Lecythidaceae
Couerobu	<i>Couepia robusta</i>	Chrysobalanaceae
Coumguia	<i>Couma guianensis</i>	Apocynaceae
Coumutil	<i>Couma utilis</i>	Apocynaceae
Courstel	<i>Couratari stellata</i>	Lecythidaceae
Cousorth	<i>Coussapoa orthoneura</i>	Urticaceae
Creprhoi	<i>Crepidosperrum rhoifolium</i>	Burseraceae
Crotlago	<i>Croton lagoensis</i>	Euphorbiaceae
Cupascro	<i>Cupania scrobiculata</i>	Sapindaceae
Cybiguya	<i>Cybianthus guyanensis</i>	Primulaceae
Dendmacr	<i>Dendropanax macropodus</i>	Araliaceae
Diniexce	<i>Dinizia excelsa</i>	Leguminosae
Dioscava	<i>Diospyros cavalcantei</i>	Ebenaceae
Diosguia	<i>Diospyros guianensis</i>	Ebenaceae
Diplmart	<i>Diplotropis martiusii</i>	Leguminosae
Diptmagn	<i>Dipteryx magnifica</i>	Leguminosae
Diptodor	<i>Dipteryx odorata</i>	Leguminosae
Dodeulea	<i>Dodecastigma uleanum</i>	Euphorbiaceae

Continued



<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Duckcest	<i>Duckeodendron cestroides</i>	Solanaceae
Duckverr	<i>Duckesia verrucosa</i>	Humiriaceae
Duguflag	<i>Duguetia flagellaris</i>	Annonaceae
Dugustel	<i>Duguetia stelechantha</i>	Annonaceae
Dugusuri	<i>Duguetia surinamensis</i>	Annonaceae
Dulacand	<i>Dulacia candida</i>	Olacaceae
Dulamacr	<i>Dulacia macrophylla</i>	Olacaceae
Durolong	<i>Duroia longifolia</i>	Rubiaceae
Duromacr	<i>Duroia macrophylla</i>	Rubiaceae
Ecclguia	<i>Ecclinusa guianensis</i>	Sapotaceae
Endlbrac	<i>Endlicheria bracteolata</i>	Lauraceae
Endouchi	<i>Endopleura uchi</i>	Humiriaceae
Entescho	<i>Enterolobium schomburgkii</i>	Leguminosae
Entetimb	<i>Enterolobium timbouva</i>	Leguminosae
Eperduck	<i>Eperua duckeana</i>	Leguminosae
Erioglob	<i>Eriotheca globosa</i>	Malvaceae
Erisbico	<i>Erisma bicolor</i>	Vochysiaceae
Erytfalc	<i>Erythrina falcata</i>	Leguminosae
Erytmacr	<i>Erythroxylum macrophyllum</i>	Erythroxylaceae
Erytmucr	<i>Erythroxylum mucronatum</i>	Erythroxylaceae
Eschalti	<i>Eschweilera altissima</i>	Lecythidaceae
Eschatro	<i>Eschweilera atropetiolata</i>	Lecythidaceae
Eschcoll	<i>Eschweilera collina</i>	Lecythidaceae
Eschcori	<i>Eschweilera coriacea</i>	Lecythidaceae
Eschcyat	<i>Eschweilera cyathiformis</i>	Lecythidaceae
Eschgran	<i>Eschweilera grandiflora</i>	Lecythidaceae
Eschparv	<i>Eschweilera parviflora</i>	Lecythidaceae
Eschpunc	<i>Eschweilera punctata</i>	Lecythidaceae
Eschtess	<i>Eschweilera tessmannii</i>	Lecythidaceae
Eschtrun	<i>Eschweilera truncata</i>	Lecythidaceae
Eschwach	<i>Eschweilera wachenheimii</i>	Lecythidaceae
Eugecupu	<i>Eugenia cupulata</i>	Myrtaceae
Eugeflor	<i>Eugenia florida</i>	Myrtaceae
Eugepatr	<i>Eugenia patrisii</i>	Myrtaceae
Eugetrun	<i>Eugenia trunciflora</i>	Myrtaceae
Euphguia	<i>Euphronia guianensis</i>	Euphroniaceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Euteprec	<i>Euterpe precatoria</i>	Arecaceae
Faracapi	<i>Faramea capillipes</i>	Rubiaceae
Ficusp1	<i>Ficus</i> sp. 1	Moraceae
Ficusp2	<i>Ficus</i> sp. 2	Moraceae
Fusalong	<i>Fusaea longifolia</i>	Annonaceae
Garcmandr	<i>Garcinia madruno</i>	Clusiaceae
Geisarge	<i>Geissospermum argenteum</i>	Apocynaceae
Geondeve	<i>Geonoma deversa</i>	Arecaceae
Goupglab	<i>Goupia glabra</i>	Goupiaceae
Guappube	<i>Guapira pubescens</i>	Nyctaginaceae
Guapsp	<i>Guapira</i> sp.	Nyctaginaceae
Guarguid	<i>Guarea guidonia</i>	Meliaceae
Guarpube	<i>Guarea pubescens</i>	Meliaceae
Guarsilv	<i>Guarea silvatica</i>	Meliaceae
Guarsp	<i>Guarea</i> sp.	Meliaceae
Guartrun	<i>Guarea trunciflora</i>	Meliaceae
Guatblep	<i>Guatteria blepharophylla</i>	Annonaceae
Guatcori	<i>Guatteria coriacea</i>	Annonaceae
Guatfoli	<i>Guatteria foliosa</i>	Annonaceae
Guatoliv	<i>Guatteria olivacea</i>	Annonaceae
Guatpube	<i>Guatteria pubens</i>	Annonaceae
Guazulmi	<i>Guazuma ulmifolia</i>	Malvaceae
Handserr	<i>Handroanthus serratifolius</i>	Bignoniaceae
Heisbarb	<i>Heisteria barbata</i>	Olacaceae
Heliscab	<i>Helicostylis scabra</i>	Moraceae
Helispru	<i>Helianthostylis sprucei</i>	Moraceae
Helitome	<i>Helicostylis tomentosa</i>	Moraceae
Hevebras	<i>Hevea brasiliensis</i>	Euphorbiaceae
Himasucu	<i>Himatanthus sucuuba</i>	Apocynaceae
Hirtmyrm	<i>Hirtella myrmecophila</i>	Chrysobalanaceae
Hirtpani	<i>Hirtella paniculata</i>	Chrysobalanaceae
Hirtphys	<i>Hirtella physophora</i>	Chrysobalanaceae
Hirtrace	<i>Hirtella racemosa</i>	Chrysobalanaceae
Hubeswie	<i>Huberodendron swietenoides</i>	Malvaceae
Hymeinte	<i>Hymenaea intermedia</i>	Leguminosae
Hymemode	<i>Hymenolobium modestum</i>	Leguminosae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Hymeoblo	<i>Hymenaea oblongifolia</i>	Leguminosae
Hymeseri	<i>Hymenolobium sericeum</i>	Leguminosae
Ingaalba	<i>Inga alba</i>	Leguminosae
Ingabico	<i>Inga bicoloriflora</i>	Leguminosae
Ingacaye	<i>Inga cayennensis</i>	Leguminosae
Ingacord	<i>Inga cordatoalata</i>	Leguminosae
Ingagrac	<i>Inga gracilifolia</i>	Leguminosae
Ingagrfl	<i>Inga graciliflora</i>	Leguminosae
Ingalaur	<i>Inga laurina</i>	Leguminosae
Ingaobid	<i>Inga obidensis</i>	Leguminosae
Ingapara	<i>Inga paraensis</i>	Leguminosae
Ingarubi	<i>Inga rubiginosa</i>	Leguminosae
Ingasube	<i>Inga suberosa</i>	Leguminosae
Ingaumbr	<i>Inga umbratica</i>	Leguminosae
Iriaseti	<i>Iriartella setigera</i>	Arecaceae
Iryahost	<i>Iryanthera hostmannii</i>	Myristicaceae
Iryajuru	<i>Iryanthera juruensis</i>	Myristicaceae
Iryalaev	<i>Iryanthera laevis</i>	Myristicaceae
Iserhypo	<i>Isertia hypoleuca</i>	Rubiaceae
Jacacopa	<i>Jacaranda copaia</i>	Bignoniaceae
Jacaspin	<i>Jacaratia spinosa</i>	Caricaceae
Laciaggr	<i>Lacistema aggregatum</i>	Lacistemataceae
Laciagre	<i>Lacistema agregatum</i>	Lacistemataceae
Lacmarbo	<i>Lacmellea arborescens</i>	Apocynaceae
Lacucren	<i>Lacunaria crenata</i>	Ochnaceae
Lacujenm	<i>Lacunaria jenmanii</i>	Ochnaceae
Laetproc	<i>Laetia procera</i>	Salicaceae
Lecyparv	<i>Lecythis parvifructa</i>	Lecythidaceae
Lecypran	<i>Lecythis prancei</i>	Lecythidaceae
Lecyzabu	<i>Lecythis zabucajo</i>	Lecythidaceae
Leonglyc	<i>Leonia glycyarpa</i>	Violaceae
Licaadol	<i>Licania adolphoduckei</i>	Chrysobalanaceae
Licacane	<i>Licania canescens</i>	Chrysobalanaceae
Licahete	<i>Licania heteromorpha</i>	Chrysobalanaceae
Licaimpr	<i>Licania impressa</i>	Chrysobalanaceae
Licamart	<i>Licaria martiniana</i>	Lauraceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Licamicr	<i>Licania micrantha</i>	Chrysobalanaceae
Licanilo	<i>Licania niloi</i>	Chrysobalanaceae
Licaoblo	<i>Licania oblongifolia</i>	Chrysobalanaceae
Licngua	<i>Licania guianensis</i>	Chrysobalanaceae
Licrguia	<i>Licaria guianensis</i>	Lauraceae
Luehrose	<i>Lueheopsis rosea</i>	Malvaceae
Mabeangu	<i>Mabea angularis</i>	Euphorbiaceae
Mabepiri	<i>Mabea piriri</i>	Euphorbiaceae
Mabespec	<i>Mabea speciosa</i>	Euphorbiaceae
Macrlimb	<i>Macrolobium limbatum</i>	Leguminosae
Manibide	<i>Manilkara bidentata</i>	Sapotaceae
Manicava	<i>Manilkara cavalcantei</i>	Sapotaceae
Manihube	<i>Manilkara huberi</i>	Sapotaceae
Maquscle	<i>Maquira sclerophylla</i>	Moraceae
Maytguia	<i>Maytenus guianensis</i>	Celastraceae
Maytguya	<i>Maytenus guyanensis</i>	Celastraceae
Metrflav	<i>Metrodorea flavida</i>	Rutaceae
Meziduck	<i>Mezilaurus duckei</i>	Lauraceae
Meziita-	<i>Mezilaurus ita-uba</i>	Lauraceae
Micoargy	<i>Miconia argyrophylla</i>	Melastomataceae
Micodisp	<i>Miconia dispar</i>	Melastomataceae
Micoerio	<i>Miconia eriodonta</i>	Melastomataceae
Micohygr	<i>Miconia hygrophila</i>	Melastomataceae
Miconerv	<i>Miconia nervosa</i>	Melastomataceae
Micopoep	<i>Miconia poeppigii</i>	Melastomataceae
Micotome	<i>Miconia tomentosa</i>	Melastomataceae
Micrcyli	<i>Micropholis cylindrocarpa</i>	Sapotaceae
Micrguya	<i>Micropholis guyanensis</i>	Sapotaceae
Micrplee	<i>Micropholis pleeana</i>	Sapotaceae
Micrscle	<i>Micrandropsis scleroxylon</i>	Euphorbiaceae
Micrsple	<i>Micropholis splendens</i>	Sapotaceae
Micrvenu	<i>Micropholis venulosa</i>	Sapotaceae
Mikaerio	<i>Mikania eriophora</i>	Compositae
Minngua	<i>Minquartia guianensis</i>	Olacaceae
Morococc	<i>Moronobea coccinea</i>	Clusiaceae
Mourcoll	<i>Mouriri collocarpa</i>	Melastomataceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Mourfico	<i>Mouriri ficoides</i>	Melastomataceae
Myrcdubi	<i>Myrciaria dubia</i>	Myrtaceae
Myrcfene	<i>Myrcia fenestrata</i>	Myrtaceae
Myrcguia	<i>Myrcia guianensis</i>	Myrtaceae
Myrchual	<i>Myrcia huallagae</i>	Myrtaceae
Myrcminu	<i>Myrcia minutiflora</i>	Myrtaceae
Myrcmult	<i>Myrcia multiflora</i>	Myrtaceae
Myrcpaiv	<i>Myrcia paivae</i>	Myrtaceae
Myrcsp1	<i>Myrcia</i> sp. 1	Myrtaceae
Naucalo	<i>Naucleopsis caloneura</i>	Moraceae
Naucmacr	<i>Naucleopsis macrophylla</i>	Moraceae
Nauculei	<i>Naucleopsis ulei</i>	Moraceae
Nealyapu	<i>Nealchornea yapurensis</i>	Euphorbiaceae
Neeaoppo	<i>Neea oppositifolia</i>	Nyctaginaceae
Neeaoval	<i>Neea ovalifolia</i>	Nyctaginaceae
Neeasp1	<i>Neea</i> sp. 1	Nyctaginaceae
Ocotbois	<i>Ocotea boissieriana</i>	Lauraceae
Ocotimme	<i>Ocotea immersa</i>	Lauraceae
Ocotnigr	<i>Ocotea nigrescens</i>	Lauraceae
Ocotoliv	<i>Ocotea olivacea</i>	Lauraceae
Oenobaca	<i>Oenocarpus bacaba</i>	Arecaceae
Oenomino	<i>Oenocarpus minor</i>	Arecaceae
Ormogros	<i>Ormosia grossa</i>	Leguminosae
Osteplat	<i>Osteophloeum platyspermum</i>	Myristicaceae
Ouradisc	<i>Ouratea discophora</i>	Ochnaceae
Ourasupe	<i>Ouratea superba</i>	Ochnaceae
Pachmacr	<i>Pachira macrocalyx</i>	Malvaceae
Palianis	<i>Palicourea anisoloba</i>	Rubiaceae
Palicory	<i>Palicourea corymbifera</i>	Rubiaceae
Pariexce	<i>Parinari excelsa</i>	Chrysobalanaceae
Parimont	<i>Parinari montana</i>	Chrysobalanaceae
Pariparv	<i>Parinari parvifolia</i>	Chrysobalanaceae
Parkmult	<i>Parkia multijuga</i>	Leguminosae
Parkniti	<i>Parkia nitida</i>	Leguminosae
Parkpend	<i>Parkia pendula</i>	Leguminosae
Pausmacr	<i>Pausandra macropetala</i>	Euphorbiaceae

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<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Paypgran	<i>Paypayrola grandiflora</i>	Violaceae
Paypguia	<i>Paypayrola guianensis</i>	Violaceae
Payplong	<i>Paypayrola longifolia</i>	Violaceae
Peltcati	<i>Peltogyne catingae</i>	Leguminosae
Peltpani	<i>Peltogyne paniculata</i>	Leguminosae
Peremoll	<i>Perebea mollis</i>	Moraceae
Picspru	<i>Picrolemma sprucei</i>	Simaroubaceae
Pipeduck	<i>Piper duckei</i>	Piperaceae
Pipelies	<i>Piper liesneri</i>	Piperaceae
Plattrin	<i>Platymiscium trinitatis</i>	Leguminosae
Plinrivu	<i>Plinia rivularis</i>	Myrtaceae
Pogoscho	<i>Pogonophora schomburgkiana</i>	Peraceae
Poraseri	<i>Poraqueiba sericea</i>	Icacinaceae
Potaamar	<i>Potalia amara</i>	Gentianaceae
Pourbico	<i>Pourouma bicolor</i>	Urticaceae
Pourcusp	<i>Pourouma cuspidata</i>	Urticaceae
Pourguia	<i>Pourouma guianensis</i>	Urticaceae
Pourmino	<i>Pourouma minor</i>	Urticaceae
Pourtome	<i>Pourouma tomentosa</i>	Urticaceae
Pourvill	<i>Pourouma villosa</i>	Urticaceae
Poutanom	<i>Pouteria anomala</i>	Sapotaceae
Pouteryt	<i>Pouteria erythrochrysa</i>	Sapotaceae
Poutfili	<i>Pouteria filipes</i>	Sapotaceae
Poutfrei	<i>Pouteria freitasii</i>	Sapotaceae
Poutguia	<i>Pouteria guianensis</i>	Sapotaceae
Poutmini	<i>Pouteria minima</i>	Sapotaceae
Poutpall	<i>Pouteria pallens</i>	Sapotaceae
Poutreti	<i>Pouteria reticulata</i>	Sapotaceae
Poutrost	<i>Pouteria rostrata</i>	Sapotaceae
Poutsple	<i>Pouteria splendens</i>	Sapotaceae
Poutvert	<i>Pouteria verticillata</i>	Sapotaceae
Poutvire	<i>Pouteria virescens</i>	Sapotaceae
Pradcoch	<i>Pradosia cochlearia</i>	Sapotaceae
Protalts	<i>Protium altsonii</i>	Burseraceae
Protamaz	<i>Protium amazonicum</i>	Burseraceae
Protapic	<i>Protium apiculatum</i>	Burseraceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Protarac	<i>Protium aracouchini</i>	Burseraceae
Protdeca	<i>Protium decandrum</i>	Burseraceae
Protgiga	<i>Protium giganteum</i>	Burseraceae
Protgran	<i>Protium grandifolium</i>	Burseraceae
Prothebe	<i>Protium hebetatum</i>	Burseraceae
Protopac	<i>Protium opacum</i>	Burseraceae
Protpilo	<i>Protium pilosum</i>	Burseraceae
Protroif	<i>Protium roifolium</i>	Burseraceae
Protstru	<i>Protium strumosum</i>	Burseraceae
Protsubs	<i>Protium subserratum</i>	Burseraceae
Protunif	<i>Protium unifoliolatum</i>	Burseraceae
Prunmyrt	<i>Prunus myrtifolia</i>	Rosaceae
Pseulaev	<i>Pseudolmedia laevis</i>	Moraceae
Pseupsil	<i>Pseudopiptadenia psilostachya</i>	Leguminosae
Psyciodo	<i>Psychotria iodotricha</i>	Rubiaceae
Psyrhod	<i>Psychotria rhodotricha</i>	Rubiaceae
Pteroffi	<i>Pterocarpus officinalis</i>	Leguminosae
Pterrohr	<i>Pterocarpus rohrii</i>	Leguminosae
Ptycolac	<i>Ptychopetalum olacoides</i>	Olacaceae
Qualpara	<i>Qualea paraensis</i>	Vochysiaceae
Quarochr	<i>Quararibea ochrocalyx</i>	Malvaceae
Quiiamaz	<i>Quiina amazonica</i>	Ochnaceae
Rhoddioi	<i>Rhodostemonodaphne dioica</i>	Lauraceae
Rhodgran	<i>Rhodostemonodaphne grandis</i>	Lauraceae
Rhodrecu	<i>Rhodostemonodaphne recurva</i>	Lauraceae
Rinoamap	<i>Rinorea amapensis</i>	Violaceae
Rinoguia	<i>Rinorea guianensis</i>	Violaceae
Rinomacr	<i>Rinorea macrocarpa</i>	Violaceae
Rinorace	<i>Rinorea racemosa</i>	Violaceae
Rouccolu	<i>Roucheria columbiana</i>	Linaceae
Roupmont	<i>Roupala montana</i>	Proteaceae
Ruizcass	<i>Ruizterania cassiquiarensis</i>	Vochysiaceae
Sacomatt	<i>Sacoglottis mattogrossensis</i>	Humiriaceae
Salainsi	<i>Salacia insignis</i>	Celastraceae
Sapiglan	<i>Sapium glandulosum</i>	Euphorbiaceae
Sapimarm	<i>Sapium marmieri</i>	Euphorbiaceae

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<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Sarcbras	<i>Sarcaulus brasiliensis</i>	Sapotaceae
Schemoro	<i>Schefflera morototoni</i>	Araliaceae
Schiamaz	<i>Schizolobium amazonicum</i>	Leguminosae
Schipara	<i>Schizolobium parahyba</i>	Leguminosae
Senepoly	<i>Senegalia polyphylla</i>	Leguminosae
Sextrubr	<i>Sextonia rubra</i>	Lauraceae
Simaamar	<i>Simarouba amara</i>	Simaroubaceae
Simacedr	<i>Simaba cedron</i>	Simaroubaceae
Simapoly	<i>Simaba polyphylla</i>	Simaroubaceae
Sipadeci	<i>Siparuna decipiens</i>	Siparunaceae
Sipagua	<i>Siparuna guianensis</i>	Siparunaceae
Sloalaur	<i>Sloanea laurifolia</i>	Elaeocarpaceae
Sloasyna	<i>Sloanea synandra</i>	Elaeocarpaceae
Socrexor	<i>Socratea exorrhiza</i>	Arecaceae
Solacrin	<i>Solanum crinitum</i>	Solanaceae
Solaleuc	<i>Solanum leucocarpon</i>	Solanaceae
Solarugo	<i>Solanum rugosum</i>	Solanaceae
Solasedt	<i>Solanum sedthnearianum</i>	Solanaceae
Soroguil	<i>Sorocea guilleminiana</i>	Moraceae
Soromuri	<i>Sorocea muriculata</i>	Moraceae
Sponmomb	<i>Spondias mombin</i>	Anacardiaceae
Sterapet	<i>Sterculia apetala</i>	Malvaceae
Sterduck	<i>Sterculia duckei</i>	Malvaceae
Sterexce	<i>Sterculia excelsa</i>	Malvaceae
Sterobov	<i>Sterigmatopetalum obovatum</i>	Rhizophoraceae
Stersp1	<i>Sterculia</i> sp. 1	Malvaceae
Sterstri	<i>Sterculia striata</i>	Malvaceae
Stryguia	<i>Stryphnodendron guianense</i>	Leguminosae
Swararbo	<i>Swartzia arborescens</i>	Leguminosae
Swararbo	<i>Swartzia arborescens</i>	Solanaceae
Swarcusp	<i>Swartzia cuspidata</i>	Leguminosae
Swarcusp	<i>Swartzia cuspidata</i>	Solanaceae
Swaringi	<i>Swartzia ingifolia</i>	Leguminosae
Swaringi	<i>Swartzia ingifolia</i>	Solanaceae
Swarpoly	<i>Swartzia polyphylla</i>	Leguminosae
Swarpoly	<i>Swartzia polyphylla</i>	Solanaceae

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<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Swarrecu	<i>Swartzia recurva</i>	Leguminosae
Swarrecu	<i>Swartzia recurva</i>	Solanaceae
Swarreti	<i>Swartzia reticulata</i>	Leguminosae
Swarreti	<i>Swartzia reticulata</i>	Solanaceae
Swarsimp	<i>Swartzia simplex</i>	Leguminosae
Swarsimp	<i>Swartzia simplex</i>	Solanaceae
Sympglob	<i>Symphonia globulifera</i>	Clusiaceae
Sympsp1	<i>Symphonia</i> sp. 1	Clusiaceae
Tabemuri	<i>Tabernaemontana muricata</i>	Apocynaceae
Tachchry	<i>Tachigali chrysophylla</i>	Leguminosae
Tachglau	<i>Tachigali glauca</i>	Leguminosae
Tachguia	<i>Tachigali guianensis</i>	Leguminosae
Tachmacr	<i>Tachigali macropetala</i>	Leguminosae
Tachmicr	<i>Tachigali micropetala</i>	Leguminosae
Tachmyrm	<i>Tachigali myrmecophila</i>	Leguminosae
Tachvenu	<i>Tachigali venusta</i>	Leguminosae
Talimoll	<i>Talisia mollis</i>	Sapindaceae
Tapiguia	<i>Tapirira guianensis</i>	Anacardiaceae
Tapuamaz	<i>Tapura amazonica</i>	Dichapetalaceae
Taraoppo	<i>Taralea oppositifolia</i>	Leguminosae
Ternurop	<i>Ternstroemia urophora</i>	Pentaphylacaceae
Tetralti	<i>Tetragastris altissima</i>	Burseraceae
Tetrpana	<i>Tetragastris panamensis</i>	Burseraceae
Theosp1	<i>Theobroma</i> sp. 1	Malvaceae
Theosp2	<i>Theobroma</i> sp. 2	Malvaceae
Theospec	<i>Theobroma speciosum</i>	Malvaceae
Theosubi	<i>Theobroma subincanum</i>	Malvaceae
Theosylv	<i>Theobroma sylvestre</i>	Malvaceae
Thyrspru	<i>Thyrsodium spruceanum</i>	Anacardiaceae
Tourguia	<i>Touroulia guianensis</i>	Ochnaceae
Tovoobov	<i>Tovomita obovata</i>	Clusiaceae
Tratrhoi	<i>Trattinnickia rhoifolia</i>	Burseraceae
Tremmicr	<i>Trema micrantha</i>	Cannabaceae
Triccipo	<i>Trichilia cipo</i>	Meliaceae
Tricplee	<i>Trichilia pleeana</i>	Meliaceae
Tripamer	<i>Triplaris americana</i>	Polygonaceae

Continued

<b>Code</b>	<b>Scientific Name</b>	<b>Family</b>
Trymamaz	<i>Trymatococcus amazonicus</i>	Moraceae
Unonduck	<i>Unonopsis duckei</i>	Annonaceae
Vantparv	<i>Vantanea parviflora</i>	Humiriaceae
Vatapara	<i>Vatairea paraensis</i>	Leguminosae
Vataseri	<i>Vatairea sericea</i>	Leguminosae
Virocalo	<i>Virola calophylla</i>	Myristicaceae
Viroguia	<i>Virola guianensis</i>	Myristicaceae
Viromich	<i>Virola michelii</i>	Myristicaceae
Viromoll	<i>Virola mollissima</i>	Myristicaceae
Viromulf	<i>Virola multiflora</i>	Myristicaceae
Viromuln	<i>Virola multinervia</i>	Myristicaceae
Viropavo	<i>Virola pavonis</i>	Myristicaceae
Virothei	<i>Virola theiodora</i>	Myristicaceae
Viroveno	<i>Virola venosa</i>	Myristicaceae
Vismcaye	<i>Vismia cayennensis</i>	Hypericaceae
Vismguia	<i>Vismia guianensis</i>	Hypericaceae
Vismjapu	<i>Vismia japurensis</i>	Hypericaceae
Vismsand	<i>Vismia sandwithii</i>	Hypericaceae
Vitetrif	<i>Vitex triflora</i>	Lamiaceae
Warsschw	<i>Warszewiczia schwackei</i>	Rubiaceae
Xyloamaz	<i>Xylopia amazonica</i>	Annonaceae
Xyloarom	<i>Xylopia aromatica</i>	Annonaceae
Xylocalo	<i>Xylopia calophylla</i>	Annonaceae
Zantdjal	<i>Zanthoxylum djalma-batistae</i>	Rutaceae
Zantrhoi	<i>Zanthoxylum rhoifolium</i>	Rutaceae
Zygirace	<i>Zygia racemosa</i>	Leguminosae