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Abstract

Forest degradation accounts for ~ 70% of total carbon losses from tropical forests. Substantial emissions are from selective logging, a land-use activity that decreases forest carbon density. To maintain carbon values in selectively logged forests, climate change mitigation policies and government agencies promote the adoption of reduced-impact logging (RIL) practices. However, whether RIL will maintain both carbon and timber values in managed tropical forests over time remains uncertain. In this study, we quantify the recovery of timber stocks and aboveground carbon at an experimental site where forests were subjected to different intensities of RIL (4 trees ha^{-1}, 8 trees ha^{-1}, and 16 trees ha^{-1}). Our census data spans 20 years post-logging and 17 years after the liberation of future crop trees from competition in a tropical forest on the Guiana Shield, a globally important forest carbon reservoir. We model recovery of timber and carbon with a breakpoint regression that allowed us to capture elevated tree mortality immediately after logging. Recovery rates of timber and carbon were governed by the presence of residual trees (i.e., trees that persisted through the first harvest). The liberation treatment stimulated faster recovery of timber albeit at a carbon cost. Model results suggest a threshold logging intensity beyond which forests managed for timber and carbon derive few benefits from RIL, with recruitment and residual growth not sufficient to offset losses. Inclusion of the breakpoint at which carbon and timber gains outpaced post-logging mortality led to high predictive accuracy, including out-of-sample R^2 values >90%, and enabled inference on demographic changes post-logging. Our modeling framework is broadly applicable to studies that aim to quantify impacts of logging on forest recovery. Overall, we demonstrate that initial mortality drives variation in recovery rates, that the second harvest depends on old growth wood, and that timber intensification lowers carbon stocks.

Keywords: carbon stocks; tropical forestry; sustainable forest management; REDD+; forest degradation; climate change mitigation; piecewise regression

Introduction

Sustainable forest management (SFM) through careful selective logging is advocated as a simultaneous means to provide timber, protect biodiversity, and reduce carbon emissions from tropical forests. The technical forestry guidelines that form the basis of SFM generally include use of reduced-impact logging (RIL) practices designed to reduce deleterious environmental impacts, sustain timber yields, and improve efficiency of logging operations (e.g., Boltz *et al.*, 2003; 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 forest workers (Hendrison, 1990; Pinard *et al.*, 1995; Dykstra & Heinrich, 1996; Van der Hout, 1999; Sist, 2000; Dykstra, 2001). Given that due to anthropogenic forest disturbance, tropical forests are a net carbon source (Baccini *et al.*, 2017), and given that most of the world's remaining tropical forests are subjected to logging (Pearson *et al.*, 2017), efforts to reduce carbon emissions from forestry activities are of global importance (Houghton *et al.*, 2015).

RIL guidelines typically include: (1) pre-harvest tree inventories and topographic mapping; (2) pre-felling vine cutting; (3) directional felling; and, (4) controls on the lengths, widths, layout, and use of pre-planned skid trails and logging roads. Use of these practices reduces both the spatial extent and severity of logging impacts (e.g., Asner *et al.*, 2004; Edwards *et al.*, 2014; Arevalo *et al.*, 2016; Vidal *et al.*, 2016). More specifically, application of RIL practices reduces soil damage (Pinard *et al.*, 1995; Sist, 2000), biodiversity loss (Bicknell *et al.*, 2015; Roopsind *et al.*, 2017a), hydrological disruption (Douglas, 1999; Miller *et al.*, 2011), and carbon emissions (e.g., Pinard & Putz, 1996) relative to unplanned or conventional logging. Post-logging recovery rates of timber and carbon stocks are also reportedly faster after RIL than after conventional logging (Lussetti *et al.*, 2016; Vidal *et al.*, 2016).

Advocates of RIL are now challenged to define timber harvest intensity thresholds that maintain timber and carbon values over multiple harvest cycles (Wadsworth & Zweede 2006; Zimmerman & Kormos 2012). If timber and carbon values do not recover under economically viable harvest intervals, these managed forests become vulnerable to conversion for more intensive land uses, with all their associated carbon emissions (Asner *et al.*, 2006). For these reasons, it is important to quantify thresholds of logging intensity beyond which benefits of RIL are lost. If intensification of forest management is pursued to maintain timber yields across harvest rotations (Putz *et al.*, 2012; Ruslandi *et al.*, 2017), such as the liberation of future crop trees, it also becomes important to quantify tradeoffs between timber and carbon values.

For a forest on the Guiana Shield, we compare the rates of recovery of timber and aboveground carbon stocks (ACS) for the first 20 years after RIL across different logging intensities. We also assess the timber-carbon tradeoffs that result from the liberation of future crop trees (FCTs; well-formed trees of commercial species smaller than the minimum cutting diameter). The Guiana Shield region is unique in that it is one of the last intact contiguous blocks of tropical forests globally, and distinct from Amazonia forests due to its ancient and nutrient-poor soils, slower ecological dynamics, and higher carbon stocks (ter Steege *et al.*, 2006; Johnson *et al.*, 2016; Piponiot *et al.*, 2016). We monitored trees ≥ 5 cm DBH from 1993 to 2013 in replicated plots subjected to RIL at one of three logging intensities, with a fourth treatment that included a post-harvest liberation treatment of FCTs after moderate intensity harvest (RIL-moderate + liberation; Table 1). This range of experimental treatments enabled us to go beyond simple comparisons of RIL and conventional logging and to quantify logging intensity thresholds for sustainable timber production with RIL. More generally, we can evaluate the role of logged forests as carbon stores and examine the tradeoffs between timber and carbon values with the use of liberation treatments to favor timber production.

We used our plot-level observations of timber stocks and ACS to evaluate the effect of logging intensity on residual tree 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 at the stand level (Piponiot *et al.*, 2016). These demographic changes include elevated mortality rates for a few years after logging followed by increased rates of tree growth and recruitment presumably due to reduced competition and increased sunlight penetration after canopy disturbance (Sist & Nguyen-Thé, 2002; Blanc *et al.*, 2009; Shenkin *et al.*, 2015; Ruslandi *et al.*, 2017). How these demographic changes interact with different logging intensities is an open question with fundamental implications for the forest dynamics that determine carbon stocks and the sustainability of timber harvests. For example, if slow recovery is a consequence of high mortality immediately after logging, implementation of RIL practices at low harvest intensities may be most effective. However, if slow recovery is a consequence of low rates of tree growth after logging, more intensive forest management practices such as liberation thinning to encourage tree growth by reducing neighborhood competition may be most effective. By simultaneously estimating both the timing of the breakpoint and effects of logging before and after the breakpoint, we were able to propagate uncertainty in breakpoint location through to model predictions (Beckage *et al.*, 2007).

We hypothesized that increasing logging intensity both increases losses of ACS during the first several years after logging and induces faster regrowth during the subsequent period. We predict that at a certain threshold logging intensity, depletion of forest ACS outweighs the longer-term gains associated with faster recovery rates. With respect to timber stock recovery, we predict that high logging intensities not only deplete commercial stocks of old growth trees but also result in higher competition between the scattered survivors of commercial species and the non-commercial species that recruit after severe forest disturbance (Villegas *et al.*, 2009). FCT liberation is expected to reduce this competition and accelerate timber stock recovery but at the cost of forest carbon. We also expect the piecewise model to improve our ability to predict timber and carbon recovery post-logging, relative to linear models that do not capture the two distinct demographic phases.

Materials and Methods

Study Site

Our data are from a long-term study in Central Guyana (5º 02` N, 58º 37` W; Fig S1) established in 1993 by Van der Hout (1999) under the Tropenbos-International sustainable forest management and conservation research program (http://www.tropenbos.org/). 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 old and quartz-rich soil derived from Cretaceous sediments on the Precambrian Guiana Shield; these soils are extremely poor compared to those of western Amazonia (Hammond, 2005; Quesada *et al.*, 2010). There are also clear differences in forest structure, floristic composition, and ecological processes between forests in Amazonia and on the Guiana Shield, with the latter characterized by higher carbon stocks and rates of wood production, higher wood densities, bigger seeds, and more dominance by species of Fabaceae (Malhi *et al.*, 2004; ter Steege *et al.*, 2006; Johnson *et al.*, 2016).

The evergreen tropical forest of the study area receives 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 m with emergent trees to 40-50 m (Vanmechelen, 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; N = 15, 1.96 ha plots), 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 are 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 a century prior to our study (Hammond & Ter Steege, 1998).

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 and on lateritic soils, *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 timber value. Prevalent understory species are *Oxandria asbeckii* (karishiri), *Tapura guianensis* (waiaballi), and *Paypayrola spp.* (adebero).

Experimental Design and Logging Treatments

The RIL experimental guidelines used in our study were based on the CELOS Harvest System developed in Suriname (Hendrison, 1990; Jonkers & Hendrison, 2011) and included: pre-harvest mapping of trees of commercial species with good stem form ≥20 cm DBH; selection of trees for harvest to avoid the creation of large canopy openings; and, limits on per species harvest intensities that reflect their respective abundances (Van der Hout, 1999). Minimum felling diameters were species-specific with harvested trees needed to contain > 6 m of defect-free log. All lianas ≥ 2 cm DBH on trees selected for harvest were cut 6 months prior to the felling operation to reduce residual stand damage; 2 years after logging, lianas on FCTs were cut in the liberation treatment only. 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 based on techniques described by Conway (1982) and Brunberg et al. (1994). 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%, downhill, or across streams and gullies. Skid trails were generally straight, spaced 80 m apart, and established with a CAT 528 wheeled skidders equipped with a winch, 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: low intensity (4 trees ha^{-1}/16 m^3 ha^{-1}); moderate intensity (8 trees ha^{-1}/24 m^3 ha^{-1}); high intensity (16 trees ha^{-1}/48 m^3 ha^{-1}); and, moderate-intensity logging followed three years later by a post-harvest liberation of FCTs (more detail provided below; Van der Hout 1999, 2000; Table 1 & Table S1). Each 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) plot for long-term monitoring. In addition to the logged and liberation-treated plots, unlogged stand dynamics were monitored in control plots in each of the three blocks. Trees ≥20 cm DBH (stem diameter at 1.3 m or above buttresses) were recorded in the 1.96 ha experimental sample plots, with twenty-five nested 10 x 10 m subplots used to census trees 5-20 cm DBH (Appendix S1: Figure S1). To enable the experimental logging treatments, blocks with high timber stocking were selected.

All plots were first censused in 1993 (pre-logging) and then the twelve experimental harvest units were 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 and defective commercial species overtopping the FCT and within 10 m radius of its base. Plots were re-censused approximately one (1995), three (1997), six (2000), and twenty years (2013) after logging occurred in 1994; and one (1997), four (2000), and seventeen (2013) years after the 1996 liberation treatment. At each census, tree diameters, mortality, and recruitment 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). We lacked measured tree heights and so used the diameter-height allometric model proposed by Chave *et al.* (2014), $\ln(H) = 0.893 - E + 0.760 * \ln(D) - 0.0340 * (\ln(D))^2$. 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 (D). Aboveground carbon stocks (ACS) were estimated by multiplying aboveground tree biomass by 0.47 (IPCC, 2003).

Stem wood densities (p) 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 average wood density for the 28 stems for which we lacked taxonomic information (Baker et al., 2004). We report ACS for trees ≥10 cm diameter to facilitate comparisons with recent studies on post-logging biomass recovery (Rutishauser *et al.* 2015, Sist *et al.* 2015, Vidal *et al.* 2016). Our biomass estimates based on the Chave *et al.*, (2014) allometry for our logged forests are potentially positively biased as the database of direct-harvest trees are primarily from undisturbed forests with only 5 secondary forests sites, and may not capture the reduction in tree heights observed in logged forests (Rutishauser *et al.*, 2016). The wood density parameter (p) captures differences in species composition (Baker *et al.*, 2004a). To correct for the downward bias in our carbon estimates introduced by diameter measurements made at heights >1.3 m (Metcalf *et al.*, 2009; Cushman *et al.*, 2014), 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 S2).

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

We applied in-country derived species-specific volumetric equations, when available, to estimate merchantable timber stocks at each census, and otherwise used a generic equation (Table S2). Our assessment of rates of post-logging merchantable timber stock recovery is restricted to the 31-species listed as commercial at the time of logging in 1994. Our timber stock estimates only include stems equal to and larger than the minimum cutting diameter for those commercial species (Table S2). We used the log grade scores to adjust our estimates of merchantable timber stocks (100% of grade 1 and 2; 90% of grade 3; and, 80% of grade 4). We used diameters measured above buttresses and trunk deformities to estimate timber stocks because these log sections are rejected during bucking. We also accounted for the subjective assignment of timber grades by multiple inventory crews by not allowing stems to improve bole grades throughout the census period.

Rates of Aboveground Biomass and Timber 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 (for more details on assumptions of new recruit growth see Appendix S1).

We partitioned our census data for timber stock recovery into recruitment rate (r) i.e. the rate at which new recruits grew into stem class ≥ 5 cm DBH, increments (m^3 ha^{-1} yr^{-1}) by advanced residuals (>20 cm DBH but < species-specific cutting diameter limits; Table S2), and increments on residual crop trees (i.e., trees that were merchantable in 1994 but were not harvested). We calculate recruitment based on the equation: $r = \frac{\ln(n_0)-\ln(S_t)}{t}$, where t is the census interval in years, n_0 is the population size at the beginning of the census interval and S_t are the survivors at its end (Condit *et al.*, 1999). The periodic annual increments ($PAIs$) for advanced regeneration and residual commercial trees (m^3 ha^{-1} yr^{-1}) were calculated for each plot as $PAI_{gross} = \frac{(V_{i+1} + I)-V_i}{t}$; where V_i and V_{i+1} represent volume of surviving trees at the beginning and end of each census, respectively, and I is the total volume of recruited trees at the end of the census interval. We also calculated net periodic annual increment as $PAI_{net} = \frac{(V_{i+1} + I)-V_i+M}{t}$, where M represents the volume of trees that died between censuses.

Piecewise Model for ACS and Timber Recovery Predictions

We applied a piecewise regression model (also referred to as a break-point model or broken-stick model; Beckage *et al.*, 2007; Bourgeois *et al.*, 2016) that captures the elevated mortality in the initial years after logging followed by a period of increased rates of residual growth and recruitment (Sist & Nguyen-Thé, 2002; Blanc *et al.*, 2009; Mazzei *et al.*, 2010; Shenkin *et al.*, 2015; Piponiot *et al.*, 2016). Compared to linear models that estimate a single slope parameter, piecewise models allow for rate-dependent changes in the slope parameter, representing threshold dynamics (Toms & Lesperance, 2003; Bourgeois *et al.*, 2016). In our case, we applied a piecewise regression model with a single breakpoint. This model structure results in two straight lines that join at the breakpoints for our ACS and timber stock recovery models:

$$[\text{Eq. } 1] \qquad y_i = \begin{cases} \beta_0 + \beta_1 x_1 + \beta_2\,(x_1 * x_2) + plot\,[i] + e_i & for\; x_1 \leq \alpha \\ \beta_0 + \beta_1 x_1 + \beta_2\,(x_1 * x_2) + \beta_3\left((x_1 - \alpha) * x_2\right) + plot\,[i] + e_i & for\; x_1 > \alpha \end{cases}$$

where y_i is the value for the i^{th} observation, x_1 is time since logged (years), x_2 is logging intensity (m^3 ha^{-1}). β_0 is the intercept term (unlogged forests), β_1 is the background effect of time (including control plots), and β_2 and β_3 are the interaction terms between time since logging and logging intensity, including a pre-breakpoint effect (β_2; elevated mortality) and a post-breakpoint effect (β_3; residual growth and recruitment overtakes post-logging mortality) slopes, respectively. The breakpoint parameter, α, is estimated as a free parameter, representing the time at which increased growth and recruitment outpace post-logging mortality. As we expected recovery of ACS and timber stocks to vary between plots due to spatial heterogeneity, we included plots as random effects ($plot[i]$).

We implement our model in a Bayesian hierarchical framework so as to interpret our results in a probabilistic manner relevant for adaptive forest management (Ghazoul & McAllister, 2003; Clark, 2005). We used non-informative priors, with the exception of the breakpoint parameter, which was parameterized with a weakly informative prior based on previous studies that report the duration of elevated post-logging mortality (Blanc *et al.*, 2009; Shenkin *et al.*, 2015; Piponiot *et al.*, 2016 ; For more details see Appendix S1).We evaluated several variants of the piecewise model, including models with and without the main effects of logging intensity and time since logging, and chose the model structure with the highest predictive accuracy, quantified with out-of-sample predictions (leave-one-out-cross validation; Dietze *et al.*, 2018). Because linear models are commonly used to estimate timber and carbon recovery after logging (Rutishauser *et al.*, 2015b; Lussetti *et al.*, 2016; Roopsind *et al.*, 2017b), we also evaluated the predictive accuracy of linear regression models without the breakpoint and the post-breakpoint interaction term (i.e., without α and β_3 parameter in [Eq. 1]).We do not include the liberated plots in our piecewise models because logging and liberation occurred at different times, and the targeted mortality from the liberation treatment has a different biological interpretation than mortality associated with logging. We expect this model formulation to be more useful for projecting losses and recovery associated with logging intensity, as timber production data are commonly available.

We forecast timber stock recovery and ACS to 30 years after logging, the cutting cycle interval implemented in most selectively logged Amazonian forests (Zarin *et al.*, 2007). Our forecast length is inclusive of the 25-year harvest rotation that most timber concessions opt to implement in Guyana based on harvests of 8.33 m^3 ha^{-1}. We also report variance explained by our random effects (plot-level) by applying the method proposed by Nakagawa & Schielzeth (2013) for mixed effect models. All models were implemented in JAGS software in R (Plummer, 2011; R Development Core Team, 2015) with model code included in Supporting information (Appendix S1).

Results

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

Merchantable timber stocks (i.e., harvestable wood volumes based on species-specific minimum cutting diameters) across all plots prior to logging (1993) averaged 40.9 m^3 ha^{-1} (SE ± 3.0). Over the 20-year observation period, timber stocks in the control plots increased by 45% (from 39.5 to 57.3 m^3 ha^{-1}; Table 1 & Figure S2). Over this same period, RIL-low and RIL-moderate + liberation plots recovered their pre-logged merchantable timber stocks plus an additional 7% (from 38.9 to 41.7 m^3 ha^{-1}) and 15% (from 44.4 to 51.0 m^3 ha^{-1}), respectively. In contrast, RIL-moderate and RIL-high logging intensity remained below their pre-logged harvestable timber stocking by 9% (from 37.0 to 33.6 m^3 ha^{-1}) and 50% (from 44.5 to 22.6 m^3 ha^{-1}), respectively. Net periodic annual increments of harvestable volume were highest in the RIL-moderate + liberated treatment (1.32 m^3 ha^{-1} yr^{-1}) and lowest at RIL-moderate (0.33 m^3 ha^{-1} yr^{-1}; Table 2). Recruitment rates of commercial species into the >5 cm DBH class were also highest in the RIL-moderate + liberation treatment with similarly high levels of recruitment of non-commercial species (Table S3).

Mean aboveground carbon stock (ACS) prior to logging across all 15 plots in 1993 was 185.1 Mg C ha^{-1} (SE ± 6.6; Table 1). Over the 20-year observation period the three control plots increased their mean ACS by 11%, from 183.8 Mg C ha^{-1} in 1993 to 204.3 Mg C ha^{-1} in 2013 (Table 1). Twenty years after logging, ACS in plots subjected to RIL-low and RIL-moderate intensity logging averaged 189.9 Mg C ha^{-1} and 194.3 Mg C ha^{-1}, respectively, which were 3% and 1% higher than pre-logging (Table 1). Initial ACS losses were highest after RIL-high and RIL-moderate + liberation, with 23% and 42% of initial ACS lost, respectively (Figure S3); at 20 and 17 years these treatments were on average 9% (164.1 Mg C ha^{-1}) and 19% (149.8 Mg C ha^{-1}) below their initial ACS (Table 1 & Figure S2). Net periodic increments in aboveground carbon were highest for RIL-moderate + liberation at 1.69 Mg C ha^{-1} yr^{-1} and lowest at 0.13 Mg C ha^{-1} yr^{-1} for low intensity logged plots (Table 3). RIL-moderate, RIL-high, and the control plots recorded similar net increments in aboveground carbon stocks (Table 3). Census-specific changes in basal area, stem density, ACS, and biomass weighted wood density by diameter classes are reported in the Supporting information (Table S1).

Piecewise Regression: Prediction of ACS and Timber Stock Recovery

The piecewise regression coefficients that capture the interaction of time (years-after-logging) and harvest intensity (m^3 ha^{-1}) both indicate significant negative slopes prior to their respective breakpoints for ACS followed by significant positive slopes (Figure 1). The negative values of the interaction terms prior to the breakpoints indicate that losses of both ACS and timber stocks increase with logging intensities. The positive values of the interaction terms after the breakpoint indicate that recovery rates increase with increasing logging intensity. Nevertheless, the higher logging intensity dampens the positive effect of time (β_1) on recovery by elevating the size of the pre-breakpoint parameter (β_2) that captures elevated mortality (Figure 2). The timing of breakpoints was estimated at 1.71 years (95% CI, 1.3 - 2.0) for carbon, and 1.30 years (95 % CI, 0.73 - 1.60) for timber (Figure S4).

Our ACS forecast to 30 years indicate that the probabilities of ACS recovery to pre-logged levels (≥185.1 Mg C ha^{-1}) after low and moderate intensity RIL logging are >90%, and only 45% after high intensity logging (Figure 3). The probabilities of full recovery of merchantable timber stocks (≥ 40.9 m^3 ha^{-1}) by 30 years after low and moderate logging intensity were also high (>90%). In contrast the probability of recovery after RIL-high logging intensity was zero (Figure 3). At the end of the 30 year forecast, ACS in low intensity logged plots average 203.6 Mg C ha^{-1} (95% CI: 184.6 – 222.7), 10% percent greater than in the high intensity logged plots (184.3 Mg C ha^{-1}, 95% CI: 164.4–203.1). Timber stocks averaged 53.0 m^3 ha^{-1} (95% CI: 44.5 – 61.2) in low intensity logged plots at 30 years, twice that in the high intensity logged plots (25.6 m^3 ha^{-1}; 95% CI: 16.7– 35.1; Figure S5).

Overall, the proportion of variance explained by our piecewise model reached values >90% based on out-of-sample R^2 (leave-one-out cross validation) for both timber and ACS recovery models (Table 4). Linear models performed poorly in comparison to the piecewise model, with near-zero proportion of variance explained by linear models for timber and ~50% variance explained for ACS. Our breakpoint model also improved the precision of our predictions (RMSE) in the leave-one-out cross validation; reducing RMSE by 1.5 and 3 times the RSME values predicted in the linear models for ACS and timber stocks, respectively (Table 4). Plot level variation (i.e., random effects) explained 38% (95% CI: 23.8 – 58.6%) and 45% (95% CI: 28.9 – 65.6%) of the total variance (R^2) captured by our piecewise model for timber and ACS recovery, respectively.

Discussion

Reduced-Impact Logging Intensity Thresholds for Sustainable Forest Management

One important challenge for tropical forest management is identification of thresholds for timber extraction and post-logging treatments that are compatible with maintenance of ecosystem values (Petrokofsky *et al.*, 2015). We evaluated logging intensity thresholds beyond which ecosystem benefits specific to carbon and timber recovery are lost. Our experimental data from a Guiana Shield forest suggest that for both carbon and timber, RIL harvests of >8 trees ha^{-1} are followed by slow recovery. A similar study conducted in dipterocarp forests in East, Kalimantan, Indonesia came up with exactly the same logging intensity threshold of 8 trees ha^{-1} with RIL beyond which residual stand resilience is compromised (Sist & Nguyen-Thé, 2002). Those recovery times depend substantially on the presence of remnant old growth trees, which is why, for example, the time-to-recover carbon stocks is even faster at the lowest observed logging intensity (4 trees ha^{-1} or 16 m^3 ha^{-1}). This finding is consistent with Amazonia- wide results that show that the time needed to recover initial carbon stocks increases with ACS losses (Rutishauser *et al.*, 2015a). For biodiversity benefits as well, the lowest logging intensity in our study is close to the purported threshold (10 m^3 ha^{-1}) above which a global meta-analysis of biodiversity impact studies revealed rapidly increasing species losses (Burivalova *et al.*, 2014).

The high probability of harvestable timber volume recovery by the end of the 30-year rotation at a logging intensity of 4 trees ha^{-1} is mostly due to the presence of commercial trees that survived the first harvest (i.e. old growth wood; Figure 3 and Table 2). In contrast, after harvests > 8 tree ha^{-1}, remnant commercial trees are scarce and volume recovery depends on recruitment and growth of advanced regeneration into harvestable size classes (Table 2). One potential pitfall from RIL-low intensity harvests is that they do not stimulate recruitment and growth of commercial species (Table 2). In primary forest in the Guianas, dynamics are slow and governed by gaps formed when large trees die and fall (ter Steege *et al.*, 1996). To the extent that gap dynamics drive growth and recruitment rates (Michela *et al.*, 2008; Villegas *et al.*, 2009), RIL-moderate logging intensity may represent a compromise as this intensity maintains some old growth commercial trees while causing enough disturbance to stimulate recruitment and growth of the advanced regeneration needed for long-term timber production (Table 2). Net ACS increments were slightly higher at our study site compared to Amazonian-averages predicted in Piponiot *et al.*, (2016) at 20 years based on the percentage of initial ACS lost to logging (Figure S3). The higher estimates can both be explained by the inclusion of 10-20 cm diameter classes in our analysis and higher ACS gains from tree growth in the Guiana Shield (Johnson *et al.*, 2016).

Intensification for Timber Production: Timber and Carbon Tradeoffs

Liberation of FCTs from liana loads and overtopping canopy competitors is often recommended as a silvicultural treatment for selectively logged tropical forests (e.g., De Graaf *et al.*, 1999; Peña-Claros *et al.*, 2008). At our study site this treatment applied after RIL-moderate intensity of 8 trees ha^{-1} resulted in a fourfold increase in net merchantable timber volume increments (Table 2) and almost twofold increase in recruitment rates of commercial species into the 5-cm DBH class compared to similarly logged but unliberated forests (Table S3). At 20 years post-logging and 17 years after liberation, the unliberated plots were 33% below pre-logged timber stocks whilst the liberated plots exceeded pre-logged timber stocks by 2% (Table 1). It is important to note that this faster recovery of timber stocks came at the cost of carbon, with liberated forests storing 19% less above-ground carbon than similarly logged but unliberated forests (Figure 4).

The liberation treatment also stimulated recruitment of twice as many non-commercial stems into the 5 cm DBH class as the logged but unliberated plots. One concern about this finding is that these non-commercial species will outcompete the slower growing high wood density commercial species (de Avila *et al.*, 2015). The changing composition of these forests was also reflected in a 3% decline in biomass-weighted wood density in the smaller diameter classes (Table S1). To maintain the high rates of timber stock increments observed after the first liberation treatment, additional liberation treatments may be required if, as in other forests, the benefits last less than a decade (Wadsworth & Zweede, 2006). Multiple liberation treatments may slowly transform these forests, from uneven-aged, high species diversity stands into more homogeneous and otherwise plantation-like stands, with concomitant losses in biodiversity (Putz & Romero, 2014). If increased yields through management intensification in suitable stands allows other, more environmentally sensitive or valuable lands to be spared from such treatments, then there could be overall landscape gains for biodiversity and other non-timber values.

Piecewise Model: Accounting for Demographic Changes After Logging

Although linear regression is often used to analyze biomass recovery after logging (e.g., Rutishauser *et al.*, 2015b; Lussetti *et al.*, 2016; Roopsind *et al.*, 2017b), post-logging recovery is non-linear, due to continued decreases in biomass after logging followed by increases in biomass as the forest recovers (Blanc *et al.*, 2009; Piponiot *et al.*, 2016). Modelling recovery of ACS and timber stocks as a linear response often entails dropping the pre-logged census data. To build a linear relationship between the logging effect and biomass dynamics, observations in logged plots must then be compared to either a static pre-logging baseline condition or to unlogged plots (i.e., controls). In the case of the latter, comparisons with different unlogged plots introduces additional uncertainty given that among plot variation in tropical forests is high due to spatial processes that drive biomass dynamics, such as blowdowns (Chave *et al.*, 2001), while comparisons with a static baseline ignore the fact that tropical forests are constantly changing (Baker *et al.*, 2004b). Our point is that comparisons to different plots and/or a static state introduce uncertainty that could mask the effect of logging intensity on recovery rates. Our piecewise model enabled us to overcome problems with among-plot variation by comparing logging recovery to pre-logged conditions at the plot level, while accounting for changing baselines in the control plots. The conceptual advantages of our piecewise model were mirrored in predictive performance, with substantial gains in out-of-sample R^2 (>90%) for both timber recovery and ACS in the piecewise model, relative to linear models (Table 4). We argue that further use of non-linear models will more accurately reflect post-logging demographic changes that vary with logging intensity.

Our piecewise model also enabled us to quantify the observed interaction between logging intensity and time-since-logging both before and after the breakpoint (Figure 1). Results confirm our expectation that ACS recovery rates increase with logging intensity. A likely demographic mechanism for this result is that residual trees benefit from reduced competition (Villegas *et al.*, 2009). Similarly, carbon losses immediately after logging increase with logging intensity as more trees are killed by felling and other harvest operations. The relative magnitudes of these slope terms suggest a dynamic in which stimulated residual tree growth is insufficient to compensate for post-logging mortality at high logging intensities. Estimating the timing of the breakpoint improved predictive accuracy and contributed to biologically-meaningful inferences. For example, our model predicts that the breakpoint for timber recovery occurs earlier than the breakpoint for carbon recovery, suggesting that RIL goals of reducing mortality of timber species, relative to the non-commercial species, were successful. Model estimates of breakpoint timing were within the range of those reported for other logged forests in the Guiana Shield (Blanc *et al.*, 2009).

Our piecewise model supports the prediction that there are logging intensity thresholds for sustainable timber production beyond which forests recovery as well as the provision of ecosystem services are at risk, even with RIL practices. Moreover, the piecewise model has clear inputs and outputs based on familiar linear regressions, which forest managers may be more comfortable with relative to simulation models that rely on multiple sub-models and the ability to modify and interpret source code (e.g., SYMFOR; Phillips & Gardingen, 2001). Although the period of elevated post-logging mortality is likely to end gradually and not with a sharp breakpoint, capturing such gradual changes requires finer scale temporal data than ours. The piecewise approach can be a useful tool as most other long-term permanent sample plot data in tropical forests are characterized by long and irregular census intervals due to funding gaps. Overall, our piecewise model serves as a compromise between no effort to model recovery and the complex application of more sophisticated models (Alder, 1992).

Implications for Sustainable Forest Management

Managed forests are expected to sustain the capacity to produce timber and provide the ecosystem services needed by society. RIL practices applied in selectively logged forests maintain timber and carbon stocks, at least up to a second harvest, if logging intensities are kept low and conditioned on site-specific characteristics (i.e., below thresholds that retain residual old growth trees). These well-managed forests that provide timber and ecosystem services (e.g., carbon and biodiversity) can potentially offset opportunity costs associated with more profitable land uses such as pastures and croplands that results in huge carbon emissions and losses in biodiversity (Sasaki *et al.*, 2012). However, such ecosystem service payments will require effective policies, governance, and monitoring structures to ensure payments for carbon sequestration and biodiversity improve forestry practices on the ground (e.g., REDD+).

If the primary goal is timber production, higher logging intensities coupled with liberation of future crop trees is recommended but with the caveat that this intensification comes at the cost of other ecosystem services, or at least carbon, for which forests are also valued (Houghton *et al.*, 2015). If intensification of timber production occurs in a portion of the landscape and satisfies timber demand, there will be more opportunities for protection of more pristine forests (i.e., land sparing; Edwards *et al.*, 2014; Griscom *et al.*, 2017)**.**

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Figure 1. Piecewise model coefficients for aboveground carbon and timber stocks. Points are the mean parameter estimate with vertical lines indicating 95% credible intervals. Parameter estimates that do not cross the zero value (dashed line) can be considered to have a significant effect. The *Time* term represents the baseline impact of time across all plots (including controls). The effects of logging before and after the breakpoint represent the interactions between logging intensity and time since logging during these two time periods.

Figure 2. Predictions from piecewise regression models for ACS (Mg C ha^{-1}) and timber stocks (m^3 ha^{-1}) in unlogged forests and at different logging intensities using RIL. Dark lines are mean predicted recovery, with 95% credible intervals indicated by the lighter shaded bands. Points are the observed values. Predictions account for both parameter and sampling uncertainty.

Figure 3. Probability of recovery of ACS and harvestable timber stocks to pre-logged carbon stocks (184 Mg C ha^{-1}) and harvestable timber volume (40 m^3 ha^{-1}) for forests logged at RIL- low, moderate and high intensity. Model forecasts span 30 years (10-years beyond observed data).

Figure 4. Recovery of ACS (left panel - a) and harvestable timber stocks (right panel - b) for forests logged at an intermediate intensity (RIL-moderate; 8 trees ha^{-1}; solid line) and forests logged at the same intensity and subjected to liberation thinning (RIL-moderate + liberation; broken line). A solid arrow on the x-axis indicates time of logging (1994) and a broken arrow indicates the time of liberation (1996).

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Table 1. Harvest information and silvicultural treatments applied in the Pibiri reduced-impact logging growth and yield experimental plots in central Guyana based on all trees ≥10 cm DBH in 1.96 ha; pre-harvest forest structure prior to logging intervention (1993), 20-years post-logging, and 17-years post-liberation of future crop trees (2013).

Silvicultural Treatment	**Plot ID**	Extracted timber (m^3 ha^{-1})	Basal area harvested (m^2 ha^{-1})	Stems harvested (ha^{-1})	**Pre-harvest stand structure (1993)**				**Post-harvest/treatment stand structure (2013)**			
					Basal area (m^2 ha^{-1})	Stem density (ha^{-1})	ACS (Mg C ha^{-1})	Merchantable timber stocks * (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Stem density (ha^{-1})	ACS (Mg C ha^{-1})	Merchantable timber stocks * (m^3 ha^{-1})
RIL – Low	3	14.30	1.10	4	30.6	461	222.89	41.05	30.7	421	232.25	45.89
RIL – Low	10	16.30	1.20	4	25.3	561	155.22	38.43	25.4	525	158.16	36.76
RIL – Low	11	18.20	1.30	4	26.7	478	177.10	37.22	26.2	423	179.40	42.50
RIL – Moderate	1	25.60	2.00	8	24.8	481	166.05	34.48	27.5	491	192.40	33.18
RIL – Moderate	8	20.80	1.80	8	29.5	668	186.48	26.42	27.4	600	176.24	26.81
RIL – Moderate	15	24.50	1.90	8	30.2	458	222.56	50.16	29.0	441	214.17	40.78
RIL – High	2	39.70	3.40	16	28.3	466	208.53	35.39	26.4	444	187.60	16.66
RIL – High	7	53.80	4.00	16	24.1	432	159.86	51.31	23.2	516	143.02	18.19
RIL – High	14	50.30	3.60	16	25.8	443	174.69	46.79	24.7	508	161.62	32.88
RIL - Moderate + liberation	4	26.30	1.9 (5.5+)	8 (49+)	25.0	511	161.28	40.05	22.6	530	135.71	39.85
RIL - Moderate + liberation	9	23.00	1.8 (7.3+)	8 (64+)	26.2	537	165.48	23.20	23.7	538	146.77	30.68
RIL - Moderate + liberation	13	38.60	2.7 (9.0+)	8 (54+)	29.6	402	224.50	69.96	24.0	447	166.82	82.36
Control (unlogged)	5	-	-	-	26.5	464	177.47	35.16	28.7	473	195.82	58.14
Control (unlogged)	6	-	-	-	24.4	442	164.20	34.53	26.3	425	177.95	49.39
Control (unlogged)	12	-	-	-	27.7	340	209.81	48.81	31.5	394	238.98	64.33

+ killed by frilled and poison

* includes only volumes in trees larger than species-specific minimum cutting diameters (Table S2)

Table 2. Periodic annual increments (m^3 ha^{-1} yr^{-1}) for advanced regeneration (>20 cm DBH and < species-specific cutting diameters) and harvestable timber volumes for commercial timber species. Note that trees that transition from advanced regeneration into the harvestable classes reduce the former.

Silvicultural Treatment	Gross volume increments of advanced regeneration (m^3 ha^{-1} $year^{-1}$; ± 1 SE)	Gross harvestable volume increments (m^3 ha^{-1} $year^{-1}$; ± 1 SE)	Net harvestable volume increments (m^3 ha^{-1} $year^{-1}$; ± 1 SE)
RIL - Low	-0.01 (± 0.19)	0.86 (± 0.15)	0.77 (±0.12)
RIL - Moderate	0.58 (± 0.19)	0.45 (± 0.14)	0.33 (±0.16)
RIL - High	0.47 (± 0.27)	0.70 (± 0.11)	0.68 (±0.12)
RIL - Moderate + liberation	0.91 (± 0.21)	1.58 (± 0.39)	1.32 (±0.31)
Control (unlogged)	-0.02 (± 0.20)	1.09 (± 0.17)	1.02 (±0.18)

Table 3. Gross and net periodic annual increments (PAI; Mg C ha^{-1} yr^{-1}) for trees ≥ 10 cm DBH for the post-logging recovery of 1997 to 2013.

Silvicultural Treatment	Gross PAI of aboveground carbon (Mg C ha^{-1} $year^{-1}$; SE)	Net PAI of aboveground carbon (Mg C ha^{-1} $year^{-1}$; SE)
RIL - Low	2.11 (± 0.32)	0.13 (± 0.42)
RIL - Moderate	2.78 (± 0.78)	1.09 (± 1.02)
RIL - High	2.88 (± 0.55)	1.04 (± 0.65)
RIL - Moderate + liberation	3.54 (± 0.63)	1.69 (± 0.88)
Control (unlogged)	2.34 (± 0.57)	1.02 (± 0.87)

Table 4. Out-of-sample predictive performance of piecewise and linear models, estimated using leave-one-out cross validation (Eq.1).

	R^2 (95% CI)	RMSE (95% CI)
Piecewise models (Eq. 1)		
Timber stocks	0.91(0.88 - 0.94)	4.35 (3.72 - 5.00)
Aboveground carbon stocks	0.92 (0.90-0.94)	8.04 (6.85 - 9.20)
Linear models – (excludes the α parameter and second term in Eq. 1)		
Timber stocks	0.00 (0.00-0.04)	16.99 (14.33 - 19.93)
Aboveground carbon stocks	0.49 (0.33 - 0.63)	20.44 (17.44 - 23.57)

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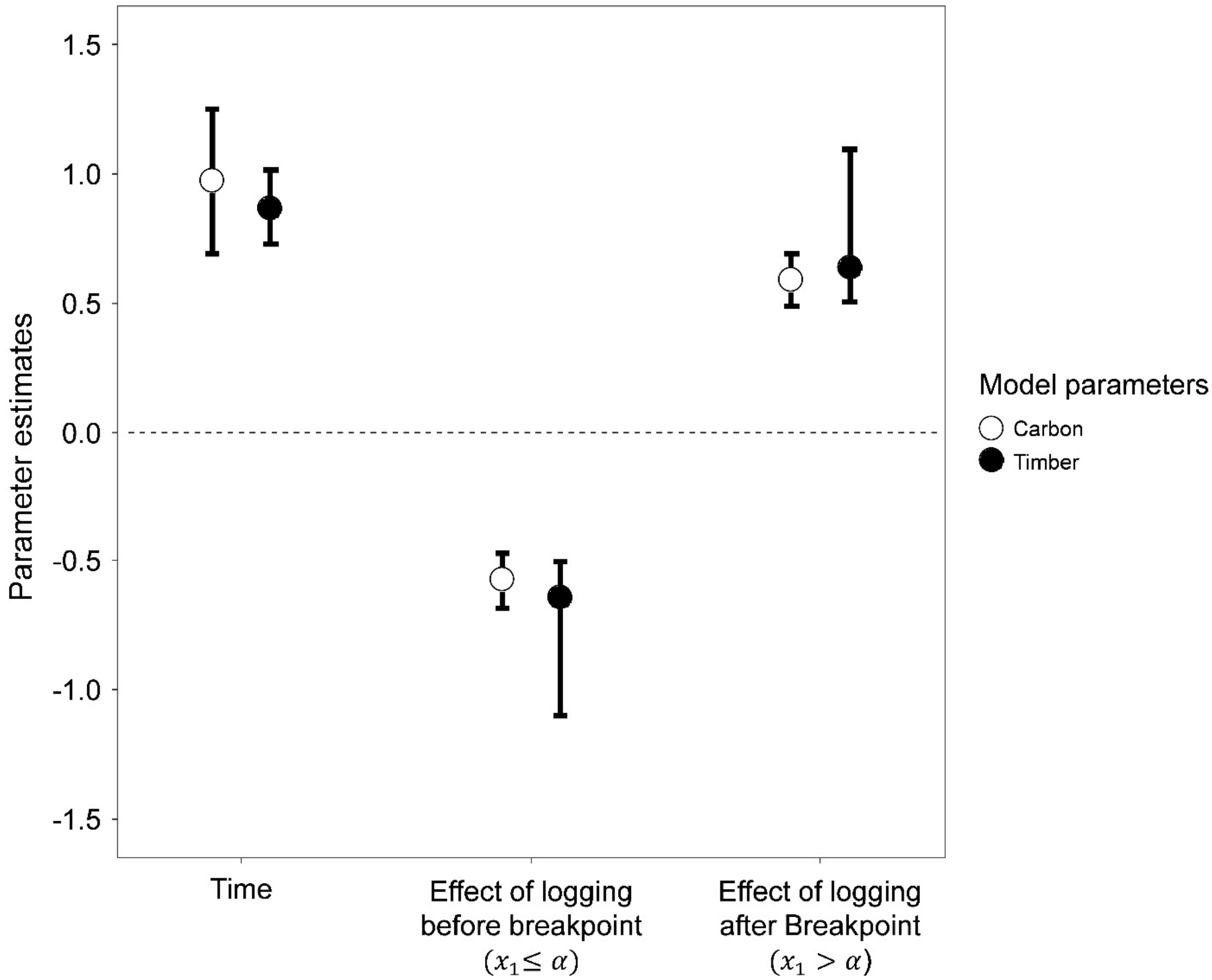


Figure 1

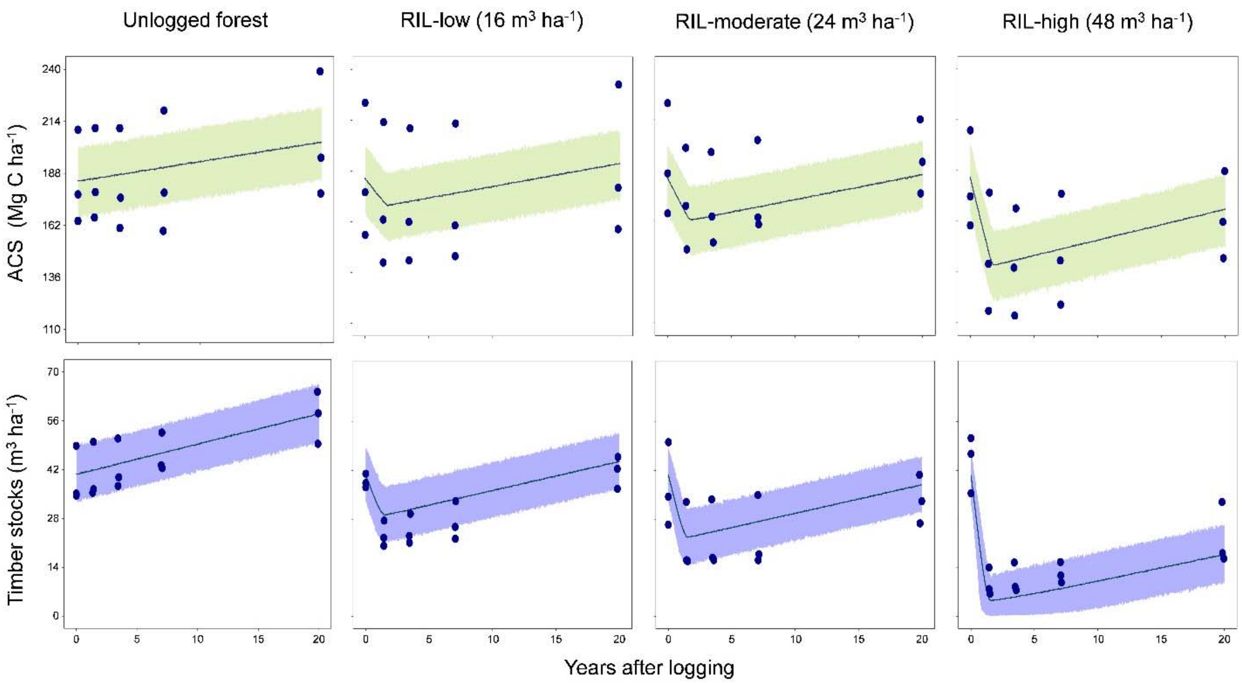


Figure 2

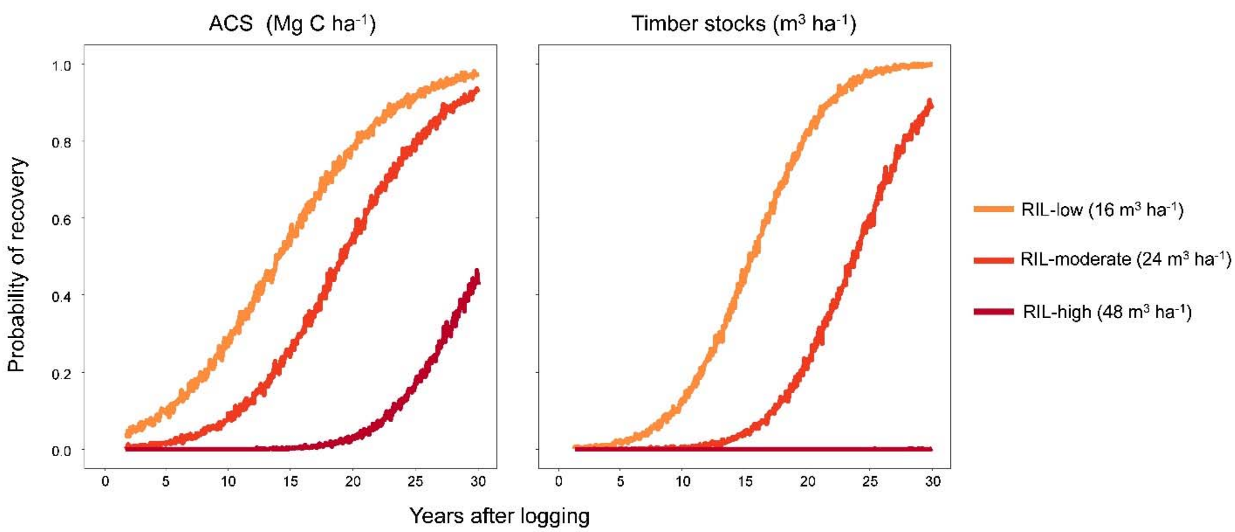
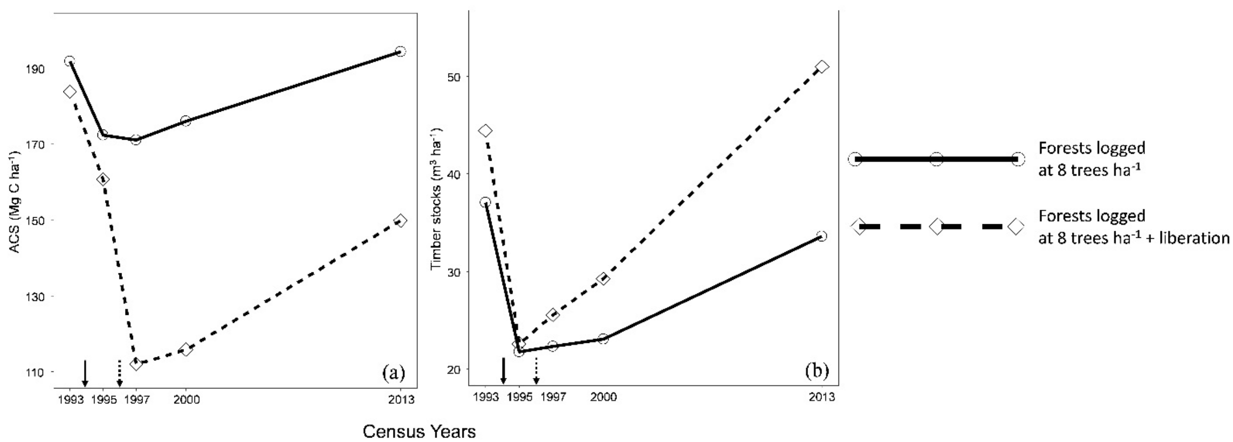


Figure 3



ACS (Mg C ha-1)
190
170
150
130
110
(a)
Timber stocks (m3 ha-1)
50
40
30
20
(b)
1993
1995
1997
2000
2013
Census Years
Forests logged
at 8 trees ha-1
Forests logged
at 8 trees ha-1 + liberation

Figure 4