

SUSTAINABLE FOREST MANAGEMENT: THE ROLE OF REDUCED IMPACT
LOGGING FOR TIMBER AND ENVIRONMENTAL SUSTAINABILITY

By

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To my mom, and sister: the pillars of my academic success

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LIST OF ABBREVIATIONS

CELOS	Centre for Agricultural Research in Suriname, a research institution that fosters applied scientific research in the agricultural and forestry sector in Suriname and the region.
RIL	Reduced-impact logging, a suite of logging techniques that reduce the undesirable impacts of logging on the forest.
SFM	Sustainable forest management, managing forests to increase their benefits, including timber and food, to meet society's needs in a way that conserves and maintains forest ecosystems for the benefit of present and future generations.

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Implementation of reduced-impact logging (RIL) practices is expected to contribute to the sustainability of selective timber harvests from tropical forests while helping to maintain ecosystem services. Decades after implementation of experiments on RIL and other silvicultural treatments (e.g., liberation thinning), there is still a scarcity of the results needed to design guidelines for sustainable forest management. In this thesis, I revisit two long-term experimental studies on improved forestry practices in Guiana Shield forests, one of the last remaining unfragmented tropical forests in the world. Data from these two experimental studies, the CELOS harvest system in Suriname and the Pibiri-RIL study in Guyana, are used to assess the rates of post-logging recovery of timber and carbon stocks, which represent the major market values of these forests. At another site in Guyana, I also assess the impacts of RIL on large neotropical vertebrates from which I disentangle the effects of hunting. We applied modern quantitative analytical methods to evaluate these long-term datasets and the impact of logging on biodiversity.

I found that in both Guyana and Suriname, RIL below a threshold intensity of 8 trees ha⁻¹ (24 m³ ha⁻¹) recovered merchantable timber stocks within 40 years, with

similarly fast recovery of carbon values. At these low logging intensities with RIL, large vertebrate diversity does not decline, except where there is substantial hunting pressure. This good news about Guiana Shield forest recovery after RIL (at least at low logging intensities) needs to be tempered by concerns about yield sustainability after the second harvest. More intensive liberation treatments that favor the growth of future crop trees may help sustain timber yields from these forests beyond the second harvest but at the cost of carbon stocks.

CHAPTER 1 INTRODUCTION

Forests and trees stabilize soils and climates, support biodiversity, regulate water flows, and contribute to the livelihoods of hundreds of millions of people for whom they provide food, energy and income (FAO 2016). As such, forests have clear contributions to make towards achievement of the United Nations Sustainable Development Goals (SDGs) that aim to reduce poverty, protect ecosystems services, improve access to sustainable energy, and combat climate change. In forested landscapes where timber production can compete with the attainment of environmental and biodiversity goals, forest managers need to holistically view the environmental, social, and economic impacts of their operations. As they work towards sustainable forest management (SFM), managers need to strive to maintain the flows of timber as well as the ecosystem services and biodiversity that society expects (Edwards, Tobias, *et al.* 2014).

Many conservationists see the adoption of SFM as an imperative step to ensure forests are not degraded by forestry activities. At the same time, by sustaining timber values, managers can reduce the likelihood of forest conversion where markets determine forest fates. SFM also contributes to livelihoods and provides safer environments for forestry workers. In regards to the environment, SFM contributes to important services such as carbon sequestration along with water, soil, and biodiversity conservation. Despite substantial financial investments in SFM in the tropics, we still lack specific technical details about which forestry practices will achieve SFM, especially at the regional level where geographical and forest attributes vary.

Arising out of initial research into SFM was a suite of practices to reduce the deleterious impacts of timber harvesting referred to as reduced-impact logging (RIL; Pinard & Putz, 1996; Bertault & Sist, 1997) . Through a highly controlled process of

planning, mapping, felling, extraction and monitoring of forest operations, damage to the forest structure can be substantially reduced (Dykstra 2001). Positive benefits are reported for biodiversity (Bicknell *et al.* 2014) as well as for rates of post-logging recovery compared to forests conventionally logged (Vidal *et al.* 2016). However, RIL alone might be insufficient to maintain a continuous flow of timber with financially viable cutting cycles (Ruslandi *et al.* 2017, Putz & Ruslandi 2015).

Information on appropriate forest management measures like RIL are especially needed for the Guiana Shield forests, one of the last remaining unfragmented blocks of tropical forests in the World. The Guiana Shield has historically suffered low deforestation rates, due to low human population, poor road infrastructure, and low land-use pressure for forest conversion for agriculture, mining, and urban development. However, as Guiana Shield countries become more integrated into the global market economy, their forests are under increasing threats from unsustainable exploitation for logs as well as from mining and infrastructure development. Guiana Shield governments have officially adopted the ideals of sustainable forest management as part of national development plans being pursued to raise the living standards and incomes of their citizens. We thus have a unique opportunity to work with forest managers across the Guiana Shield to apply more effective measures for forest conservation and management.

Recognizing and responding to the vulnerability of over-exploitation of timber is key to designing improved logging practices that does not jeopardize future production. Timber sustainability in Guiana Shield forests is expected to be especially challenging due to characteristically low stocking of commercial timber trees compared to forests in

South East Asia and West Africa (ter Steege *et al.* 1996, Werger 2011). Long-term sustainability could also prove difficult to achieve on the nutrient-poor soils of the Guyana shield. These poor soils, which were derived from the crystalline rocks of the Guiana Shield over millions of years of weathering, support unique vegetation with about 40% of the tree species being endemic (ter Steege *et al.* 2013). The sensitivity of these forests to logging disturbances and their ability to recover might both be limited by these nutrient-poor soils and the tree species they support. Evidence of this is the low growth rates, and smaller stature trees of the high wood density species that are found in these forests. Using stand-level increments, cutting cycles of at least 60 years are recommended in Guyana (Zagt *et al.* 1997), with the CELOS system in Suriname utilizing a 25 year cycle (de Graaf 1986). These harvest cycles are however biased as they are generally based on growth increments from unlogged forests. In order to truly quantify timber sustainability, we need to account for changes in forest structure and growth rates after multiple timber harvests in managed forests.

The advancement of SFM beyond the initial core elements of RIL has been hampered by the paucity of research on forest responses to timber harvesting and other silvicultural interventions post-logging. The lack of information on forest recovery is especially deplorable given that most tropical forest agencies started to install and periodically re-measure permanent sample plots (PSPs) at least since the middle of the last century in logged tropical forests. Analysis of the data from these PSPs is primarily hampered by insufficient analytical capacities in the data-holding institutions and high costs of remeasuring these long-term experiments. In the cases in which PSP data are analyzed by extra-tropical researchers, the influence of any resulting publications on

forest policies in tropical countries seems to be limited (Ruslandi *et al.* 2014). At the same time, the results of these studies are especially important due to the poor spatial coverage of RIL research and the high variability among natural forests in the tropics.

In this thesis, I take a regional perspective on SFM practices appropriate for Guiana Shield forests in Guyana and Suriname. I use long-term PSP data on the post-logging dynamics of forests logged with RIL from both countries to identify logging thresholds beyond which timber and other ecosystem services are degraded. These experimental RIL studies were designed to inform discussions about how to sustain timber yields with financially viable cutting cycles while not jeopardizing the provision of other ecosystem services. We apply modern quantitative analyses to evaluate these long-term datasets in order to provide the information that is needed by policy makers to update forestry codes of practices for sustainable timber harvests and carbon stock management.

In the first of these studies (Chapter 2), I use data from the CELOS Harvest System experiment in Suriname, which has PSPs monitored for 32 years post-logging. The CELOS approach to timber harvesting involves the selective removal of a few trees per hectare in a manner that minimizes collateral damage to the residual forest and improves recovery of utilizable timber. The specific logging practices employed included: (1) mapping all trees of commercial timber species ≥ 35 cm measured at 1.3 m above the ground (DBH); (2) selecting trees to be felled to avoid creation of large, multiple-tree felling gaps; (3) planning and construction of roads and skid trails prior to felling; (4) directional felling to facilitate log extraction; (5) winching of logs during extraction; and, (6) the use of wheeled skidders for long-distance log yarding (de Graaf

1986, Jonkers 1987). These practices are common components of what are now referred to as reduced-impact logging (RIL) practices (e.g., Putz *et al.*, 2008). The full CELOS Management System also includes the release of future crop trees from competition through poison girdling of non-marketable stems.

The second long-term study (Chapter 3) is based on data from the Tropenbos Pibiri Growth and Yield experiment in Guyana that represents a modified version of the CELOS harvest system. It considers RIL with three logging intensities and one post-harvest silvicultural treatment in PSPs monitored for 20 years post-logging and 17 years post-liberation of future crop trees (FCTs) (van der Hout 1999). The Pibiri experiment also tested species-specific felling diameters and the application of directional felling to promote worker safety, minimize damage to the bole of the felled tree, and to aid extraction (Conway 1982, Brunberg, B. & Lindgren 1984). By reporting on the uncertainty in post-logging dynamics associated with timber and carbon stock recovery from these experiments, I hope that the results of this dissertation will help inform the management of Guiana Shield forest for both, the former associated with commitments to climate change mitigation (e.g., REDD+, Intended Nationally Determined Contribution (INDCs) associated with COP12; UFCCC 2016).

In addition to the focus on silviculture, I address a gap in our knowledge about the impacts of RIL on large neotropical vertebrates. Even though many of these animals are threatened with extinction and many are of critical ecological importance for seed dispersal, data about their reactions to logging are limited (Vetter *et al.* 2011). The assessment of logging impacts on these group of animals is rendered additionally challenging by the frequent association between logging and hunting. In Chapter 4, I

partition the effects of selective logging and subsistence hunting by indigenous people on large terrestrial vertebrates (> 1 kg) with animal surveys using camera traps and spatially explicit surveys of indigenous hunting. I apply a hierarchical multi-species occupancy model to the binary detection data to account for species-specific differences in detectability associated with behaviour and abundance (Iknayan *et al.* 2014). I assess the biodiversity outcomes specific to large vertebrates in the Iwokrama Forest in central Guyana. This forest is unique insofar as its forest management policies include: (1) the ability to exclude non-sanctioned uses that can lead to forest cover loss and forest degradation; (2) co-management institutions with indigenous communities who are legally guaranteed access for hunting and other traditional forest uses and benefit financially from the timber business; (3) adherence to high standards of RIL with third-party Forest Stewardship council (FSC) certification; and, (4) forest zoning so that protected areas equal in size to timber production forests are established in adjacent wilderness reserves.

CHAPTER 2 QUANTIFYING UNCERTAINTY ABOUT FOREST RECOVERY 32-YEARS AFTER SELECTIVE LOGGING IN SURINAME

Summary

The inclusion of managed tropical forests in climate change mitigation has made it important to find the sustainable sweet-spot for timber production, carbon retention, and the quick recovery of both. Here we focus on recovery of aboveground carbon and timber stocks over the first 32 years after selective logging with the CELOS Harvest System in Suriname. Our data are from twelve 1-ha permanent sample plots in which growth, survival, and recruitment of trees ≥ 15 cm diameter were monitored between 1978 and 2012. We evaluate plot-level changes in basal area, stem density, aboveground carbon, and timber stock in response to average timber harvests of 15, 23, and 46 m³ ha⁻¹. We use a linear mixed-effects model in a Bayesian framework to quantify recovery time for aboveground carbon and timber stock, as well as annualized increments for both. Our statistical models accounted for the uncertainty associated with the height and biomass allometries used to estimate aboveground carbon and increased precision of annualized aboveground carbon increments by including data from forty-one plots located elsewhere on the Guiana Shield. The probabilities of aboveground carbon recovery to pre-logging levels 32 years after harvests of 15, 23 and 46 m³ ha⁻¹ were 45%, 40%, and 24%, respectively. Net aboveground carbon increment for logged forests across all harvest intensities was 0.64 Mg C ha⁻¹ yr⁻¹, more

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than twice the rate observed in unlogged forests ($0.26 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). The probabilities of timber stock recovery at the end of the 32-year period were highest after harvest intensities of 15 and $23 \text{ m}^3 \text{ ha}^{-1}$ (with 80% probability) and lowest after the harvest of $46 \text{ m}^3 \text{ ha}^{-1}$ (with 70% probability). Timber stock recovery across all harvest intensities was driven primarily by residual tree growth. Application of the legal cutting limit of $25 \text{ m}^3 \text{ ha}^{-1}$ will require more than 70 and 40 years to recover aboveground carbon and timber stocks, respectively, with 90% probability. Based on the low recruitment rates of the twelve species harvested, the 25 year cutting cycle currently implemented in Suriname is too short for long-term timber stock sustainability. We highlight the value of propagating uncertainty from individual tree measurements to statistical predictions of carbon stock recovery. Ultimately, our study reveals the trade-offs that must be made between timber and carbon services as well as the opportunity to use carbon payments to enable longer cutting rotations to capture carbon from forest regrowth.

Background

Technological advancements (e.g., development of chainsaws and bulldozers) coupled with growth of global shipping industries and increased demand for tropical timbers during the mid-20th Century led to the degradation of large expanses of tropical forests by unnecessarily destructive logging (Dawkins & Philip 1998). Concerns about sustained timber production and the environmental degradation caused by bad logging practices motivated research to identify management prescriptions for improved tropical forest management. These logging studies aimed to reconcile tropical timber production with the provision of other ecosystem services, and to ensure continued timber production with economically viable cutting cycles (van der Hout 1999, Jonkers 1987, Nicholson 1979, FAO 2004, Nicholson 1958).

The CELOS Harvest System experiments in Suriname, the results of which were recently reviewed by Werger (2011), are among the oldest on-going studies of improved forest management in the tropics. The CELOS approach involves the selective removal of a few trees per hectare in a manner that minimizes collateral damage to the residual forest and improves recovery of utilizable timber. The specific logging practices employed include: (1) mapping all trees of commercial timber species ≥ 35 cm measured at 1.3 m above the ground (DBH); (2) selecting trees to be felled to avoid aggregations that would result in large felling gaps; (3) planning and construction of roads and skid trails prior to felling; (4) directional felling to facilitate log extraction; and, (5) winching of logs during extraction and the use of wheeled skidders for long-distance log yarding (de Graaf 1986, Jonkers 1987). These practices are common components of what are now referred to as reduced-impact logging (RIL) systems (e.g., Putz *et al.* 2008). The full CELOS Management System also includes the release of future crop trees (FCTs) from competition through poison girdling of non-marketable stems, but no post-harvest silvicultural treatments were applied in the plots we studied.

Although the primary goal of the CELOS Management System was to sustain timber stocks, reduction in residual stand damage relative to unplanned or conventional logging also has positive effects on standing stocks of forest carbon and rates of post-logging recovery (Pinard and Putz, 1996; Putz *et al.* 2012; Vidal *et al.* 2016). By reporting on the post-logging dynamics of aboveground carbon stocks (ACS) and timber stocks, we hope that this study helps inform the management of Suriname's forest for both, the former associated with the country's commitment to climate change mitigation (e.g., REDD+, Intended Nationally Determined Contribution (INDCs) associated with

COP12; UFCCC 2016). In particular, with permanent sample plot data for the first 32-years after logging, we evaluate changes in tree density, basal area, ACS, and timber stocks.

We use permanent sample plot data collected between 1978 to 2012 to build statistical models in a Bayesian framework to predict recovery time and forest stand increments as a function of harvest intensity ($\text{m}^3 \text{ha}^{-1}$ of commercial timber). Our Bayesian analytical approach also provided a means to address the long and irregular census intervals that would otherwise result in underestimated aboveground carbon increments (Clark *et al.* 2001; Sheil and May, 1996; Talbot *et al.* 2014). Specifically, we include results from previous research on aboveground carbon increments for the Guiana Shield as informed priors to reduce uncertainty in our model predictions (Crome *et al.* 1996; McCarthy and Masters, 2005; Morris *et al.* 2013). In addition to leveraging knowledge gained from other studies, our Bayesian approach enabled us to propagate uncertainty associated with our height and biomass allometries into our ACS recovery predictions.

Methods

Study Site

The experimentally logged plots are in a 1150 ha research area (hereafter Kabo; $5^{\circ} 15' \text{N}$, $55^{\circ} 43' \text{W}$) in north-central Suriname (Figure A-1). Common canopy tree species in this lowland moist tropical forest are *Dicorynia guianensis* Amshoff (Fabaceae), *Qualea rosea* Aubl. (Vochysiaceae), and *Dendrobangia boliviana* Rusby (Cardiopteridaceae). The understory is composed mainly of palms, with *Astrocaryum sciophyllum* Pulle and *Astrocaryum paramaca* Mart. the most abundant (Jonkers 1987). The soil is an ultic haplorthox, a low pH sandy loam that is characteristic of the highly

weathered Precambrian Guiana Shield (Hammond 2005, Poels 1987, Quesada *et al.* 2010). Annual precipitation is 2385 mm with a mean of 98 mm in each of the driest months of September and October (Dekker & de Graaf 2003).

Experimental Design and Logging Treatments

Trees of commercial timber species (DBH \geq 15 cm; Table A-1) were marked, mapped, and measured across a 140-ha forest compartment in 1978. Experimental logging treatments designed to remove 1, 2, and 4 m² ha⁻¹ of basal area were applied between 1979-1980 based on a randomized block design. Each logging treatment was applied to 4 ha with 3 replicates per logging treatment (Table 2-1; Figure A-1.). The basal areas removed corresponded to average harvests of 15, 23, and 46 m³ ha⁻¹ of commercial log volumes (hereafter low, medium, and high-intensity timber harvests; Jonkers, 1987, 2011). Trees of commercial timber species \geq 15 cm DBH were re-censused immediately after logging in 1980 in 1 ha permanent sample plots established within each of the 4 ha treatment blocks.

Growth, recruitment, and mortality of trees \geq 15 cm DBH of all species, commercial and non-commercial, were subsequently monitored in these 1-ha plots (100 x 100 m) for each replicated treatment four times (1981, 1983, 2000 and 2012). Unlogged control plots of 1-ha were established within the study site in 1983 and remeasured in 2000 and 2012 (Figure A-1). Censuses adhered to protocols established by Jonkers (1983) based on standards set out in Synnott (1979). Tree species were identified by para-botanists (tree-spotters) based on common names and converted to their scientific names by a trained botanist. In instances where species were unknown, botanical collections were made for comparison with herbarium specimens. In cases of irregular stem form associated with buttresses and bole deformities, the point of

measurement was moved to 1 m above the end of the deformity to continue growth monitoring.

When the forest was selectively logged by trained and closely supervised crews, the main skid trails were opened with a D6 bulldozer within 25-m wide strips between the 1-ha permanent sample plots. Trees were directionally felled to aid extraction with wheeled skidders. Tree location maps developed from a 100% pre-harvest inventory of harvestable trees, together with topographic maps, were used to inform the selection of trees to be harvested and to plan the most appropriate routes for extraction. There were a total of six skid trail entry points into the 1-ha permanent sample plots, three on the western side and three located on the east.

Stem Densities and Basal Areas ($\text{m}^2 \text{ha}^{-1}$)

We report changes over time in basal area, stem density, and diameter class distributions for the twelve 1-ha permanent sample plots. As pre-logging data were only available for commercial stems prior to logging, we track the changes in forest structure for the logged plots between the first census completed post-logging (1981) when all stems, commercial and non-commercial species, were recorded to the last census in 2012, except for timber stocks where we use the plot census data from 1980. We also report on the observed changes for the control plots between 1983 and 2012 as well as the basal area-weighted average wood density across censuses and diameter classes for all plots. We acknowledge that forest structure can vary greatly across small spatial scales, and the use of only three 1-ha control plots as baseline reference values is not ideal. We address this limitation in our statistical models for ACS recovery through the estimation of plot-level ACS prior to logging based on an emissions factor associated with logging intensity (Appendix A).

Aboveground Carbon Stocks (ACS; Mg C ha⁻¹)

To estimate aboveground biomass for each tree across censuses we applied the pan-tropical allometric model of Chave et al. (2014; Eq. 4): *aboveground biomass* = $\beta_0 * (pD^2H)^{\beta_1}$, where p is species-specific wood density (g cm⁻³), D is stem diameter (cm), and H is total tree height (m). Tree heights were not measured so we estimated them with the diameter-height allometry model also proposed by Chave et al. (2014; Eq. 6a), $\ln(H) = \theta_0 - E + \theta_1 * \ln(D) - \theta_2 * (\ln(D))^2$. The E parameter is a site-specific bioclimatic stress variable that includes temperature seasonality, precipitation seasonality, and climatic water deficit. We estimate the β_i and θ_i parameters in the allometric equations using the Chave et al. (2014) destructive harvest dataset (Appendix A). We propagate the uncertainty around the β_i and θ_i parameters into 1350 posterior predictions of biomass for each individual tree in our census data. Aboveground carbon stocks (ACS) were estimated by multiplying aboveground tree biomass by 0.47 (IPCC 2003).

Stem wood densities [p] used in our biomass allometry were extracted from a global pan-tropical database (Chave *et al.* 2009); in the absence of species-level p values (9% of trees), the mean wood density was used for congeneric trees in tropical South America; if genus-level wood density data were unavailable (2% of trees), we used mean family values; and, for a single stem for which we had no taxonomic information, we used the basal area-weighted average wood density for the plot (Baker *et al.* 2004).

Timber Stocks (m³ ha⁻¹)

We applied in-country derived species-specific allometric equations to estimate timber stocks when available, but otherwise used a generic equation (Table A-1). Our estimates of rates of post-logging timber stock recovery are restricted to the 10 species harvested in 1979 (Table A-1) and to trees ≥ 35 cm DBH, the legal minimum cutting diameter in Suriname. Only stems of commercial value, as indicated by log quality assessments made at each census were included in our timber stock estimation. We retained class code 1 stems (trees with straight and long boles without defects), and class code 2 stems (trees slightly leaning, somewhat crooked, or with minor defects) for reporting timber stocks (Alder & Synnott 1992). To account for the lower timber stock recovery associated with minor defects for trees with stem class code 2, we reduced our timber stock estimates by 20% for those trees. We were not able to propagate uncertainty associated with our allometric equations used to estimate timber stock, as we did for ACS, because the original destructive harvest data used to build the timber stock allometric equations were not available.

Statistical Models: ACS and Timber Stock Recovery

We weighted our response variables, ACS and timber stock, by their respective plot-level initial values (i.e., prior to logging). This proportional approach facilitates interpretation of model predictions; values ≥ 1 indicate full plot recovery to the initial forest state prior to logging. As we did not have initial ACS values for the logged plots, we estimate these values by applying a carbon emissions factor based on logging intensity from a study conducted in Guyana on the same weathered Precambrian Guiana Shield substrate as our study site in Suriname (Pearson *et al.* 2014). The emissions factor of 1.52 Mg C m⁻³ ha⁻¹ accounted for carbon emissions associated with

the extracted log, damage to the residual stand, and logging infrastructure associated with skid trails (Appendix A). The weighted ACS values we consider to be conservative estimates of recovery as the emissions factors reported in the Pearson *et al.* (2014) included stems with DBH ≥ 10 cm, whilst our census data are restricted to stems with DBH ≥ 15 cm. We estimate ACS stored in stems 10-15 cm DBH to be approximately 1.97 Mg C ha⁻¹ (SD ± 0.37), based on permanent sample plot data from Guyana (unpublished data; Chapter 3).

We used a linear mixed-model approach to predict the time needed for ACS and timber stocks to recover to pre-logging values. Our mixed-model approach allows us to account for correlations among repeated measures at the plot level that would otherwise violate the assumption of independence. We incorporated plot-level random effects in our models to account for these correlations under the assumption of heterogeneous variance (Barnett *et al.* 2010).

We partitioned the additional variation in our models into fixed effects for harvest intensity (timber volume extracted) and time-since-logging (years), which are continuous covariates:

$$\mu_{ij} = \alpha_0 + \beta_1 * harv.intensity + \beta_2 * time.since.logged + (\beta_3 * harv.intensity * time.since.logged) + plot[i]$$

where μ_{ij} represents the mean from a normal distribution for the i^{th} plot and j^{th} census.

α_0 is the intercept term that represents the unlogged forest state; and, β_1 , β_2 and β_3 capture the effect of harvest intensity, time-since-logging, and the interaction between harvest intensity and time, respectively. Plot level variance is captured by $plot[i]$. We explored several models that included different combinations of covariates and also treated censuses as a fixed categorical random effect. We use the Deviance

Information Criterion (DIC) to select the best model and present results from those models (Spiegelhalter *et al.* 2002). We also assessed the goodness-of-fit of our models based on the variance explained (R^2), and partitioned the explained variance into fixed and random factors (Nakagawa and Schielzeth, 2013; Appendix A).

Our final model predictions accounts for uncertainty associated with our model parameters as well as sampling uncertainty based on a Gaussian distribution. The flexibility of our Bayesian modeling framework also enabled us to propagate the uncertainty associated with our height and biomass allometries into our statistical model for estimation of ACS. We ran all our models for 300,000 iterations, discarded the first 20,000 draws, and thinned our remaining posterior samples by 2000 using JAGS in R (Plummer 2011, R Development Core Team 2015).

Annualized Increments for Aboveground Carbon and Timber

We calculated annualized increments for aboveground carbon and timber based on the methodology recommended by Clark *et al.* (2001) for forest stands that are re-measured after long intervals. We estimated the difference in carbon stock from all surviving trees at the plot-level between censuses, subtracted carbon gained from newly recruited trees and added the biomass of trees that died between censuses (Clark *et al.* 2001). To account for uncertainty in aboveground carbon increments due to the long census intervals, we used aboveground carbon increments ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$) reported from forty-one plots across the Guiana Shield in our statistical model. Failure to correct for the long census intervals would otherwise result in underestimates of annualized aboveground carbon increments due to (1) unobserved growth of residual trees that died between censuses and (2) trees that grew to exceed 15 cm DBH but died before they were recorded (Clark *et al.* 2001). We incorporate the results from the

Johnson *et al.* (2016) as informative priors for the unlogged forest state in our statistical model because we were unable to implement the parametric technique recommended by Malhi *et al.* (2004). That approach partitions sequential censuses into increasing time intervals, but we are limited by two census intervals, 1983-2000 and 2000-2012, that averages 15 years between censuses. We also did not use the method recommended by Talbot *et al.* (2014) to deal with the same problem, which estimates the number of unobserved recruits based on mean annual mortality and recruitment rates, because it seems more suited for shorter time spans between censuses.

Instead of the Malhi *et al.* (2004) and Talbot *et al.* (2014) corrections for underestimated aboveground productivity, we rely on Bayes' principle that allows us to include published rates of aboveground carbon increments for the Guiana Shield in the form of a prior distribution to increase the precision of our model predictions for aboveground carbon productivity. The combination of this prior information, with the likelihood function that relates our observed data to the statistical model, enables us to obtain a posterior distribution that characterizes the parameter of interest under Bayes' theorem. If the prior information specified does not reduce the model fit, the model DIC value (which is analogous to the AIC in a likelihood framework) will improve (Spiegelhalter *et al.* 2002). Improvements indicate that the prior information specified is consistent with the data and that the data had an overwhelmingly large influence on the posterior distribution (Morris *et al.* 2013). Bayes' principle is especially suited to our needs given that we aim to quantify and communicate uncertainty around post-logging recovery in a probabilistic manner, and overcome data limitations with a quantitatively

rigorous approach to better inform forest managers (Hobbs & Hooten 2015, McCarthy & Masters 2005).

Results

Stem Density and Basal Area ($\text{m}^2 \text{ha}^{-1}$) Recovery

Average density of trees ≥ 15 cm DBH in the control plots declined by 4% over the 29-year observation period, from 265 stems ha^{-1} in 1983 to 254 stems ha^{-1} in 2012. After logging at medium and high intensities, stem densities increased by 14% and 16% between 1981 and 2012, from 248 to 282 stems ha^{-1} and from 218 to 254 stems ha^{-1} , respectively; average density after low intensity logging increased by 4%, from 251 to 261 stems ha^{-1} (Table 2-1; Figure 2-1).

Basal area in the control plots increased by 6% between 1983 ($27.23 \text{ m}^2 \text{ha}^{-1}$) and 2012 ($28.93 \text{ m}^2 \text{ha}^{-1}$). On average high intensity logged plots had the lowest basal area in 1981 ($21.12 \text{ m}^2 \text{ha}^{-1}$) after logging with the largest increase of 33% by 2012 ($28.09 \text{ m}^2 \text{ha}^{-1}$). Basal area in the low intensity logged plots increased by 19% (from 23.38 to $27.92 \text{ m}^2 \text{ha}^{-1}$) and medium intensity logged plots by 11% (from 23.69 to $26.36 \text{ m}^2 \text{ha}^{-1}$; Table 2-1; Figure 2-1). Between 1981 and 2012, basal area-weighted average wood density for control, low, and medium intensity logged plots remained relatively constant at 0.64 g cm^{-3} whereas it declined by 4% after the highest intensity of logging, from 0.66 g cm^{-3} in 1981 to 0.63 g cm^{-3} in 2012 (Table 2-1).

ACS (Mg C ha^{-1}) and Timber Stock ($\text{m}^3 \text{ha}^{-1}$) Recovery

Average control plot ACS increased by 8% over the 29-year observation period, from $156.75 \text{ Mg C ha}^{-1}$ in 1983 to $169.10 \text{ Mg C ha}^{-1}$ in 2012. On average, ACS in low, medium, and high intensity logged plots 32 years after the harvest were below the 2012

control plot mean values by 7% (157.94 Mg C ha⁻¹), 13% (146.99 Mg C ha⁻¹), and 4% (162.94 Mg C ha⁻¹), respectively, with highly variable plot-level ACS gains (Figure 2-1).

Commercial timber in stems \geq 35 cm DBH that were judged to have merchantable boles (Grade 1 plus 80% of Grade 2) was estimated at 100 m³ ha⁻¹ (SE \pm 9.2) prior to logging in 1978 across the entire harvest block. Control forest stands recorded an increase in standing stocks of timber of 25% from 1983 (87.4 m³ ha⁻¹) to 2012 (109.30 m³ ha⁻¹). Plots logged at low and high intensity had recovered their initial (1978) commercial timber of 81.56 m³ ha⁻¹ and 120.21 m³ ha⁻¹, respectively; in 2012 their commercial timber stocks were 49% (121.62 m³ ha⁻¹) and 24% (148.57 m³ ha⁻¹) higher than their initial commercial timber stocks. Over the same 32-year period, plots logged at medium intensity recovered to 84% of commercial timber stocks measured in 1978, from 98.22 m³ ha⁻¹ before the harvest to 82.58 m³ ha⁻¹ in 2012.

Model Predictions of ACS and Timber Stock Recovery

The probability of ACS recovery 32 years post-logging was 45%, 40% and 24% after low, medium, and high logging intensity (Figure 2-2). At the currently instituted legal harvest intensity of 25 m³ ha⁻¹, more than 70 years will be required to recover ACS with 90% probability. The mean predicted time to recover initial ACS, estimated at 184.95 Mg C ha⁻¹ across all plots, after 25 m³ ha⁻¹ harvest intensity is 37 years (95%; CI, 140.56 to 229.34 Mg C ha⁻¹). Logging intensity (β_1) had a negative effect on ACS recovery with time-since-logging (β_2) and the interaction term (β_3) with positive but non-significant effects (Figure 2-3).

Model predictions of timber stock recovery at the end of 32 years after logging was 82%, 80% and 70% after low, medium, and high logging intensity. The mean recovery time needed at harvest intensity of 25 m³ ha⁻¹ was estimated at 20 years (95%

CI: 60.00 to 137.00 m³ ha⁻¹). For more than 90% probability that timber stock would have recovered to pre-logged values, 40 years will be required. Logging intensity had a negative effect on timber stock recovery with small positive effects for time-since-logging and the interaction term (Figure 2-3).

Our ACS and timber stock models explained 0.74 (95% CI, 0.60 to 0.86) and 0.84 (95% CI, 0.75 to 0.91) of the variance captured by our fixed and random effects (conditional R²; Figure A-2 and Figure A-3). Fixed factors (i.e. logging intensity, time-since-logging, and an interaction term) accounted for 85% and 65% of the explained variance (marginal R²) in our ACS and timber stock recovery models, respectively. Our random-effects (plot identity) accounted for 15% and 33% of the variance explained by our ACS and timber stock recovery models, respectively.

Annualized Increments for Aboveground Carbon (Mg C ha⁻¹ yr⁻¹) and Timber (m³ ha⁻¹ yr⁻¹)

Predicted increments of aboveground carbon were highest for plots logged at 46 m³ ha⁻¹ (2.91 Mg C ha⁻¹ yr⁻¹; CI, 1.99 to 3.82) and slowest in the unlogged forests (2.39 Mg C ha⁻¹ yr⁻¹; CI, 1.51 to 3.26; Table 2-2). Observed carbon losses were highest in medium intensity logged plots, with annual mortality rates of 2.26 Mg C ha⁻¹ yr⁻¹, resulting in the slowest net increase of ACS. The model that used results from previous research as informed priors was indistinguishable from the model that had vague priors based on their DIC metric. Predictions for aboveground carbon increments for unlogged forests were 4% higher in the model with informed priors compared to the model with non-informative priors.

Increases in timber stocks were faster in plots logged at 46 m³ ha⁻¹ (3.56 m³ ha⁻¹ yr⁻¹; CI, 1.44 to 3.56). Net timber stock increments were slowest in unlogged forests

($0.86 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) with residual tree growth driving timber stock recovery, with little or no recruitment of stems of commercial value (Table 2-3).

Discussion

Model predictions for recovery time after careful selective logging in Suriname revealed a 55% probability that forests logged at the lowest harvest intensity ($15 \text{ m}^3 \text{ ha}^{-1}$) would not recover initial ACS within 32 years (Figure 2-2). At an estimated loss of 14% of initial ACS associated with the lowest logging intensity, we expected a higher probability of recovery after 32 years based on a recent Amazon-wide study on ACS that found recovery time (years) is close to the proportional losses in ACS due to logging (Rutishauser *et al.* 2015; $[100 * \text{ACS}_{\text{loss}}/\text{ACS}_{\text{initial}}]^{1.106}$). Similarly, 60% and 76% of model predictions at 32 years after logging indicated that ACS would not have recovered after medium and high logging intensity, with average losses of 22% and 37% of initial ACS, respectively. As our study lacked pre-logging plot-level ACS data, we applied an emissions factor based on harvested timber volume to estimate initial ACS prior to logging in 1979 and weighted our post-logging ACS data by their respective plot-level initial ACS estimates (Appendix A). Our recovery predictions may thus be conservative as the carbon emissions factor ($1.52 \text{ Mg C m}^{-3} \text{ ha}^{-1}$) accounted for tree mortality for stems $\geq 10 \text{ cm DBH}$, whilst our census data includes stems $\geq 15 \text{ cm DBH}$. Additionally, the logging emissions factor reported by Pearson *et al.* (2014) could be higher than those at our study site as it spanned a wide range of logging practices, whilst the CELOS System was designed to reduced collateral damage to the forest based on RIL principles.

In contrast to the low confidence in ACS recovery, confidence about timber stock recovery was higher. There is an 80% probability that plots logged at intensities of 15-

23 m³ ha⁻¹ would have recovered initial timber stocks within 32 years after logging. Recovery was slower for forests logged at 46 m³ ha⁻¹, with 30% of model predictions at 32 years indicating failure to recover initial timber stocks (Figure 2-2). However, recovery of timber stocks was driven primarily by biomass accumulation from residual tree growth (Table 2-1), as reported for a forest in Eastern Amazonia after RIL (Mazzei *et al.* 2010). The low recruitment of commercial species may not be sufficient to sustain timber stocks beyond a third harvest. Perversely, if market preferences change to favor additional timber species beyond those harvested during the study, timber stocks could be sustained beyond a third harvest (Keller *et al.* 2007). Stand improvement interventions such as liberation thinning that stimulates recruitment and growth of commercial timber species (Gourlet-Fleury *et al.* 2004, Peña-Claros *et al.* 2008) or enrichment planting (Ruslandi *et al.* 2017) can also be used to promote long-term timber yield sustainability.

The average net recovery rate of aboveground carbon across all nine of our logged plots was 0.62 Mg C ha⁻¹ yr⁻¹ (95% CI, 0.24 to 1.01), half of the 1.3 Mg C ha⁻¹ yr⁻¹ for Amazonia reported by Rutishauser *et al.* (2015) study. The net rate of change in aboveground carbon (residual growth and recruitment minus mortality) in our unlogged forest was similar to those reported for old-growth Amazonian forests (0.28 Mg C ha⁻¹ yr⁻¹; Brienen *et al.* 2015) but slower than observed rates reported for Guiana Shield old-growth forests (0.45 Mg C ha⁻¹ yr⁻¹; Johnson *et al.* 2016). The slower carbon increments relative to other studies in the Brazilian Amazon, which dominated the Rutishauser *et al.* (2015) was also found in a nearby logging study in Paracou, French Guiana. In that study, at harvest intensity of 23 m³ ha⁻¹, the average time to recover initial ACS was 45

years with conventional logging (Blanc *et al.* 2009). In our study, average predicted time to recover initial ACS based on logging intensity of 25 m³ ha⁻¹ was 37 years, 8 years less than at the Paracou research site. The shorter recovery time with the CELOS system could be associated with the lower reduction in ACS, estimated to be one fifth of initial ACS. In Paracou, ACS loss immediately after logging with conventional logging was estimated at one third of initial ACS.

Analytically, the Bayesian framework employed in our analysis enabled us to make probabilistic statements about recovery at different time points after logging. In particular, the use of data from forty-one plots across the Guiana Shield helped address two major shortcomings of our dataset that would otherwise have resulted in lower precision and less confidence in our annualized increments: (1) long census intervals that lead to unrecorded growth of trees that die between censuses as well as the contributions of trees that recruited but died before being measured (Clark *et al.* 2001); and, (2) our small sample size (N = 12) of small (1-ha) plots that can lead to prediction bias due to failure to capture much of the characteristic spatial heterogeneity of carbon stocks in tropical forests (Phillips *et al.* 2002). The mean rate of aboveground carbon productivity was 4% higher in the model with informative priors, which is similar to the ~1-3% underestimates caused by not accounting for growth and recruitment of trees that die between censuses (Carey 1994). The combination of the results from other studies with our own data represents a cost-effective statistical method to improve confidence associated with model inferences when census intervals are long and there is high uncertainty associated with carbon stocks across the landscape (McCarthy & Masters 2005).

Forest Management Implications. Our model predictions indicate a 67% probability that timber stocks will recover in 25 years to pre-logging levels after careful harvests of 25 m³ ha⁻¹; in Suriname, 25 years is the minimum cutting cycle duration and 25 m³ ha⁻¹ is the maximum harvest intensity. Similarly, we estimate the probability of ACS recovery under these same rules as only 27%. If forest managers want >90% confidence in both ACS and timber stock recovery to pre-logged levels, cutting cycles will have to be set at 70 and 40 years, respectively. These results indicate a trade-off between carbon and timber values, with higher reductions in carbon sequestration between cutting cycles with higher harvest intensities. Carbon payments can potentially be used to offset higher logging intensities that lead to greater reductions in carbon stocks and longer cutting cycles to recover timber stocks.

The CELOS system, intended to be environmentally good logging, may not ensure long term profitable timber management alone due to the low recruitment of commercial timber species. To sustain yields and profits across multiple cutting cycles, timber stand improvements aimed at increasing growth rates and recruitment of commercial timber species could be used (Putz & Ruslandi 2015). The application of stand improvement treatments to increase timber stocks could however further decrease carbon storage and sequestration between cutting cycles (Blanc *et al.* 2009). Nevertheless, adoption of the CELOS harvest system that is guided by RIL practices improves post-logging recovery rates of both timber stocks and ACS compared to conventional logging (Sasaki *et al.* 2016).

Table 2-1. Stem density, basal area (m² ha⁻¹), and ACS (Mg C ha⁻¹) by stem diameter class in 1981 (2-years post-logging) and 2012 (32-years post-logging). Commercial timber stocks (m³ ha⁻¹) are reported for 1978 (pre-logging) and 2012. ACS values reported are the mean from 1350 posterior predictions based on uncertainty associated with our allometric models. Control plot values are from 1983 to 2012.

Plot ID	41	42	43	19	28	34	14	26	38	12	22	32												
Logging intensity (basal area - m ² ha ⁻¹)	0.0 0	0.0 0	0.0 0	1.1 9	1.6 1	1.7 4	2.8 1	2.7 4	2.6 0	3.5 1	4.0 4	3.8 2												
Logging intensity (m ³ ha ⁻¹)	0.0 0	0.0 0	0.0 0	14. 30	15. 30	14. 60	22. 50	30. 30	22. 50	49. 10	56. 40	42. 20												
Logging intensity (stems ha ⁻¹)	0	0	0	4	3	3	7	6	6	13	11	12												
Census year (1) Stem density (ha ⁻¹)	19 83	20 12	19 83	20 12	19 83	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12	19 81	20 12
15-30	17 0	15 0	18 0	15 3	14 7	13 7	14 2	13 9	15 8	14 5	18 2	18 4	17 2	18 6	14 0	17 8	16 5	18 7	13 1	13 4	13 2	13 7	15 5	13 4
30-45	54	71	60	73	54	44	48	53	58	45	64	65	50	65	34	56	62	50	52	57	51	48	61	47
45-60	22	24	24	25	18	22	22	31	19	29	18	26	21	16	23	20	22	32	15	40	17	25	18	32
>60	20	22	28	27	18	14	18	23	17	23	9	20	22	17	18	18	15	20	10	13	19	25	15	29
Total	26 6	26 7	29 2	27 8	23 7	21 7	23 0	24 6	25 2	24 2	27 3	29 5	26 5	28 4	21 5	27 2	26 4	28 9	20 8	24 4	21 9	25 5	22 9	26 2
(2) Basal area (m ² ha ⁻¹)	6.4	5.5	6.4	5.8	5.4	5.2	5.5	5.3	5.4	5.1	6.5	6.5	5.9	6.7	4.6	6.4	5.8	6.7	4.8	5.1	4.6	5.5	4.8	5.6
15-30	1	0	5	5	9	9	6	2	2	8	1	7	6	2	1	5	4	6	3	6	8	8	3	4
30-45	5.5	7.6	6.1	7.6	5.6	4.9	5.4	5.4	6.1	4.9	6.6	6.5	5.3	6.5	3.4	5.9	6.3	5.3	5.4	6.1	5.5	5.4	6.2	4.8
30-45	3	2	0	8	1	0	1	2	6	1	8	8	9	9	5	9	7	8	4	3	4	5	6	6

Table 2-1. Continued.

	4.5	5.0	5.3	5.2	3.8	4.6	4.9	6.4	3.9	5.9	3.6	5.3	4.3	3.4	5.0	4.4	4.5	7.0	3.3	8.6	3.5	5.3	3.8	6.8
45-60	3	9	3	1	3	0	9	8	0	9	1	4	2	6	0	2	7	0	0	0	1	2	4	6
>60	3	12	43	16	43	6	3	09	3	06	6	9	25	1	6	1	4	8	8	8	7	75	7	56
Total	01	34	31	90	37	55	68	31	02	15	45	29	91	28	33	67	82	12	86	27	50	09	99	92
(4) Wood specific gravity (g cm ⁻³)																								
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
15-30	4	4	6	5	2	3	6	3	4	5	2	2	4	9	1	2	6	4	3	0	3	2	3	0
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
30-45	5	4	8	8	3	1	6	5	4	5	0	2	0	9	8	1	8	5	9	4	4	0	2	5
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
45-60	3	3	6	6	3	5	6	6	6	0	7	3	3	1	3	6	8	6	5	8	9	5	2	0
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.6	0.7	0.6	0.6	0.6	0.7	0.6
>60	2	2	8	5	2	0	8	5	3	6	9	8	9	8	3	6	0	7	3	3	9	6	1	7
Mean plot level wood density	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
	3	3	7	6	2	2	6	5	4	4	2	1	1	2	4	4	6	5	8	4	6	3	5	3
(4) ACS (Mg ha ⁻¹)																								
	25.	22.	26.	24.	21.	21.	23.	21.	21.	21.	25.	25.	23.	24.	17.	25.	24.	27.	18.	19.	18.	21.	19.	21.
15-30	98	08	60	18	60	38	45	51	36	15	11	67	52	76	34	13	04	14	79	46	74	57	37	34
	28.	38.	32.	40.	27.	23.	28.	27.	30.	25.	31.	31.	25.	30.	18.	29.	33.	27.	28.	31.	28.	26.	30.	24.
30-45	29	39	24	91	99	90	22	71	69	36	76	92	88	70	54	23	71	63	75	30	22	27	77	98
	25.	29.	32.	31.	21.	27.	30.	39.	23.	32.	21.	30.	24.	19.	28.	26.	27.	40.	19.	52.	21.	31.	21.	37.
45-60	79	18	27	21	65	25	31	32	47	33	20	34	70	58	96	89	76	84	04	82	89	47	76	10
				11																				10
	55.	67.	99.	0.6	73.	70.	56.	76.	67.	88.	29.	54.	65.	54.	64.	72.	37.	61.	24.	36.	65.	85.	74.	0.9
>60	26	93	28	8	28	21	28	04	87	13	91	34	60	51	77	78	07	79	16	36	68	04	46	2

Table 2-1. Continued.

	13	15	19	20	14	14	13	16	14	16	10	14	13	12	12	15	12	15		14	13	16	14	18
	5.3	7.5	0.3	6.9	4.5	2.7	8.2	4.5	3.3	6.9	7.9	2.2	9.7	9.5	9.6	4.0	2.5	7.4	92.	0.1	4.5	4.3	6.3	4.3
Total	2	7	9	7	2	5	6	8	9	7	8	8	0	6	1	3	7	0	38	1	3	5	6	4
(5) Timber																								
stocks	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20	19	20
(m ³ ha ⁻¹)	83	12	83	12	83	12	78	12	78	12	78	12	78	12	78	12	78	12	78	12	78	12	78	12
	9.3	4.3	8.7	5.3	2.2	0.3	8.1	0.8	11.	6.6	15.	6.9	8.9	5.1	5.6	1.1	5.6	7.6	5.3	1.7	11.	5.5	15.	11.
15-30	3	0	2	5	5	4	4	2	55	4	83	8	9	3	2	5	8	1	2	7	19	7	12	94
	21.	27.	12.	18.	9.4	7.1	13.	12.	32.	22.	21.	29.	17.	14.	9.6	11.	15.	18.	18.	15.	23.	25.	32.	27.
30-45	10	96	56	71	9	4	15	59	88	84	62	07	10	15	4	03	58	72	99	64	92	27	52	43
	30.	27.	22.	23.	7.3	10.	25.	25.	20.	31.	11.	26.	29.	13.	30.	13.	27.	31.	32.	42.	26.	31.	44.	56.
45-60	05	53	62	91	7	25	14	92	46	21	30	30	09	42	04	00	37	15	21	60	03	95	02	20
				10					10															12
	60.	89.	80.	9.8	32.	23.	15.	64.	80.	6.0	40.	64.	51.	36.	67.	47.	60.	68.	53.	48.	77.	88.	76.	6.4
>60	88	74	52	8	61	00	83	33	38	0	08	47	13	70	64	90	09	58	22	52	57	00	15	8
	12	14	12	15				10	14	16		12	10		11		10	12	10	10	13	15	16	22
	1.3	9.5	4.4	7.8	51.	40.	62.	3.6	5.2	6.6	88.	6.8	6.3	69.	2.9	73.	8.7	6.0	9.7	8.5	8.7	0.7	7.8	2.0
Total	6	3	3	4	71	73	26	6	7	9	83	3	1	40	4	09	2	6	3	3	0	8	1	5

Table 2-2. Components of aboveground woody carbon production and model predictions with uninformed and informed priors for stand-level increments (Mg C ha⁻¹ yr⁻¹) at logging intensities of 15, 23, and 46 m³ ha⁻¹. We estimated aboveground carbon increment at the plot level as: ($\sum ACS$ at $t_2 - \sum ACS$ at $t_1 = residual\ growth$) + ($\sum ACS$ mortality between t_1 and t_2) - (ACS of tree at 15 cm DBH * number of new recruits between t_1 and t_2) for the 1983-2000 and 2000-2012 census intervals to account for unobserved increments. We used these values to estimate ACS increments across logging intensities, with both vague Gaussian priors [$N(\mu = 0, sd = 0.0001)$] and informative priors [$N(\mu = 3.51, sd = 4.04$; Johnson et al., 2016)].

Logging intensity	Mg C ha ⁻¹ yr ⁻¹			Aboveground carbon increments Mg C ha ⁻¹ yr ⁻¹ (95% CI)	
	<i>Residual growth</i> (± SE)	<i>Recruitment</i> (± SE)	<i>Mortality</i> (± SE)	<i>Uninformed priors</i>	<i>Informed priors</i>
15 m ³ ha ⁻¹	2.39 (± 0.09)	0.14 (± 0.03)	1.91 (± 0.32)	2.54 (1.68 to 3.44)	2.55 (1.71 to 3.46)
23 m ³ ha ⁻¹	2.25 (± 0.20)	0.27 (± 0.03)	2.26 (± 0.35)	2.65 (1.73 to 3.51)	2.65 (1.71 to 3.52)
46 m ³ ha ⁻¹	2.65 (± 0.22)	0.31 (± 0.10)	2.10 (± 0.39)	2.93 (2.04 to 3.83)	2.91 (1.99 to 3.82)
Control	2.23 (± 0.19)	0.11 (± 0.02)	2.13 (± 0.21)	2.35 (1.47 to 3.22)	2.39 (1.51 to 3.26)

Table 2-3. Timber stock increments ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) for stems ≥ 15 cm DBH and classified as having commercial log value. We applied the stand increment formula presented in Clark *et al.* (2001): $\sum \text{Residual growth} + \sum \text{mortality} - \sum (\text{number of recruited trees} * \text{volume of a tree @ 15 cm DBH})$ to estimate timber stock recovery rates.

Logging intensity	$\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$			Timber stock increment (95% credible interval)
	Residual growth (\pm SE)	Recruitment (\pm SE)	Mortality (\pm SE)	
15 $\text{m}^3 \text{ha}^{-1}$	2.35 (\pm 0.19)	0.000 (\pm 0.00)	1.35 (\pm 0.20)	2.62 (1.16 to 4.06)
23 $\text{m}^3 \text{ha}^{-1}$	1.86 (\pm 0.31)	0.006 (\pm 0.00)	1.20 (\pm 0.31)	2.25 (0.72 to 3.83)
46 $\text{m}^3 \text{ha}^{-1}$	3.22 (\pm 0.48)	0.023 (\pm 0.02)	0.91 (\pm 0.30)	3.56 (1.44 to 3.56)
Control	1.58 (\pm 0.36)	0.003 (\pm 0.00)	1.04 (\pm 0.18)	1.90 (-0.13 to 3.57)

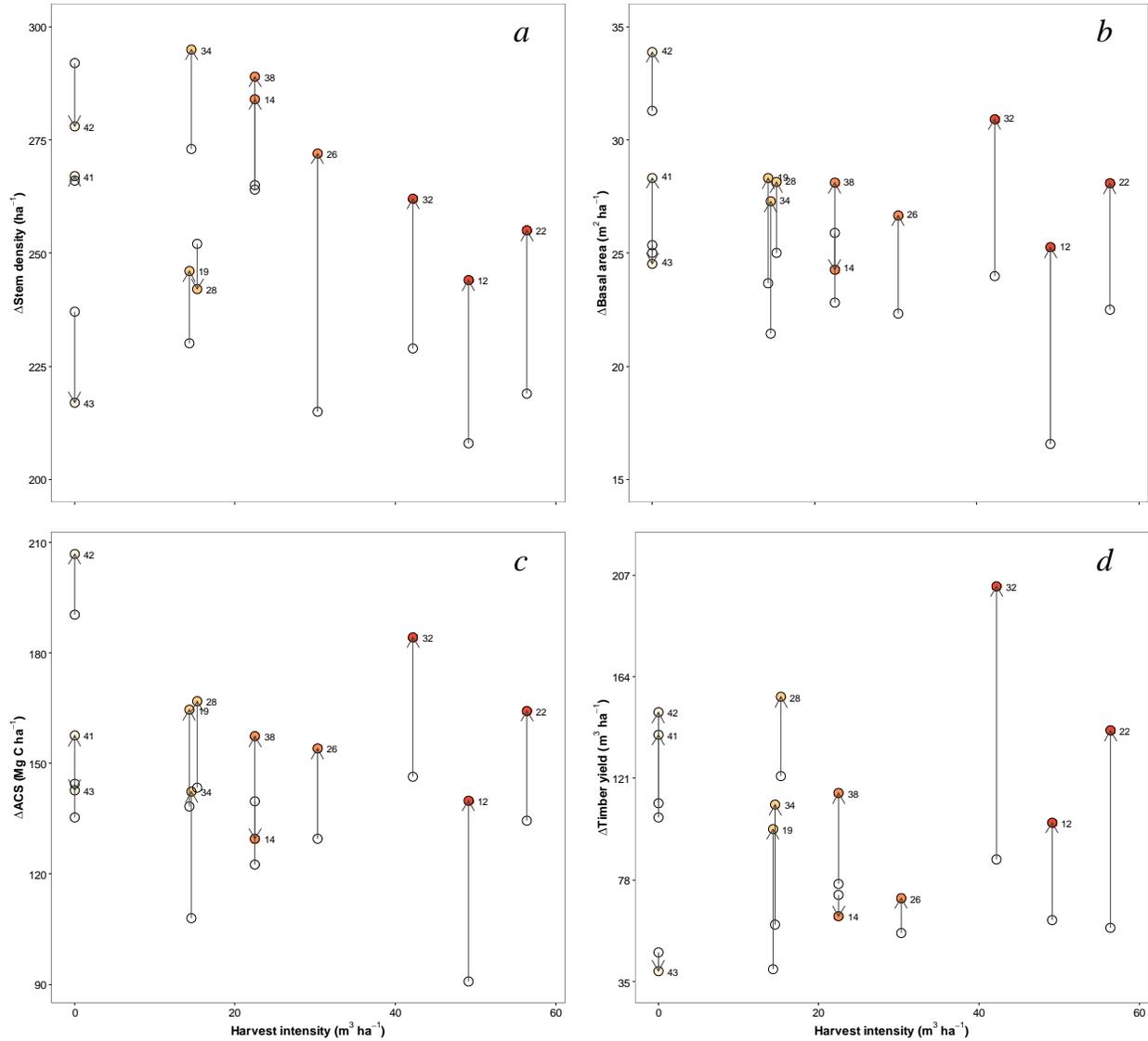


Figure 2-1. Changes (Δ) in stem density (a), basal area (b), and ACS (c) from 2 years (1981) to 32 years (2012) after selective logging. Changes in timber stock (d) are from 1 year (1980) to 32 (2012) years after selective logging. Numbers on graph identify the plots and corresponds to the meta-data presented in Table 2-1 with arrows indicating direction of change over the period reported. Changes across the unlogged forest plots are located at the zero point of the x-axis (plots 41, 42, and 43) and are from 1983 to 2012. We propagate the uncertainty of our allometric models used to estimate ACS (c) and plotted the mean values.

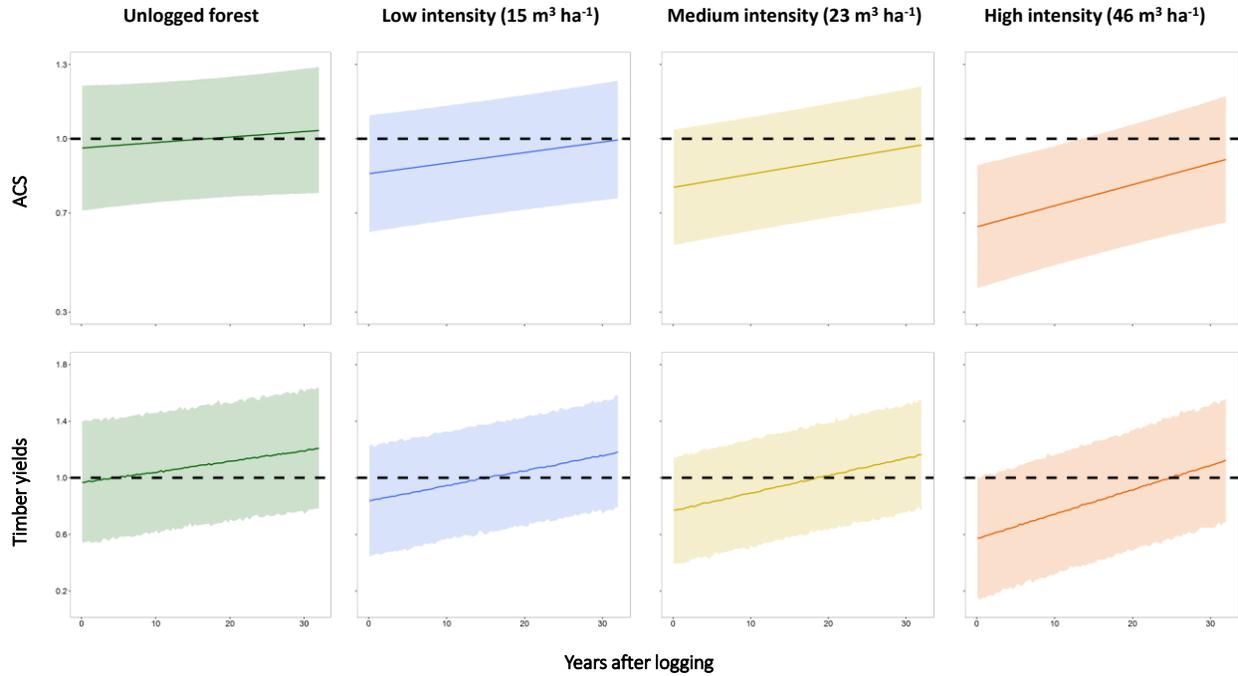


Figure 2-2. Model predictions of recovery of ACS (*a*, *b*, and *c*) and timber stock (*d*, *e*, and *f*) at low, medium and high logging intensities. Observed ACS post-logging is weighted by initial ACS (Mg C ha^{-1}) and timber stock ($\text{m}^3 \text{ha}^{-1}$). Solid lines are the mean predictions based on parameter and sampling uncertainty, with 95% credible intervals represented by the lighter colored ribbons. Predictions above the dashed horizontal line ($y\text{-intercept} = 1.0$) indicate recovery to pre-logging values.

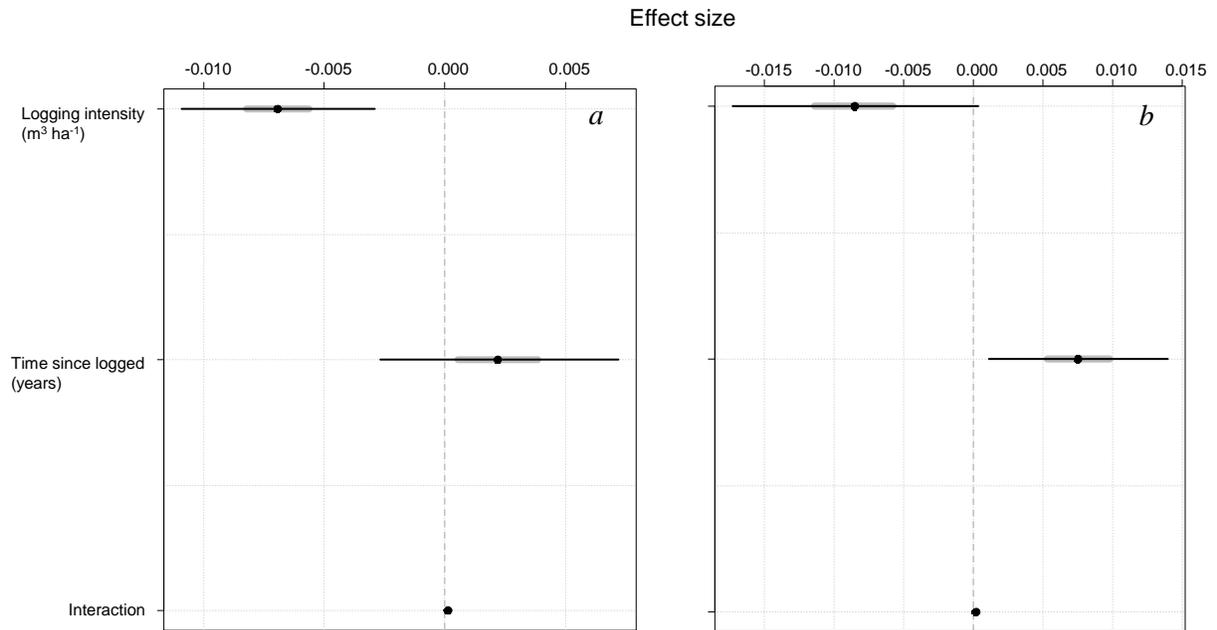


Figure 2-3. Regression coefficients from recovery models for ACS (a) and timber (b) based on logging intensity ($\text{m}^3 \text{ha}^{-1}$), time-since-logging (years), and an interaction-term for logging intensity and time-since-logging. Thin vertical lines indicate the 95% credible intervals (CIs), thicker lines capture the 50% CIs based on posterior draws, and points indicate the mean effect size. Coefficients with 95% CIs that do not cross the zero value (dashed line) can be considered statistically significant.

CHAPTER 3
MANAGING TROPICAL FORESTS FOR TIMBER AND CARBON: INTENSITY
THRESHOLDS WITH REDUCED-IMPACT LOGGING AND LIBERATION THINNING

Summary

Reduced-impact logging (RIL) techniques are considered critical for sustainable forest management in the tropics insofar as they reduce the deleterious environmental impacts to the residual forest stand compared to unplanned logging. Forest managers have championed the adoption of RIL to maintain carbon stocks in selectively logged forests and mitigate climate change. It is less clear whether use of RIL alone will guarantee timber stock recovery within economically viable cutting cycles. In this 20-year study we quantify the losses and recovery of aboveground carbon and timber stocks in forests subjected to different intensities of RIL (16 m³ ha⁻¹ and 4 trees ha⁻¹, 24 m³ ha⁻¹ and 8 trees ha⁻¹, and 48 m³ ha⁻¹ and 16 trees ha⁻¹) and liberation of future crop trees (FCTs; well-formed trees of commercial species 20-40 cm DBH) after medium intensity RIL. Our study site is in a wet forest on the Guiana Shield, a region known for its nutrient-poor soils, unique suite of functional traits of its dominant species, and high carbon stocks. We model recovery of aboveground carbon (Mg C ha⁻¹) and timber stocks (m³ ha⁻¹) with a piecewise regression that represents both the effects of elevated mortality immediately after logging, as well as increased growth during post-logging recovery. Recovery of ACS and timber stocks across all RIL treatments was mostly due to growth of residual trees (i.e., trees present at the time of logging). Stands logged at low and moderate intensities were highly likely to recover their timber stocks for a harvest at 40 years. FCT liberation promoted growth into merchantable DBH classes but slowed ACS recovery. Guiana Shield forests managed for timber seem to lose the benefits of RIL with harvests of >8 trees ha⁻¹ (24 m³ ha⁻¹); at higher intensities,

recruitment and growth are not sufficient to offset logging-induced mortality. The use of FCT liberation in combination with moderate RIL however doubled annual increments of timber stocks but it also resulted in 30% less carbon stocks compared to unliberated forests. Though a second harvest at RIL-low and RIL-moderate harvest intensities should be possible after 40 years, recovery trajectories after the second harvests may resemble forests logged at intensities >8 trees ha^{-1} without treatments to promote growth of trees into the harvestable size classes. If management is intensified, carbon stocks will be traded for timber.

Background

Sustainable forest management (SFM), through careful and low-intensity selective logging is advocated as a way to simultaneously provide income, maintain biodiversity, and conserve ecosystem services in tropical forests (Edwards, Tobias, *et al.* 2014). The ecological basis of SFM includes the use of reduced-impact logging (RIL) practices designed to reduce deleterious environmental impacts and to sustain timber yields (Putz *et al.* 2008, 2012). RIL guidelines typically cover a suite of activities that emphasize strict planning and control of logging operations as well as training of forestry workers (Dykstra & Heinrich 1996, Dykstra 2001). Planning generally includes: (1) pre-harvest tree inventories and topographic mapping; (2) vine cutting; (3) the use of crews trained in directional felling; and, (4) controls on the lengths, widths, layout, and use of skid trails and logging roads (Sist 2000, Pinard *et al.* 1995). By following these guidelines, the spatial extent and severity of logging impacts are reduced (e.g., Arevalo *et al.* 2016, Edwards *et al.* 2014).

We know now that RIL causes less soil damage (Sist 2000, Pinard *et al.* 1995), biodiversity loss (Bicknell, Struebig, *et al.* 2015), hydrological disruption (Douglas 1999),

and carbon emissions (Putz & Pinard 1993) relative to unplanned logging. Furthermore, post-logging recovery rates of aboveground carbon and timber stocks after RIL are also reportedly faster than after conventional logging (Vidal *et al.* 2016, Lussetti *et al.* 2016). However, as tropical forests approach their second and third harvests, timber volumes may not recover within the time allocated for subsequent harvests solely with RIL and no other silvicultural treatments (Putz *et al.* 2012, Ruslandi *et al.* 2017). Opportunity costs of retention of these production forests increase with restrictions on logging intensities and longer cutting cycles, which may translate into increased vulnerability to conversion to crop and range lands (Asner *et al.* 2006). These deforestation drivers demonstrate the need to quantify thresholds of logging intensity beyond which benefits of RIL are lost and additional silvicultural treatments are needed to sustain timber yields within financially acceptable cutting cycles (Putz & Ruslandi 2015).

In this study, we compare the rates of recovery of aboveground carbon (ACS) and timber stocks for the first 20 years after RIL at different intensities, and assess the carbon-timber dynamics that result from the liberation of future crop trees (FCTs; well-formed trees of commercial species 20-40 cm DBH) from competition. We monitored trees ≥ 10 cm DBH from 1993 to 2013 in replicated plots subjected to RIL at three logging intensities in forests located on the Guiana Shield: RIL-low ($16 \text{ m}^3 \text{ ha}^{-1}$), RIL-moderate ($24 \text{ m}^3 \text{ ha}^{-1}$), RIL-high ($48 \text{ m}^3 \text{ ha}^{-1}$) and a fourth treatment that included a post-harvest liberation treatment of FCTs after moderate intensity harvest (RIL-moderate + liberation; van der Hout 1999).

We used our plot-level observations of ACS and timber stocks to evaluate the effect of logging intensity on residual mortality and recovery with a piecewise linear

regression (broken-stick model; Bourgeois *et al.* 2016). The structure of the piecewise regression can accommodate our theoretical expectation of post-logging demographic changes that result in non-linear biomass dynamics (Piponiot *et al.* 2016). Specifically elevated mortality rates for a few years after logging is followed by increased levels of growth and recruitment due to reduced competition (Sist & Nguyen-Thé 2002, Shenkin *et al.* 2015, Ruslandi *et al.* 2017). How these expected thresholds in tree biomass fluxes interact with different logging intensities is an open question with fundamental implications for the forest dynamics that determine carbon fluxes and the sustainability of timber harvests.

We hypothesized that increasing logging intensity with RIL results in both increased losses of ACS in the first several years after logging and faster regrowth in the subsequent period. We predict that after a threshold of logging intensity, the decreased ACS immediately after logging outweighs the benefits of the increased recovery rate. The faster regrowth is premised on the lower competition for light and other resources that residual trees benefit from with the removal of trees during logging, whilst log damaged trees may take several years to die during which mortality rates are elevated. In contrast, we expect that rates of recovery of merchantable timber stocks decreases with logging intensity because of the typically low densities of FCTs and low growth rates. We also expected that after moderate intensity RIL and FCT liberation, merchantable timber stock recovery will be accelerated, but at the cost of ACS. We use our piecewise model to explore stand dynamics across logging intensities to demarcate the period post-logging when mortality rates are elevated.

One challenge for advocates of SFM is to define appropriate thresholds for timber extraction with RIL and to prescribe silvicultural treatments that are compatible with the long-term goal of reconciling production with protection (Putz & Ruslandi 2015, Wadsworth & Zweede 2006, Zimmerman & Kormos 2012). Given the wide variation in the silvics of tropical trees and forests (e.g., Johnson *et al.* 2016, Quesada *et al.* 2010, Rutishauser *et al.* 2015), these thresholds and prescriptions will need to be tailored regionally. For example, our study site on the ancient and nutrient-poor Guiana Shield is quite distinct from forests in Amazonia insofar as the trees live longer, the wood is denser, carbon stocks are higher, and the forest is dominated by trees that produce large seeds (ter Steege *et al.* 2006, Pioniot *et al.* 2016). Here we explore different silvicultural approaches to sustaining the flow of products and services from these forests.

Methods

Study Site

Our data are from a long-term study in Central Guyana ($5^{\circ} 02' N$, $58^{\circ} 37' W$; Fig B-1) established in 1989 by Tropenbos International (<http://www.tropenbos.org/>) as part of its sustainable forest management and conservation research program. The research site is within an active timber concession, Demerara Timbers Limited (DTL), at elevations of 50-100 m above-sea-level on undulating sedimentary plains with slopes mostly $< 20\%$. The forest grows on the old and extremely nutrient-poor quartz-rich soil derived from Cretaceous sediments on the Precambrian Guiana Shield; these soils are extremely poor compared to those of western Amazonia (Quesada *et al.* 2010, Hammond 2005). There is also a clear geographical pattern in forest structure, floristic

composition and function across the Amazon and Guiana Shield, with the latter characterized by higher carbon stocks and rates of wood production, higher wood densities and seed sizes, and more dominance by species of Fabaceae (Malhi *et al.* 2004, Johnson *et al.* 2016, ter Steege *et al.* 2006).

The evergreen tropical forest of the study area receives about 2772 mm of precipitation per year with dry seasons in March-April and September-November, but on average no month receives <60 mm of rain (Van Dam 2001). The average canopy height is 30-40 m with emergent trees to 50-60 m (Vanmeschelen 1994). Prior to logging in 1993, density of stems ≥ 10 cm DBH (diameter measured at 1.3 m or above buttresses) in unlogged forests was 476 stems ha⁻¹ (SE ± 19), with species composition that varied with local soil characteristics, topographic position, and water availability (Ter Steege *et al.* 1993, Van der Hout 1996). Approximately 10% of tree species produce large buttresses, palms are sparse and mostly confined to the understory, and lianas >2 cm DBH estimated at 453 stems ha⁻¹ (Zagt *et al.* 2003). In unlogged forest, the crowns of 9% of trees ≥ 20 cm are liana-covered. There were no signs of previous logging but soil charcoal indicates scattered small-scale fires during the last century (Hammond & Ter Steege 1998).

Monodominant patches of *Chlorocardium rodiei* (greenheart) and *Lecythis confertiflora* (wirimiri kakaralli) frequently dominate the forest canopy layer with *Licania spp.* (kautaballi), *Swartzia leiocalycina* (wamara), and *Catostemma fragans* (sand baromalli) as prevalent co-dominants. In some parts of the research site, particularly uphill of gullies, *Mora gongrijpii* (morabukea) dominates while *Carapa spp.* (crabwood) and *Pentaclethra macroloba* (trysil) are common on wetter soils. Among the emergent

species, *Peltogyne venosa* (purpleheart) and *Hymenaea courbaril* (locust) are the most common and have high commercial value. Prevalent understory species are *Oxandria asbeckii* (karishiri), *Tapura guianensis* (waiaballi), and *Paypayrola* spp. (adebero).

Experimental Design and Logging Treatments

The approach to RIL used in our study was based on the CELOS Harvest System developed in Suriname (Werger 2011, Jonkers 1987, Roopsind *et al.* 2017). The practices implemented included: pre-harvest enumeration and mapping of commercial species with good stem form ≥ 20 cm DBH; trees selected to be harvested are spaced to assure excessively large gaps are created; and, the number of stems harvested per species is representative of their abundance. Minimum felling diameters were species-specific and based on growth patterns but all harvested trees need > 6 m of defect-free bole. As an additional criterion designed to improve future timber yields, the selection of the tree to be harvested took into consideration how many high-value FCTs would be released from canopy competition from the harvest. All lianas ≥ 2 cm DBH connected to trees selected for harvest were cut 6 months prior to the felling operation to reduce residual stand damage. Directional felling was carried out (in order of priority) to promote worker safety, to minimize damage to the bole of the felled tree, and to aid extraction; the techniques described by Conway (1982), as modified by Brunberg *et al.* (1994) were utilized. All fellers were trained and used STIHL AV66 chainsaws. Planned skid trails were constructed in a herringbone pattern to minimize skidding distances, with no skidding on slopes $>20\%$, as well as no skidding downhill or across streams and gullies. Skid trails generally followed a straight alignment with 80 m spacing and were built with a CAT 528 wheeled skidders equipped with a cable arch and 35 m of winch line; winching distances averaged 12.2 m (sd = 8.2 m, n = 163).

The study employed a randomized block design with three intensities of RIL [low intensity (4 trees ha⁻¹/16 m³ ha⁻¹), moderate intensity (8 trees ha⁻¹/24 m³ ha⁻¹), high intensity (16 trees ha⁻¹/48 m³ ha⁻¹)], and moderate-intensity RIL followed three years later by a post-harvest liberation of FCTs (van der Hout 1999, 2000; see Table 3-1 for plot-level losses of basal area and harvested timber volumes). Each logging treatment was replicated three times in 5.76 ha (240 x 240 m) plots with a centrally located 1.96 ha (140 x 140 m) permanent sample plot (PSP). In addition to the logged and liberation treated plots, unlogged stand dynamics were also monitored in a control plot in each of the three blocks. Trees ≥ 20 cm DBH were recorded in the 1.96 ha PSPs, with twenty-five nested 10 x 10 m subplots used to census trees >10 cm (Figure B-1).

All plots were first censused in 1993 (pre-logging) with the twelve experimental harvest units logged in 1994. Future crop trees (FCTs), defined as trees 20-40 cm DBH of commercial species and good form, were liberated in 1996 by cutting all impinging lianas and poison girdling taller non-commercial trees within 10 m of the FCT's bole. Plots were re-censused approximately one (1995), three (1997), six (2000), and twenty years (2013) after the 1994 logging and one (1997), four (2000), and seventeen (2013) years after the 1996 liberation treatment. At each census, tree diameters, mortality, and in-growth were recorded, along with the apparent cause of mortality; each tree was also assigned a timber grade that reflects commercial utilization potential.

Aboveground Carbon Stocks (Mg C ha⁻¹)

To estimate the aboveground biomass of each stem we used the pan-tropical allometric model of Chave et al. (2014): $aboveground\ biomass_{estimate} = 0.0673 * (pD^2H)^{0.976}$, where p is stem wood density (g cm⁻³), D is DBH (cm), and H is total tree height (m). As we did not have measured tree heights, we used the diameter-height

allometry model also proposed by Chave et al. (2014), $\ln(H) = 0.893 - E + 0.760 * \ln(D) - 0.0340 * (\ln(D))^2$ to estimate tree heights. The E parameter is a georeferenced bioclimatic stress variable that includes temperature seasonality, precipitation seasonality, and climatic water deficit that utilizes a linear relationship to estimate height (m) based on tree diameters. Aboveground carbon stocks (ACS) were estimated by multiplying aboveground tree biomass by 0.47 (IPCC 2003).

Stem wood densities were extracted from a global pan-tropical database (Chave et al., 2009); in the absence of species-level data (9.4% of trees), the mean wood density was used for congeneric trees in tropical South America; we used the plot-level basal area-weighted average wood density for the 28 stems for which we lacked taxonomic information (Baker et al. 2004). We employ the Chave et al. (2014) biomass allometric model in part to facilitate comparisons with recent studies on post-logging biomass recovery (Rutishauser et al. 2015, Sist et al. 2015, Vidal et al. 2016, Roopsind et al. 2017). In addition the Chave et al. (2014) allometry incorporates datasets from both primary and secondary forests, which addresses potential changes in forest structure in logged forest (such as reductions in tree heights; Rutishauser et al. 2016) with the wood density parameter capturing differences in species composition (Baker et al. 2004). To correct for the downward bias in our carbon estimates introduced by diameter measurements recorded at heights >1.3 m (Metcalf et al. 2009, Cushman et al. 2014), primarily due to buttresses, we developed and implemented a taper correction model using a local dataset with multiple diameter measurements along the trunks of 150 trees across 23 genera (Appendix B).

Merchantable Timber Stocks ($\text{m}^3 \text{ha}^{-1}$)

We applied in-country derived species-specific volumetric equations to estimate merchantable timber stocks at each census, when available, and otherwise used a generic equation (Table B-1). Our assessment of rates of post-logging merchantable timber stock recovery is restricted to the 31-species listed as having commercial value at the time of logging in 1994. Our timber stock estimates only include stems that have reached the minimum cutting diameter for those commercial species, with the majority of species with a minimum felling diameter of 45 cm (Table B-1). We used the log grade scores to adjust our estimates of merchantable timber stocks (100% of grade one; 90% of grade 2 and 3; and 80% of grade 4). We used diameters measured above buttresses and trunk deformities to estimate timber stocks because logs with either are rejected during bucking.

Rates of Aboveground Biomass Productivity

We divide aboveground biomass productivity into residual tree growth, recruitment into the smallest size class (10 cm DBH), and mortality. We followed the recommendation of Clark *et al.* (2001) for the treatment of recruits, which is to subtract the biomass of a 10 cm DBH tree from the biomass of each new tree when first recorded. Our aboveground biomass productivity rates are thus for trees ≥ 10 cm. Our approach differs from the recommendation of Talbot *et al.* (2014) that assumes newly recruited trees grew from 0 cm between censuses. This procedure results in an overestimation of total aboveground biomass productivity that is mitigated by the underestimation caused by not accounting for trees that do not grow from zero but remain < 10 cm DBH at the time of the census. We deemed the Talbot *et al.* (2014)

technique inappropriate for our study as it assumes that the populations of trees <10 cm DBH are stable (Malhi *et al.* 2004), which is unlikely in our logged and liberated forests.

Despite a very long inter-census interval in our data (12.8 years, 2000-2013), we do not correct for the expected underestimation of aboveground biomass productivity associated with unrecorded growth of previously measured stems that died during the interval and from unmeasured stems that passed the minimum diameter threshold but then died before they were recorded (Sheil & May 1996). We both lack sufficient data and believe the parametric census interval correction suggested by Malhi *et al.* (2004) is not suited to our logged forests as it assumes that unmeasured growth and mortality will converge as is expected in mature forests that are in equilibrium (Phillips *et al.* 2009). We report mortality rates (% yr⁻¹) in the supplemental materials (Appendix B).

Statistical Analysis of ACS and Merchantable Timber Stock Recovery

We applied a piecewise regression model (also referred to as a broken stick model) that corresponds to the typical dynamics of logged forests, specifically elevated mortality in the initial years after logging followed by increased rates of residual growth and recruitment (Sist & Nguyen-Thé 2002, Mazzei *et al.* 2010, Blanc *et al.* 2009). Compared to linear models that estimate a single intercept and slope parameter, the piecewise model allows for changes in the intercept and slope parameters at the different points in time to correspond with threshold dynamics (Toms & Lesperance 2003, Bourgeois *et al.* 2016). In our case, we applied the simplest piecewise regression model with a single breakpoint. This model structure results in two straight lines that join sharply at these breakpoints for our ACS and timber stock recovery models:

$$y_i = \begin{cases} \beta_0 + \beta_1 X_i + plot [i] + e_i & \text{for } X_1 \leq \alpha \\ \beta_0 + \beta_1 X_i + \beta_2 (X_1 - \alpha) + plot [i] + e_i & \text{for } X_1 > \alpha \end{cases}$$

where y_i is the value for the i^{th} observation; x_i is a k vector of covariates that includes time-since-logged (years; X_1), logging intensity (timber volume – $m^3 ha^{-1}$), and an interaction term for time-since-logged and logging intensity; β_i is a k vector of regression coefficients; and α is the breakpoint in years, with e_i assumed to be independent additive errors with a mean of zero. Plot level variance is captured by $plot[i]$. Although the period of elevated post-logging mortality probably ends gradually, modelling it that way requires frequent censuses. We set our breakpoints, α , at 3.6 and 1.4 years for ACS and merchantable timber stocks, respectively. Based on previous studies (Piponiot *et al.* 2016) and our data, we use 3.6 years as the breakpoint for elevated losses of ACS. In contrast, for merchantable timber stocks we use 1.4 years after the harvest as the period of elevated mortality because the logging system used was explicitly designed to avoid damage to FCTs. This intervention resulted in lower mortality rates for merchantable timber trees than stand-wide rates.

Our model allows us to account explicitly for both the loss and recovery periods of ACS and merchantable timber stocks across different logging intensities. Other studies typically report the census data immediately after logging as the beginning of the recovery period (Lussetti *et al.* 2016, Ruslandi *et al.* 2017, Vidal *et al.* 2016), even though we know mortality is elevated for several years post-logging (Shenkin *et al.* 2015, Mazzei *et al.* 2010, Sist & Nguyen-Thé 2002). We are thus able to quantify both the impact of logging intensity on residual losses and subsequent recovery rates. The piecewise model also enables us to draw off the framework of linear regression to interpret the slope parameters in our models and test our hypotheses of post-logging recovery at different logging intensities.

We implement our model in a Bayesian hierarchical framework. We used uninformed normally distributed priors for all coefficient parameters. The hierarchical model structure allows us to distinguish observation error from natural process variation, and is well suited for ecological time-series datasets (Webb and Kerry, 2009). We tested several models with and without different predictor variables, including with and without the interaction term, as well as linear models without the breakpoint, and present the best fit models based on out-of-sample model fit (Appendix B). We do not include the liberation treatment of FCTs in our models as we wanted to maintain logging intensity ($\text{m}^3 \text{ha}^{-1}$) as a continuous predictor variable. We expect this model formulation to be more useful to forest managers for projecting losses and recovery associated with logging intensity, as harvest volume data is commonly available. Forest managers can use the intensity of harvest to scale their losses and recovery predictions. All models were implemented in the JAGS software in R (Plummer 2011, R Development Core Team 2015).

Results

Observed Recovery: ACS (Mg C ha^{-1}) and Timber Stocks ($\text{m}^3 \text{ha}^{-1}$)

Mean aboveground carbon stocks (ACS) prior to logging across all 15 plots in 1993 was $185.1 \text{ Mg C ha}^{-1}$ ($\text{SE} \pm 6.6$; Table 3-1). Over the 20-year observation period the three control plots increased their mean ACS by 11%, from $183.8 \text{ Mg C ha}^{-1}$ in 1993 to $204.3 \text{ Mg C ha}^{-1}$ in 2013 (Table 3-1). After 20 years, ACS in plots subjected to low and moderate intensity logging averaged $189.9 \text{ Mg C ha}^{-1}$ and $194.3 \text{ Mg C ha}^{-1}$, respectively, which were 3% and 1% higher than their pre-logging ACS (Table 3-1). ACS losses were highest after high intensity logging and moderate intensity logging + liberation, with 23% and 42% of initial ACS lost, respectively (Figure B-2); at 20 and 17

years after these treatments the plots still respectively averaged 9% (164.1 Mg C ha⁻¹) and 19% (149.8 Mg C ha⁻¹) below their initial ACS (Table 3-1 & Figure 3-1). Census-specific changes in basal area, stem density, and weighted wood density by diameter classes are reported in Table B-1.

Timber stocks (i.e., volumes of wood in trees larger than the species-specific minimum cutting diameter of merchantable quality) across all plots prior to logging (1993) averaged 42.2 m³ ha⁻¹ (SE ± 3.0). Over the 20-year observation period, timber stocks in the control plots increased by 52% (from 41.2 to 62.6 m³ ha⁻¹; Table 3-1). Plots logged at low intensity and moderate intensity followed by liberation recovered their initial timber stocks plus 9% (to 44.0 m³ ha⁻¹) and 13% (to 50.7 m³ ha⁻¹), respectively (Table 3-1 & Figure 3-1). Over the same 20-year period, the plots logged at moderate and high intensities were still below their initial timber stocks by 12% (34.03 m³ ha⁻¹) and 46% (25.03 m³ ha⁻¹), respectively (Table 3-1).

Observed Recovery: Aboveground Biomass Productivity

Aboveground carbon increments between 1997-2000 and 2000-2013 were similar between the control plots (1.18 Mg C ha⁻¹ yr⁻¹, SE ± 0.4) and the low intensity logged plots (0.83 Mg C ha⁻¹ yr⁻¹, SE ± 0.3). Recovery rates were higher after moderate (1.41 Mg C ha⁻¹ yr⁻¹, SE ± 0.4) and high intensity logging (1.50 Mg C ha⁻¹ yr⁻¹, SE ± 0.2). The plots logged at moderate intensity followed by FCT liberation showed the fastest annual increments of aboveground carbon (1.85 Mg C ha⁻¹ yr⁻¹, SE ± 0.5).

Aboveground productivity across all treatments was primarily due to residual tree growth and not recruits that grew into the smallest DBH class (10 cm; Figure 3-2). Recruitment was highest in the logged and liberated plots (0.35 Mg C ha⁻¹ yr⁻¹), three times the rate observed in the control plots (0.11 Mg C ha⁻¹ yr⁻¹), low (0.12 Mg C ha⁻¹ yr⁻¹),

¹) and after moderate intensity RIL alone ($0.12 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). At the end of 20 years, stem turnover rates for low (1.74 \% yr^{-1} ; $\text{SE} \pm 0.19$) and moderate intensity logging (1.73 \% yr^{-1} ; $\text{SE} \pm 0.21$) returned to resemble unlogged forest (1.67 \% yr^{-1} ; $\text{SE} \pm 0.38$). Mortality rates remained elevated relative to the unlogged control plots 20 years after high intensity RIL (1.96 \% yr^{-1} ; $\text{SE} \pm 0.23$) and 17 years after moderate intensity logging and FCT liberation ($2.87\% \text{ yr}^{-1}$; $\text{SE} \pm 0.19$; Figure B-S3).

Similarly, gains in timber stocks were mostly due to residual growth, with unlogged forests increasing at a rate of $1.41 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, higher than RIL-moderate ($0.83 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) and RIL-high ($1.03 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) but similar to RIL-low ($1.44 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). Timber stock increments were highest in the logged and liberated plots ($1.94 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). Recruitment of stems into the harvestable classes for the liberation treatment was also three times the recruitment rates in the control, low, moderate and high logging intensities plots (Figure B-S4).

Piecewise Regression: Statistical Analysis of ACS and Timber Stock Recovery

The piecewise regression coefficients that capture the interaction of time (years-after-logging) and harvest intensity on ACS and timber stocks both indicated significant negative slopes to their respective breakpoints (3.6 and 1.4 years) followed by significant positive slopes (Figure 3-3). The negative values of the interaction terms for both the breakpoints indicate that losses of ACS and timber stocks increases with higher logging intensities. In contrast, higher logging intensities had the opposite effect after the breakpoints, as the significant positive interaction terms indicate that, over time, recovery rates increase with logging intensity. The effects of increased logging intensity on residual tree mortality before the threshold point was not fully compensated by subsequent increases in recovery rates of either ACS or timber stocks (Figure 3-4).

The probabilities of initial ACS recovery by 20 years after low and moderate intensity logging are 75% and 60%, respectively (Figure 3-4), but only 15% after high intensity logging. The probabilities of recovery of initial harvestable timber stocks by 20 years after low and moderate intensity logging are 73% and 45%, respectively, whereas the probability was almost zero after the high intensity treatment (Figure 3-4). If average recovery rates after the breakpoint are maintained at 1.25, 1.60 and 1.93 Mg C ha⁻¹ yr⁻¹ for the low, medium, and high intensity logged plots, respectively, 26, 29, and 44 years will be needed to recover initial ACS with >90% probability. At mean model recovery rates of 0.92, 0.88, and 0.71 m³ ha⁻¹ yr⁻¹ for harvestable timber stocks after the same treatments, 28, 35, and 88 years will be needed for full recovery with >90% probability.

Silvicultural Intensification

Forest subjected to moderate intensity RIL followed by FCT liberation recovered harvestable timber stocks at a rate of 1.94 m³ ha⁻¹ yr⁻¹ between 1997-2013, twice the rate for forests logged at the same intensity but without liberation (Figure 3-5). At 17 years post-liberation, harvestable timber stocks were 50% higher than in forests logged at the same intensity but without the liberation treatment (Table 3-1).

Recovery rate of ACS was also faster in the logged and liberated plots, 2.42 Mg C ha⁻¹ yr⁻¹ compared to 1.82 Mg C ha⁻¹ yr⁻¹ in the similarly logged but not liberated plots. At 17 years post-liberation, ACS was however 30% lower in the liberated areas (149.77 Mg C ha⁻¹) than in the unliberated stands (194.27 Mg C ha⁻¹). Faster recovery did not fully offset the >30% loss of initial ACS that resulted from the liberation treatment.

Discussion

Sustainable Forest management and Reduced-Impact Logging

The underlying principle of SFM is to reconcile timber production in natural forests without compromising the social and ecological value of these forests. This is an attractive concept to both conservationists, hoping to extend positive biodiversity outcomes, and timber managers, who wish to adhere to environmentally and socially responsible forestry practices. Experimental logging studies have identified reduced-impact logging (RIL) as a tool for SFM based on both the reduction in harvest damage to the residual forest stand and comparable timber extraction volumes to unplanned logging (Putz *et al.* 2012). However, RIL alone may not be sufficient for the long term sustainability of timber production in natural forest stands (Peña-Claros *et al.* 2008).

At our study site RIL implemented at logging intensities of 8 trees ha⁻¹ or 24 m³ ha⁻¹ and below were on a recovery trajectory that would enable a second harvest at the end of 40 years. At these logging intensities, forests had returned to similar stem turnover rates as unlogged forests 20 years post-logging (Figure B-3). Similarly, ACS is predicted to recover within a 40 year period with high confidence at RIL-low and RIL-moderate logging intensities. At higher logging intensities the benefits of RIL on post-logging recovery are lost, and are consistent with other studies that have identified a logging intensity threshold of 8 trees ha⁻¹ (Sist *et al.* 2003). However, a cutting rotation of 40 years might not be sustained after the second harvest in Guyana shield forests at RIL-low and RIL-moderate logging intensities. Recovery of merchantable timber stocks at our study site was driven primarily by residual growth of trees present prior to logging for both RIL-low and RIL-moderate logging intensities. After a second harvest when those residual trees would have been depleted, insufficient ingrowth of commercial

species within the prescribed diameter harvest class, will likely require more than 40 years to recover initial timber stocks. Poor recovery when the majority of harvestable trees are removed at the first harvest is evident from the RIL-high logging intensity treatment (Figure C-B4). If the residual timber stocks are reduced to levels observed after RIL-high logging intensities at the second harvest, we would also expect similarly long cutting rotations of 80 years to the third harvest.

Silvicultural Intensification: Liberation of Future Crop Trees

Aside from the deceptive concept of timber yield sustainability achieved by reducing minimum felling diameters and expanding the list of commercial tree species, post-harvest liberation treatments may be required to favour the growth of FCTs to sustain timber production. Maintaining the harvest criteria used in the selection of harvestable trees in our study, recovery was twice as fast in the forests where FCTs were liberated relative to similarly logged forests not subjected to any silvicultural intensification. Ingrowth into the harvestable stem diameter classes was notably higher in the liberated forests compared to forests only logged with RIL and had no liberation treatment. This bodes well for timber yield sustainability at regular cutting rotations as trees harvested are replaced and prevents the depletion of harvestable crop trees. The improvement in recruitment rates is especially important as commercial species in tropical forests tend to occur at low densities, as per norm in species rich tropical forests (Rosin 2014).

Though harvestable timber stocks recover faster with the liberation treatment after RIL, the carbon value of these forests is 30% less at 20 years post-logging compared to similarly logged forests that had no liberation treatment. As forests logged only with RIL will likely require longer cutting rotations than forests undergoing

silvicultural intensification, the global carbon market should focus on financial instruments that reward low impact logging that retains high carbon stocks. Payments associated with these ecosystem services can provide the needed revenue to enable forest managers to extend the cutting rotations when only RIL is applied with a natural regeneration system.

Piecewise Model

Our piecewise model provides insight into the recovery trajectory of managed forests. The model quantifies the tradeoff between post-logging mortality and residual growth at different logging intensities. We found significant effects of the interaction between logging intensity and time since logging both before and after the breakpoint. These results conform to our expectation that recovery rates of ACS increase with logging intensity as residual trees take advantage of improved growing conditions associated with access to sunlight and lower competition created by logging related mortality. Biomass loss immediately after logging similarly increases with logging intensity as more trees are killed from felling, and logging infrastructure. The relative magnitude of these slope terms suggests a dynamic where residual growth rates are unable to compensate for post-logging mortality at high logging intensities.

Similarly, we found support for stagnated recovery of harvestable timber stocks at the highest logging intensity (Figure 3-2). Though the timber volume harvested doubled between RIL-moderate and RIL-high, the recovery time for harvestable timber stocks at RIL-high logging intensity was almost three times the recovery time needed at RIL-moderate logging intensity to achieve >90% probability of recovery. Our piecewise model supports the concept that logging intensity thresholds for sustainable timber production do exist, beyond which the ability of the forests to recover from logging

interventions and continue to provide timber and other services are put at risk (Bertault & Sist 1997, Sist *et al.* 1998). Moreover, the piecewise model enabled us to use a straightforward linear model approach to quantify the non-linear threshold dynamics of post-logging recovery.

Implications for Forest Management in Guyana Shield Forests

Logging at high intensities is detrimental to biodiversity (Burivalova *et al.* 2014, de Avila *et al.* 2015), reduces carbon storage, and compromises future timber production in these forests, even with the use of RIL. To achieve sustainable timber yields based on a polycyclic system that relies on natural regeneration, forest managers should plan not to harvest beyond RIL-moderate (8 tree ha⁻¹ or 24 m³ ha⁻¹) in Guyana shield forests. Our results are consistent with the current forest management regulations in Guyana that allow for a maximum removal of 20 m³ ha⁻¹ of timber, estimated at 10 trees ha⁻¹. Additional rules implemented in the Guyanese forest sector such as an 8 m minimum spacing distance between harvested trees also help to ensure felling intensity remains under the threshold limit. The annual allowable cut of 0.33 m³ ha⁻¹ yr⁻¹ used to calculate harvest rotations may however be inappropriate as it does not account for the loss of residual tree growth from commercial trees after logging, which accounts for the majority of timber stock recovery.

If forest managers plan to employ only a natural regeneration system for timber production, financial benefits provided by the global carbon market focused on forestry activities that reduce levels of global greenhouse gases will be important to offset the economic disadvantages of longer harvest rotations. Otherwise if forest managers intend to manage primarily for timber production, some form of intensification will be required that will have a concomitant reduction in other ecosystem services these

forests provide. If intensification is done across multiple cycles, we should acknowledge that these forests are no longer natural forests stands but more akin to plantations, and not managed equally for the dual goals of timber production and conservation.

Table 3-1. Harvest information, aboveground carbon (ACS; Mg C ha⁻¹) and timber stocks (m³ ha⁻¹) before logging (1993), 20 and 17 years post-logging and liberation respectively.

Treatment	Plot ID	Harvest information			Pre-harvest stand structure (1993)		Post-harvest stand structure (2013)	
		Extracted timber (m ³ ha ⁻¹)	Basal area (m ² ha ⁻¹)	Stems ha ⁻¹	ACS (Mg C ha ⁻¹)	Timber stocks (m ³ ha ⁻¹)	ACS (Mg C ha ⁻¹)	Timber stocks (m ³ ha ⁻¹)
RIL - Low	3	14.30	1.10	4	222.89	41.63	232.25	47.67
RIL - Low	10	16.30	1.20	4	155.22	38.43	158.16	38.21
RIL - Low	11	18.20	1.30	4	177.10	41.19	179.40	46.06
RIL - Moderate	1	25.60	2.00	8	166.05	34.73	192.40	34.24
RIL - Moderate	8	20.80	1.80	8	186.48	27.24	176.24	26.96
RIL - Moderate	15	24.50	1.90	8	222.56	53.44	214.17	40.88
RIL - High	2	39.70	3.40	16	208.53	36.38	187.60	17.63
RIL - High	7	53.80	4.00	16	159.86	52.42	143.02	20.88
RIL - High	14	50.30	3.60	16	174.69	49.11	161.62	36.57
RIL - Moderate + liberation	4	26.30	1.90	8 + liberation	161.28	40.66	135.71	40.69
RIL - Moderate + liberation	9	23.00	1.80	8 + liberation	165.48	23.20	146.77	31.07
RIL - Moderate + liberation	13	38.60	2.70	8 + liberation	224.50	70.44	166.82	80.33
Control	5	0.00	0.00	0	177.47	36.16	195.82	60.86
Control	6	0.00	0.00	0	164.20	37.36	177.95	54.28
Control	12	0.00	0.00	0	209.81	50.01	238.98	72.74

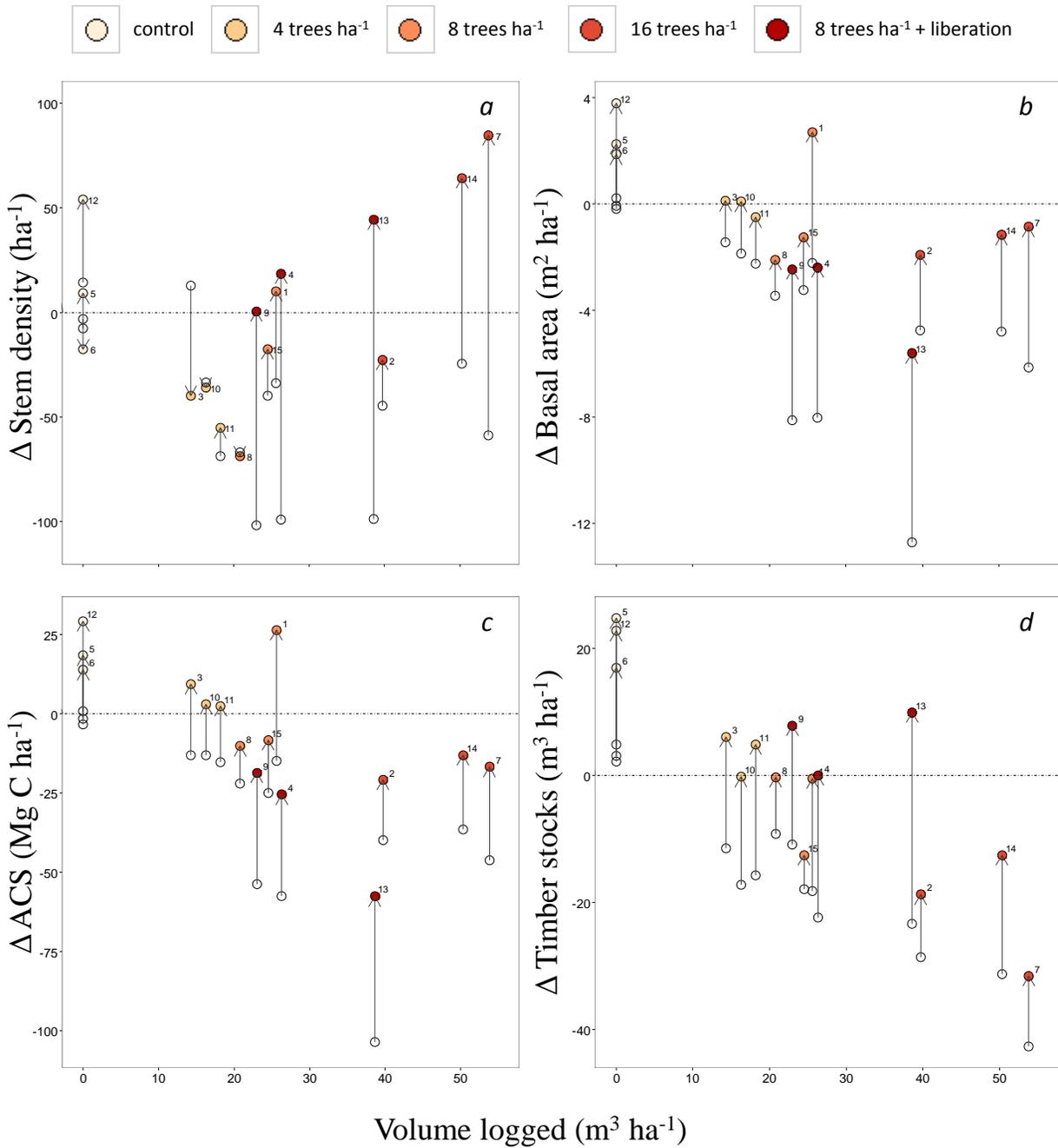


Figure 3-1. Observed changes from pre-logging (1993; dashed horizontal line) basal area (a), stem density (b), aboveground carbon stocks -ACS (c), and commercial timber stocks (d), 3 years after logging and 1 year after liberation thinning (1997; unfilled symbols); and 20 years after logging and 17 years after FCT liberation (2013; filled circles). Arrows indicate the direction of change between 1993 to 2013. Plot numbers refer to Table 3-1.

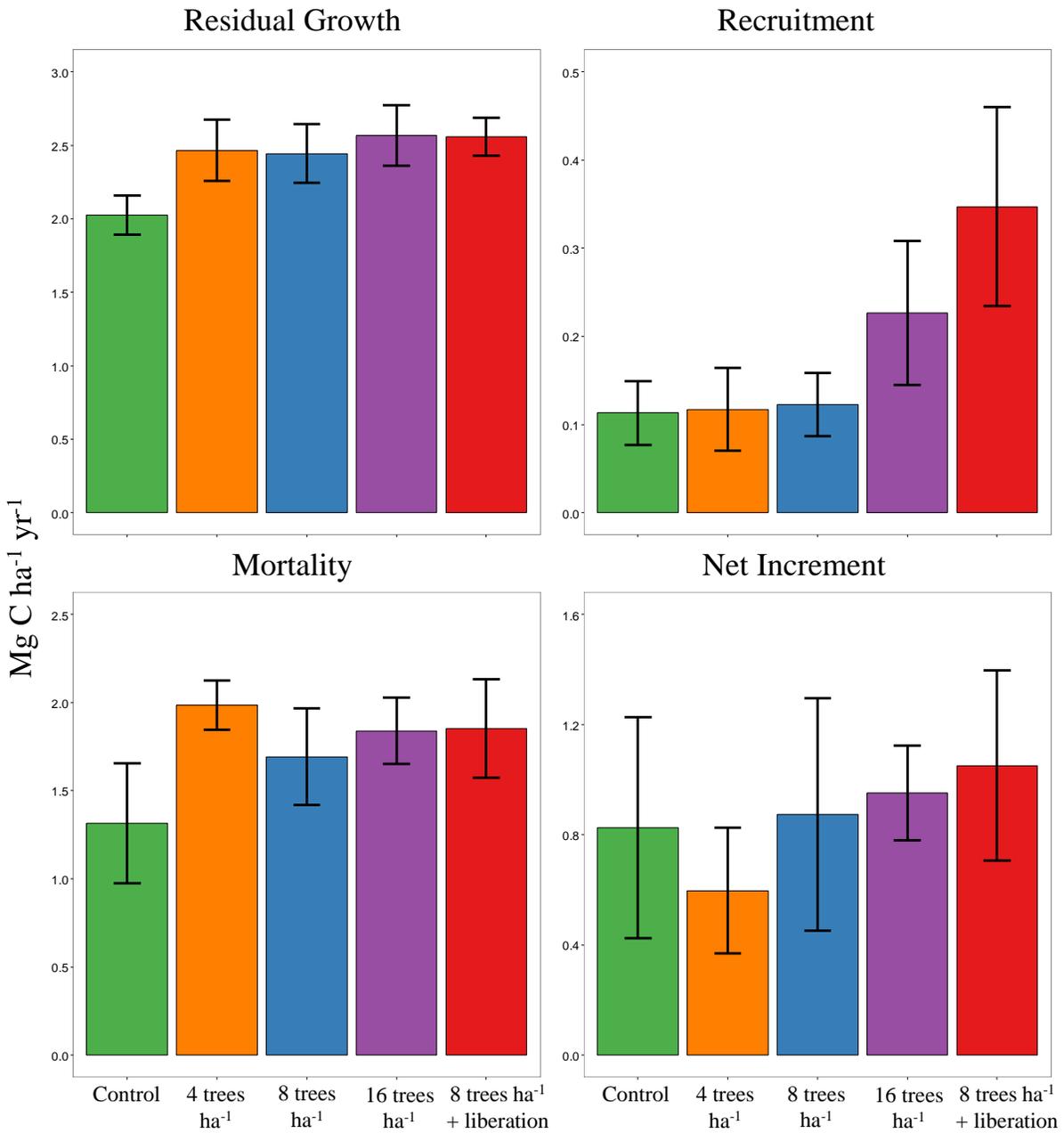


Figure 3-2. Aboveground biomass production for trees ≥ 10 cm broken down into residual growth, recruitment (i.e. trees that grow above 10 cm diameter between censuses), and mortality rates. We used the two post-logging and post-liberation censuses, 1997-2000 and 2000-2013, to estimate our aboveground biomass production.

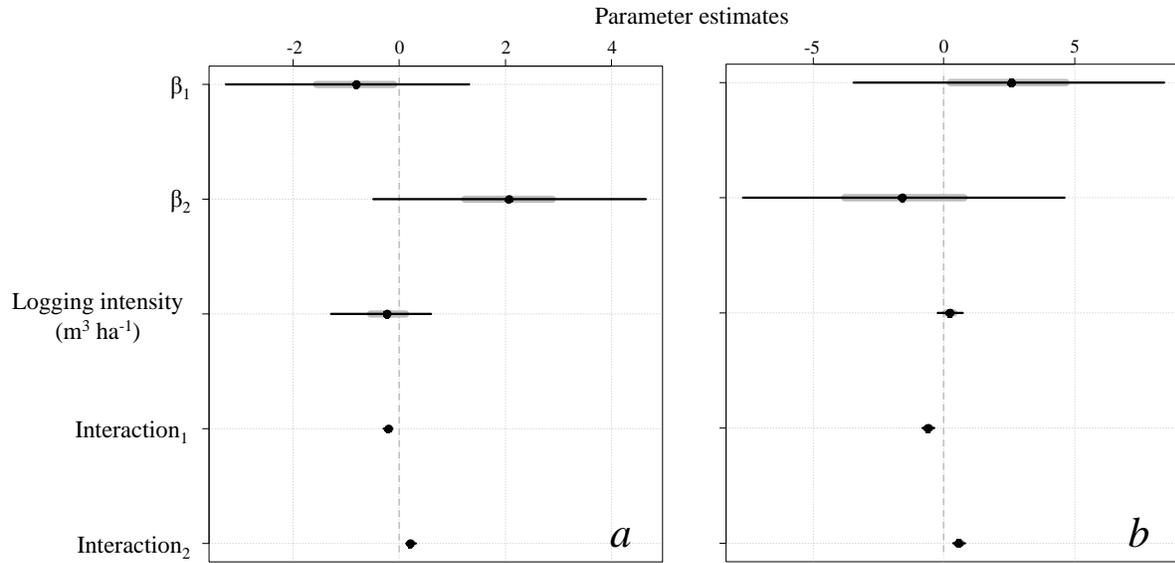


Figure 3-3. Piecewise model coefficients for aboveground carbon (a) and timber stock recovery (b). Points are the mean parameter estimates with thick grey lines capturing the 50% credible intervals and thin black lines the 95% credible intervals. Parameter estimates that do not cross the zero value (dashed grey line) can be considered to have a significant effect. Interaction1 captures the period of elevated mortality to 3.6 years after logging (breakpoint) and Interaction2 represents the recovery period.

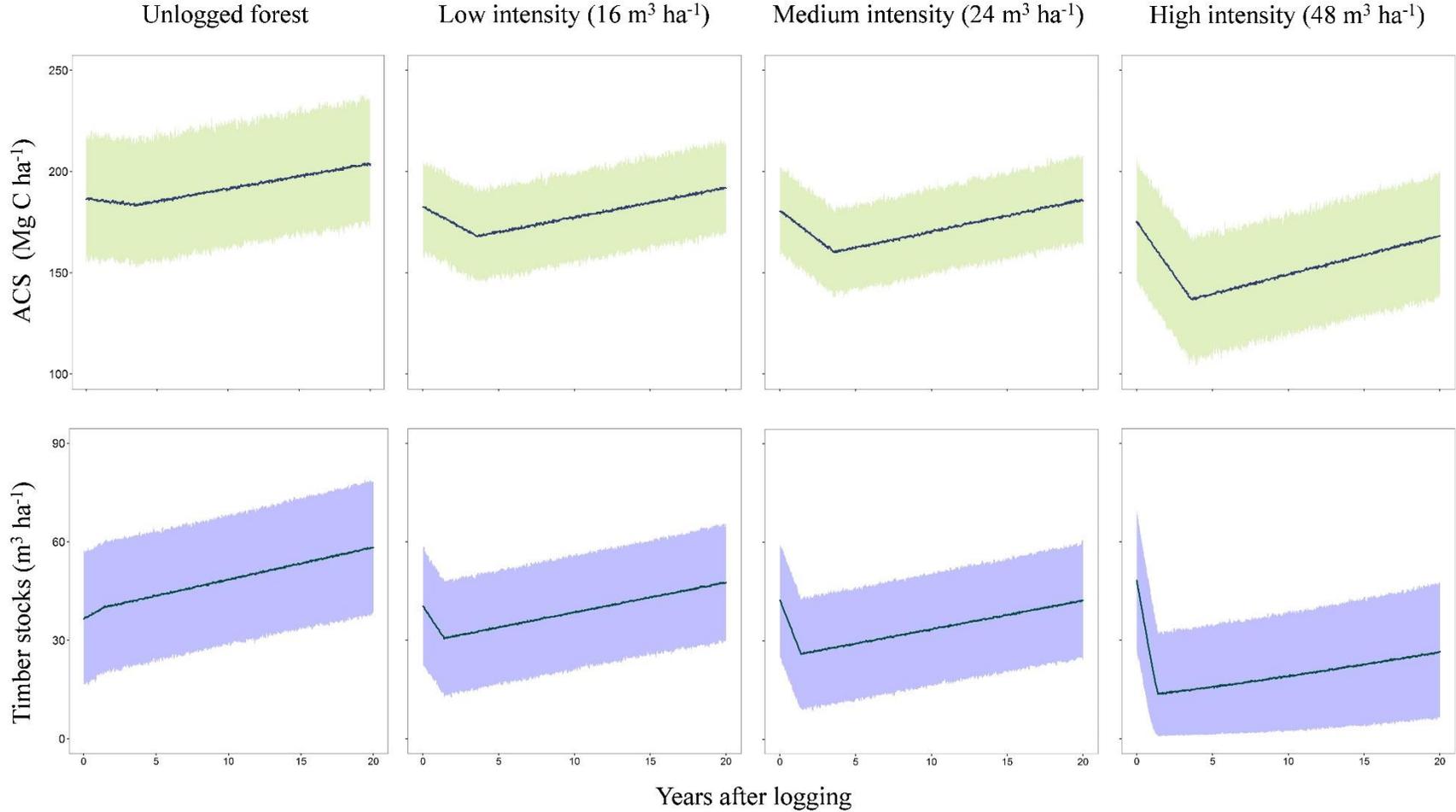


Figure 3-4. Predictions from piecewise regression models for ACS (Mg C ha⁻¹) and merchantable timber stocks (m³ ha⁻¹) over the 20-year post-logging observational period. Dark lines are mean predicted recovery rates, with lighter shaded bands capturing the 95% credible intervals from predictions that account for parameter and natural process variation.

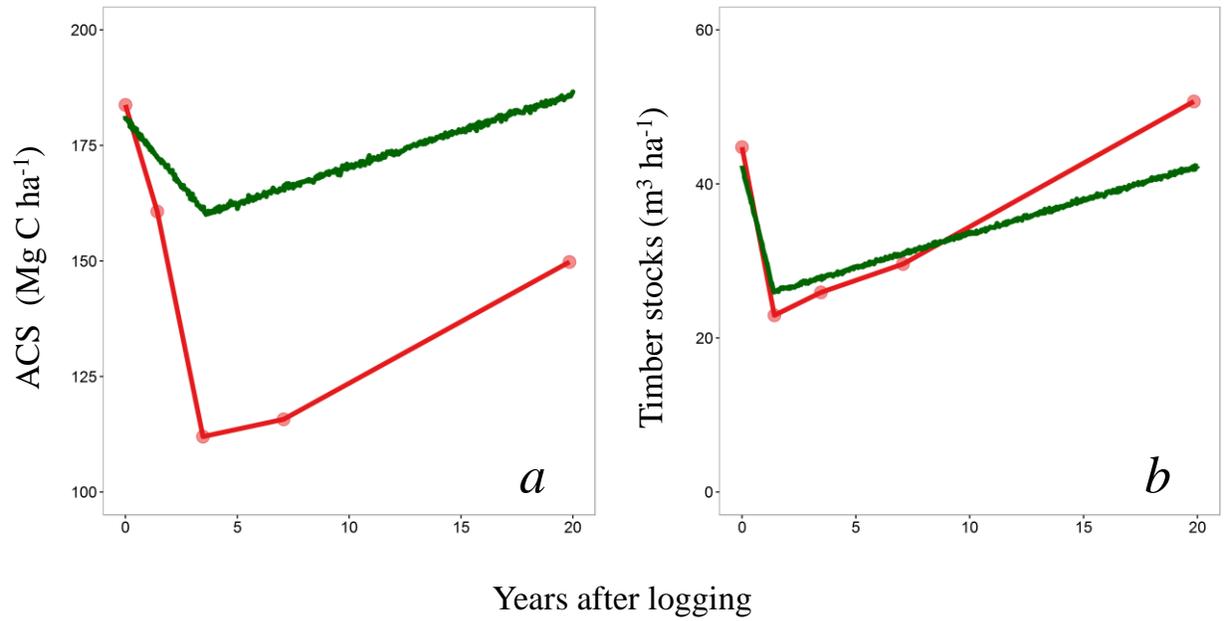


Figure 3-5. Recovery of ACS (a) and harvestable timber stocks (b) for forests logged at $24 \text{ m}^3 \text{ ha}^{-1}$ (RIL-moderate; green line) and forests logged at the same intensity and subjected to a liberation thinning (RIL-moderate + liberation; red line).

CHAPTER 4 LOGGING AND INDIGENOUS HUNTING IMPACTS ON PERSISTENCE OF LARGE NEOTROPICAL ANIMALS

Summary

Areas allocated for industrial logging and community-owned forests account for over 50% of all remaining tropical forests. Landscape-scale conservation strategies that include these forests are expected to have substantial benefits for biodiversity, especially for large mammals and birds that require extensive habitat but that are susceptible to extirpation due to synergies between logging and hunting. Additionally, their responses to logging alone are poorly understood due to their cryptic behaviour and low densities. In this study, we assessed the effects of logging and hunting on detection and occupancy rates of large vertebrates in a multiple-use forest on the Guiana Shield. Our study site was certified as being responsibly managed for timber production and indigenous communities are legally guaranteed use-rights to the forest. We coupled camera trap data for wildlife detection with a spatially-explicit dataset on indigenous hunting. A multi-species occupancy model found a weak positive effect of logging on occupancy and detection rates, whilst hunting had a weak negative effect. Model predictions of species richness were also higher in logged forest sites compared to unlogged forest sites. Density estimates for jaguars and ocelots in our multiple-use area were similar to estimates reported for fully protected areas. Involvement of local communities in forest management, control of forest access, and nesting production

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forests in a landscape that includes protected areas seemed important for these positive biodiversity outcomes. The maintenance of vertebrate species bodes well for both biodiversity and the humans that depend on multiple-use forests.

Background

Managed forests can extend the formal “conservation estate” beyond the boundaries of protected areas (e.g., Clark & Poulsen 2009; Putz *et al.* 2012; Edwards *et al.* 2014a). For tropical forests managed principally for timber, the magnitude of this conservation benefit depends on the policies and practices implemented during timber harvests and in the periods between harvests. Control of forest access is of especially high priority to curb the illegal hunting that has contributed to global declines of vertebrate populations (Redford 1992, Wilkie *et al.* 2000, Laurance & Edwards 2014, Bicknell *et al.* 2015). Faunal loss may affect forest productivity, tree species composition, and the food security of forest-dependent people (Levi *et al.* 2009, Dirzo *et al.* 2014).

Hunting pressure in tropical timber concessions is especially high due to the improved access provided by logging roads and the influx of forestry workers, miners, and other people (Robinson & Bennett 2000, Wilkie *et al.* 2000). The largest vertebrates are the preferred prey of most human hunters and the first to decline due to their characteristically low fecundities and sparse populations (Peres 2000). Their population recovery rates are also impeded if their home ranges are reduced subsequently by forest conversion to croplands or pastures (Morrison *et al.* 2007). Depletion of large vertebrates may directly affect recruitment and survival of many tree species through loss of their dispersal services (Harrison *et al.* 2013, Caughlin *et al.* 2014). For example,

tapirs (*Tapirus* spp.), the largest mammal native to the neotropics, and an often over-hunted herbivore, are important seed dispersers for many large-seeded tree species such as *Manilkara zapota*, a canopy tree species commercially important for both its timber and latex (Fragoso & Huffman 2000, O’Farrill *et al.* 2013). The ability of vertebrates to persist in and move around tropical forests is thus of great importance for natural regeneration processes that contribute to the recovery of timber species and carbon stocks in managed forests (Jansen & Zuidema 2001, Rosin 2014, Osuri *et al.* 2016).

Strictly protected areas are and will remain critical for conservation but many are not large enough to maintain viable populations of vertebrates with large home ranges, including apex predators (Cantú-Salazar & Gaston 2010, Peres 2005). As selective logging leaves most of the forest intact, large production forests adjacent to protected areas will allow continued animal movements and thereby reduce fragmentation (Elkin & Possingham 2008, Edwards *et al.* 2014). Despite the critical ecological importance and threatened status of many large vertebrates, knowledge about the impacts of logging on this group of animals remains limited (Vetter *et al.* 2011). For example, a recent meta-analysis of logging impacts on biodiversity that utilized 48 studies included only one study on large vertebrates (Burivalova *et al.* 2014).

Given that the majority of timber concessions experience substantial hunting pressure, it is difficult to untangle the effects of logging from those associated with hunting (Vetter *et al.* 2011, Brodie *et al.* 2015). Hunting is an especially complex issue where subsistence hunting by indigenous people is legally sanctioned and managed forests abut or overlap with their traditional lands. This study was able to address both

of these issues because it was conducted in a sustainable use reserve co-managed by a non-governmental organization (Iwokrama International Centre; <http://iwokrama.org>) and local indigenous communities (North Rupununi District Development Board; <http://nrddb.org>) who jointly develop forest use policies. Iwokrama's forest operations were certified by the Forest Stewardship Council (FSC) as responsible managed, access and hunting by non-indigenous people is strictly controlled, and the permanency of the forest estate is nationally legislated. We assess the biodiversity outcomes specific to large vertebrates that derive in part from these resource-use policies.

We partition the effects of selective logging and subsistence hunting by indigenous people on large terrestrial vertebrates (> 1 kg) with animal surveys using camera traps and spatially explicit surveys of indigenous hunting. We apply a hierarchical multi-species occupancy model to our binary detection data that enables us to account for species-specific differences in detectability associated with behaviour and abundance (Iknayan *et al.* 2014). This statistical method quantifies the impacts of both logging and hunting on the occupancy state of large vertebrates in a lowland neotropical forest in Guyana that is known to harbour substantial populations of game animals such as tapirs (*Tapiris terrestris*), deer (*Mazama spp.*), giant armadillos (*Priodontes maximus*), paca (*Cuniculus paca*), peccaries (*Tayassuidae*), as well as large predators such as jaguars (*Panthera onca*) and pumas (*Puma concolor*) that are rare or absent in degraded forests (Lim & Engstrom 2005, Read *et al.* 2010).

Methods

Study Site

Field work was conducted in Iwokrama Forest in central Guyana (4-5° N, 58.5-59.5°W; Figure 4-1), a 370,000-ha conservation area. Iwokrama is zoned into a

sustainable-use area where selective logging and other resource-use activities are permitted (e.g., ecotourism and non-timber forest product extraction), a wilderness preserve where anthropogenic disturbances are prohibited, and a titled indigenous community resource-use area. This moist tropical rainforest, with small areas that are seasonally flooded, is located on the Guiana Shield and receives 2693 mm of annual rainfall with a marked September - November dry season (<150 mm month⁻¹; Bovolo et al. 2012). The area is characterized by highly weathered and nutrient-poor soils, slow canopy dynamics, and high forest biomass as a result of high densities of trees of species with high density wood that mostly produce large seeds (Hammond 2005, Malhi et al. 2009). The canopy of these species-rich forests is dominated by *Catostemma* spp., *Eperua falcata*, *Eschweilera* spp., *Swartzia leiocalycina*, *Mora excelsa*, *Carapa guianensis*, and *Chlorocardium rodiei* (ter Steege 2000). Iwokrama is part of one of the least fragmented lowland tropical rainforests in the Americas and supports an intact community of large vertebrates (Watkins 2010; Figure C-1).

Timber harvesting operations in Iwokrama followed reduced-impact logging (RIL) standards that included a pre-harvest inventory, liana cutting, road planning, directional felling, and cable winching. Harvesting is carried out with a 60-year harvest cycle and a minimum cutting diameter of 40 cm DBH (diameter at 1.3m above the ground). Average harvest intensity in our study area was 12.4 m³ ha⁻¹ (~6 trees ha⁻¹) but was spatially heterogeneous (minimum = 9.1 m³ ha⁻¹ and maximum = 16.4 m³ ha⁻¹) with an average of 72 m ha⁻¹ of roads and skid trails (Rodney 2013a). Densities of trees ≥20 cm DBH in 12 ha of permanent sample plots in unlogged forest and 169 ha of plots in logged

forests averaged 228 trees ha⁻¹ and 161.4 trees ha⁻¹, respectively (Rodney 2013b). The forest was FSC certified during the study period.

Iwokrama is remote, approximately 240 km from the nearest non-indigenous settlement, but accessible by an all-weather dirt road with entry controlled at several checkpoints; these characteristics together lead to minimal hunting other than for subsistence purposes by local indigenous people. Other land-use practices such as swidden agriculture are controlled by co-management protocols negotiated with the Makushi and Wapishana tribes, who have utilised these forests for thousands of years (see Plew 2005, Read et al. 2010, Luzar et al. 2011 for a detailed description of the biophysical and social environments).

Camera Trap Data

A total of 52 camera-trap stations were monitored in June-August 2011 with 27 in logged and 25 in an adjacent unlogged forest (Figure 4-1). The unlogged forest is a 6000 ha contiguous buffer zone for the 5747 ha logged area. Timber was harvested during 2007-2011, with the majority completed prior to the study. Camera trap stations (Cuddeback® Capture, Non-typical Inc.) were arranged 1-1.5 km apart at sites with signs of animal activity (e.g. animal tracks, scat) to increase chances of photo captures. Each station comprised two cameras installed on opposite sides of the presumed animal path to increase captures and to buffer against camera failure. The effective sample area of each camera-trap station was assumed to be a circle with a diameter of 1.5 km (see TEAM Network 2011). Frames were captured 24 hours per day with a 1-min delay between exposures with the date and time recorded. Consecutive photographs of the same species at the same site were considered new individuals when there was at least a 1-hour interval between “captures”, except for when

individuals were identifiable by unique markings (following Bowkett et al. 2007). Due to limitations on equipment and personnel, cameras were deployed sequentially, first in the logged forest and immediately after in the adjacent unlogged forest. Cameras were active for 30-33 days at each site (i.e., 1613 trap nights).

We used spatially explicit capture-recapture models (SECR) to estimate densities of species with uniquely identifiable individuals across the entire multiple use area surveyed (jaguars and ocelots; Gopalaswamy et al. 2012) and mean camera trapping rates as proxies for densities between logged and unlogged sites for all species (Rovero & Marshall 2009). The SECR density estimates for jaguars and ocelots were not partitioned into logged and unlogged forests due to the large home ranges of these carnivores (e.g. jaguars >10 km²; Rabinowitz & Nottingham 1986, Maffei et al. 2011), and the contiguous spatial nature of the logged and unlogged forests. Our goal of estimating density is to compare overall SECR density estimates in the multiple-use area from our study with protected forests with little to no anthropogenic disturbance.

Hunting Data

Survey data on animal kills by hunters from the indigenous community within Iwokrama Forest were collected from 2007-2010 as part of a wider regional study on subsistence livelihood strategies (see Read et al. 2010, Luzar et al. 2011, Fragoso et al. 2016). Hunting surveys were administered to every household in the community by locally recruited indigenous technicians who were residents of the community and trained by project researchers. A hunting record consisted of a hunter ID, the spatial location of the kill site identified by the hunter on a topographic map, and the species hunted. Quality control checks were carried out throughout the data-collection process to identify mistakes and potential falsification of self-reported hunting events. For a

discussion of the strengths and limitations of these self-reported hunting data, see Luzar et al. (2011).

We filtered the hunting records to include only large terrestrial vertebrates (> 1 kg; Table C-1), which led to the exclusion of mainly aquatic species (e.g., river turtles). Kill sites marked by the hunters on a topographic map were used to estimate hunting rates for 400 m x 400 m grid cells across a minimum convex polygon (39,000 ha) that captured all kills as well as the logged and unlogged forest areas where camera traps were deployed. Total number of kills for the entire study period was then extracted for each grid cell and used as a response variable. As our question here concerns how hunting affects wildlife occupancy, we used total number of kills as a cumulative metric of spatial hunting rates across the 21 months of data from the livelihood study. We used a negative binomial distribution to account for over-dispersion because the number of kills is heavily skewed towards zero with a few large outliers (Bolker 2008; Figure C-3). We then predicted mean hunting rate (μ) for each grid cell (j) as a function of distance from the village within Iwokrama with an integrated nested Laplace approximation (INLA; Lindgren et al. 2011) to account for spatial autocorrelation, where ξ_j represents a spatial random effect. Distance ($\beta_{hunting}^1$) from the village was the only fixed effect in our hunting model (distance from the nearest road and river did not improve model fit and were excluded in the final model):

$$\log(\mu_j) = \alpha_{hunting} + \beta_{hunting}^1 \times Village_{distance_j} + \xi_j$$

Our analysis improves on recent efforts to decouple hunting and logging effects on wildlife by explicit inclusion of spatially referenced kill locations. This approach contrasts with other studies that relied on categorical classifications of hunting (often

just, un hunted vs. hunted) or metrics such as hunter encounter rates (Poulsen *et al.* 2011, Brodie *et al.* 2015). The advantage of predicting a mean hunting rate as a covariate in the occupancy model is that the continuous nature of a hunting rate prevents a loss of statistical power compared to when continuous variables are discretized into binary categories such as “hunted vs. non-hunted” (Gelman & Park 2009). One caveat to our hunting rate approach is that our surveys did not contain information to allow us to define the catch-per-unit-effort. If catch-per-effort is high in areas where animal abundance is low, our simple hunt rate could be misleading. However, agent-based simulations of hunting at our study region found that confined hunting territory leads to source-sink meta-population dynamics around villages where forest cover is maintained, potentially leading to relatively constant catch-per-unit-effort (Iwamura *et al.* 2014). Additionally, we found that our model-derived hunt rate led to much better model fit of occupancy models, compared to the simpler metric of distance-from-village (Appendix B: description of the spatial vs. non-spatial models).

Multispecies Occupancy Model

For our occupancy model, we extracted detection records (present/absent) from the camera trap data and used these binary observations as our response variable. Camera trap location was used to situate each trap in either logged or unlogged forest and to predict hunting rates from our spatially-explicit hunting model. We used standard hierarchical occupancy models that are widely used for wildlife camera trap data (Ahumada *et al.* 2013, Tobler *et al.* 2015, Rich *et al.* 2016). Our model represents a multi-species approach to obtain composite information by estimating occurrence probabilities for each species (Dorazio & Royle 2005). The hierarchical model structure permits distinction between non-detection and true absence by an explicit and formal

representation of the data into constituent models of the observations (detections) and of the underlying ecological processes (occupancy; Clark 2005, Royle & Dorazio 2008, Iknayan et al. 2014). The advantage of a community-level approach is that parameter estimates for data-poor species are more precise because they borrow strength from data-rich species (Zipkin *et al.* 2010, Pacifici *et al.* 2014). We refer to community-level occupancy as the mean occupancy rate across all species, with species-level occupancy drawn from this global distribution (Royle & Dorazio 2008, Zipkin *et al.* 2010). The point-level occurrence model is specified as a Bernoulli distribution, $z(i, j) = \text{Bern}(\psi_{i,j})$ where $\psi_{i,j}$ is the probability that species i occurs at site j . We accounted for species identity in our models of detection and occupancy using species-level random effects for both the intercept term as well as the parameters that describe effects of hunting and logging. Site levels effects are incorporated into the model linearly on the logit probability scale:

$$\text{Logit}(\psi_{i,j}) = \alpha_i + \beta_i^{\text{logged}} \times \text{LOGGED}_j + \beta_i^{\text{Hunt}} \times \mu_j$$

in which α_i is the intercept term for the occurrence probability of species i in unlogged forests, and β_i^{logged} and β_i^{Hunt} are parameters that capture the effects of logging and hunting pressure for species i . LOGGED_j indicates whether a grid cell is located in logged or unlogged forests and μ_j is the hunting rate predicted by our INLA model. The detection-level model was similar to the occupancy-level model above insofar as it included the same covariates in a logit-transformed linear model, with intercept, logging and hunting parameters estimated as species-level random effects. As an additional metric of community-level response to hunting and logging, we calculated species richness as the sum of species occupancy values at each site.

Of the many ways to account for space in this modeling framework, we chose to use spatially-varying covariates to address spatial non-independence; we explicitly modeled the environmental factors that drive variability in the response variable. This approach is desirable because parameters that represent the effect size of these spatially-varying covariates have direct biological interpretations (Burton *et al.* 2012). Another (non-mutually exclusive) approach is to estimate the effect of space with models for between-point spatial autocorrelation (Royle *et al.* 2009). We found little evidence for additional spatial autocorrelation in our models once the effects of hunting rate and logging were included (Appendix C: Description of the spatial vs. non-spatial models) and so we present hierarchical occupancy models with hunting rate as a spatially-varying covariate. We also compared our occupancy model that used hunt-rate derived from our INLA analysis with a model that substituted distance-to-village and found that hunt-rate outperformed distance-from-village as a predictor of occupancy (Appendix C: Model results using distance-to-village as a metric of hunting rather than hunt rate).

We parameterized our models in a hierarchical Bayesian framework, constructed in the R coding platform (R Core Team, 2015) using R-INLA and JAGS (Plummer 2011), with non-informative priors (Appendix C: model description and complete R and JAGS code). We ran three chains of length 1,500,000 after a burn-in of 500,000, thinned the posterior chains by 2800, and assessed model convergence using the Gelman-Rubin statistic (Gelman & Hill 2007). To assess statistical power, we simulated occupancy data across a range of parameter values and tested whether our sample size was sufficient to estimate parameter values (Appendix C: Power analysis). We

present our data, model, and simulation code as supplementary materials and online in an open access repository (doi:10.5061/dryad.t2s27).

Results

Camera Trap Data

We captured 270 and 180 independent photographs of 17 and 15 species in the logged and unlogged forest, respectively (Figure C-1 & Figure C-2). Detections were highest for frugivores (e.g. agoutis and trumpeters) and lowest for omnivores and insectivores (e.g. armadillos, tayras, and coatis; Table 4-1). Tayras and coatis were detected in logged but not unlogged forest. Mean camera trapping rates were 18 times greater in the logged forest for the largest carnivores (jaguars and pumas) and 3 times greater for the largest herbivores (tapirs and red-brocket deer) compared to the unlogged forest (Table 4-1). Animal densities based on uniquely identifiable individuals for jaguars and ocelots across the combined logged and unlogged forests were estimated at 1.72 individuals/100 km² (95% CI; 1.55 – 2.32) and 16.20 individuals/100 km² (95% CI; 6.92 – 26.7), respectively (Figure 4-2). These values are similar to those reported in the literature for protected areas.

Hunting Data

We recorded 210 spatially unique hunting kill sites for 13 terrestrial species over 21 months of surveys. All species in the hunting data were also detected with camera traps except two tortoise species, accouchi, and white-lipped peccaries that together account for 23% of all reported kills (Table C-1). Seven species, mainly from the order Carnivora (jaguars, pumas, ocelots, margays, coatis, and tayras) and grey-winged trumpeters, accounted for 38% of all photographs but were not recorded in the hunting data. Species with the highest monthly kill rates were agoutis, pacas, and two peccary

species (Figure 4-2). Although distance from the village had a non-significant mean effect (-0.0002; 95% CI, -0.0006 to 0.0001), it was a better predictor of hunting intensity than distance from the nearest road or river. The majority of kill sites were <10 km and mostly upstream from the village (Figure 4-1 & Figure C-3). Although much of the logged forest was <10 km from the village, it hosted little hunting.

Multispecies Occupancy Model

Across all species and sites (logged and unlogged forests), detection had a median value of 4.12% (95% CI, 0.4 to 28.91%), and occupancy had a median value of 54.43% (95% CI, 8.36 to 94.01%). Both logging and hunting had relatively small and non-significant effects on occupancy and detection rates (Figure 4-3). Logging resulted in a median increase of 8.81% (95% CI, -16.97% to 34.48%) in community-level occupancy. Species-level effects of logging on occupancy were weak and uncertain, with 50% CI overlapping zero for most species (Figure 4-4 & Figure C-4). Results from our power analysis suggest that if there had been a significantly negative effect of logging on occupancy, we would have had sufficient statistical power to detect it (Appendix C: Power analysis). Community-level occupancy at the sites with the highest hunting pressure declined by a median value of 25.01% (95% CI, -57.04 to 17.38%) relative to sites that experienced no hunting. Species-level effects of hunting on occupancy were consistently negative for most species, with the strongest (although non-significant) effects on agoutis (Figure 1-4; Figure 4-4). Using posterior samples, we estimate the probability of negative effects of logging and hunting on community-level occupancy as 24.49% and 88.45%, respectively.

We estimated median observed species richness per sample site at 10 species (95% CI, 5 to 11) in logged forests and 8 species (95% CI, 2 to 12) in unlogged forests

(Figure 4-6). Compared to logging, there was a greater effect of hunt rate on estimated species richness, with a median of 10 species at the sites with no hunting (95% CI, 7 to 12), compared to a median value of 3 species (95% CI, 0 to 6) at the site with the highest hunting rate.

Overall, logging was associated with higher community-level detection of large vertebrates by a median value of 1.76% (95% CI, -0.97 to 6.08%). The strongest species-level effects of logging on detection were observed for the three terrestrial cat species (i.e., jaguars, pumas, and ocelots), with a significant positive effect of logging on puma and jaguar detection (Figure C-5). Compared to the community-level effect of hunting on occupancy, the community-level effect of hunting on detection was relatively weak (Figure 4-3). Similarly, species-level effects of hunting on detection had a median near zero with wide credibility intervals for all species (Figure C-5).

Discussion

Our results shed light on conservation-compatible policies for managed forests for species susceptible to extirpation from anthropogenic impacts due to intrinsic demographic and life history traits correlated with body size (Bodmer *et al.* 1997). The community of large vertebrate species at our study site remained intact in areas subjected to both reduced-impact logging and traditional indigenous hunting. Community partnerships, like the one in this case study, can increase conservation gains through improved forest management while they contribute to local livelihoods and achievement of development aspirations. Although generalisations based on a study in a single logging operation and a single community need to be made with caution (Ramage *et al.* 2013), our results contribute to knowledge about the conservation benefits to large vertebrates of improved forest management. More

specifically, the benefits for biodiversity conservation are clear for policies that require RIL and restrict forest access to people without legitimate claims on forest resources (Edwards *et al.* 2012, Putz *et al.* 2012, Bicknell *et al.* 2014).

In forests that do not benefit from the community partnerships and ecologically sound management practices employed in Iwokrama Forest, the potential loss of ground-dwelling vertebrates can affect the nutrition of local people, forest dynamics, and biodiversity (Iwamura *et al.* 2014). The large-bodied vertebrates that were retained in our study area are especially important in Guiana Shield forests where seeds of most canopy tree species are too large to be dispersed by wind or small animals (Hammond *et al.* 1996). Loss of these dispersers will result in decreased populations of these large-seeded tree species, a guild that accounts for the above-average carbon content of the forests at our study site that is so important for national climate mitigation programs associated with REDD+ (Malhi *et al.* 2009, Johnson *et al.* 2016). From a sustainable timber production perspective, regeneration of commercial timber species depends on the maintenance of these plant-animal interactions due to the high costs of silvicultural interventions to promote the regeneration and growth of commercial timber species (Rosin 2014). Avoidance of conversion of production forest to non-forest land uses, which leads to massive biodiversity losses and carbon emissions, is to some extent dependent on the continued regeneration of these commercially important species (Edwards *et al.* 2014).

The observed lack of a negative effect of RIL on large vertebrates is in line with other studies on birds, bats, amphibians and primates conducted in Iwokrama Forest (Bicknell & Peres 2010, Bicknell *et al.* 2015, Holting *et al.* 2016). Similar to those

studies, we attribute our finding to the low intensity of timber harvests coupled with the use of specific harvesting practices that minimize undesirable logging damage. With planned roads and skid trails coupled with directional felling and log extraction by trained workers, much of the area designated for logging suffers no direct impacts from RIL (Arevalo *et al.* 2016) and therefore remains suitable for species that normally avoid disturbed forests. It should be noted, however, that the higher animal detections observed in logged forests, especially of carnivores, might be a result of the changes in forest structure that improves visual animal detection, animals making use of logging roads, and/or potential increases in food resources (Fragoso 1991, Costa & Magnusson 2003).

The current level of subsistence hunting in Iwokrama may in time reduce the animal populations within the hunting catchment area, as evident from the negative effect of hunting on detection and occupancy. Nevertheless, our overall results and those from other studies in the same area indicate that hunting at our study site is and has been sustainable (Read *et al.* 2010, Iwamura *et al.* 2014). Hunting may reduce animal abundances in areas that experience the highest hunting rates, but these same areas may also represent favourable habitats for wildlife and continue to receive dispersing individuals from surrounding forests (Mayor *et al.* 2015, Iwamura *et al.* 2016). Thus, repeated kills at specific sites likely reflect both traditional hunter knowledge and locations favoured by their preferred bush meat species. We believe this effect to hold true over time as the hunting data cover multiple years that span the first 4 years of logging during which the 30-year old village experienced a 150% population increase (Iwokrama, unpublished data).

The negative effect of hunting on occupancy and detection that we observed perhaps indicates the sensitivity of this region to overhunting. For example, mean camera trapping rates were highest for agoutis, a small bodied rodent that comes to dominate community composition as overall species diversity and animal abundance declines within village hunting zones (Shepard *et al.* 2012). Additionally, the density estimated for jaguars, the apex predators at our study site, across the multiple-use forest, that included both logged and unlogged forests, falls on the lower range of values reported for protected areas (Maffei *et al.* 2011). The low densities of jaguars may indicate larger individual home-ranges that might reflect population reductions of prey species hunted by humans (Novack *et al.* 2005) or inherently low animal densities associated with Guiana Shield forests (Emmons 1984, Eisenberg 1979). Density estimates for ocelots, a meso-predator, in contrast, were similar to those reported for protected areas, 80% higher than the minimum values reported (Di Bitetti *et al.* 2008). The lack of photo captures of white-lipped peccaries, though recorded in the hunting surveys, may reflect the range-wide declines reported for this species (Fragoso 2004, Richard-Hansen *et al.* 2014, Mayor *et al.* 2015).

Conclusions

Our results provide support for the conservation value of managed forests for large vertebrates that are sensitive to human-induced environmental changes (Laurance *et al.* 2012). The policies and practices specific to our study site that enabled such an outcome included: (1) the ability to exclude non-sanctioned uses that can lead to forest cover loss and forest degradation; (2) co-management institutions with indigenous communities who are legally guaranteed access for hunting and other traditional forest uses and benefit financially from the timber business; (3) adherence to

high standards of RIL with third-party certification; and, (4) forest zoning so that protected areas equal in size to timber production forests are established in adjacent wilderness reserves. The existence and enforcement of such policies might serve as indicators of good forest management under global conservation initiatives such as REDD+. An outcome that leads to well-managed tropical forests will be good for biodiversity, enhance indigenous people's livelihoods, and contribute to national development, but only where supported by strong policies and effective enforcement.

The impact of selective logging on tropical biodiversity is dependent on the policies, practices, and enforcement contexts in which forest management occurs. Logging and other forest uses such as subsistence hunting by indigenous people are important livelihood activities that can be conducted in ways that do not result in losses of forest cover. Control of forest access through road closure coupled with co-management mechanisms with indigenous communities can clearly serve to improve forest management and prevent illegal hunting, unplanned colonization, and deforestation that leads to massive biodiversity loss (Robinson et al. 1999, Fimbel et al. 2001, Bicknell et al. 2015). To better understand the suite of policies that would lead to the most conservation gains in managed tropical forest, future research should aim to quantify wildlife densities across multiple sites governed by a range of policies (Ferraro 2013, Angrist & Pischke 2014).

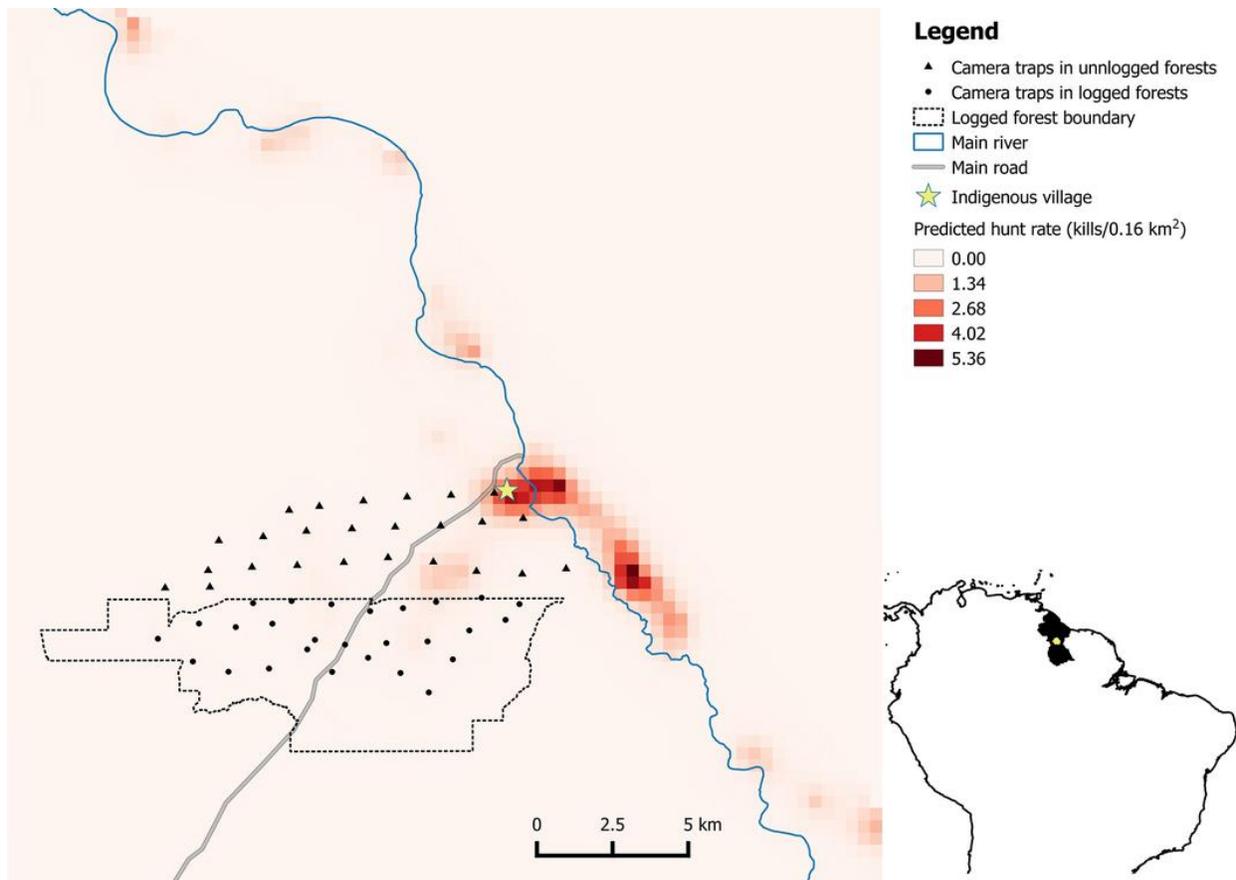


Figure 4-1. Study site location overlain with the predicted hunting surface extracted from a model that uses spatial locations of successful kills over 21 months (2007-2010, total number of kills = 210). Camera traps were installed in 2011 for 808 camera trap nights in logged forests and 805 camera trap nights in unlogged forests. The effective camera trap sample areas were ~ 5747 ha and ~ 6000 ha in logged and unlogged forests, respectively. The indigenous village studied is the only settlement within the sustainable-use reserve. All camera traps outside of the logged forest boundary are located in unlogged forests within Iwokrama. [Inset-map: Guyana is indicated by the dark outline on the South American map, with Iwokrama in the center of Guyana].

Scientific name	Common name	Feeding guild (active period)	Size (kg)	Density estimates (individuals/km ²)	IUCN Status	Mean (SE) camera trapping rate		Mean (SE) monthly hunting rate
						Logged	Unlogged	
<i>Crax alector</i>	Black Curassow	Frugivore (diurnal)	2.4 - 3.7	6.90*	Vulnerable	4.33 (± 0.68)	2.61 (± 5.15)	0.24 (± 0.19)
<i>Cuniculus paca</i>	Spotted Paca	Frugivore (nocturnal)	5.0 - 13.0	84.00 - 93.00	Least concern	0.25 (± 5.76)	0.37 (± 1.55)	2.24 (± 0.63)
<i>Dasyprocta leporina</i>	Red-rumped Agouti	Frugivore (diurnal)	3.0 - 5.9	10.50*	Least concern	7.80 (± 9.36)	6.34 (± 9.12)	2.38 (± 1.06)
<i>Dasyopus sp</i>	Armadillo	Insectivore (nocturnal)	2.7 - 6.3	Unknown	Least concern	0.25 (± 1.35)	0.37 (1.55)	0.86 (± 0.28)
<i>Eira barbara</i>	Tayra	Omnivore (diurnal)	2.7 - 7.0	9	Least concern	0.50 (± 1.27)	0 (± 0.00)	No hunting record
<i>Leopardus pardalis</i>	Ocelot	Carnivore (nocturno-crepuscular)	8.0 - 14.5	0.03 - 0.80 (0.16 ± 0.06)	Least concern	2.10 (± 4.40)	0.37 (± 1.17)	No hunting record
<i>Leopardus wiedii</i>	Margay	Carnivore (nocturnal)	3.0 - 9.0	0.01 - 0.05	Near threatened	0.12 (± 0.68)	0.37 (± 1.55)	No hunting record
<i>Mazama americana</i>	Red-brocket Deer	Herbivore (nocturno-crepuscular)	24.0 - 48.0	0.10 - 0.30	Data deficient	1.36 (± 3.12)	0.87 (± 2.60)	0.14 (± 0.10)
<i>Mazama gouazoubira</i>	Grey-brocket Deer	Herbivore (nocturno-crepuscular)	11.0 - 18.0	0.35 - 1.00	Least concern	0.99 (± 1.91)	0.62 (± 1.76)	0.10 (± 0.10)
<i>Myrmecophaga tridactyla</i>	Giant Anteater	Insectivore (diurnal)	22.0 - 39.0	0.12 - 0.41	Vulnerable	0.12 (± 0.68)	0.25 (± 0.98)	0.05 (± 0.05)
<i>Nasua nasua</i>	Coati	Omnivore (diurnal)	3.0 - 7.2	6.20 - 13.00	Least concern	0.12 (± 0.68)	0 (± 0.00)	No hunting record
<i>Panthera onca</i>	Jaguar	Carnivore (nocturno-crepuscular)	31.0 - 158.0	0.01 - 0.11 (0.02 ± 0.003)	Near Threatened	2.60 (± 5.19)	0.12 (± 0.70)	No hunting record
<i>Pecari tajacu</i>	Collared Peccary	Frugivore (diurnal)	17.0 - 35.0	3.00 - 7.00	Least concern	0.74 (± 2.25)	1.12 (± 3.20)	1.33 (± 0.58)
<i>Priodontes maximus</i>	Giant Armadillo	Insectivore (nocturnal)	18.7 - 32.3	0.05 - 0.06	Vulnerable	0.25 (± 0.94)	0.5 (± 1.32)	0.05 (± 0.05)
<i>Psophia crepitans</i>	Grey-winged Trumpeter	Frugivore (diurnal)	1.0 - 1.5	15.30*	Least concern	4.46 (± 8.22)	7.83 (± 11.96)	No hunting record
<i>Puma concolor</i>	Puma	Carnivore (nocturnal)	29.0 - 120.0	0.02 - 0.05	Least concern	4.95 (± 5.10)	0.25 (± 0.98)	No hunting record
<i>Tapirus terrestris</i>	Tapir	Herbivore (nocturno-crepuscular)	227.0 - 250.0	0.20 - 3.70	Vulnerable	2.35 (± 4.23)	0.37 (± 1.55)	0.29 (± 0.10)

Figure 4-2. Species photographed in Iwokrama Forest by feeding guild (activity period), body size (kg), density (individuals/km²), threatened status (Emmons & Feer 1990, IUCN 2016), and hunting pressure. Hunting rate is based on 21 months of monitoring (see methods). Mean camera trapping rates are used as proxies for species abundance and based on independent photo captures over the sample period. Size and density estimates are minimum and maximum values reported in Emmons & Free (1997) and IUCN (2016) respectively; Density estimates with "*" are based on studies in unlogged forests in Iwokrama (Bicknell & Peres 2010). Mean densities (individuals/km²) were estimated for ocelots and jaguars with SECR models with our data shown in parenthesis (means and standard deviations). Mean camera trapping rates is the ratio of independent photo captures to the number of trap days multiplied by 100 (Rovero & Marshall 2009).

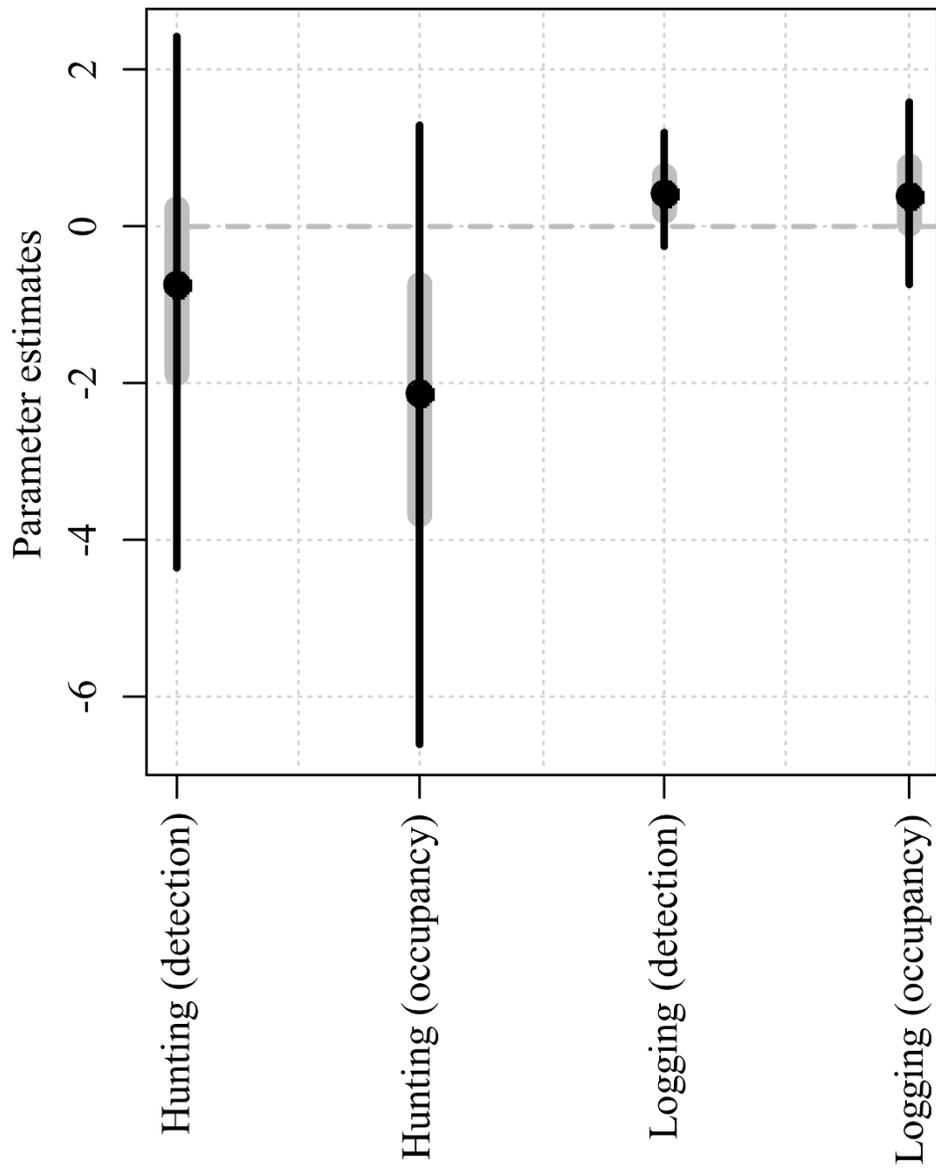


Figure 4-3. Community-level effects of logging and hunting on occupancy and detection. Dark vertical lines represent 95% credible intervals and grey bands represent the 50% credible intervals.

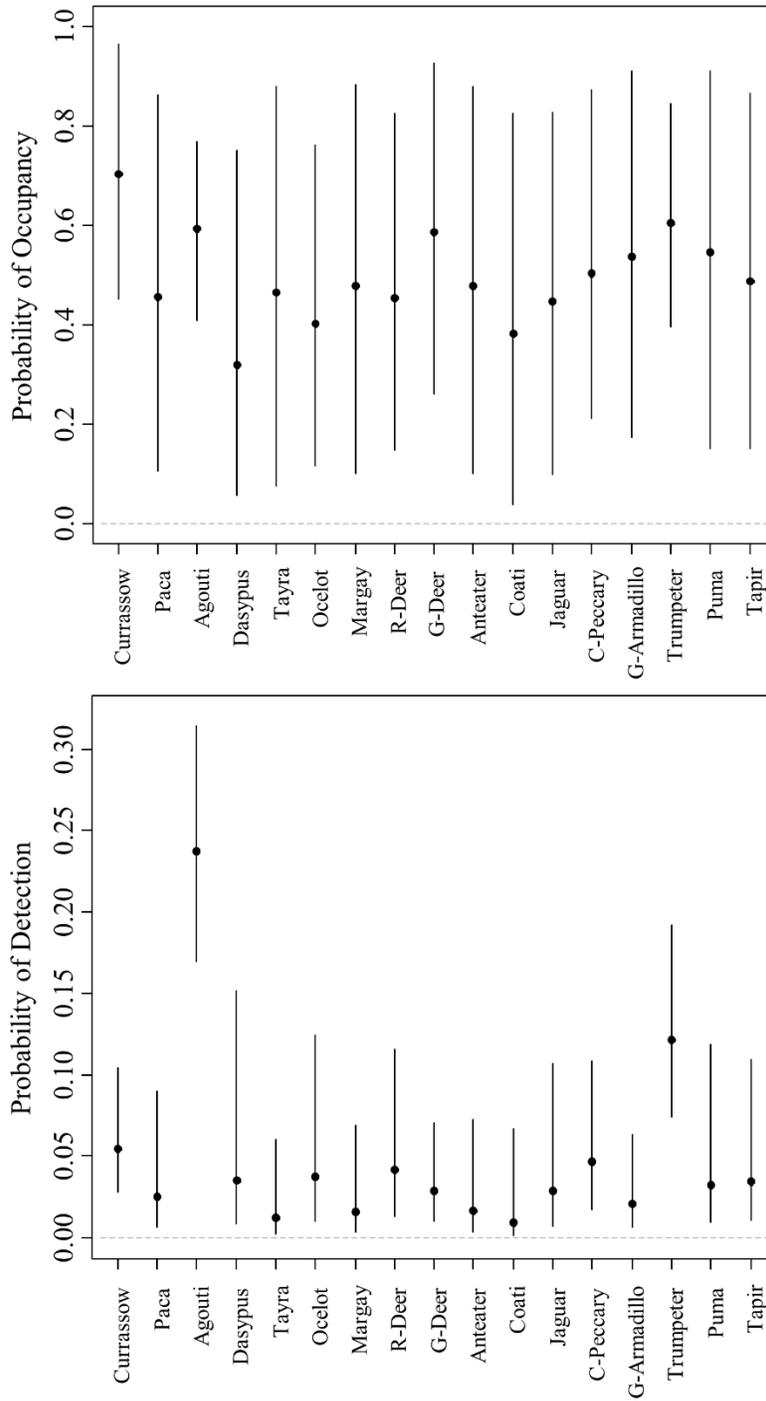


Figure 4-4. Probability of detection (a) and occupancy (b) in unlogged forests for all species recorded in camera traps.

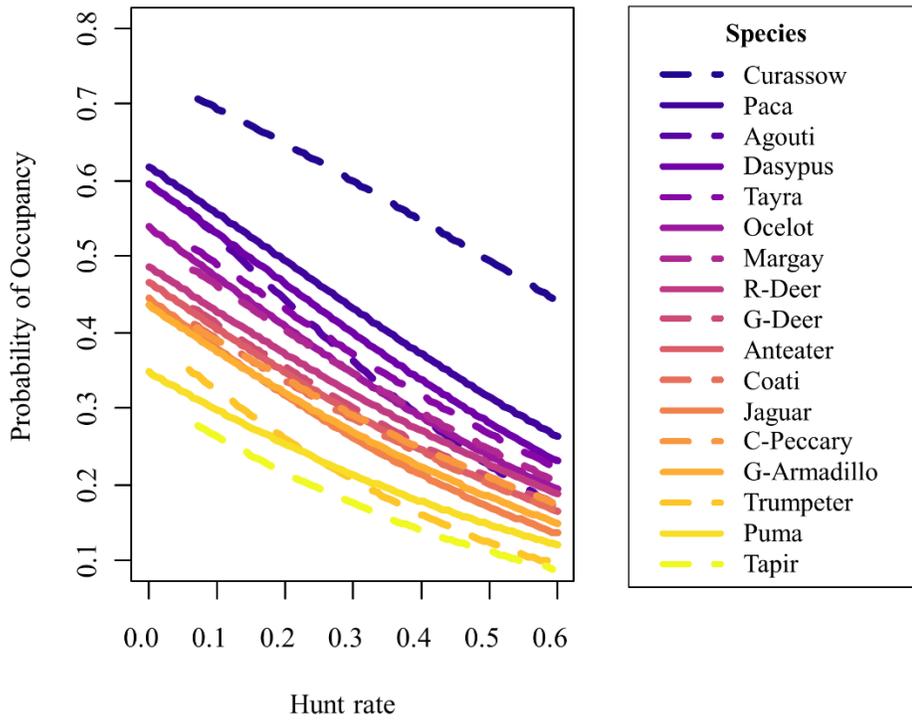


Figure 4-5. Changes in probability of occupancy at the species level across the range of observed hunting rates. Each coloured line represents a single species.

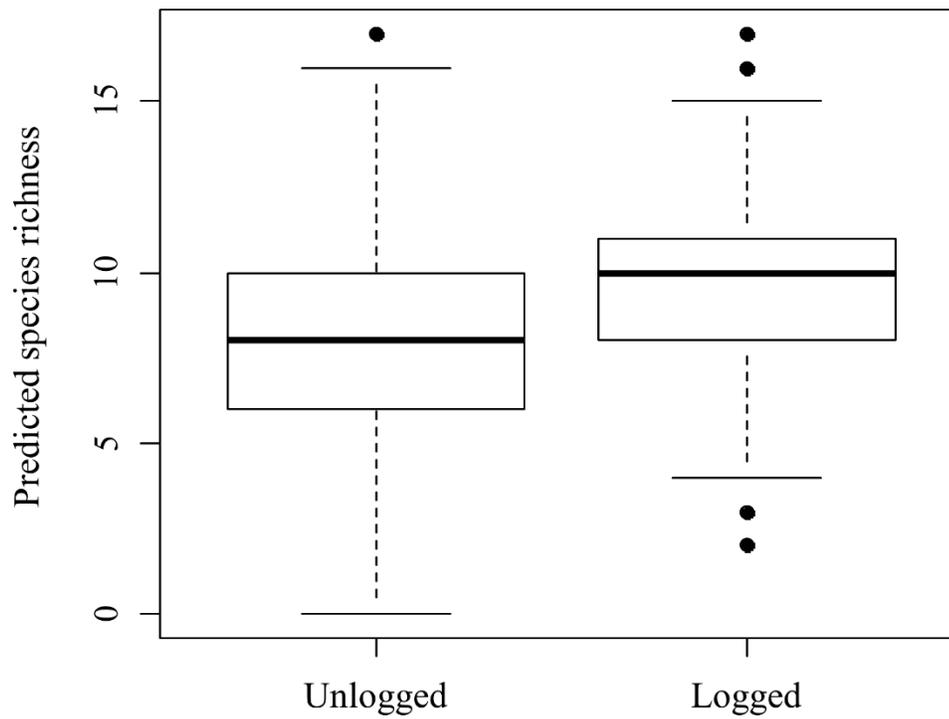


Figure 4-6. Predicted species richness for sites in unlogged and unlogged forests. The upper and lower edges of the box plots represent first and third quartiles, the thick black line within each box represents the median value, 'whiskers' represent minimum and maximum observations within 1.5 times of the upper and lower quartiles, and dots represents outliers.

APPENDIX A
 SUPPLEMENTARY DETAILS: QUANTIFYING UNCERTAINTY ABOUT FOREST
 RECOVERY 32-YEARS AFTER SELECTIVE LOGGING IN SURINAME

Supplemental Figures and Tables for Main Text

Table A-1. Commercial timber species harvested in 1979 from the plots we studied botanical names, trade names, and locally derived volumetric equations are noted for commercial species ≥ 35 cm DBH, with a generic volumetric equation for stems < 35 cm DBH.

Botanical Name	Trade Name	Commercial Volume Equation
<i>Carapa</i> spp.	Andiroba, Crabwood	$-0.2335 + (1.125 \times 10^{-3}) * DBH^2$
<i>Dicorynia guianensis</i>	Angelique	$-0.3232 + (1.208 \times 10^{-3}) * DBH^2$
<i>Goupia glabra</i>	Cupiuba, Kabukalli	$-0.3152 + (1.020 \times 10^{-3}) * DBH^2$
<i>Jacaranda copaia</i>	Gobaja, Para-para, Caroba	$-0.0239 + (1.040 \times 10^{-3}) * DBH^2$
<i>Manilkara bidentata</i>	Macaranduba	$-0.3018 + (1.133 \times 10^{-3}) * DBH^2$
<i>Micropholis guyanensis</i>	Moraballi, Apixuna	$-0.3481 + (1.189 \times 10^{-3}) * DBH^2$
<i>Ocotea rubra</i>	Louro vermelho	$-0.2335 + (1.125 \times 10^{-3}) * DBH^2$
<i>Qualea rosea</i>	Mandio, Quaruba	$-0.1486 + (1.213 \times 10^{-3}) * DBH^2$
<i>Simarouba amara</i>	Marupa, Simaruba	$-0.2335 + (1.125 \times 10^{-3}) * DBH^2$
<i>Tetragastris altissima</i>	Sali	$-0.0836 + (0.759 \times 10^{-3}) * DBH^2$
<i>Virola michelii</i>	Virola, Babun	$-0.2169 + (1.199 \times 10^{-3}) * DBH^2$
<i>Vochysia tomentosa</i>	Quaruba, Iteballi	$-0.2335 + (1.125 \times 10^{-3}) * DBH^2$
<i>Generic volumetric equation (DBH < 35 cm)</i>		$0.0005107 * DBH_m^{2.2055}$

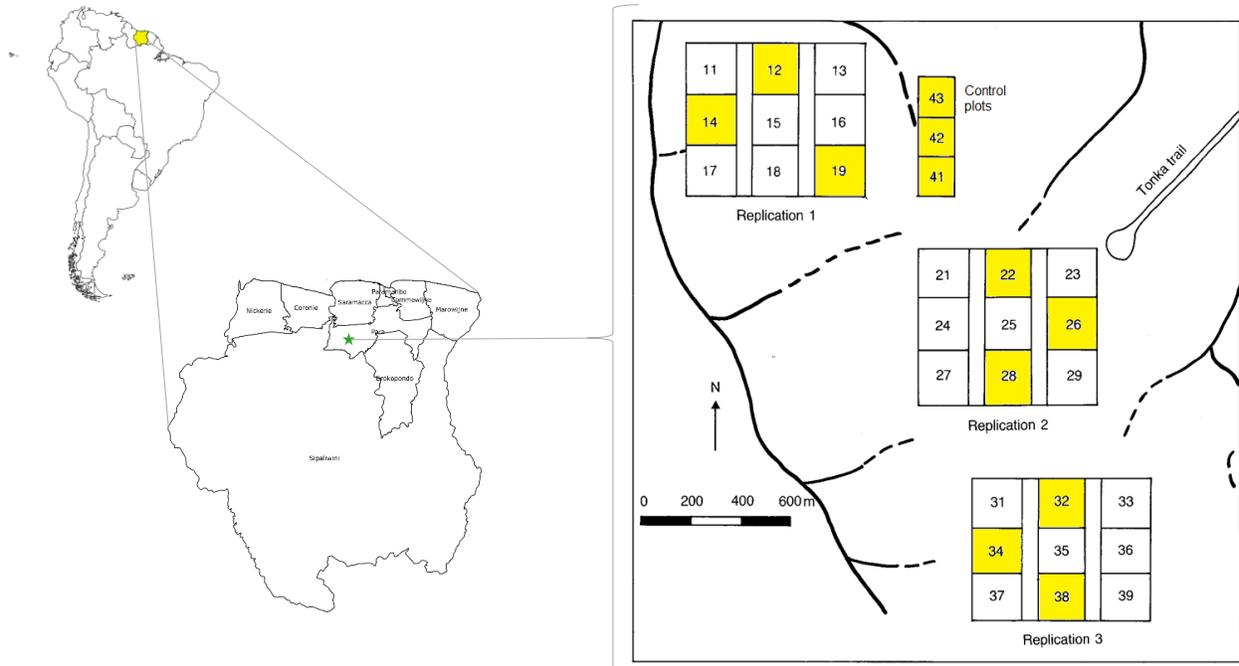
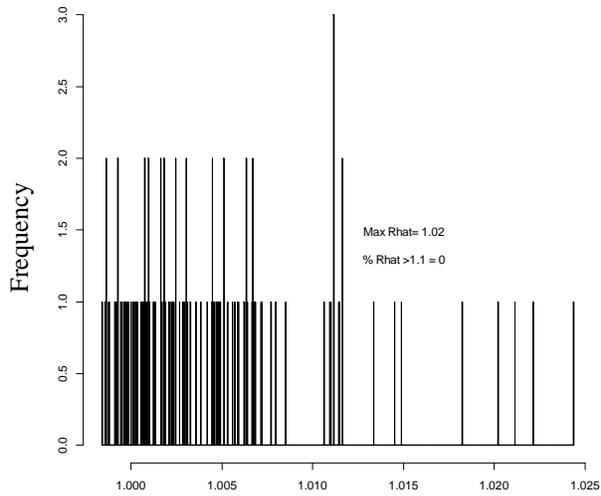


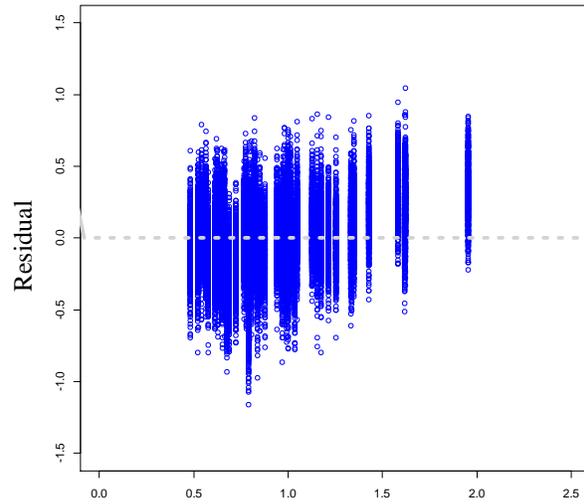
Figure A-1. Location of the Kabo research site and layout of the randomized block design for the experimental logging treatments. The yellow highlighted plots, which are the ones included in our analysis, were selectively logged in 1979 using the CELOS Harvesting System and numbers correspond to Table 2-1. Control plots in unlogged forest were established in 1983. Suriname is highlighted in yellow on the map of South America.

Model Convergence



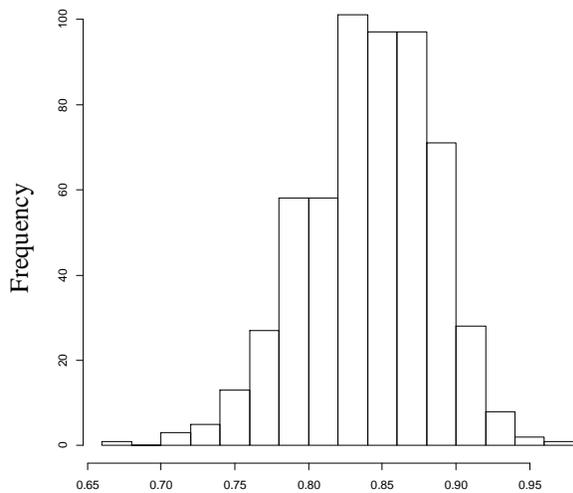
Gelman-Rubin statistic (Rhat)

Residuals vs. Fitted



Fitted value (weighted timber yield)

Conditional R-squared



Marginal R-squared

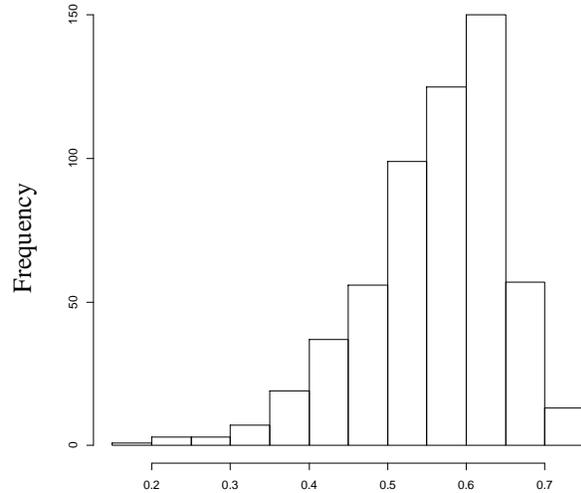


Figure A-2. Model assessment and goodness-of-fit for timber yield recovery. Conditional R-square is the variance explained by both random and fixed effects whereas the marginal R-Squared is the variance explained only by fixed effects.

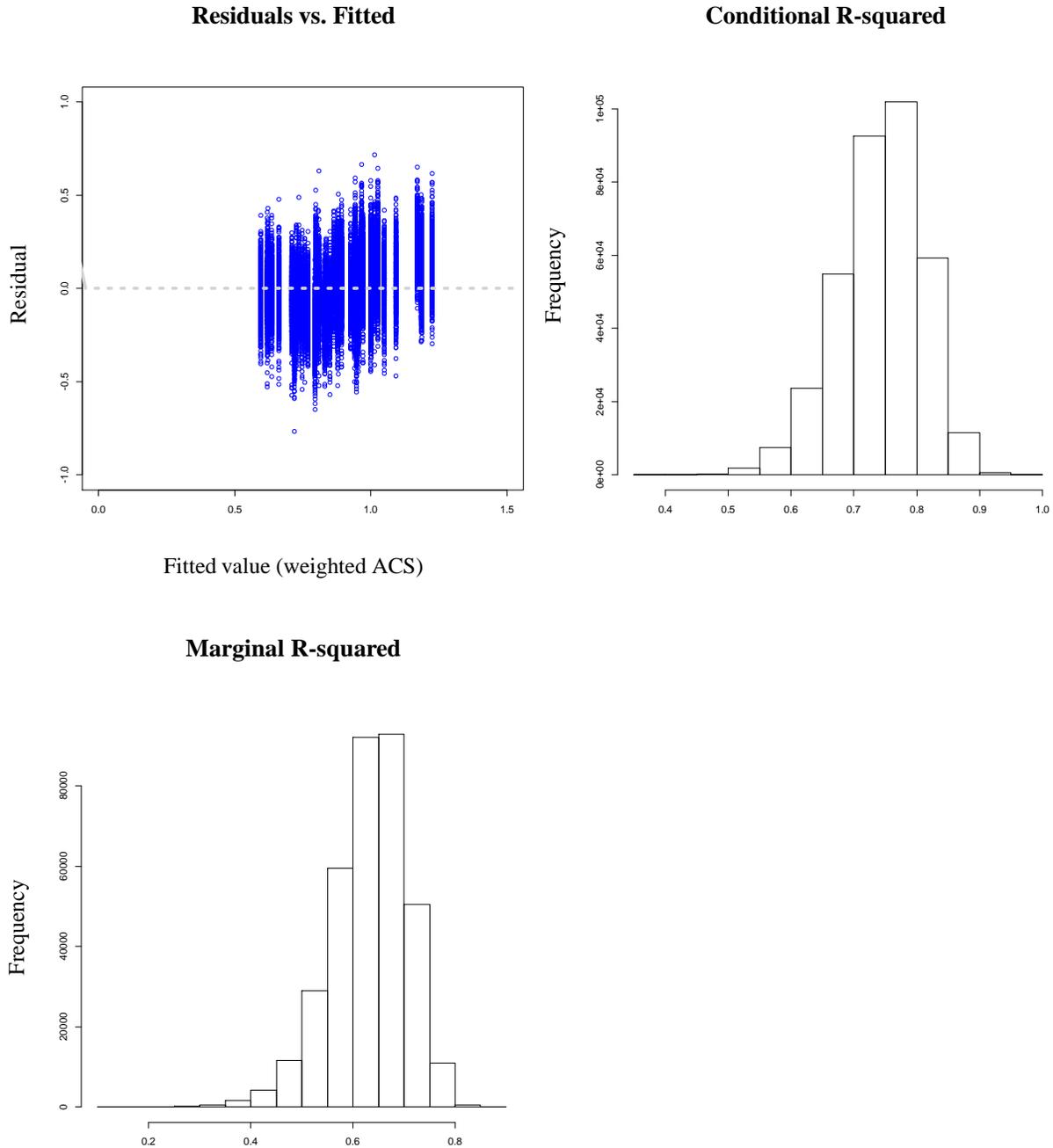


Figure A-3. Model assessment and goodness-of-fit for ACS recovery. We do not present the Gelman-Ruben statistic for model convergence due to the propagation of uncertainty associated with the Chave et al. (2014) biomass allometry that resulted in 1350 ACS predictions for each tree.

Estimation of Plot Level Initial ACS

In 1978, prior to logging in 1979, only commercial species (DBH \geq 15 cm) were censused. After logging, all trees \geq 15 cm DBH of both commercial and non-commercial species were monitored from 1981 to 2012. Because we lack pre-logged values for ACS, we estimate them by applying a carbon emissions factor reported for selectively logged forests located elsewhere on the Guiana Shield. We add these carbon emission estimates based on recorded plot-level logging intensities to the ACS from the 1981 census, our first post-logging census to include all stems \geq 15 cm DBH. This approach allowed us to approximate the pre-logged ACS at the plot level.

The total emission factor (TEF) from selective logging is estimated as the sum of three parts based on a study conducted in Guyana (Pearson *et al.* 2014) and include:

- (1) Logging damage factor (LDF): dead wood stocks in the logging gap, which is equal to the total biomass of the tree felled for timber minus the biomass of the extracted log (parts of the harvested trees left behind in the forest), plus the biomass of trees incidentally uprooted or snapped (i.e., logging related tree mortality), and the biomass of any broken branches from surviving trees. $LDF = 0.99 \text{ Mg C m}^{-3}$.
- (2) Emissions from the extracted log portion (ELE): This is the carbon emissions associated with the extracted logs from the harvested trees. $ELE = 0.36 \text{ Mg C m}^{-3}$.
- (3) Logging infrastructure factor (LIF): This accounts for emissions resulting from the creation of logging roads, skid trails, and logging decks. As the CELOS experimental design established logging roads and decks outside the permanent sample plots, we only account for skid trails used to extract felled logs. Specifically, two 25 m wide strips (running N-S) were located between the treatment plots. These strips were used as the main skid trails, with the wheeled skidders allowed to enter the logged plots at six points

to extract felled logs i.e., three on the western side and three on the east (Jonkers 1983). We used an emissions factor of 0.17 Mg C m⁻³ that is specific to skid trails as reported in Pearson et al. (2014).

Our estimated pre-logged carbon stocks for plot j was calculated as follows:

$$ACS_j \text{ (Mg C ha}^{-1}\text{)} = (0.99 + 0.36 + 0.17) * \textit{logging intensity}_j \text{ (m}^3\text{ha}^{-1}\text{)} + 1980 ACS_j$$

Propagation of Uncertainty Associated with *Chave et al. (2014)* Allometric Models

We accounted for uncertainty around the allometric equations used to estimate tree height and aboveground biomass (AGB) by downloading the tree harvest dataset used to build these allometric models (http://chave.ups-tlse.fr/pantropical_allometry.htm). We directly include these dataset to estimate the model parameters for AGBest [Eq. 4] and heightest [Eq. 6a] based on the best-fit pantropical models presented by Chave et al. (2014). This method directly propagates the uncertainty associated with the parameters presented for these allometric models into our estimates for height and AGB for our Suriname tree census data, that results in 1350 posterior predictions of AGB for each tree in our dataset. We have uploaded our r code on an open access repository (<https://github.com/aroopsind/Quantifying-uncertainty-about-forest-recovery-32-years-after-selective-logging-in-Suriname.git>).

APPENDIX B
SUPPLEMENTARY DETAILS: MANAGING TROPICAL FORESTS FOR TIMBER AND
CARBON: INTENSITY THRESHOLDS WITH REDUCED-IMPACT LOGGING AND
LIBERATION THINNING

Supporting Text, Figures and Tables for the Main Text

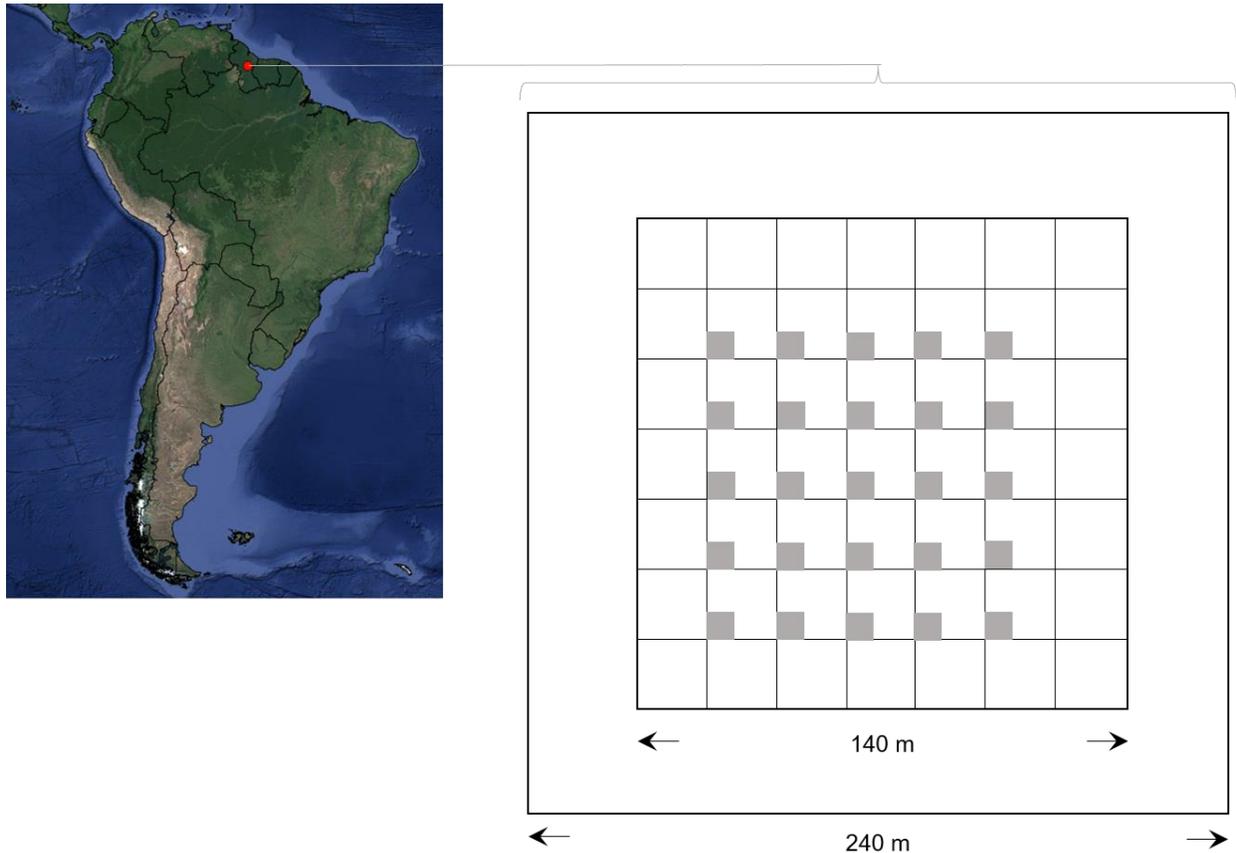


Figure B-1. Location of the Pibiri research site and plot layout. Pibiri is indicated by a red dot on the South American map. Logging treatments were applied to 240 x 240 m (5.76 ha) harvest units, with 140 x 140 m (1.96 ha) permanent sample plots established in the center of each for long-term monitoring of growth, mortality, and recruitment of trees with DBH \geq 20 cm. Shaded areas are 10 x 10 m nested plots (0.25 ha) used to monitor trees with 10-20 cm DBH.

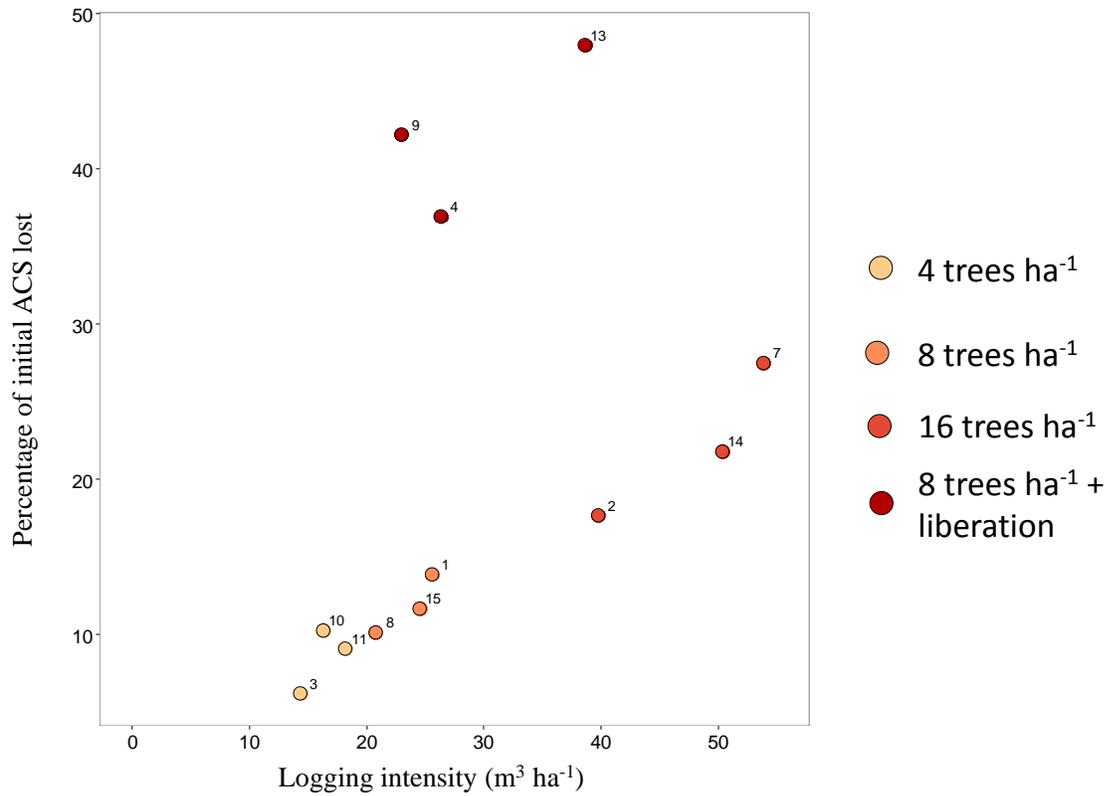


Figure B-2. Percentage of initial aboveground carbon stocks (ACS), estimated in 1993, that were lost as a result of logging mortality (trees harvested plus trees killed by felling and skidding) based on the 1995 assessment except for the logged and liberated plots, which were assessed in 1996. Plot numbers from Table 3-1.

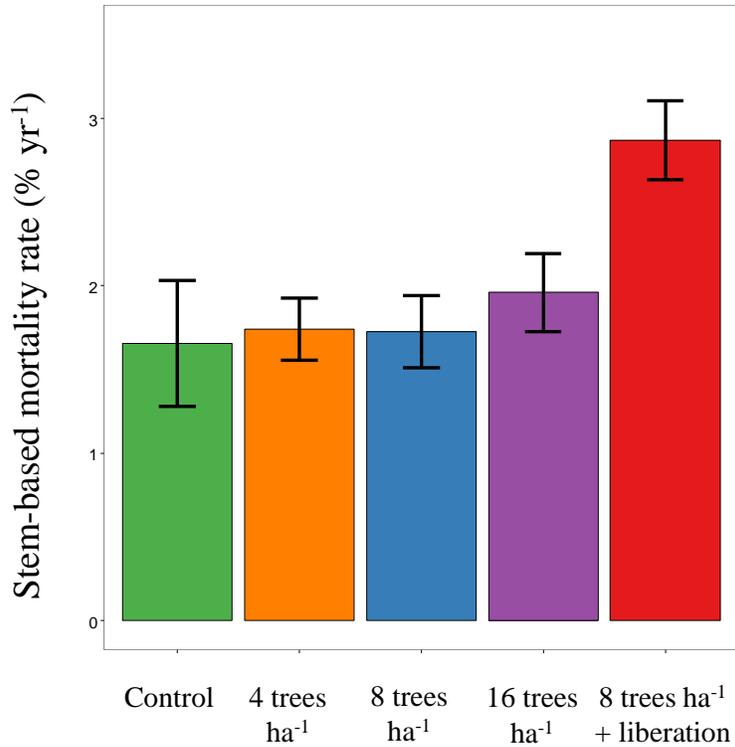


Figure B-3. Stem mortality rates (% yr⁻¹) by treatment at the end of 20 years post logging and 17 years post liberation. Stem mortality rates are calculated based on an exponential mortality coefficient: $mortality = \frac{\ln(N_0) - \ln(N_0 - N_D)}{t} * 100$; Sheil & May (1996). N_0 is the number of stems at the first census (pre-logging), N_D is the number of stems that died in the interval, and t is the census interval length (years).

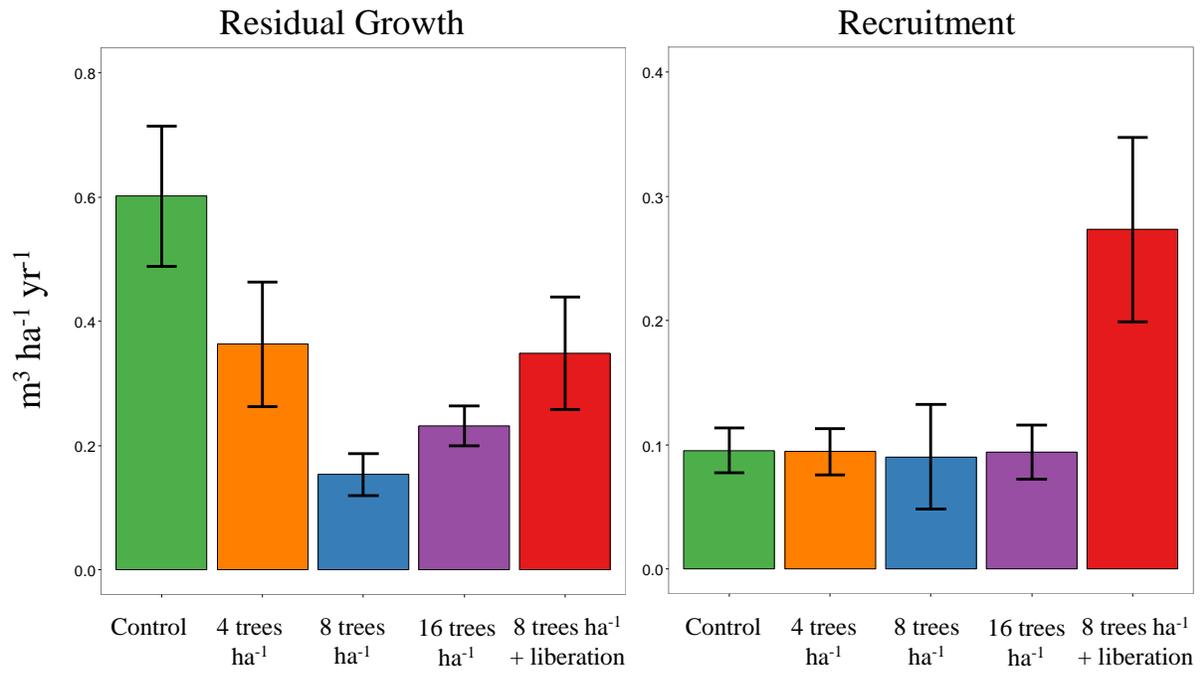


Figure B-4. Gains in timber stocks from residual tree growth and recruitment of commercial trees into their minimum species specific size classes for harvesting.

Table B-1. Commercial timber species and the volumetric equations used to assess recovery of timber stocks.

Scientific Name	Botanical Family	Vernacular name	Wood density (g cm ⁻³)	Minimum cutting diameter (cm)	Volume equations
<i>Anacardium giganteum</i>	Anacardiaceae	Ubudi	0.45	45	
<i>Aspidosperma album</i>	Apocynaceae	Shibadan, smooth leaf	0.78	60	
<i>Aspidosperma desmanthum</i>	Apocynaceae	Shibadan, boat leaf	0.61	60	
<i>Parahancornia fasciculata</i>	Apocynaceae	Dukali	0.48	45	
<i>Jacaranda copaia</i>	Bignoniaceae	Futui	0.35	45	0.55985 +
<i>Protium decandrum</i>	Burseraceae	Kurokai	0.52	45	0.0000123 * D ³
<i>Trattinnickia demerarae</i>	Burseraceae	Ulu, rough skin	0.40	45	(>20 DBH)
<i>Trattinnickia rhoifolia</i>	Burseraceae	Ulu, smooth skin	0.45	45	
<i>Goupia glabra</i>	Celastraceae	Kabukalli	0.72	45	
<i>Clathrotropis brachypetala</i>	Fabaceae	Aromata	0.81	45	
<i>Diploctropis purpurea</i>	Fabaceae	Tatabu	0.78	60	
<i>Eperua falcata</i>	Fabaceae	Wallaba, soft	0.74	45	0.14588 + 0.0000129 * D ³ (>30 cm DBH)
<i>Hymenaea courbaril</i>	Fabaceae	Locust	0.77	70	0.55985 + 0.0000123 * D ³ (>20 DBH)
<i>Mora excelsa</i>	Fabaceae	Mora	0.81	45	- 6.75364 + 0.0042053 D ² - 0.0000227 * D ³ (>45 cm DBH)
<i>Mora gonggrijpii</i>	Fabaceae	Morabukea	0.82	45	0.55985 +
<i>Peltogyne venosa</i>	Fabaceae	Purpleheart	0.72	70	0.0000123 * D ³
<i>Swartzia leiocalycina</i>	Fabaceae	Wamara	0.97	45	(>20 DBH)
<i>Aniba hypoglauca</i>	Lauraceae	silverballi, yellow	0.53	45	
<i>Chlorocardium rodiei</i>	Lauraceae	Greenheart	0.86	45	- 4.4496 + 0.13441 * D (>45 cm DBH)

Table B-1. Continued

<i>Licaria cannella</i>	Lauraceae	silverballi, brown	0.94	45	
<i>Ocotea canaliculata</i>	Lauraceae	Silverballi, sawari skin	0.46	45	
<i>Ocotea floribunda</i>	Lauraceae	Silverballi, pea's leaf	0.40	45	
<i>Ocotea puberula</i>	Lauraceae	Silverballi, kereti	0.46	45	
<i>Couratari guianensis</i>	Lecythidaceae	Wadara	0.52	45	
<i>Lecythis zabucajo</i>	Lecythidaceae	Monkey pot	0.86	45	
<i>Catostemma commune</i>	Malvaceae	Baromalli, swamp	0.51	45	
<i>Catostemma fragrans</i>	Malvaceae	Baromalli, sand	0.56	45	$0.55985 + 0.0000123 * D^3$
<i>Sterculia pruriens</i>	Malvaceae	Maho, smooth leaf	0.47	45	(>20 DBH)
<i>Sterculia rugosa</i>	Malvaceae	Maho, rough leaf	0.47	45	
<i>Carapa guianensis</i>	Meliaceae	Crabwood	0.53	45	
<i>Brosimum guianense</i>	Moraceae	Tibokushi	0.91	45	
<i>Virola sebifera</i>	Myristicaceae	Dalli	0.47	45	
<i>Chrysophyllum pomiferum</i>	Sapotaceae	Paripiballi	0.75	45	
<i>Chrysophyllum sanguinolentum</i>	Sapotaceae	Barataballi	0.65	45	
<i>Pouteria speciosa</i>	Sapotaceae	Suya	0.61	45	
<i>Simarouba amara</i>	Simaroubaceae	Simarupa	0.37	45	
<i>Ruizterania albiflora</i>	Vochysiaceae	Muneridan	0.60	45	$0.55985 + 0.0000123 * D^3$
<i>Vochysia surinamensis</i>	Vochysiaceae	Iteballi	0.60	45	(>20 DBH)

Recovery of Basal Area ($m^2 ha^{-1}$) and Stem Density

We report on the changes over time in basal area, and stem density for trees \geq 10 cm across diameter classes for the fifteen 1.96-ha permanent sample plots. To quantify logging-related reductions in these forest attributes, we subtract plot level values observed 3 years (1997) after logging, which captures the majority of logging-induced mortality losses (Shenkin *et al.* 2015, Mazzei *et al.* 2010), from their values pre-logging (1993). To quantify recovery, we compare the pre-logged forest attributes to the last census conducted in 2013, 20 years post-logging, and 17 years post-liberation. We

also report on changes in basal area-weighted average wood densities across plots and diameter classes (Table 1).

Average total basal area of trees ≥ 10 cm DBH across all 15 plots prior to logging in 1993 was $27.0 \text{ m}^2 \text{ ha}^{-1}$ (SE ± 0.5). Over the 20-year study period the control plots increased their basal area by an average of 10% ($28.8 \text{ m}^2 \text{ ha}^{-1}$; SE ± 1.5). Plots subjected to low and medium logging intensities had recovered their pre-logging basal areas within 20 years, to 27.4 and $28.0 \text{ m}^2 \text{ ha}^{-1}$, respectively (Table 1; Figure 1). Plots subject to the highest logging intensity, which resulted in plot-level basal area losses that averaged 20% ($5 \text{ m}^2 \text{ ha}^{-1}$), had recovered to $24.8 \text{ m}^2 \text{ ha}^{-1}$ (SE ± 0.9) in 2013, 5% less than observed values in 1993. Plots that were logged and then treated with liberation thinning in 1996, showed the largest reduction in basal area (36%; $9.8 \text{ m}^2 \text{ ha}^{-1}$), and recovered in 2013 to a basal area of $23.4 \text{ m}^2 \text{ ha}^{-1}$ (SE ± 0.4).

Average density of trees ≥ 10 cm DBH in unlogged forests was $476 \text{ stems ha}^{-1}$ (SE ± 19) in 1993. Stem density in the control plots increased by 4% between 1993 ($415 \text{ stems ha}^{-1}$; SE ± 38) and 2013 ($431 \text{ stems ha}^{-1}$; SE ± 23). The low and medium logging intensity plots had stem densities of 456 and $510 \text{ stems ha}^{-1}$ in 2013, which are, respectively, 9% and 5% below their pre-logging values. In contrast, the highest intensity logged plots increased in stem density by 9% (to $489 \text{ stems ha}^{-1}$) and the liberated plots by 4% (to $505 \text{ stems ha}^{-1}$) in 2013 compared to their initial values. Mean wood density weighted by plot-level basal area was 0.76 g cm^{-3} in 1993 across all unlogged plots, and remained unchanged in the control and logged plots over the 20-year observation period.

Taper Correction Model

Tree diameter measurements recorded above the standard height of 1.3 m (diameter at breast height - DBH) to avoid buttresses and other trunk irregularities cause a systematic downward bias in plot-level biomass estimates and biomass change especially if the point of measurement moves up the tree trunk over repeated censuses (Shield 1995). The downward bias arises as allometric equations generally reference diameters measured at 1.3 m above-ground to estimate tree biomass (Chave *et al.* 2005). Additionally, if biomass change is assessed over time and the measurement height changes, a tree diameter measured at a point higher than the previous census will have a smaller diameter measurement compared to the same tree measured at the initial point of measurement because of natural taper in tree trunks.

Given that >50% of the tree diameter measurements in this study were made above 1.3 m (Figure B-5), such downward bias could be substantial. To correct for the bias associated with measurement heights >1.3 m and changing points of measurement, we employed a taper correction model developed by Metcalf *et al.* (2009) and evaluated by Cushman *et al.* (2014). We used a local dataset of diameter measurements at different heights on the trunks of 150 trees representing 23 genera, to parameterize our taper model:

$$d = DBH * e^{-b(h-1.3)}$$

where d is diameter (cm) at height h ; DBH is diameter (cm) at 1.3 m above the ground; h is the height above-ground for the diameter measurement d ; with b as a free parameter. Our taper model varied with measured diameter (tree size), height of measurement, and genera (random effects) with our model implemented in a Bayesian

framework. We used the mean value by genus to apply the taper correction to our dataset to estimate diameters at 1.3 m and the mean value across all genera for those genera not present in our taper dataset (Table 3-1).

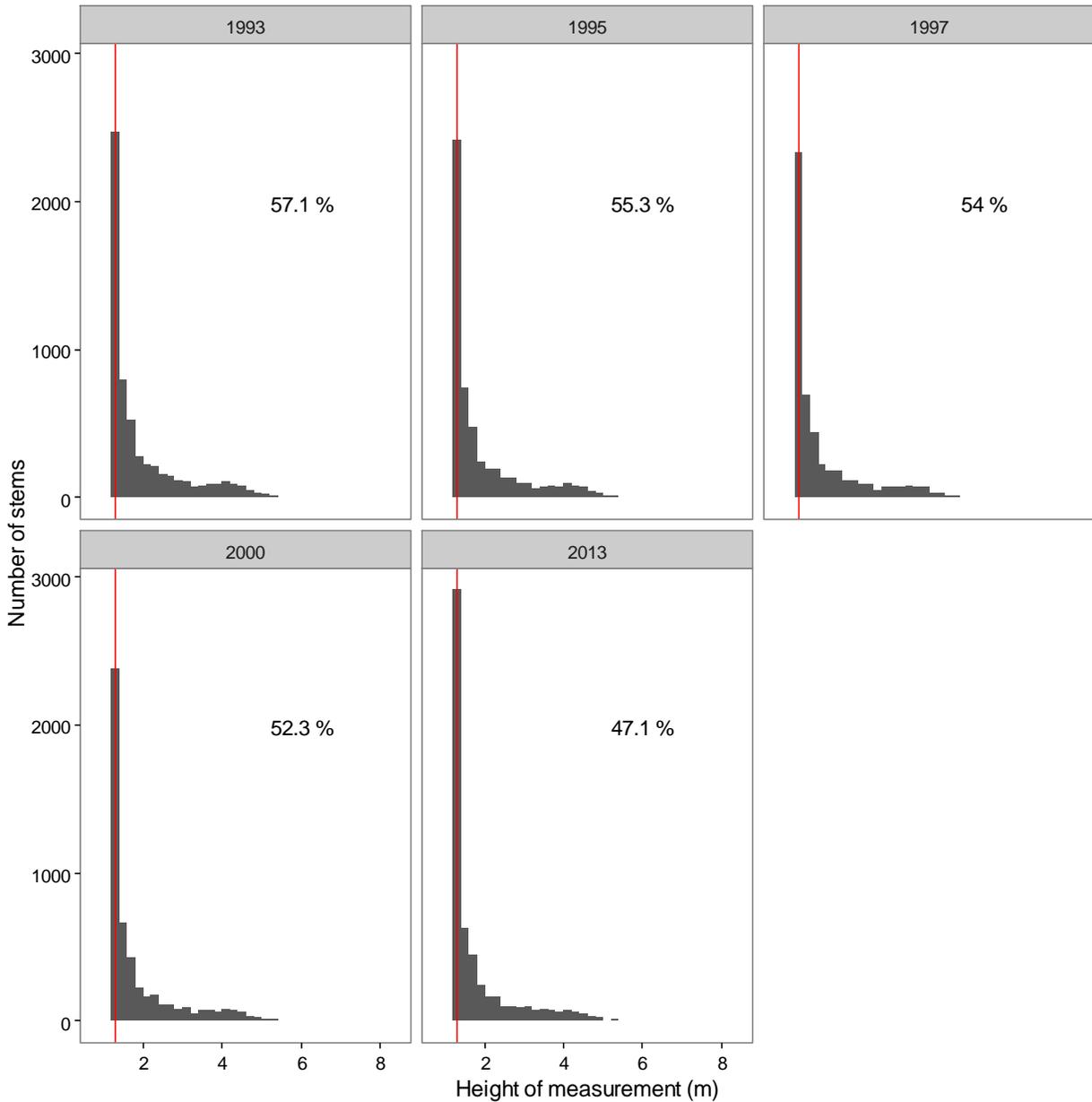


Figure B-5. Distribution of heights (m) aboveground at which stem diameter measurements (cm) were recorded for each census. Vertical red line indicate the 1.3 m reference height used to develop allometric equations to estimate biomass. Percentages indicate stems for which diameters were not measured at 1.3 m.

Table B-2. Estimates of rate parameter by genus and the overall mean value applied to estimate diameters at a reference height of 1.3 m.

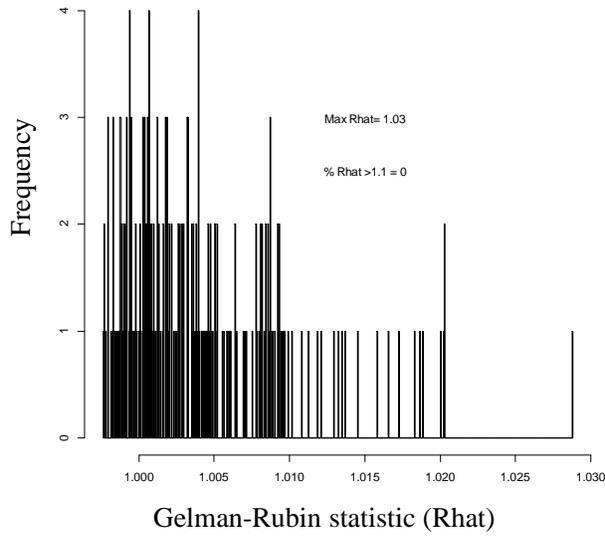
Genus	Rate parameter
<i>Aniba</i>	0.023487151
<i>Aspidosperma</i>	0.025057735
<i>Carapa</i>	0.024412216
<i>Chlorocardium</i>	0.024391744
<i>Clathrotropis</i>	0.021675118
<i>Dicorynia</i>	0.025106525
<i>Eperua</i>	0.024970046
<i>Eschweilera</i>	0.026747864
<i>Goupia</i>	0.026568666
<i>Humiria</i>	0.029561457
<i>Hymenaea</i>	0.016490418
<i>Licaria</i>	0.024488084
<i>Manilkara</i>	0.025585501
<i>Mora</i>	0.015258628
<i>Ocotea</i>	0.026124428
<i>Ormosia</i>	0.022554006
<i>Peltogyne</i>	0.014138812
<i>Pouteria</i>	0.020215935
<i>Simarouba</i>	0.026632951
<i>Swartzia</i>	0.022177786
<i>Symphonia</i>	0.02844094
<i>Tabebuia</i>	0.024277345
<i>Talisia</i>	0.01781887
Mean (all genera)	0.02329429

Model Evaluation and Goodness-of-Fit

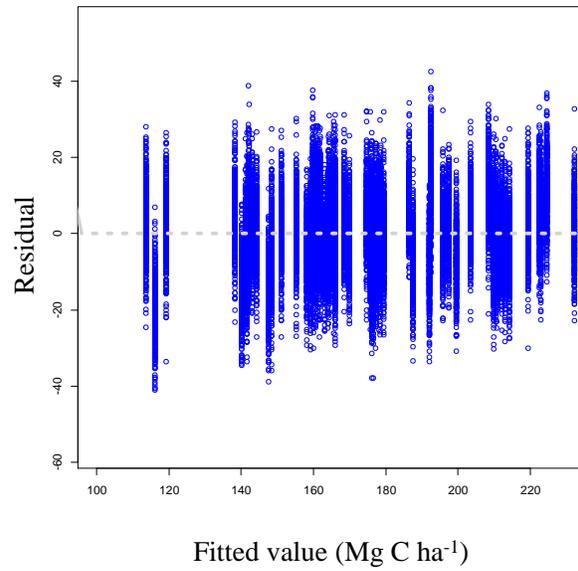
Table B-3. Model comparison of piecewise versus linear formulations; we report the coefficients of determination (R^2) and the residual mean square errors (RSME).

Model structure		ACS	Merchantable timber stocks
piecewise	RSME	10.29 (95% CI, 8.44-12.56)	10.84 (95% CI, 8.74 - 13.37)
	R^2	0.87 (95% CI, 0.81 - 0.91)	0.58 (95% CI, 0.37 - 0.73)
linear	RSME	12.69 (95% CI, 9.9 - 16.4)	12.69 (95% CI, 9.85 - 16.42)
	R^2	0.93 (95% CI, 0.90 - 0.96)	0.46 (95% CI, 0.13 - 0.69)

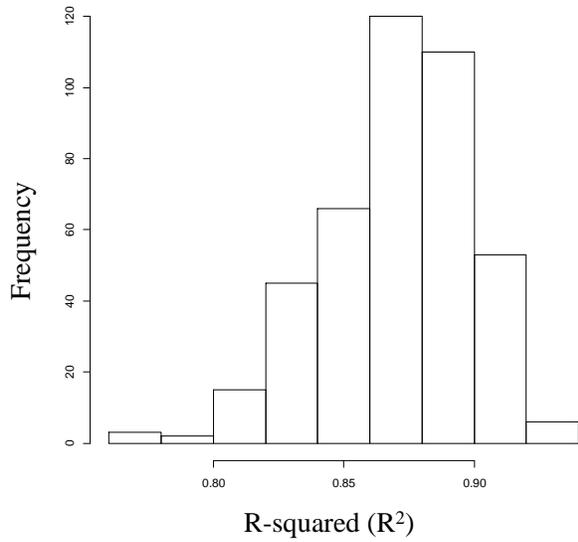
Model Convergence



Residuals vs. Fitted



R-squared (R²) statistic



Mean squared error (MSE)

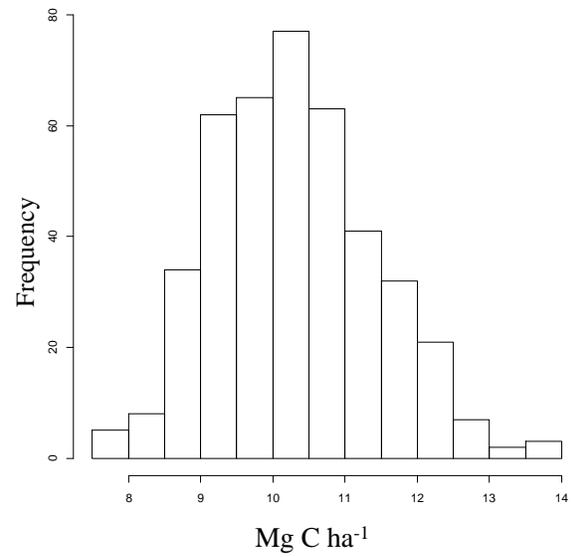


Figure B-6. Piecewise model assessment for aboveground carbon stock recovery.

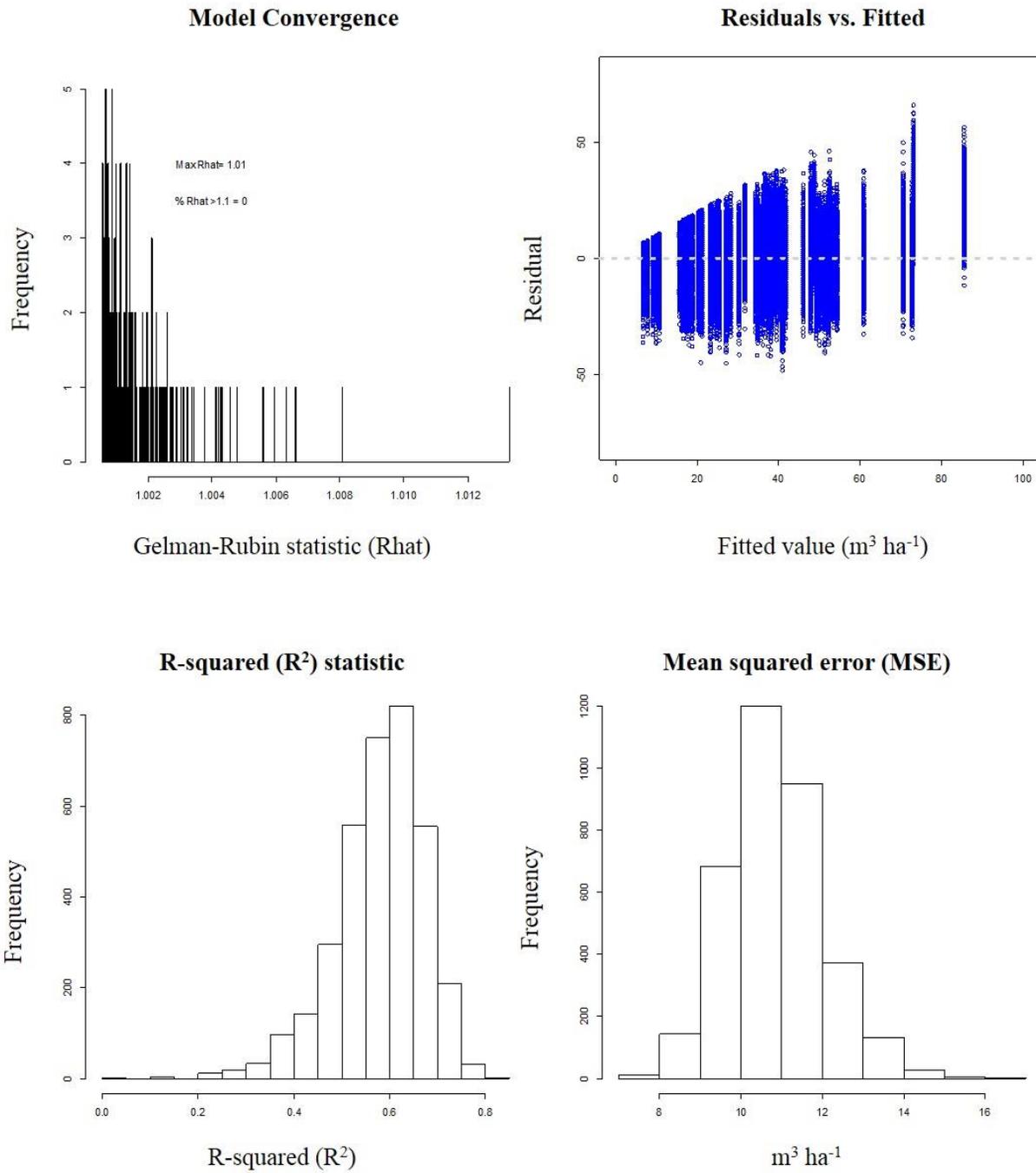


Figure B-7. Piecewise model assessment for timber stock recovery.

APPENDIX C
SUPPLEMENTARY DETAILS: LOGGING AND HUNTING IMPACTS ON THE
PERSISTENCE OF NEOTROPICAL ANIMALS

Table C-1. Terrestrial species killed by hunters over a 21 month period (total number of unique kills=210).

Scientific name	Common name	Feeding guild (active period)	Size (kg)	Density estimates (individuals/km ²)	IUCN Status (2016)	Mean number of kills per month (SE)	Percentage of total kills*
<i>Crax alector</i>	Black Currasow	Frugivore (diurnal)	2.4 - 3.7	6.9	Vulnerable	0.24 (± 0.19)	2.4
<i>Cuniculus paca</i>	Spotted paca	Frugivore (nocturnal)	5.0 - 13.0	84.00 - 93.00	Least concern	2.24 (± 0.63)	22.4
<i>Chelondis sp.</i>	Yellow/red foot tortoise	Frugivore (diurnal)	4.0	5.68	Vulnerable	0.95 (± 0.25)	9.5
<i>Dasyprocta leporina</i>	Red-rumped Agouti	Frugivore (diurnal)	3.0 - 5.9	10.5	Least concern	2.38 (± 1.06)	23.8
<i>Dasyopus sp.</i>	Armadillo	Insectivore (nocturnal)	2.7 - 6.3	Unknown	Least concern	0.86 (± 0.28)	8.6
<i>Mazama americana</i>	Red-brocket Deer	Herbivore (nocturno-crepuscular)	24.0 - 48.0	0.10 - 0.30	Data deficient	0.14 (± 0.10)	1.4
<i>Mazama gouazoubira</i>	Grey-brocket Deer	Herbivore (nocturno-crepuscular)	11.0 - 18.0	0.35 - 1.00	Least concern	0.10 (± 0.10)	1.0
<i>Myoprocta acouchy</i>	Accouchi	Frugivore (diurnal)	1.1 - 1.5	64	Least concern	0.05 (± 0.05)	0.5
<i>Myrmecophaga tridactyla</i>	Giant Anteater	Insectivore (diurnal)	22.0 - 39.0	0.12 - 0.41	Vulnerable	0.05 (± 0.05)	0.5
<i>Pecari tajacu</i>	Collared Peccary	Frugivore (diurnal)	17.0 - 35.0	3.00 - 7.00	Least concern	1.33 (± 0.58)	13.3
<i>Priodontes maximus</i>	Giant Armadillo	Insectivore (nocturnal)	18.7 - 32.3	0.05 - 0.06	Vulnerable	0.05 (± 0.05)	0.5
<i>Tapirus terrestris</i>	Tapir	Herbivore (nocturno-crepuscular)	227.0 - 250.0	0.20 - 3.70	Vulnerable	0.29 (± 0.10)	2.9
<i>Tayassue pecari</i>	white-lipped peccary	Frugivore (diurnal)	25.0 - 45.0	7.58	Vulnerable	1.33 (± 0.98)	3.3

Ecological characteristics (diet, size and density) extracted from Emmons & Feer (1990) ; Percentage of kills do not sum to 100% because aquatic species (primarily river turtles; Podocnemis sp.) hunted are excluded from the analysis.

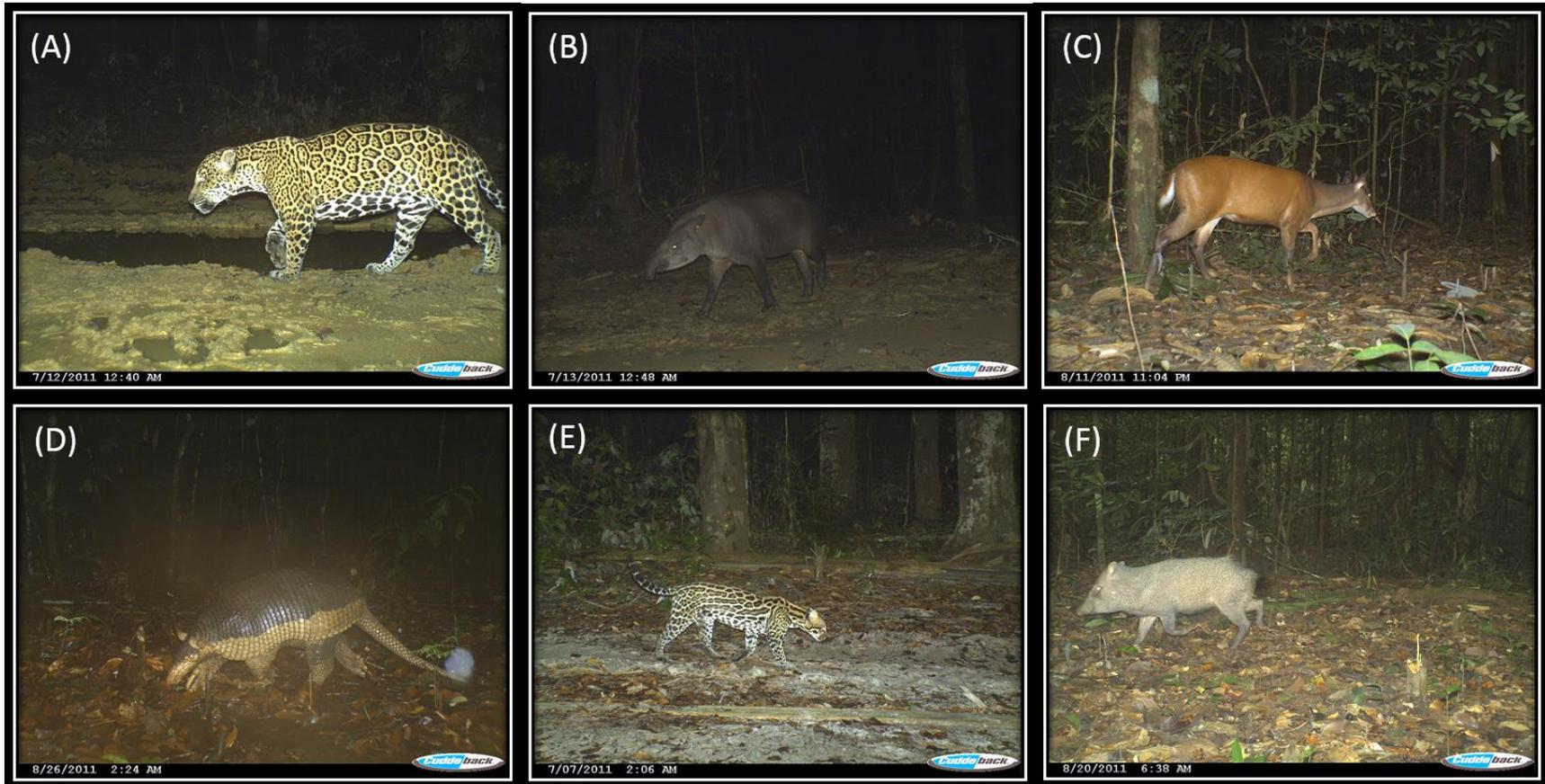


Figure C-1. Species captured in the logged forest (A) *Panthera onca* (jaguar), carnivore; (B) *Tapirus terrestris* (lowland tapir), the largest neotropical frugivore; (C) *Mazama americana* (red-brocket deer), browsing herbivore; (D) *Priodontes maximus* (giant armadillo), a rare and cryptic insectivore; (E) *Leopardus weidii* (ocelot), a meso-carnivore; (F) *Pecari tajacu*, (collared peccary). Tapirs, deer, armadillos, and peccaries experience substantial hunting pressure across the neotropics.

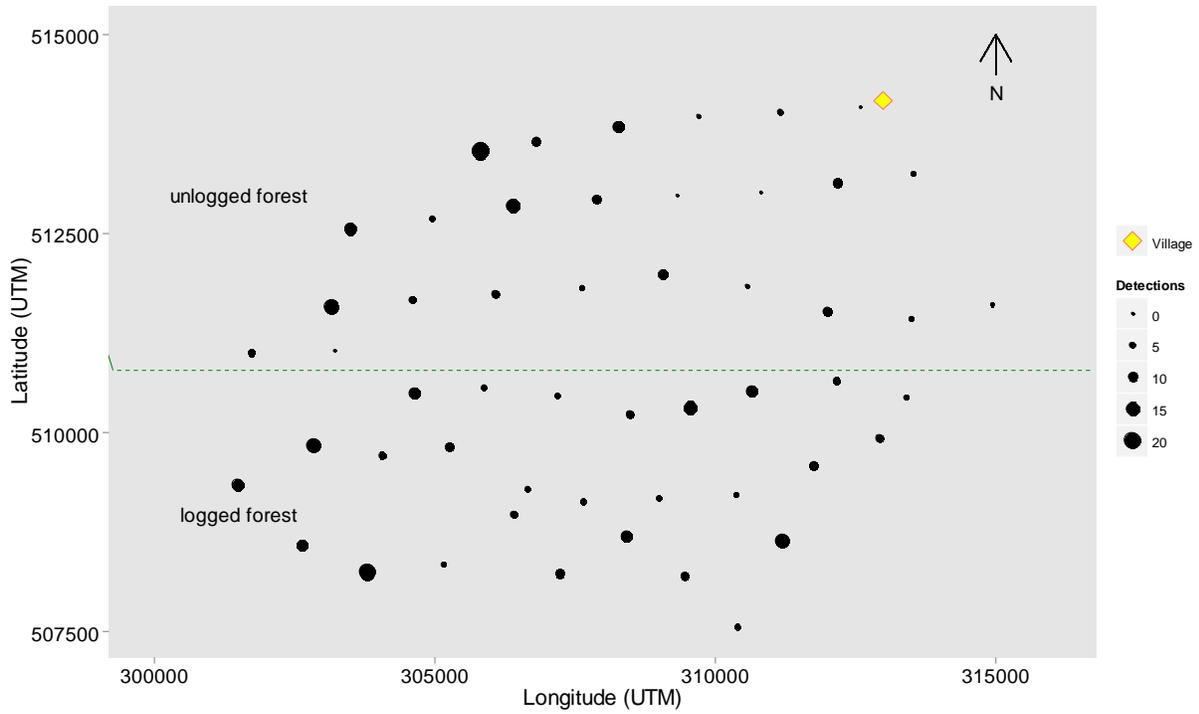


Figure C-2. Total number of independent animal detections pooled for all species (N=450) for 808 and 805 camera trap nights in June-August 2011 for logged and unlogged forest, respectively. The horizontal dashed green line indicates the boundary between unlogged and forests that was logged between 2007-2011.

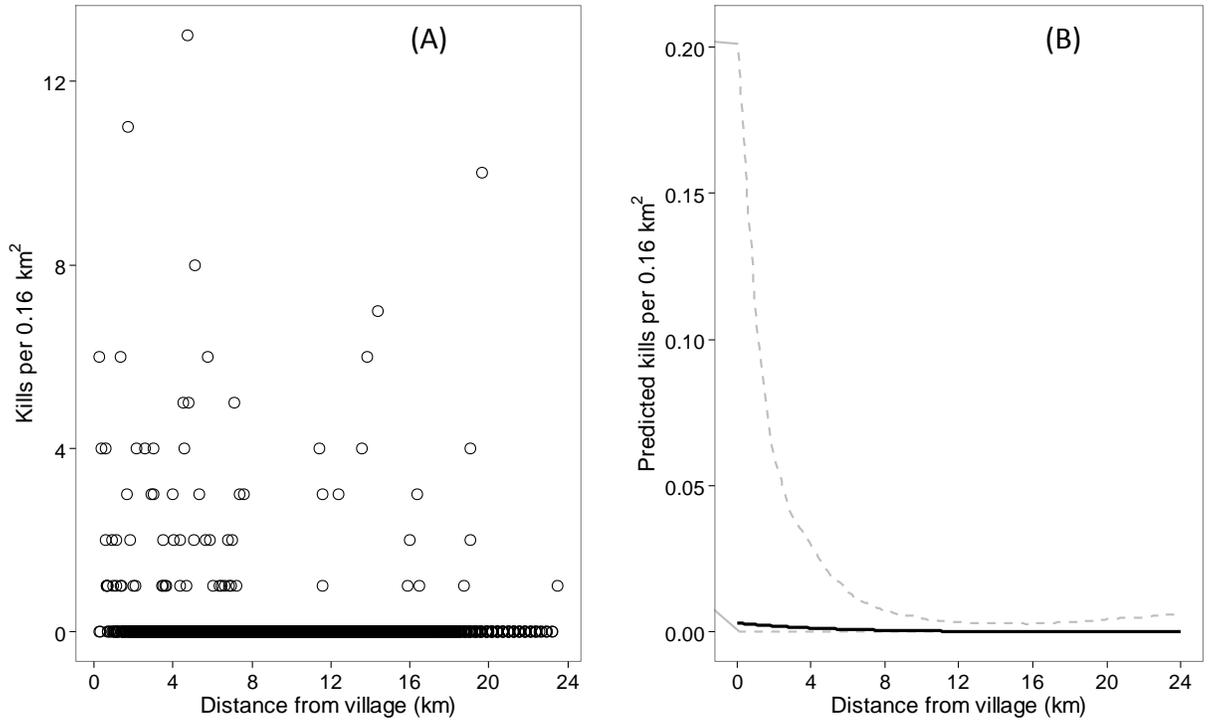


Figure C-3. Distance-from-village as the main predictor of hunting intensity. *Panel A:* number of kills recorded in the 0.16 km² grid cells. *Panel B:* Predicted hunting rate from the spatial hunting model with 95% credibility intervals (CI) – note the high variation close to the village that declines towards the mean rate of ~ 0.11 kills per 0.16 km² by 10 km from the village.

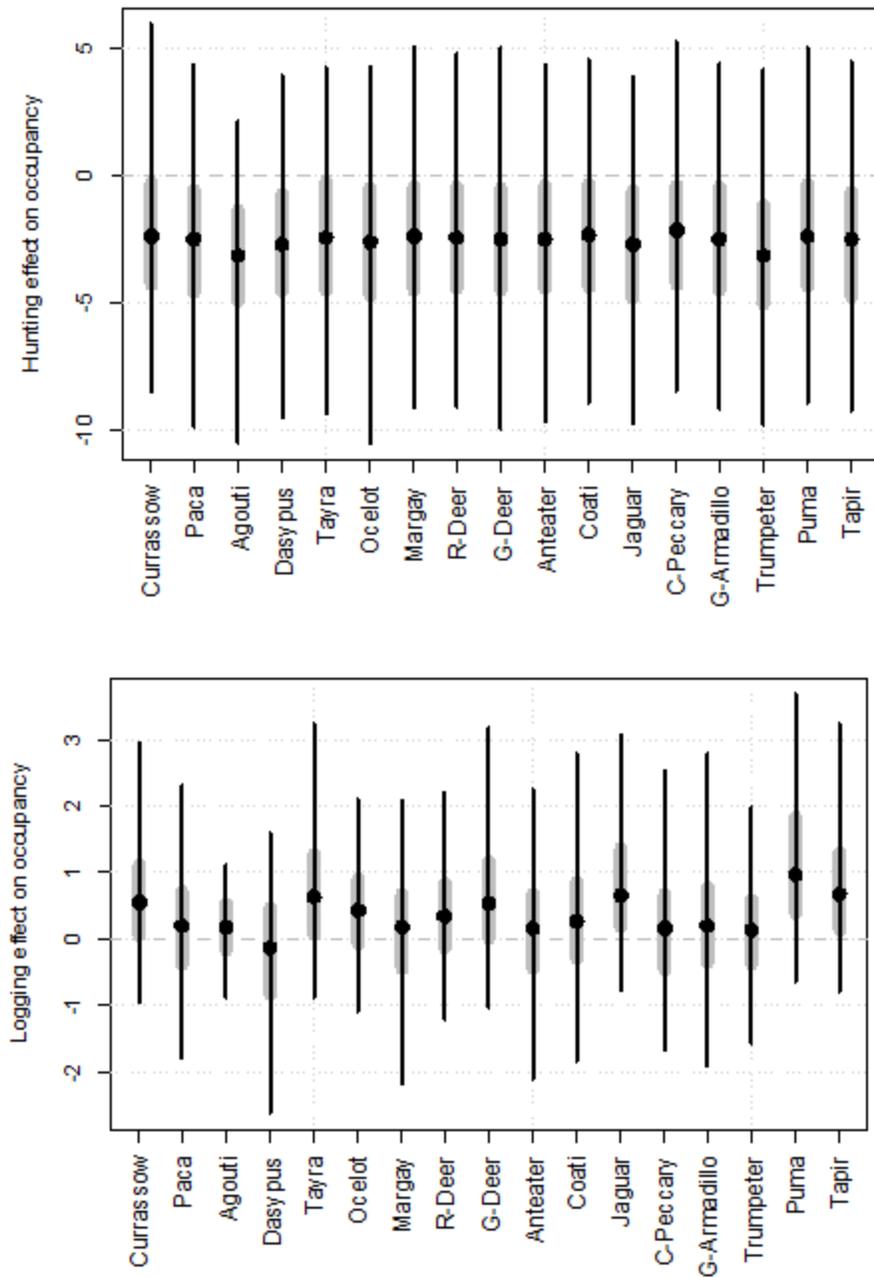


Figure C-4. Effects of logging and hunting on species-level occupancy. Thick gray lines indicate 50% CI, and thin black lines indicate 95% CI.

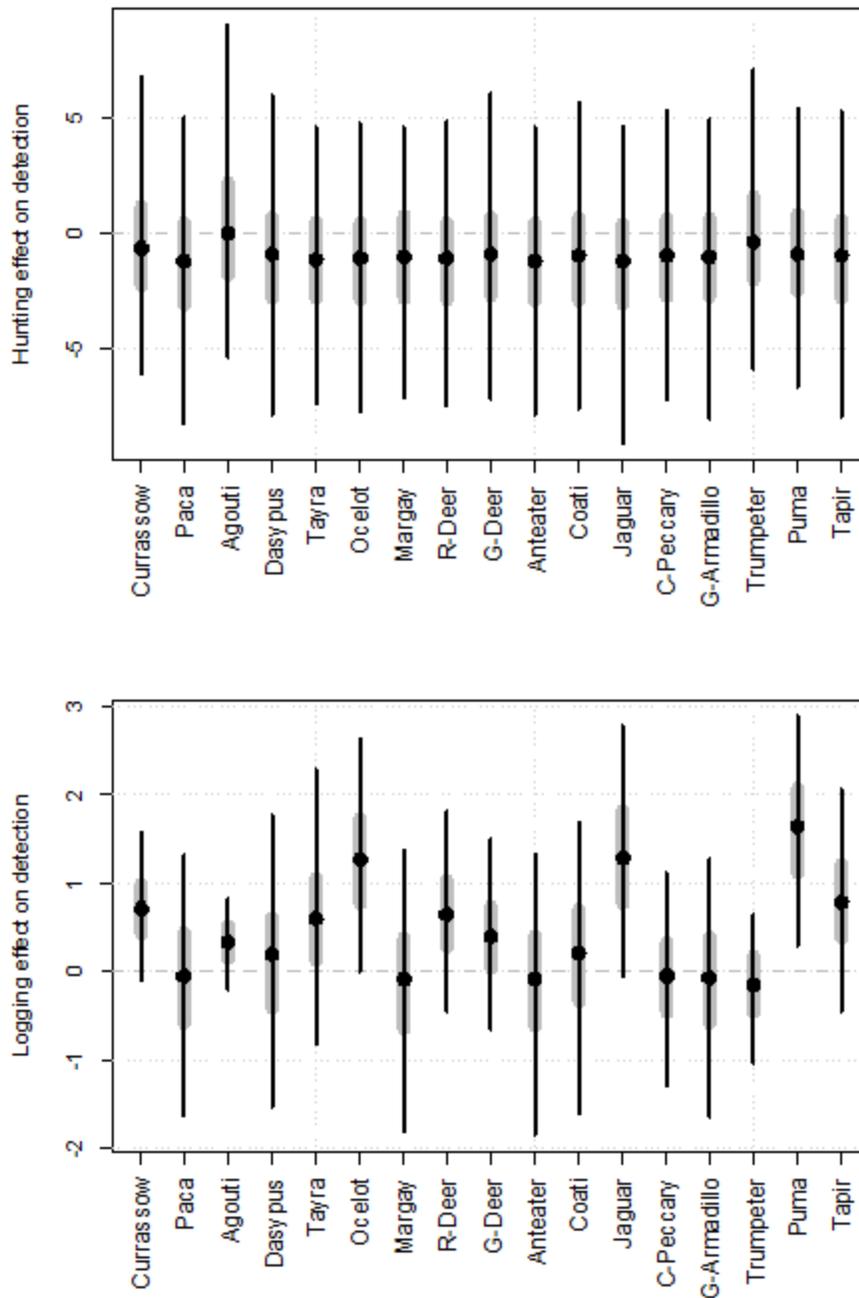


Figure C-5. Effects of logging and hunting on species-level detection for the seventeen observed species. Thick gray lines indicate 50% CI and thin black lines indicate 95% CI. Estimates with 95% CI that do not overlap with zero (horizontal dashed gray line) can be considered statistically significant.

Description of the Spatial vs. Non-Spatial Models

Similar to many other tropical forestry studies, our design includes blocks of camera traps and potentially risks violating assumptions of spatial independence between neighboring camera trap stations (Ramage et al. 2013). To test whether residual spatial autocorrelation, after the effects of hunting rate and logging were taken into account, affects our conclusions, we compared spatial and non-spatial models for occupancy for our wildlife species. Although hierarchical models for wildlife occupancy that account for imperfect detection and include spatial random effects are possible (Johnson et al. 2012), preliminary analyses suggested that our sample size was insufficient to parameterize these complex models. Consequently, to examine the effects of space, we explored models with a binary response variable to represent occupancy, coded as “1” if a species was ever detected at a camera trap site and “0” otherwise. We then fit models in INLA (Lindgren et al. 2011) for binary detection as a response variable, predicted hunting rate and logged vs. unlogged treatments as fixed effects and species as a random effect. We compared a model that included a spatial random effect with a model that included no spatial effects. If spatial autocorrelation had a significant effect on our model structure, we would expect that (1) effect of logging and hunting rate would differ in the spatial vs. non-spatial model and (2) the spatial model would fit the observed data better than the non-spatial model.

We found no evidence that accounting for spatial autocorrelation would change our primary conclusions with similar effect sizes and uncertainty for logging and hunting parameters in both models (Figure C-6). Additionally, the DIC and WAIC values for the spatial vs. non-spatial model were similar (Table C-2), suggesting that there is no clear

evidence in favor of one model over the other. For these reasons, we present the non-spatial hierarchical model for occupancy in the main text.

Table C-2. Deviance information criterion (DIC) and Wantanabe-Akaike information criterion (WAIC) for our spatial and non-spatial models. Model selection criteria reveal minimal difference between spatial and non-spatial models for wildlife occupancy at our study site.

<i>Model</i>	DIC	WAIC
Spatial	399.72	397.01
Non-spatial	402.97	397.49

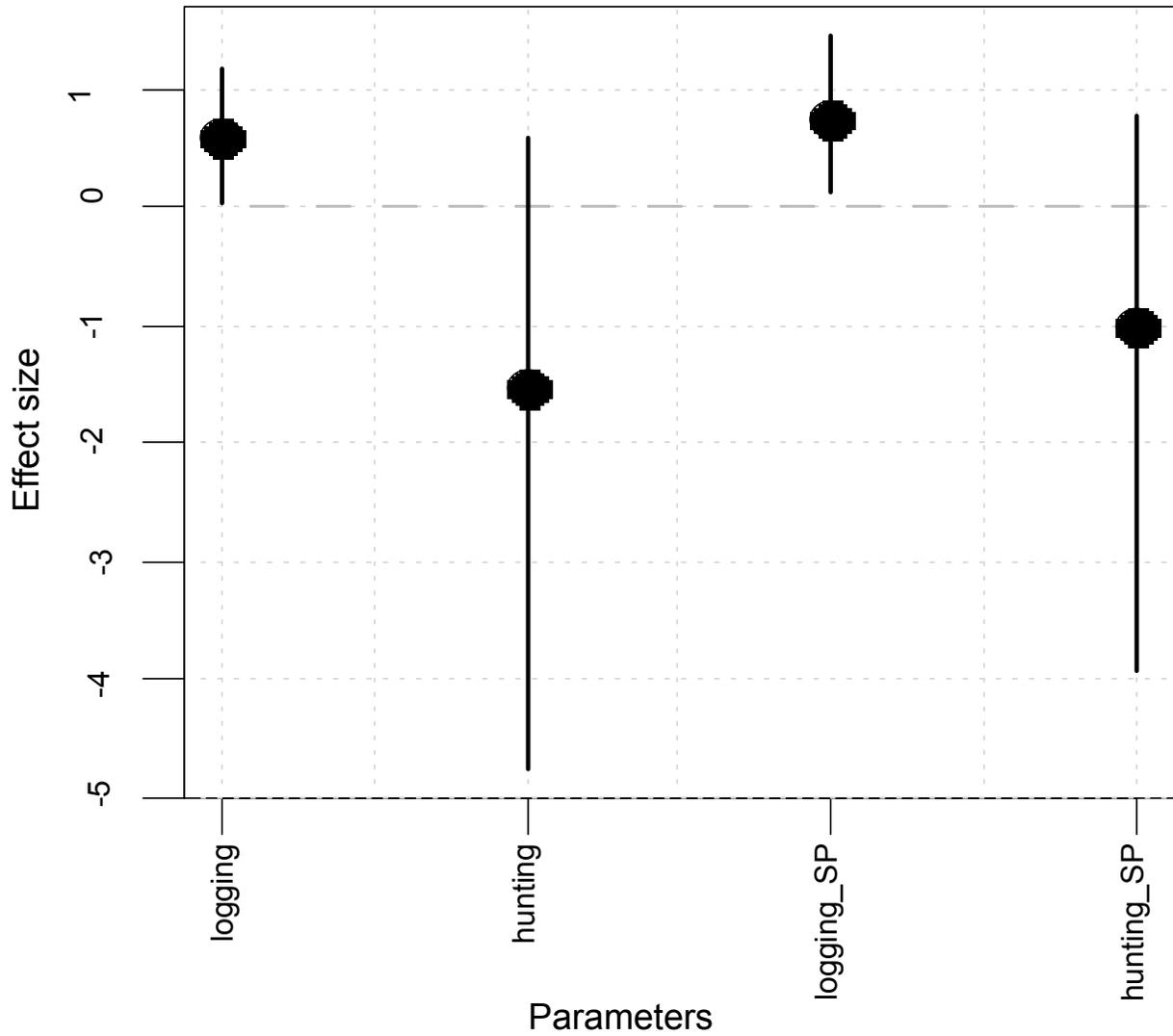


Figure C-6. Mean effect size and 95% credible interval (vertical lines) of effects on logging and hunting from the non-spatial model (left) compared to the spatial model (right, indicated by “SP”).

Model Results Using Distance-to-Village as a Metric of Hunting Rather than Hunt Rate

In the main text, we present a multi-species occupancy model that uses a model-derived hunt rate as a covariate for occupancy and detection. The hunt rate is derived from a spatial model that includes distance-to-village as a covariate, in addition to accounting for spatial patterns in number of kills per grid cell (see Figure 4-2 in main text). As an alternative, we fit an occupancy model that included distance-to-village as a metric of hunting, rather than model-derived hunt rate. Metrics of model selection (DIC and WAIC) revealed that the hunt rate provided better model fit than distance-to-village (Table C-3). Therefore, in the main text, we present the occupancy model with hunt rate as a covariate. Nevertheless, we found that our main results (lack of a negative impact of logging on occupancy rates; negative effect of hunting on occupancy rates) were nearly identical between the model with distance-to-village vs. the model with hunt rate. Note that a positive correlation between distance-to-village and wildlife occupancy (Figure C-1), means that camera traps at further distances from the village have higher wildlife occupancy. In other words, we would expect model-derived hunt rate and distance-to-village to have opposite effects. In this appendix, Figures C-7, C-8 and C-9 present results from the occupancy model with distance-to-village as a covariate and correspond to Figures 4-3, 4-4, and 4-6 in the main text.

Table C-3. Deviance information criterion (DIC) and Wantanabe-Akaike information criterion (WAIC) for models that include hunt rate (estimated from INLA analysis) verses distance-to-village.

<i>Model</i>	DIC	WAIC
Hunt rate as a covariate	1849.8	9508.6
Distance-to-village as a covariate	1944.5	9821.502

Model selection criteria reveal a better fit of the hierarchical occupancy model with hunt rate, derived from kill data, as a covariate for occupancy and detection compared to the occupancy model with the same structure but with distance-to-village as a covariate instead of hunt rate. Lower values for DIC and WAIC indicate better model fit.

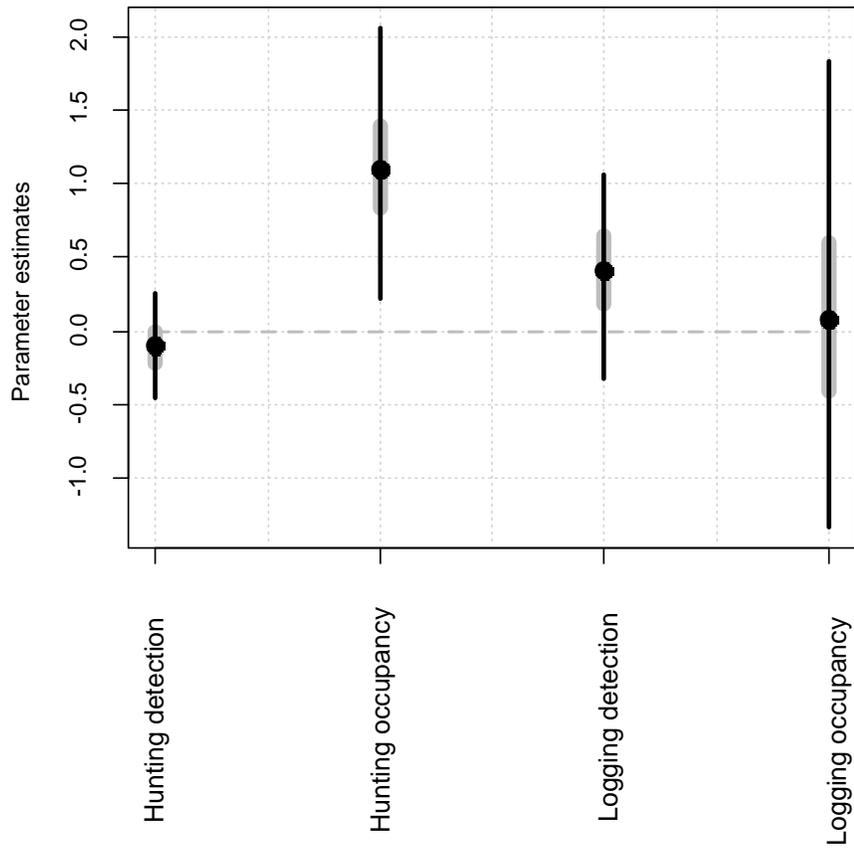


Figure C-7. Community-level effects of logging and hunting on occupancy and detection. Dark vertical lines represent 95% credible intervals and grey bands represent the 50% credible intervals. In contrast to the main text, the “hunting” covariate referred to in this figure is distance-to-village, rather than model-derived hunt rate.

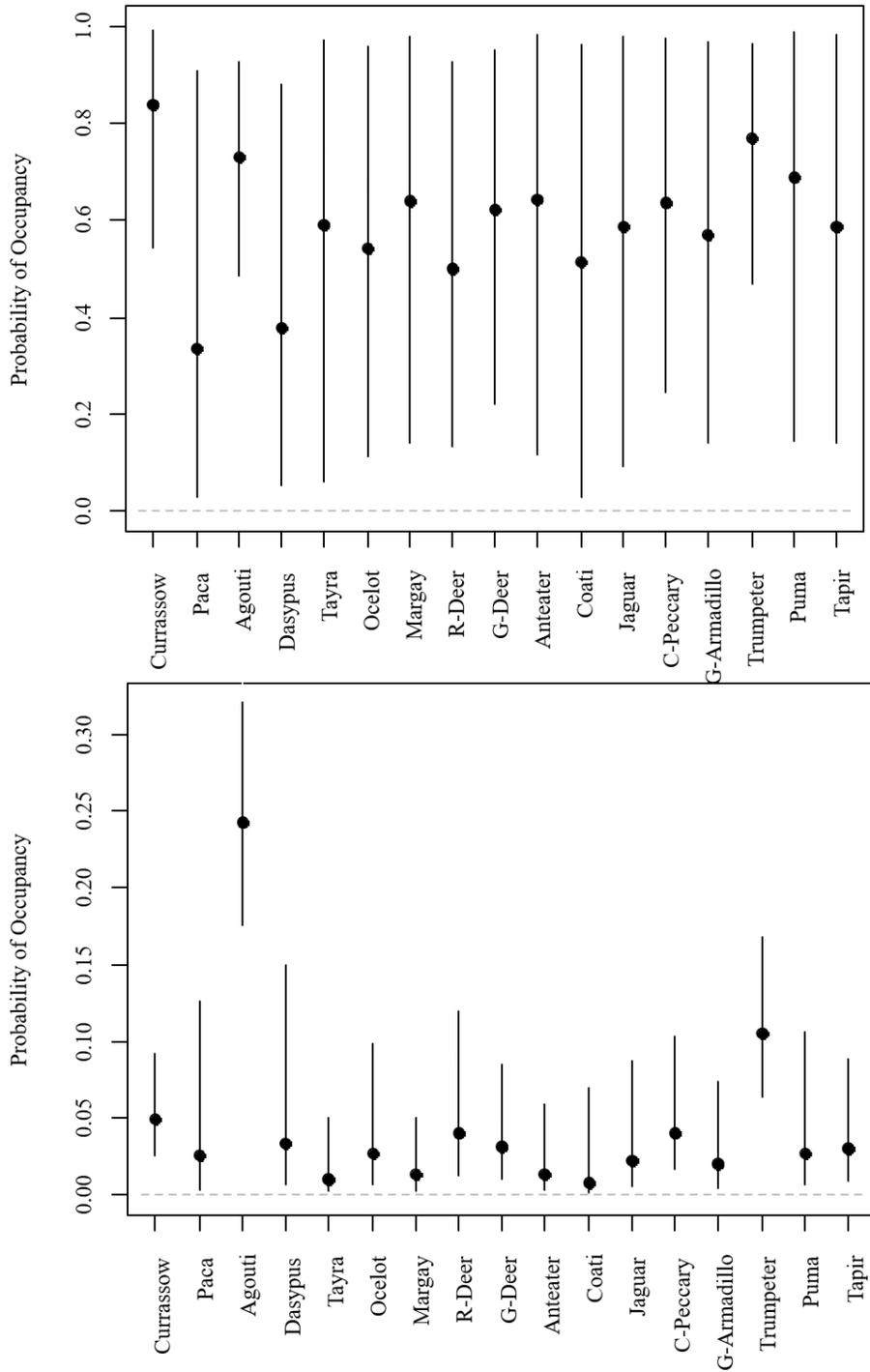


Figure C-8. Probability of detection (a) and occupancy (b) in unlogged forests for all species recorded in camera traps. Lines as in Fig C-5. Note that this figure presents results from an occupancy model with distance-to-village, rather than hunt rate, as a covariate.

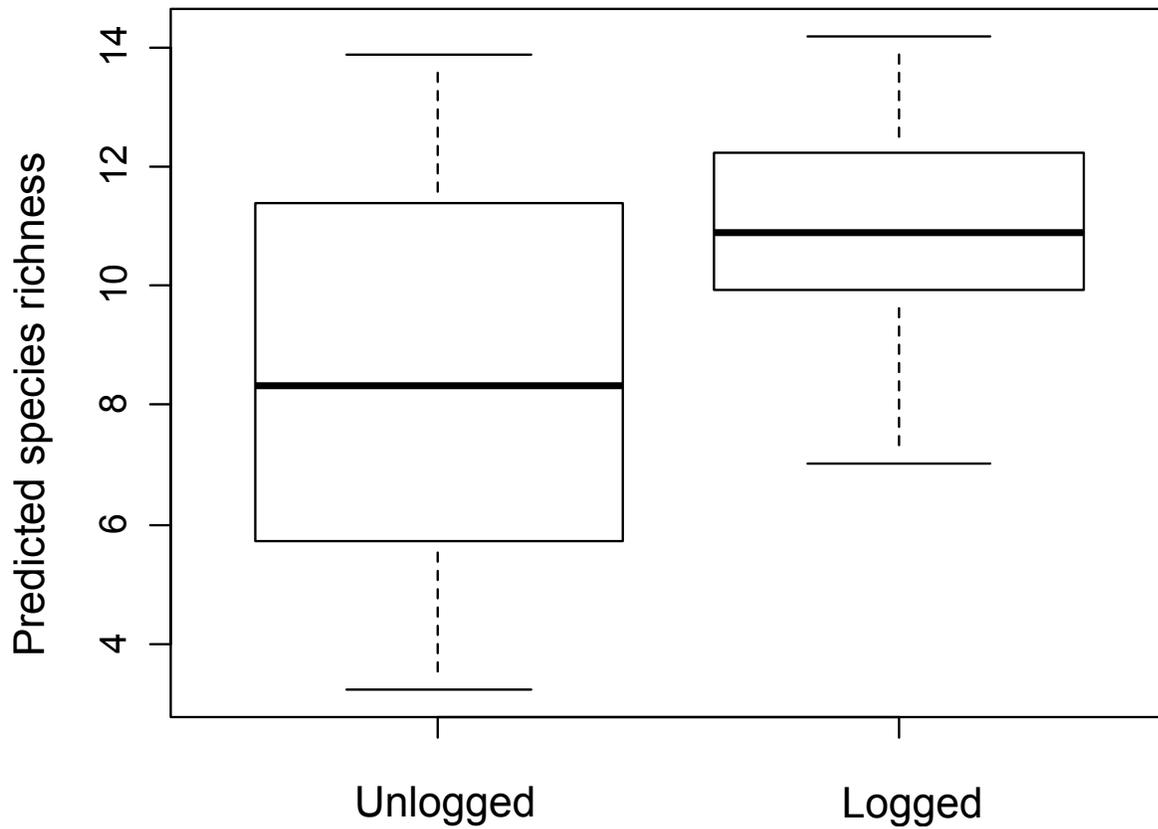


Figure C-9. Predicted species richness for sites in unlogged and logged forests. The upper and lower edges of the box plots represent first and third quartiles, the thick black line within each box represents the median value, 'whiskers' represent minimum and maximum observations within 1.5 times the upper and lower quartiles, and dots represents outliers.

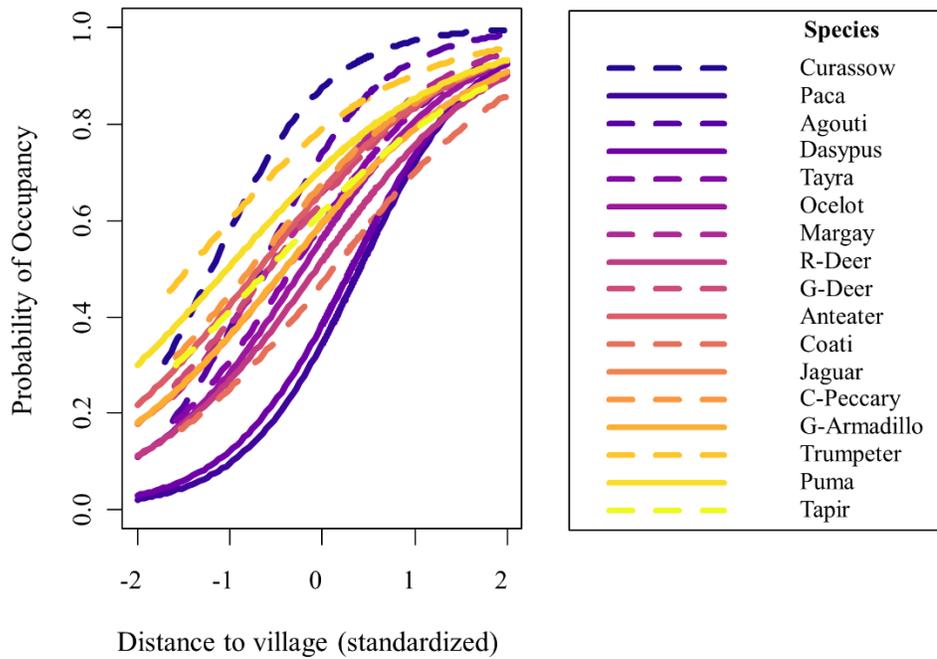


Figure C-10. Changes in probability of occupancy at the species level across the range of observed distances from the village (standardized by centering around the mean and dividing by two standard deviations). Each coloured line represents a single species

Hierarchical Community Occupancy Model – JAGS Code

We estimated Bayesian parameters using a Markov Chain Monte Carlo algorithm with the program JAGS (using the 'R2jags' R package) in R for 3 chains of length 1,500,000 after a burn-in of 500,000 and thinned by 2800. The burn-in discards samples from the analysis drawn prior to model convergence and thinning help reduce the correlation between neighboring iterations. Convergence was assessed by examining the Gelman-Rubin statistics for each parameter estimate (Gelman & Hill 2007). The model code, including the prior distributions is presented below.

JAGS model code:

```
model {  
  # Prior distributions on the community level occupancy and detection  
  covariates  
  
  mu.INTERCEPT ~ dbeta (1, 1)  
  LOGGED ~ dnorm (0, 0.001) #Fixed effect of logging on occupancy  
  HUNTING ~ dnorm (0, 0.001) # Fixed effect of hunting on occupancy  
  HUNT_det ~ dnorm (0,0.001) # Fixed effect of logging on detection  
  LOG_det ~ dnorm (0,0.001) # Fixed effect on detection  
  
  sigma.INTERCEPT ~ dunif(0, 10)  
  tau_INTERCEPT<-1/(sigma.INTERCEPT*sigma.INTERCEPT)  
  # Community level priors for species random effects  
  mu.SP~dbeta(1, 1)  
  sigma.SP~dunif(1, 10)  
  tau_SP <-1/(sigma.SP*sigma.SP)
```

```

    for (i in 1:Nspecies) {
      p.detect[i] ~ dnorm(logit(mu.SP),tau_SP)
      INTERCEPT[i] ~ dnorm(logit(mu.INTERCEPT),tau_INTERCEPT)
    }

# Estimating true occupancy
  For (i in 1:Nobs) {
    logit(psi[i]) <- INTERCEPT[Species[i]] + LOGGED * Site [i] + HUNTING *
HUNT_rate [i]
    z[i] ~ dbern(psi[i])
    # Detection probabilities
    logit(p[i])<- (p.detect [Species[i]] + HUNT_det * HUNT_rate[i] + LOG_det*
Site [i])
    Y[i] ~ dbinom(z[i] *p[i], J[i])
    Y.predict[i] ~ dbinom(p[i], J[i])  }
  }

```

Power Analysis

Our occupancy models suggest that the community-level effect of logging is slightly positive with an estimated median value of 0.37 (95% CI: -0.72 to 1.57). Thus, we did not find a significant, negative impact of logging on wildlife occupancy across our community of 17 species. To guard against a Type II error (accepting a null hypothesis that is actually false), we conducted a power analysis that asks, given our observed rates of occupancy, detection, and our sample size, what is the probability of estimating a positive effect of logging on occupancy when the true effect is negative?

To answer this question, we simulated 21,480 datasets using a hierarchical model for occupancy (z) with imperfect detection:

(C3 – 1)

$$\text{Logit}(\psi_{i,j,k,l}) = \alpha_{i,k} + \beta_{i,l}^{\text{logged}} \times \text{LOGGED}_j + \beta_{i,k}^{\text{Hunt}} \times \mu_j$$
$$z_{i,j,k,l} \sim \text{Bernoulli}(\psi_{i,j,k,l})$$

In Equation C3-1, the variables LOGGED and μ represent observed logging treatment and hunting rate, respectively, with one measurement for each of j sites. The intercept parameter (α) as well as the effect of hunting rate (β^{Hunt}) were drawn as k th value of the posterior distribution for these estimated parameters for site j and species i . In contrast, the effect of logging (β^{logged}) was drawn for species i from a normal distribution with a true value, l , of community logging effect (L^μ) that included twenty values in an evenly-spaced sequence from a strong negative effect (-5) to a weakly negative effect (-1e-05):

(C3 – 2)

$$\beta_{i,l}^{logged} \sim \text{Normal}(L_l^\mu, \sigma)$$

The reason for replicating different “true” values of the community-level logging effect, was to ensure that our occupancy model was capable of correctly estimating the sign of the community-level logging parameter even when this effect is fairly small.

(C3 – 3)

$$\text{Logit}(p_{i,j,k}) = \alpha_{i,k}^{detect} + \beta_{i,k}^{Hunt(detect)} \times \mu_j$$

$$Y_{i,j,k,l} \sim \text{Binomial}(\psi_{i,j,k,l} * p_{i,j,k}, S_j)$$

The detection-level of the model (Equation C3-3) included draws from the posterior distribution of the parameters for hunting effect ($\beta^{Hunt(detect)}$) and intercept (α^{detect}), but did not include a logging effect. This simplification reduced computation time and enabled us to focus on our key question of whether we could measure an effect of logging on occupancy.

We simulated datasets for each of 1,074 posterior draws and the twenty values of community logging effect, for a total of 21,480 datasets. These simulations propagate uncertainty from our statistical estimation of effects as well as sampling uncertainty. To analyse these simulated datasets, we used a generalized linear mixed model (GLMM) approach in a frequentist framework, where we recorded $Y_{i,j,k,l}$ as a binary variable, with 1 representing any number of detection ≥ 1 , and 0 representing site and species combinations where no animals were observed. Species was included as a random intercept in the GLMM and logging was included as a fixed effect. Analysis of the simulated data with the GLMM enabled us to rapidly estimate parameters for a large number of models. In Table C-4, we compare the parameter estimates from the GLMM

for the intercept and logged-effect parameter to the community-level parameters for the intercept and logged-effect from the hierarchical occupancy model:

Table C-4. Comparison of parameter estimates from the GLMM and the hierarchical occupancy model.

GLMM model			Hierarchical Occupancy model		
Parameter	Point estimate	95% CI	Parameter	Estimate (median of posterior distribution)	95% CI
Intercept	-2.03	-2.66 to -1.45	Community-level intercept	0.003	-1.01 to 1.02
Logging effect	0.75	0.39 to 1.12	Community-level logging effect	0.37	-0.72 to 1.57

As Table C-4 shows, although the intercept parameters were fairly different (as expected from the different model frameworks), the logging effect estimated by the two different models was qualitatively similar.

Using the GLMM described above, we estimated the logging-effect for all 21,480 datasets. We discarded models with convergence issues, leading to a total of 19,681 models. We found that the parameter estimates from the GLMM reasonably estimated the true parameters (Figure C-11), with a correlation of 57% between estimates and true values (Pearson’s product-moment correlation). The largest estimation errors occurred when the true value of logging effect was moderately to strongly negative (< -3), in which case, there was a chance of overestimating the magnitude of this effect.

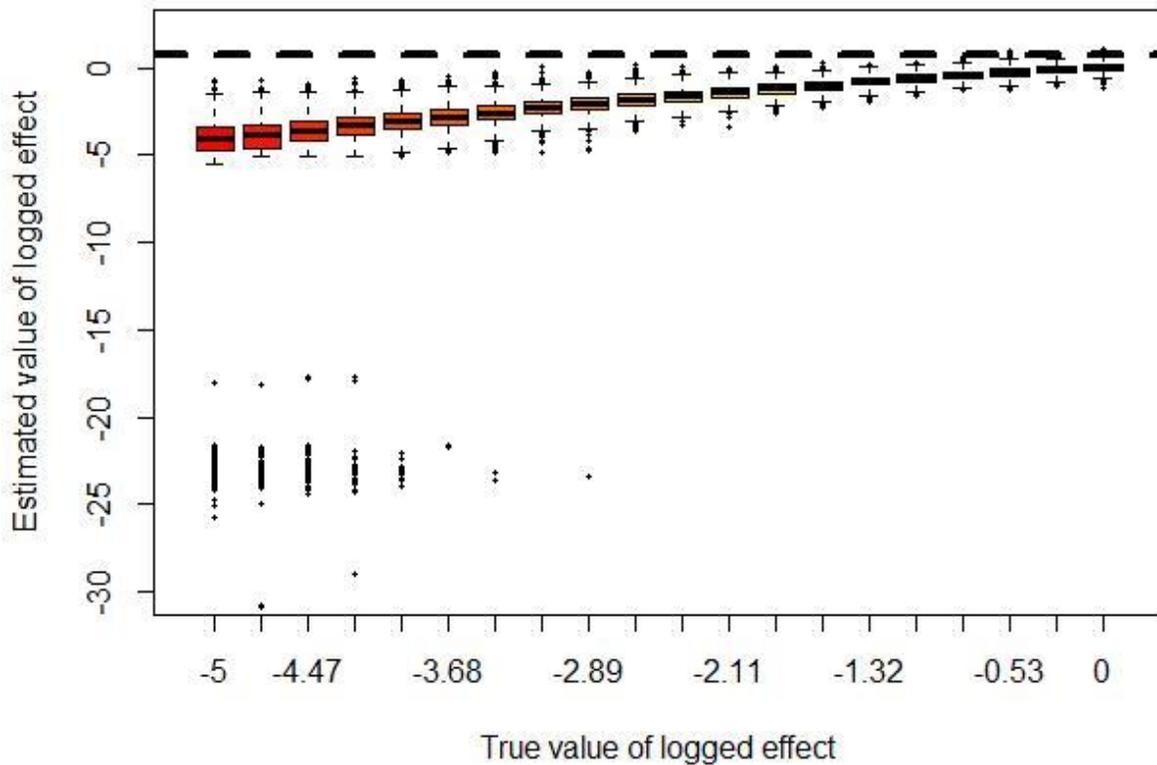


Figure C-11. Parameter estimates from the GLMM compared to the true effect size for logging across our simulated datasets. The broken horizontal line indicates the estimated value of logging effect from the real data. The upper and lower edges of the box plots represent first and third quartiles, the thick black line within each box represents the median value, 'whiskers' represent minimum and maximum observations within 1.5 times of the upper and lower quartiles, and dots represents outliers.

Out of the 19,681 GLMM models, 1,212 incorrectly estimated the effect of community-level logging as positive whereas 3,844 estimated a non-significant effect of logging at a level of $\alpha=0.05$. Most importantly, only 14 out of 19,681 models estimated the community level-effect of logging to be greater than the observed level of 0.75 (Figure C-12).

Overall, results from our power analysis suggest that we have sufficient statistical power, given our occupancy and detection rates and sample size, to capture a negative effect of logging on wildlife occupancy if it existed in our observations.

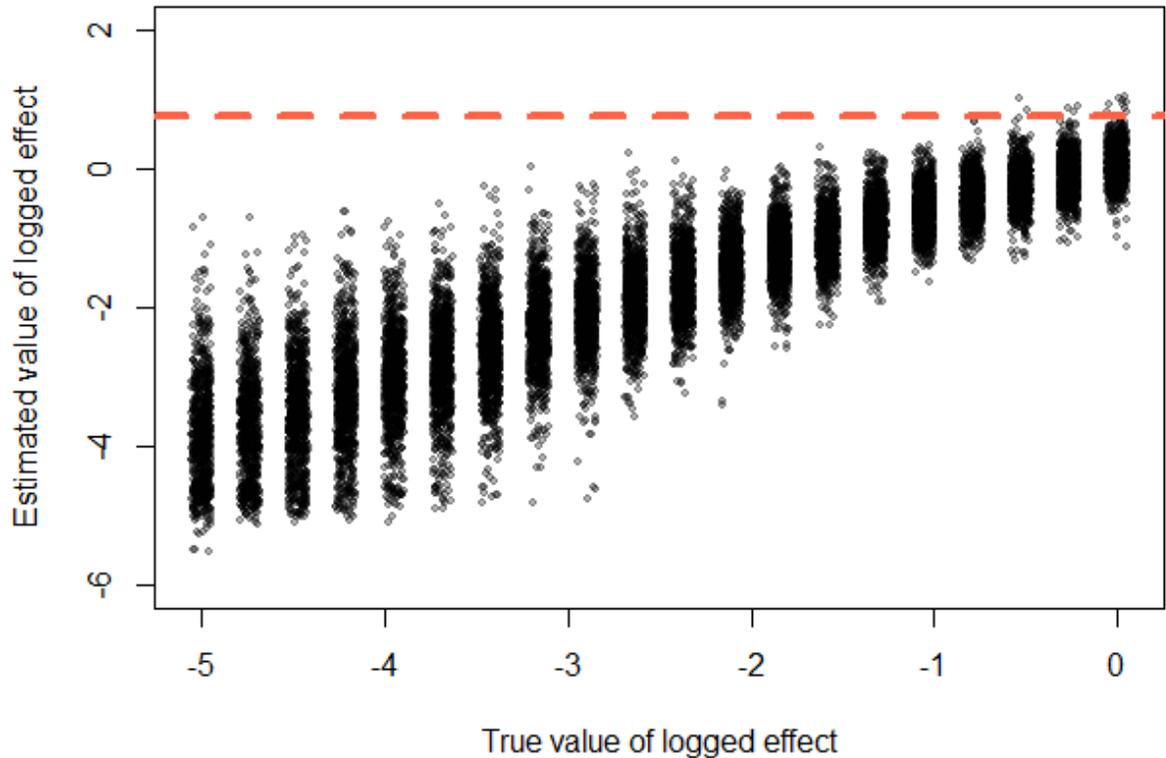


Figure C-12. Model estimates for the simulated datasets relative to our result from the hierarchical model (broken red line). A single dot in this figure represents one simulated dataset. To better visualize the 14 estimated values that were larger than our observed values, we truncated extreme outliers in estimated values from this plot (entire range visible in Figure C-11).

LIST OF REFERENCES

- AHUMADA, J. A., J. HURTADO, and D. LIZCANO. 2013. Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. *PLoS One* 8: e73707.
- ALDER, D., and T. J. SYNNOTT. 1992. Permanent sample plot techniques for mixed tropical forest. Oxford Forestry Institute.
- ANGRIST, J. D., and J.-S. PISCHKE. 2014. *Mastering 'Metrics: The Path from Cause to Effect*. Princeton University Press.
- AREVALO, B., J. VALLADAREZ, S. MUSCHAMP, E. KAY, A. FINKRAL, A. ROOPSIND, and F. E. PUTZ. 2016. Effects of reduced-impact selective logging on palm regeneration in Belize. *For. Ecol. Manage.* 369: 155–160.
- ASNER, G. P., E. N. BROADBENT, P. J. C. OLIVEIRA, M. KELLER, D. E. KNAPP, and J. N. M. SILVA. 2006. Condition and fate of logged forests in the Brazilian Amazon. *Proc. Natl. Acad. Sci. U. S. A.* 103: 12947–50.
- DE AVILA, A. L., A. R. RUSCHEL, J. O. P. DE CARVALHO, L. MAZZEI, J. N. M. SILVA, J. DO C. LOPES, M. M. ARAUJO, C. F. DORMANN, and J. BAUHUS. 2015. Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest. *Biol. Conserv.* 191: 577–586.
- BAKER, T., O. PHILLIPS, Y. MALHI, S. ALMEIDA, L. ARROYO, A. DI FIORE, T. ERWIN, T. J. KILLEEN, S. G. LAURENCE, W. F. LAURANCE, S. L. LEWIS, J. LLOYD, A. MONTEAGUDO, D. A. NEILL, S. PATIÑO, N. C. PITMAN, J. N. M. SILVA, and R. V. MARTÍNEZ. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Chang. Biol.* 10: 545–562.
- BARNETT, A. G., N. KOPER, A. J. DOBSON, F. SCHMIEGELOW, and M. MANSEAU. 2010. Using information criteria to select the correct variance–covariance structure for longitudinal data in ecology. *Methods Ecol. Evol.* 1: 15–24.
- BERTAULT, J. G., and P. SIST. 1997. An experimental comparison of different harvesting intensities with reduced-impact and conventional logging in East Kalimantan, Indonesia. *For. Ecol. Manage.* 94: 209–218.
- BICKNELL, J. E., D. L. A. GAVEAU, Z. G. DAVIES, and M. J. STRUEBIG. 2015. Saving logged tropical forests: Closing roads will bring immediate benefits: peer-reviewed letter. *Front. Ecol. Environ.* 13: 73–74.
- BICKNELL, J. E., M. J. STRUEBIG, and Z. G. DAVIES. 2015. Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *J. Appl. Ecol.* 52: 379–388.
- BICKNELL, J. E., M. J. STRUEBIG, D. P. EDWARDS, and Z. G. DAVIES. 2014. Improved timber harvest techniques maintain biodiversity in tropical forests. *Curr. Biol.* 24: R1119-20.
- BICKNELL, J., and C. A. PERES. 2010. Vertebrate population responses to reduced-impact logging in a neotropical forest. *For. Ecol. Manage.* 259: 2267–2275.

- DI BITETTI, M. S., A. PAVIOLO, C. D. DE ANGELO, and Y. E. DI BLANCO. 2008. Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). *J. Trop. Ecol.* 24: 189–200.
- BLANC, L., M. ECHARD, B. HERAULT, D. BONAL, E. MARCON, J. CHAVE, and C. BARALOTO. 2009. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecol. Appl.* 19: 1397–404.
- BODMER, R. E., J. F. EISENBERG, and K. H. REDFORD. 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conserv. Biol.* 11: 460–466.
- BOLKER, B. 2008. *Ecological models and data in R*. Princeton University Press.
- BOURGEOIS, B., A. VANASSE, E. GONZALEZ, R. ANDERSEN, M. POULIN, and B. WILSEY. 2016. Threshold dynamics in plant succession after tree planting in agricultural riparian zones. *J. Appl. Ecol.* 53: 1704–1713.
- BOVOLO, C. I., R. PEREIRA, G. PARKIN, C. KILSBY, and T. WAGNER. 2012. Fine-scale regional climate patterns in the Guianas, tropical South America, based on observations and reanalysis data. *Int. J. Climatol.* 32: 1665–1689.
- BOWKETT, A., F. ROVERO, and A. MARSHALL. 2007. The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *Afr. J. Ecol.* 46: 479–487.
- BRIENEN, R. J. W. ET AL. 2015. Long-term decline of the Amazon carbon sink. *Nature* 519: 344–8.
- BRODIE, J. F., A. J. GIORDANO, E. F. ZIPKIN, H. BERNARD, J. MOHD-AZLAN, and L. AMBU. 2015. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conserv. Biol.* 29: 110–121.
- BRUNBERG, B., R., and P. LINDGREN. 1984. *Felling manual*. Forskningsstiftelsen “Skogsarbeten.” Stockholm.
- BURIVALOVA, Z., C. SEKERCIOĞLU, and L. KOH. 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* 24: 1893–1898.
- BURTON, A. C., M. K. SAM, C. BALANGTAA, and J. S. BRASHARES. 2012. Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS One* 7: e38007.
- CANTÚ-SALAZAR, L., and K. J. GASTON. 2010. Very Large Protected Areas and Their Contribution to Terrestrial Biological Conservation. *Bioscience* 60: 808–818.
- CAUGHLIN, T. T., J. M. FERGUSON, J. W. LICHSTEIN, A. ZUIDEMA, S. BUNYAVEJCHEWIN, D. J. LEVEY, and T. T. CAUGHLIN. 2014. Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. R. Soc. B* 282: 20142095.
- CHAVE, J. ET AL. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* 20: 3177–3190.

- CHAVE, J., C. ANDALO, S. BROWN, M. A CAIRNS, J. Q. CHAMBERS, D. EAMUS, H. FÖLSTER, F. FROMARD, N. HIGUCHI, T. KIRA, J.-P. LESCURE, B. W. NELSON, H. OGAWA, H. PUIG, B. RIÉRA, and T. YAMAKURA. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.
- CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, and A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12: 351–66.
- CLARK, C. J., J. R. POULSEN, R. MALONGA, and P. W. ELKAN. 2009. Logging concessions can extend the conservation estate for central African tropical forests. *Conserv. B* 23: 1281–1293.
- CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, and J. NI. 2001. Measuring net primary production in forest concepts and field methods. *Ecol. Appl.* 11: 356–370.
- CLARK, J. S. 2005. Why environmental scientists are becoming Bayesians. *Ecol. Lett.* 8: 2–14.
- CONWAY, S. 1982. *Logging Practices: Principles of Timber Harvesting Systems*.
- COSTA, R. C., and W. E. MAGNUSSON. 2003. Effects of Selective Logging on the Diversity and Abundance of Flowering and Fruiting Understory Plants in a Central Amazonian Forest. *Biotropica* 35: 103–114.
- CROME, F. H. J., M.R. THOMAS, and L. A. MOORE. 1996. A Novel Bayesian Approach to Assessing Impacts of Rain Forest Logging. *Ecol. Appl.* 6: 1104–1123.
- CUSHMAN, K. C., H. C. MULLER-LANDAU, R. S. CONDIT, and S. P. HUBBELL. 2014. Improving estimates of biomass change in buttressed trees using tree taper models. *Methods Ecol. Evol.* 5: 573–582.
- DAWKINS, H. C., and M. S. PHILIP. 1998. *Tropical moist forest silviculture and management: a history of success and failure*. CAB International, Wallingford.
- DEKKER, M., and N. R. DE GRAAF. 2003. Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. *For. Ecol. Manage.* 172: 183–190.
- DIRZO, R., H. S. YOUNG, M. GALETTI, G. CEBALLOS, N. J. B. ISAAC, and B. COLLEN. 2014. Defaunation in the Anthropocene. *Science* (80-.). 345: 401–406.
- DORAZIO, R. R. M., and J. A. J. ROYLE. 2005. Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *J. Am. Stat. Assoc.* 100: 389–398.
- DOUGLAS, I. 1999. Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 354: 1725–1738.
- DYKSTRA, D. 2001. The old and the new of reduced impact logging. *Trop. For. Updat.* 3–4.
- DYKSTRA, D., and R. HEINRICH. 1996. *Forest codes of practice: Contributing to environmentally sound forest operations* FAO Forest. D. Dykstra and R. Heinrich (Eds.). Rome, Italy.

- EDWARDS, D. P. D., P. WOODCOCK, F. A. EDWARDS, T. H. LARSEN, W. W. HSU, S. BENEDICK, and D. S. WILCOVE. 2012. Reduced-impact logging and biodiversity conservation: a case study from Borneo. *Ecol. Appl.* 22: 561–71.
- EDWARDS, D. P., J. J. GILROY, P. WOODCOCK, F. A. EDWARDS, T. H. LARSEN, D. J. R. ANDREWS, M. A. DERHÉ, T. D. S. DOCHERTY, W. W. HSU, S. L. MITCHELL, T. OTA, L. J. WILLIAMS, W. F. LAURANCE, K. C. HAMER, and D. S. WILCOVE. 2014. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Glob. Chang. Biol.* 20: 183–91.
- EDWARDS, D. P., J. A. TOBIAS, D. SHEIL, E. MEIJAARD, and W. F. LAURANCE. 2014. Maintaining ecosystem function and services in logged tropical forests. *Trends Ecol. Evol.* 29: 511–520.
- EISENBERG, J. F. 1979. Habitat, economy, and society: some correlations and hypotheses for the Neotropical primates. *In* I. Bernstein and E. Smith (Eds.) *Primate Ecology and Human Origins*. pp. 215–262, Garland STMP Press, New Jersey.
- ELKIN, C. M., and H. POSSINGHAM. 2008. The role of landscape dependent disturbance and dispersal in metapopulation persistence. *Am. Nat.* 172: 563–575.
- EMMONS, L. H. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16: 210–222.
- EMMONS, L. H., and F. FEER. 1990. *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press.
- FAO. 2004. *Reduced impact logging in tropical forests. Literature synthesis, analysis and prototype statistical framework*. Rome, Italy.
- FAO. 2016. *State of the World's Forests 2016. Forests and agriculture: land-use challenges and opportunities*. Rome, Italy.
- FERRARO, P. J. 2013. Counterfactual thinking and impact evaluation in environmental policy. *New Dir. Eval.* 137: 107–114.
- FIMBEL, R. A., A. GRAJAL, and J. G. ROBINSON. 2001. *The cutting edge- Conserving wildlife in logged tropical forest*. Columbia University Press, New York.
- FRAGOSO, J. M. V. 1991. The effect of selective logging on Baird's tapir in Belize. *In* M. A. Mares and D. J. Schmidly (Eds.) *Latin American Mammalogy: History, Biodiversity, and Conservation*. University of Oklahoma Press, Norman, Oklahoma.
- FRAGOSO, J. M. V. 2004. A long-term study of white-lipped peccary (*Tayassu pecari*) population fluctuations in northern Amazonia - anthropogenic versus "natural" causes. *In* K. M. Silvius, R. E. Bodmer, and J. M. V. Fragoso (Eds.) *People in Nature: Wildlife Conservation in South and Central America*. p. 464, Columbia University Press.
- FRAGOSO, J. M. V., and J. M. HUFFMAN. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *J. Trop. Ecol.* 16: 369–385.

- FRAGOSO, J. M. V., T. LEVI, L. F. B. OLIVEIRA, J. B. LUZAR, H. OVERMAN, J. M. READ, and K. M. SILVIUS. 2016. Line Transect Surveys Underdetect Terrestrial Mammals: Implications for the Sustainability of Subsistence Hunting. *PLoS One* 11: e0152659.
- GELMAN, A., and J. HILL. 2007. *Data Analysis using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.
- GELMAN, A., and D. K. PARK. 2009. Splitting a Predictor at the Upper Quarter or Third and the Lower Quarter or Third. *Am. Stat.* 63: 1–8.
- GOPALASWAMY, A. M., J. A. ROYLE, J. E. HINES, P. SINGH, D. JATHANNA, N. S. KUMAR, and K. U. KARANTH. 2012. Program SPACECAP: software for estimating animal density using spatially explicit capture-recapture models. *Methods Ecol. Evol.* 3: 1067–1072.
- GOURLET-FLEURY, S., J. M. GUEHL, and O. LAROUSSINIE. 2004. *Ecology and management of a neotropical rainforest : lessons drawn from Paracou, a long-term experimental research site in French Guiana*. Elsevier, Paris.
- DE GRAAF, N. R. 1986. *A Silvicultural System for Natural Regeneration of Tropical Rain Forest in Suriname*. Agricultural University, Wageningen, The Netherlands.
- HAMMOND, D. S. 2005. *Tropical forests of the Guiana shield: ancient forests in a modern world*. CABI.
- HAMMOND, D. S., S. GOURLET-FLEURY, P. VAN DER HOUT, H. TER STEEGE, and V. K. BROWN. 1996. A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. *For. Ecol. Manage.* 83: 99–116.
- HAMMOND, D. S., and H. TER STEEGE. 1998. Propensity for fire in Guianan rainforests. *Conserv. Biol.* 12: 944–947.
- HARRISON, R. D. R., S. TAN, J. B. J. PLOTKIN, F. SLIK, M. DETTO, T. BRENES, A. ITOH, and S. J. DAVIES. 2013. Consequences of defaunation for a tropical tree community. *Ecol. Lett.* 16: 687–694.
- HOBBS, N. T., and M. B. HOOTEN. 2015. *Bayesian Models: A Statistical Primer for Ecologists*. Princeton University Press, Oxford, UK.
- HOLTING, M., C. I. BOVOLO, and R. ERNST. 2016. Facing Complexity in Tropical Conservation : How Reduced Impact Logging and Climatic Extremes Affect Beta Diversity in Tropical Amphibian Assemblages. *Biotropica* 1–9.
- VAN DER HOUT, C. 1999. *Reduced impact logging in the tropical rain forest of Guyana*. Tropenbos-Guyana Series 6.
- VAN DER HOUT, P. 1996. *Effects of logging with different intensities of low impact harvesting*. Georgetown, Guyana.
- HOUT, P. VAN DER. 2000. *Pibiri permanent plots-objectives, design and database management*. Tropenbos-Guyana Ser. 1–73.
- IKNAYAN, K. J., M. W. TINGLEY, B. J. FURNAS, and S. R. BEISSINGER. 2014. Detecting diversity: Emerging methods to estimate species diversity. *Trends Ecol. Evol.* 29: 97–106.

- IPCC. 2003. Good practice guidance for land use, landuse change and forestry (GPG-LULUCF). *In* Good Practice Guidance for Land Use, Land-Use Change and Forestry.
- IUCN. 2016. The IUCN Red List of Threatened Species. Available at: <http://www.iucnredlist.org> [Accessed April 19, 2016].
- IWAMURA, T., E. F. LAMBIN, K. M. SILVIUS, J. B. LUZAR, and J. M. V FRAGOSO. 2016. Socio-environmental sustainability of indigenous lands: Simulating coupled human-natural systems in the Amazon. *Front. Ecol. Environ.* 14: 77–83.
- IWAMURA, T., E. F. LAMBIN, K. M. SILVIUS, J. B. LUZAR, and J. M. V. V FRAGOSO. 2014. Agent-based modeling of hunting and subsistence agriculture on indigenous lands: Understanding interactions between social and ecological systems. *Environ. Model. Softw.* 58: 109–127.
- JANSEN, P., and P. ZUIDEMA. 2001. Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees. *In* R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.) *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*. pp. 35–59, Columbia University Press, New York.
- JOHNSON, M. O. ET AL. 2016. Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: implications for dynamic global vegetation models. *Glob. Chang. Biol.* 44: 1–18.
- JONKERS, W. B. . 1983. Exploitation, Natural regeneration and increment- experiment plan and progress report on Experiment 78/5.
- JONKERS, W. B. . 2011. Tree growth, recruitment and mortality after logging and refinement. *In* M. Werger (Ed.) *Sustainable Management of Tropical Rainforests: the CELOS Management System*. Tropenbos International, Paramaribo, Suriname.
- JONKERS, W. B. J. 1987. *Vegetation structure, logging damage and silviculture in a tropical rain forest in suriname*. Wageningen, The Netherlands.
- KELLER, M., G. P. ASNER, G. BLATE, J. MCGLOCKLIN, F. MERRY, M. PEÑA-CLAROS, and J. ZWEEDE. 2007. Timber production in selectively logged tropical forests in South America. *Front. Ecol. Environ.* 5: 213–216.
- LAURANCE, W., and D. EDWARDS. 2014. Saving logged tropical forests. *Front. Ecol. Environ.* 12: 147.
- LAURANCE, W. F. ET AL. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489: 290–294.
- LEVI, T., G. H. SHEPARD, J. OHL-SCHACHERER, C. A. PERES, and D. W. YU. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: Landscape-scale management implications for Amazonia. *J. Appl. Ecol.* 46: 804–814.
- LIM, B. K., and M. D. ENGSTROM. 2005. Mammals of Iwokrama Forest. *Proc. Acad. Nat. Sci. Philadelphia* 154: 71–108.

- LINDGREN, F., H. H. RUE, J. LINDSTRÖM, and J. LINDSTRÖM. 2011. An explicit link between gaussian fields and gaussian markov random fields: The stochastic partial differential equation approach. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73: 423–498.
- LUSSETTI, D., E. P. AXELSSON, U. ILSTEDT, J. FALCK, and A. KARLSSON. 2016. Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo. *For. Ecol. Manage.* 381: 335–346.
- LUZAR, J. B., K. M. SILVIUS, H. OVERMAN, S. T. GIERY, J. M. READ, and J. M. V. FRAGOSO. 2011. Large-scale Environmental Monitoring by Indigenous Peoples. *Bioscience* 61: 771–781.
- MAFFEI, L., A. J. NOSS, S. C. SILVER, and M. J. KELLY. 2011. Abundance/Density Case Study: jaguars in the Americas. Camera traps in animal ecology. *In* A. F. O’Connell, J. D. Nichols, and K. U. Karanth (Eds.) pp. 119–144, Springer, New York.
- MALHI, Y. ET AL. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Glob. Chang. Biol.* 10: 563–591.
- MALHI, Y., L. E. O. C. ARAGÃO, D. B. METCALFE, R. PAIVA, C. A. QUESADA, S. ALMEIDA, L. ANDERSON, P. BRANDO, J. Q. CHAMBERS, A. C. L. DA COSTA, L. R. HUTYRA, P. OLIVEIRA, S. PATIÑO, E. H. PYLE, A. L. ROBERTSON, and L. M. TEIXEIRA. 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Glob. Chang. Biol.* 15: 1255–1274.
- MAYOR, P., P. PÉREZ-PEÑA, M. BOWLER, P. E. PUERTAS, M. KIRKLAND, and R. BODMER. 2015. Effects of selective logging on large mammal populations in a remote indigenous territory in the northern peruvian amazon. *Ecol. Soc.* 20.
- MAZZEI, L., P. SIST, A. RUSCHEL, F. E. PUTZ, P. MARCO, W. PENA, and J. E. R. FERREIRA. 2010. Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *For. Ecol. Manage.* 259: 367–373.
- MCCARTHY, M. A., and P. MASTERS. 2005. Profiting from prior information in Bayesian analyses of ecological data. *J. Appl. Ecol.* 42: 1012–1019.
- METCALF, C. J. E., J. S. CLARK, and D. A. CLARK. 2009. Tree growth inference and prediction when the point of measurement changes: modelling around buttresses in tropical forests. *J. Trop. Ecol.* 25: 1.
- MORRIS, W. K., P. A. VESK, and M. A. MCCARTHY. 2013. Profiting from pilot studies: Analysing mortality using Bayesian models with informative priors. *Basic Appl. Ecol.* 14: 81–89.
- MORRISON, J. C., W. SECHREST, E. DINERSTEIN, D. S. WILCOVE, and J. F. LAMOREUX. 2007. Persistence of Large Mammal Faunas as Indicators of Global Human Impacts. *J. Mammal.* 88: 1363–1380.
- NAKAGAWA, S., and H. SCHIELZETH. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4: 133–142.
- NICHOLSON, D. 1958. An analysis of logging damage in tropical rain forest, North Borneo. *Malaysian For.* 21: 235–45.

- NICHOLSON, D. I. 1979. The effects of logging and treatment on the mixed dipterocarp forests of Southeast Asia.
- NOVACK, A. J., M. B. MAIN, M. E. SUNQUIST, and R. F. LABISKY. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *J. Zool.* 267: 167–178.
- O’FARRILL, G., M. GALETTI, and A. CAMPOS-ARCEIZ. 2013. Frugivory and seed dispersal by tapirs: An insight on their ecological role. *Integr. Zool.* 8: 4–17.
- OSURI, A. M., J. RATNAM, V. VARMA, P. ALVAREZ-LOAYZA, J. H. ASTAIZA, C. BRADFORD, M., FLETCHER, M. NDOUNDOU-HOCKEMBA, P. A. JANZEN, D. KENFACK, A. R. MARSHALL, B. R. RAMESH, F. ROVERO, and M. SANKARAN. 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nat. Commun.* 7: 1–7.
- PACIFICI, K., E. F. E. ZIPKIN, J. A. COLLAZO, J. I. IRIZARRY, and A. DEWAN. 2014. Guidelines for a priori grouping of species in hierarchical community models. *Ecol. Evol.* 4: 877–888.
- PEARSON, T. R. H., S. BROWN, and F. M. CASARIM. 2014. Carbon emissions from tropical forest degradation caused by logging. *Environ. Res. Lett.* 9: 34017.
- PEÑA-CLAROS, M., T. S. FREDERICKSEN, A. ALARCÓN, G. M. BLATE, U. CHOQUE, C. LEAÑO, J. C. LICONA, B. MOSTACEDO, W. PARIONA, Z. VILLEGAS, and F. E. PUTZ. 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *For. Ecol. Manage.* 256: 1458–1467.
- PERES, C. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conserv. Biol.* 14: 240–253.
- PERES, C. A. 2005. Why We Need Megareserves in Amazonia. *Conserv. Biol.* 19: 728–733.
- PHILLIPS, O. L. ET AL. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323: 1344–7.
- PHILLIPS, O. L., Y. MALHI, B. VINCETI, T. BAKER, S. L. LEWIS, N. HIGUCHI, W. F. LAURANCE, P. N. VARGAS, R. V. MARTINEZ, and S. LAURANCE. 2002. Changes in growth of tropical forests: evaluating potential biases. *Ecol. Appl.* 12: 576–587.
- PINARD, M. A., and F. E. PUTZ. 1996. Retaining Forest Biomass by Reducing Logging Damage. *Biotropica* 28: 278–295.
- PINARD, M. A., F. E. PUTZ, J. TAY, and T. E. SULLIVAN. 1995. Creating Timber Harvest Guidelines for a Reduced-Impact Logging Project in Malaysia. *J. For.* 41–45.
- PIPONIOT, C., P. SIST, L. MAZZEI, and M. PE. 2016. Carbon recovery dynamics following disturbance by selective logging in Amazonian forests. *Elife* 5.
- PLEW, M. G. 2005. The Archaeology of Iwokrama and the North Rupununi. *Proc. Acad. Nat. Sci. Philadelphia* 154: 7–28.
- PLUMMER, M. 2011. JAGS Version 3.1. 0 user manual. Int. Agency Res. Cancer.
- POELS, R. L. . 1987. Soils, water, and nutrients in a forest ecosystem in Suriname. Wageningen.

- POULSEN, J. R., C. J. CLARK, and B. M. BOLKER. 2011. Decoupling the effects of logging and hunting on an afrotropical animal community. *Ecol. Appl.* 21: 1819–1836.
- PUTZ, F. E., and RUSLANDI. 2015. Intensification of tropical silviculture. *J. Trop. For. Sci.* 27: 285–288.
- PUTZ, F. E., P. SIST, T. FREDERICKSEN, and D. DYKSTRA. 2008. Reduced-impact logging: Challenges and opportunities. *For. Ecol. Manage.* 256: 1427–1433.
- PUTZ, F. E., P. A. ZUIDEMA, T. SYNNOTT, M. PEÑA-CLAROS, M. A. PINARD, D. SHEIL, J. K. VANCLAY, P. SIST, S. GOURLET-FLEURY, B. GRISCOM, J. PALMER, and R. ZAGT. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conserv. Lett.* 5: 296–303.
- PUTZ, F., and M. PINARD. 1993. Reduced-impact logging as a carbon-offset method. *Conserv. Biol.* 7: 755–757.
- QUESADA, C. A. ET AL. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* 7: 1515–1541.
- RABINOWITZ, A. R., and B. G. NOTTINGHAM. 1986. Ecology and behavior of the jaguar (*Panthera onca*) in Belize, Central-America. *J. Zool.* 210: 149–159.
- R DEVELOPMENT CORE TEAM. 2015. R: A language and environment for statistical computing.
- RAMAGE, B. S., D. SHEIL, H. M. W. W. SALIM, C. FLETCHER, N. Z. A. MUSTAFA, J. C. LURUTHUSAMAY, R. D. HARRISON, E. BUTOD, A. D. DZULKIPLY, A. R. KASSIM, and M. D. POTTS. 2013. Pseudoreplication in Tropical Forests and the Resulting Effects on Biodiversity Conservation. *Conserv. Biol.* 27: 364–372.
- READ, J. M., J. M. V. FRAGOSO, K. M. SILVIUS, J. LUZAR, H. OVERMAN, A. CUMMINGS, S. T. GIERY, and L. FLAMARION DE OLIVEIRA. 2010. Space, Place, and Hunting Patterns among Indigenous Peoples of the Guyanese Rupununi Region. *J. Lat. Am. Geogr.* 9: 213–243.
- REDFORD, K. 1992. The empty forest. *Bioscience* 42: 412–422.
- RICH, L. N., D. A. W. MILLER, H. S. ROBINSON, J. W. MCNUTT, and M. J. KELLY. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *J. Appl. Ecol.*
- RICHARD-HANSEN, C., N. SURUGUE, K. KHAZRAIE, M. LE NOC, and P. GRENAND. 2014. Long-term fluctuations of white-lipped peccary populations in French Guiana. *Mammalia* 78: 291–301.
- RIFAI, S. W., T. A. P. WEST, and F. E. PUTZ. 2015. “Carbon Cowboys” could inflate REDD+ payments through positive measurement bias. *Carbon Manag.* 1–8.
- ROBINSON, J. G., and E. L. BENNETT eds. 2000. *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York.
- ROBINSON, J. G., K. H. REDFORD, and E. L. BENNETT. 1999. Conservation - Wildlife harvest in logged tropical forests. *Science* (80-.). 284: 595–596.
- RODNEY, K. 2013a. Lessons learned on the sustainability of Iwokrama’s timber harvesting operation 2007 to 2011. Georgetown, Guyana.

- RODNEY, K. 2013b. Post harvest silvicultural survey (MUs K-39 and K-41). Georgetown, Guyana.
- ROOPSIND, A., V. WORTEL, W. HANOEMAN, and F. E. PUTZ. 2017. Quantifying uncertainty about forest recovery 32-years after selective logging in Suriname. *For. Ecol. Manage.* 391: 246–255.
- ROSIN, C. 2014. Does hunting threaten timber regeneration in selectively logged tropical forests? *For. Ecol. Manage.* 331: 153–164.
- ROVERO, F., and A. R. MARSHALL. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *J. Appl. Ecol.* 46: 1011–1017.
- ROYLE, J. A., and R. M. DORAZIO. 2008. *Hierarchical Modeling and Inference in Ecology*. Academic Press.
- ROYLE, J. A., K. U. KARANTH, A. M. GOPALASWAMY, and N. S. KUMAR. 2009. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology* 90: 3233–3244.
- RUSLANDI, W. P. CROPPER, and F. E. PUTZ. 2017. Effects of silvicultural intensification on timber yields, carbon dynamics, and tree species composition in a dipterocarp forest in Kalimantan, Indonesia: An individual-tree-based model simulation. *For. Ecol. Manage.* 390: 104–118.
- RUSLANDI, A. ROOPSIND, P. SIST, M. PEÑA-CLAROS, R. THOMAS, and F. E. PUTZ. 2014. Beyond equitable data sharing to improve tropical forest management. *Int. For. Rev.* 16: 497–503.
- RUTISHAUSER, E. ET AL. 2015. Rapid tree carbon stock recovery in managed Amazonian forests. *Curr. Biol.* 25: R787–R788.
- RUTISHAUSER, E., B. HÉRAULT, P. PETRONELLI, and P. SIST. 2016. Tree Height Reduction After Selective Logging in a Tropical Forest. *Biotropica* 48: 285–289.
- SASAKI, N., G. P. ASNER, Y. PAN, W. KNORR, P. B. DURST, H. O. MA, A. J. LOWE, L. P. KOH, and F. E. PUTZ. 2016. Sustainable Management of Tropical Forests Can Reduce Carbon Emissions and Stabilize Timber Production. *Front. Environ. Sci.*
- SHEIL, D., and R. M. MAY. 1996. Mortality and Recruitment Rate Evaluations in Heterogeneous Tropical Forests. *J. Ecol.* 84: 91–100.
- SHENKIN, A., B. BOLKER, M. PEÑA-CLAROS, J. C. LICONA, and F. E. PUTZ. 2015. Fates of trees damaged by logging in Amazonian Bolivia. *For. Ecol. Manage.* 357: 50–59.
- SHEPARD, G. H., T. LEVI, E. G. NEVES, C. A. PERES, and D. W. YU. 2012. Hunting in Ancient and Modern Amazonia: Rethinking Sustainability. *Am. Anthropol.* 114: 652–667.
- SIST, P. 2000. Reduced-impact logging in the tropics: Objectives, principles and impacts. *Int. For. Rev.* 2: 3–10.
- SIST, P. ET AL. 2015. The Tropical managed forests Observatory: A research network addressing the future of tropical logged forests. *Appl. Veg. Sci.* 18: 171–174.

- SIST, P., D. DYKSTRA, and R. FIMBEL. 1998. Reduced-Impact Logging Guidelines for Lowland and Hill Dipterocarp Forests in Indonesia. *CIFOR Occas. Pap.* 15 62: 1–18.
- SIST, P., and N. NGUYEN-THÉ. 2002. Logging damage and the subsequent dynamics of a dipterocarp forest in East Kalimantan (1990-1996). *For. Ecol. Manage.* 165: 85–103.
- SIST, P., D. SHEIL, K. KARTAWINATA, and H. PRIYADI. 2003. Reduced-impact logging in Indonesian Borneo: some results confirming the need for new silvicultural prescriptions. *For. Ecol. Manage.* 179: 415–427.
- SPIEGELHALTER, D. J., N. G. BEST, B. P. CARLIN, and A. VAN DER LINDE. 2002. Bayesian measures of model complexity and fit. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 64: 583–616.
- TER STEEGE, H. 2000. *Plant Diversity in Guyana. with Recommendations for a National Protected Area Strategy.* Wageningen.
- TER STEEGE, H. ET AL. 2013. Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092.
- TER STEEGE, H., R. G. A. BOOT, L. C. BROUWER, J. C. CAESAR, R. C. EK, D. S. HAMMOND, P. P. HARIPERSAUD, P. VAN DER HOUT, V. G. JETTEN, A. J. VAN KEKEM, M. A. KELLMAN, Z. KHAN, A. M. POLAK, T. L. PONS, J. PULLES, D. RAAIMAKERS, S. A. ROSE, J. J. VAN DER SANDEN, and R. J. ZAGT. 1996. *Ecology and logging in a tropical rain forest in Guyana. With recommendations for forest management.*
- TER STEEGE, H., V. JETTEN, A. POLAK, and M. WERGER. 1993. Tropical rain forest types and soil factors in a watershed area in Guyana. *J. Veg. Sci.* 4: 705–716.
- TER STEEGE, H., N. C. A PITMAN, O. L. PHILLIPS, J. CHAVE, D. SABATIER, A. DUQUE, J.-F. MOLINO, M.-F. PRÉVOST, R. SPICHIGER, H. CASTELLANOS, P. VON HILDEBRAND, and R. VÁSQUEZ. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443: 0–2.
- SYNNOTT, T. J. 1979. *A manual of permanent plot procedure for tropical rainforests.* Commonweal.
- TALBOT, J. ET AL. 2014. Methods to estimate aboveground wood productivity from long-term forest inventory plots. *For. Ecol. Manage.* 320: 30–38.
- TEAM NETWORK. 2011. *Terrestrial Vertebrate Protocol Implementation Manual, v. 3.1.* Tropical Ecology, Assessment and Monitoring Network. Arlington, VA, USA.
- TOBLER, M. W., A. ZÚÑIGA HARTLEY, S. E. CARRILLO-PERCASTEGUI, and G. V. N. POWELL. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *J. Appl. Ecol.* 52: 413–421.
- TOMS, J. D., and M. L. LESPERANCE. 2003. Piecewise regression: A tool for identifying ecological thresholds. *Ecology* 84: 2034–2041.
- UFCCC. 2016. *Aggregate effect of the intended nationally determined contributions : an update.*

- VANMESCHELEN, E. 1994. Vegetatiestructuur en lichtklimaat van een Greenheartbos in Guyana. Katholieke Universiteit Louvain, Belgium.
- VETTER, D., M. M. HANSBAUER, Z. VÉGVÁRI, and I. STORCH. 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: A quantitative review. *Ecography (Cop.)*. 34: 1–8.
- VIDAL, E., T. A. P. WEST, and F. E. PUTZ. 2016. Recovery of biomass and merchantable timber volumes twenty years after conventional and reduced-impact logging in Amazonian Brazil. *For. Ecol. Manage.* 376: 1–8.
- WADSWORTH, F. H., and J. C. ZWEEDE. 2006. Liberation: Acceptable production of tropical forest timber. *For. Ecol. Manage.* 233: 45–51.
- WATKINS, G. G. 2010. Baseline Assessment of Ecosystem services from the Iwokrama Forest. Georgetown, Guyana.
- WERGER, M. ed. 2011. Sustainable Management of Tropical Rainforests: The CELOS Management System. Tropenbos International, Paramaribo, Suriname.
- WEST, T. A. P., E. VIDAL, and F. E. PUTZ. 2014. Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. *For. Ecol. Manage.* 314: 59–63.
- WILKIE, D., E. SHAW, F. ROTBERG, G. MORELLI, and P. AUZEL. 2000. Roads, Development, and Conservation in the Congo Basin. *Conserv. Biol.* 14: 1614–1622.
- ZAGT, R. J., R. EK, and N. RAES. 2003. Logging effects on liana diversity and abundance in Central Guyana. Tropenbos International, Wageningen, The Netherlands.
- ZAGT, R. J., M. J. A. WERGER, E. J. MALTA, M. H. RIJKS, D. S. HAMMOND, J. L. MACHADO, P. B. REICH, and R. G. A. BOOT. 1997. Tree demography in the tropical rain forest of Guyana.
- ZIMMERMAN, B. L., and C. F. KORMOS. 2012. Prospects for Sustainable Logging in Tropical Forests. *Bioscience* 62: 479–487.
- ZIPKIN, E. F., J. ANDREW ROYLE, D. K. DAWSON, and S. BATES. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biol. Conserv.* 143: 479–484.

BIOGRAPHICAL SKETCH

Anand Roopsind is a faithful representative of the immigrant nature and diversity of the Americas; West Indian in identity and culture, ethnically Indian from historical trafficking of people from the Indian subcontinent, and intellectually and spiritually rooted in the mainland forests of South America. He was born in Guyana to first generation non-agrarian parents, but spent the majority of his childhood on his grandparents' farm, which may have been a cause or an effect of his dislike for school. He attended St. Joseph's High School and then the University of Guyana, where he completed his degree in Forestry in 2004; his choice of a field of study was partially to be antithetical to his sister's major in Wildlife Conservation. After graduation, Anand worked for the Guyana Forestry Commission as a Forest Planning Officer, but that job involved too much planning from the inside of an air-conditioned office. After that experience in government service, he spent 2005-2007 mostly outdoors as a Professional Development Fellow at the Iwokrama International Centre, which placed him on the same path as his sister with the same employer. Anand resided with great pleasure at the Iwokrama Field Station in the heart of Guyana's forest belt. By staying in the forest he avoided having to travel back and forth to Georgetown on an "all weather road" along which bridge failures and floods frequently left people stranded in the middle of the forest for days. In 2008, Anand was awarded a British Commonwealth Fellowship to pursue a master's in Environment and Development at the University of Reading. His thesis, on community-based natural resource management, was inspired by his work with the Makushi indigenous communities that live around Iwokrama. Upon completion of his Master's, he returned to Iwokrama as the Assistant Forest Manager, eager to further his work with communities. After substantial personal reflection, Anand

realized that he was better suited for the management of trees than for the Herculean tasks associated with social science work. His job from 2009 through mid-2012 was to assist his long time mentor, Ken Rodney, a Canadian forester who found his way to Guyana via Peru, with the sustainable forest management program for Iwokrama's 370,000 ha reserve. Anand once again became a full-time resident at the Iwokrama Field Station because, in addition to the continued poor conditions, travelers often had to contend with gun-toting robbers holding up buses. For him these conditions provided a perfect excuse for 6-month long work shifts in the forest. The only down side was that after years of a mutually respectful relationship with Sankar, the resident caiman, he was banned from swimming in the river due to safety concerns. At the end of his second stint at Iwokrama, through professional and personal relationships, Anand met Francis E. ('Jack') Putz during a training course in Suriname. Prior to meeting Jack in person, he had already experienced the electronic swiftness at which Jack wields his track-changes sword; few lines in his PhD research proposal escaped those slashes. Having survived the field course and multiple drafts of his research proposal, in mid-2012 Anand felt he was sufficiently resilient to join Jack's lab in the Department of Biology at the University of Florida to pursue a PhD. At the University of Florida, Anand cultivated numerous fruitful professional and personal relationships with people from across the tropics and enjoyed many opportunities to collaborate with a wide array of researchers, forest managers, and NGO practitioners. He received his PhD from the University of Florida in the summer of 2017. Anand's passion as he moves forward with his professional career continues to be the training of fellow Guyanese in the skills they need to responsibly manage their national heritage.