



Trade-offs between carbon stocks and timber recovery in tropical forests are mediated by logging intensity

Anand Roopsind¹  | T. Trevor Caughlin¹ | Peter van der Hout² | Eric Arets³  | Francis E. Putz⁴

¹Biological Sciences, Boise State University, Boise, ID, USA

²Van der Hout Forestry Consulting, Rotterdam, The Netherlands

³Wageningen University and Research, Wageningen, The Netherlands

⁴Department of Biology, University of Florida, Gainesville, FL, USA

Correspondence

Anand Roopsind, Biological Sciences, Boise State University, Boise, ID, USA.

Email: anandroopsind@boisestate.edu

Funding information

WWF-Guianas Program; WWF-Russell E. Train Fellow; NSF

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, 8, and 16 trees/ha). Our census data span 20 years postlogging 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 postlogging mortality led to high predictive accuracy, including out-of-sample R^2 values >90%, and enabled inference on demographic changes postlogging. 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, climate change mitigation, forest degradation, piecewise regression, REDD+, sustainable forest management, tropical forestry

1 | 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, Holmes, & Carter, 2003; Putz, Sist, Fredericksen, & Dykstra, 2008; Putz et al., 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 (Dykstra, 2001; Dykstra & Heinrich, 1996; Hendrison, 1990; Pinard, Putz, Tay, & Sullivan, 1995; Sist, 2000; Van der Hout, 1999). 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, Brown, Murray, & Sidman, 2017), efforts to reduce carbon emissions from forestry activities are of global importance (Houghton, Byers, & Nassikas, 2015).

Reduced-impact logging guidelines typically include: (i) preharvest tree inventories and topographic mapping; (ii) prefalling vine cutting; (iii) directional felling; and (iv) controls on the lengths, widths, layout, and use of preplanned skid trails and logging roads. Use of these practices reduces both the spatial extent and severity of logging impacts (e.g., Arevalo et al., 2016; Asner, Keller, Pereira, Zweede, & Silva, 2004; Edwards et al., 2014; Vidal, West, & Putz, 2016). More specifically, application of RIL practices reduces soil damage (Pinard et al., 1995; Sist, 2000), biodiversity loss (Bicknell, Struebig, & Davies, 2015; Roopsind, Caughlin, Sambhu, Fragoso, & Putz, 2017), hydrological disruption (Douglas, 1999; Miller et al., 2011), and carbon emissions (e.g., Pinard & Putz, 1996) relative to unplanned or conventional logging. Postlogging recovery rates of timber and carbon stocks are also reportedly faster after RIL than after conventional logging (Lussetti, Axelsson, Ilstedt, Falck, & Karlsson, 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 & Ruslandi, 2015; Ruslandi, Cropper, & Putz, 2017), such as the liberation of future crop trees, it also becomes important to quantify trade-offs 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 trade-offs 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 (Johnson et al., 2016; Pioniot et al., 2016; ter Steege et al., 2006). We monitored trees ≥ 5 cm diameter

at breast height (DBH) from 1993 to 2013 in replicated plots subjected to RIL at one of three logging intensities, with a fourth treatment that included a postlogging 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 trade-offs 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 postlogging demographic changes that result in nonlinear biomass dynamics at the stand level (Pioniot 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 (Blanc et al., 2009; Ruslandi et al., 2017; Shenkin, Bolker, Peña-Claros, Licona, & Putz, 2015; Sist & Nguyen-Thé, 2002). 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, Joseph, Belisle, Wolfson, & Platt, 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 noncommercial 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 postlogging, relative to linear models that do not capture the two distinct demographic phases.

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; preharvest forest structure prior to logging intervention (1993), 20 years postlogging, and 17 years postliberation of future crop trees (2013)

Silvicultural treatment	Plot ID	Preharvest stand structure (1993)			Postlogging/treatment stand structure (2013)							
		Extracted timber (m ³ /ha)	Basal area harvested (m ² /ha)	Stems harvested (ha ⁻¹)	Basal area (m ² /ha)	Stem density (ha ⁻¹)	ACS (Mg C ha ⁻¹)	Merchantable timber stocks ^a (m ³ /ha)	Basal area (m ² /ha)	Stem density (ha ⁻¹)	ACS (Mg C ha ⁻¹)	Merchantable timber stocks ^a (m ³ /ha)
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 ^b)	8 (49 ^b)	25.0	511	161.28	40.05	22.6	530	135.71	39.85
RIL—Moderate + liberation	9	23.00	1.8 (7.3 ^b)	8 (64 ^b)	26.2	537	165.48	23.20	23.7	538	146.77	30.68
RIL—Moderate + liberation	13	38.60	2.7 (9.0 ^b)	8 (54 ^b)	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

^aIncludes only volumes in trees larger than species-specific minimum cutting diameters (Table S2).

^bKilled by frilled and poison.

2 | MATERIALS AND METHODS

2.1 | Study site

Our data are from a long-term study in Central Guyana (5°02'N, 58°37'W; Figure 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 (Johnson et al., 2016; Malhi et al., 2004; ter Steege et al., 2006).

The evergreen tropical forest of the study area receives 2,772 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 ($SE \pm 19$; $N = 15$, 1.96 ha plots), with species composition that varied with local soil characteristics, topographic position, and water availability (Ter Steege, Jetten, Polak, & Werger, 1993). Approximately 10% of the 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 (Zagt, Ek, & Raes, 2003). In unlogged forest, the crowns of 9% of trees ≥ 20 cm DBH are liana infested. 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 codominants. 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).

2.2 | Experimental design and logging treatments

The RIL experimental guidelines used in our study were based on the CELOS Harvest System developed in Suriname (Henderson,

1990; Jonkers & Hendrison, 2011) and included: preharvest 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 Brunberg and Lindgren (1984) and Conway (1982). 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 or 16 m³/ha); moderate intensity (8 trees/ha or 24 m³/ha), high intensity (16 trees/ha or 48 m³/ha), and moderate-intensity logging followed 3 years later by a postlogging liberation of FCTs (more detail provided below; Van der Hout, 1999, 2000; Tables 1 and S1). Each treatment was replicated three times in 5.76 ha (240 × 240 m) plots with a centrally located 1.96 ha (140 × 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 were recorded in the 1.96 ha sample plots, with 25 nested 10 × 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 (prelogging) and then the 12 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 noncommercial trees and defective commercial species overtopping the FCT and within 10 m radius of its base. Plots were re-censused approximately 1 (1995), 3 (1997), 6 (2000), and 20 years (2013) after logging in 1994; and 1 (1997), 4 (2000), and 17 years (2013) 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.

2.3 | 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/cm³), 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), $\ln(H) = 0.893 - E + 0.760 \cdot \ln(D) - 0.0340 \cdot (\ln(D))^2$. 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 (ρ) were extracted from a global pan-tropical database (Chave et al., 2009); in the absence of species-level data (9.4% 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., 2004a). We report ACS for trees ≥ 10 cm diameter to facilitate comparisons with recent studies on postlogging 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 five secondary forest sites, and may not capture the reduction in tree heights observed in logged forests (Rutishauser, Hérault, Petronelli, & Sist, 2016). The wood density parameter (ρ) 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 (Cushman, Muller-Landau, Condit, & Hubbell, 2014; Metcalf, Clark, & Clark, 2009), we developed and implemented a taper correction model using a local dataset with multiple diameter measurements along the trunks of 150 trees in 23 genera (Appendix S2).

2.4 | Merchantable timber stocks (m^3/ha)

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 postlogging 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 between the census period.

2.5 | 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), that is, the rate at which new recruits grew into the ≥ 5 cm DBH class, increments ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) 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 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 ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) were calculated for each plot as $\text{PAI}_{\text{gross}} = \frac{(V_{i+1} + I) - V_i}{t}$, 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 $\text{PAI}_{\text{net}} = \frac{(V_{i+1} + I) - V_i + M}{t}$, where M represents the volume of trees that died between censuses.

2.6 | Piecewise model for ACS and timber recovery predictions

We applied a piecewise regression model (also referred to as a breakpoint 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 (Blanc et al., 2009; Mazzei et al., 2010; Pioniot et al., 2016; Shenkin et al., 2015; Sist & Nguyen-Thé, 2002). Compared to linear models that estimate a single slope parameter, piecewise models allow for rate-dependent changes in the slope parameter, representing threshold dynamics (Bourgeois et al., 2016; Toms & Lesperance, 2003). 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:

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

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). 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 prebreakpoint effect (β_2 ; elevated mortality) and a postbreakpoint effect (β_3 ; residual growth and recruitment overtakes postlogging mortality) slopes, respectively. The breakpoint parameter, α , is estimated as a free parameter, representing the time at which increased growth and

TABLE 2 Periodic annual increments ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) for advanced regeneration (>20 cm DBH and $<$ species-specific cutting diameters) and harvestable timber volumes for commercial timber species

Silvicultural treatment	Gross volume increments of advanced regeneration ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$; ± 1 SE)	Gross harvestable volume increments ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$; ± 1 SE)	Net harvestable volume increments ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$; ± 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)

Note that trees that transition from advanced regeneration into the harvestable classes reduce the former.

recruitment outpace postlogging 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 (Clark, 2005; Ghazoul & McAllister, 2003). We used noninformative 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 postlogging mortality (Blanc et al., 2009; Shenkin et al., 2015; Pioniot 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 (Lussetti et al., 2016; Roopsind, Wortel, Hanoeman, & Putz, 2017; Rutishauser et al., 2015), we also evaluated the predictive accuracy of linear regression models without the breakpoint and the postbreakpoint interaction term (i.e., without α and β_3 parameter in [Equation 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, Schulze, Vidal, & Lentini, 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 $8.33 \text{ m}^3/\text{ha}$. We also report variance explained by our random effects (plot level) by applying the method proposed by Nakagawa and 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 (Appendix S1).

3 | RESULTS

3.1 | Observed recovery: merchantable timber stocks (m^3/ha) 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 $40.9 \text{ m}^3/\text{ha}$ ($SE \pm 3.0$). Over the 20 year observation period, timber stocks in the control plots increased by 45% (from 39.5 to $57.3 \text{ m}^3/\text{ha}$; Table 1 & Figure S2). Over this same period, RIL-low and RIL-moderate + liberation plots recovered their prelogged merchantable timber stocks plus an additional 7% (from 38.9 to $41.7 \text{ m}^3/\text{ha}$) and 15% (from 44.4 to $51.0 \text{ m}^3/\text{ha}$), respectively. In contrast, RIL-moderate and RIL-high logging intensity remained below their prelogged harvestable timber stocking by 9% (from 37.0 to $33.6 \text{ m}^3/\text{ha}$) and 50% (from 44.5 to $22.6 \text{ m}^3/\text{ha}$), respectively. Net periodic annual increments of harvestable volume were highest in the RIL-moderate + liberated treatment ($1.32 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$) and lowest at RIL-moderate ($0.33 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$; 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 noncommercial species (Table S3).

Mean aboveground carbon stock (ACS) prior to logging across all 15 plots in 1993 was $185.1 \text{ Mg C ha}^{-1}$ ($SE \pm 6.6$; Table 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 1). Twenty years after logging, ACS in plots subjected to RIL-low and RIL-moderate-intensity logging averaged 189.9 and $194.3 \text{ Mg C ha}^{-1}$, respectively, which were 3% and 1% higher than prelogging (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% ($164.1 \text{ Mg C ha}^{-1}$) and 19% ($149.8 \text{ Mg C ha}^{-1}$) below their initial ACS (Table 1 & Figure S2). Net periodic increments in aboveground carbon were highest for RIL-moderate + liberation at $1.69 \text{ Mg C ha}^{-1} \text{year}^{-1}$ and lowest at $0.13 \text{ Mg C ha}^{-1} \text{year}^{-1}$ for low-intensity logged plots (Table 3). RIL-moderate, RIL-high, and the control plots recorded similar net

TABLE 3 Gross and net periodic annual increments (PAI; Mg C ha⁻¹ year⁻¹) for trees ≥10 cm DBH for the postlogging recovery of 1997–2013

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)

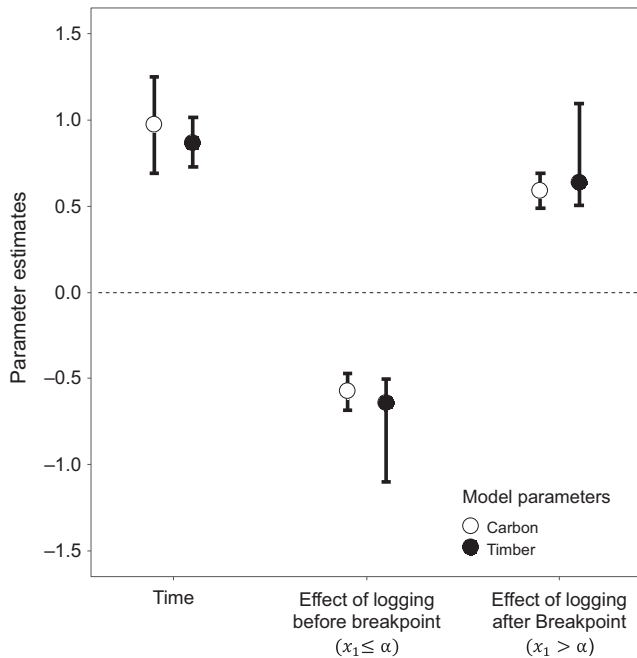


FIGURE 1 Piecewise model coefficients for aboveground carbon and timber stocks. Points are the mean parameter estimate with vertical lines indicating 95% credible intervals. Parameter estimates that do not cross the zero value (dashed line) can be considered to have a significant effect. The *Time* term 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

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 (Table S1).

3.2 | 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 (m³/ha) 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, higher logging intensity dampen the positive effect of time (β_1) on recovery by elevating the size of the prebreakpoint 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 prelogged levels (≥ 185.1 Mg C ha⁻¹) after low- and moderate-intensity RIL logging are >90%, but only 45% after high-intensity logging (Figure 3). The probabilities of full recovery of merchantable timber stocks (≥ 40.9 m³/ha) 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 m³/ha (95% CI: 44.5–61.2) in low-intensity logged plots at 30 years, twice that in the high-intensity logged plots (25.6 m³/ha; 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.

4 | DISCUSSION

4.1 | Reduced-impact logging intensity thresholds for sustainable forest management

One important challenge for tropical forest management is identification of thresholds for timber extraction and postlogging 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 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 with RIL beyond which residual stand resilience is compromised (Sist & Nguyen-Thé, 2002). Those recovery times depend substantially on the presence

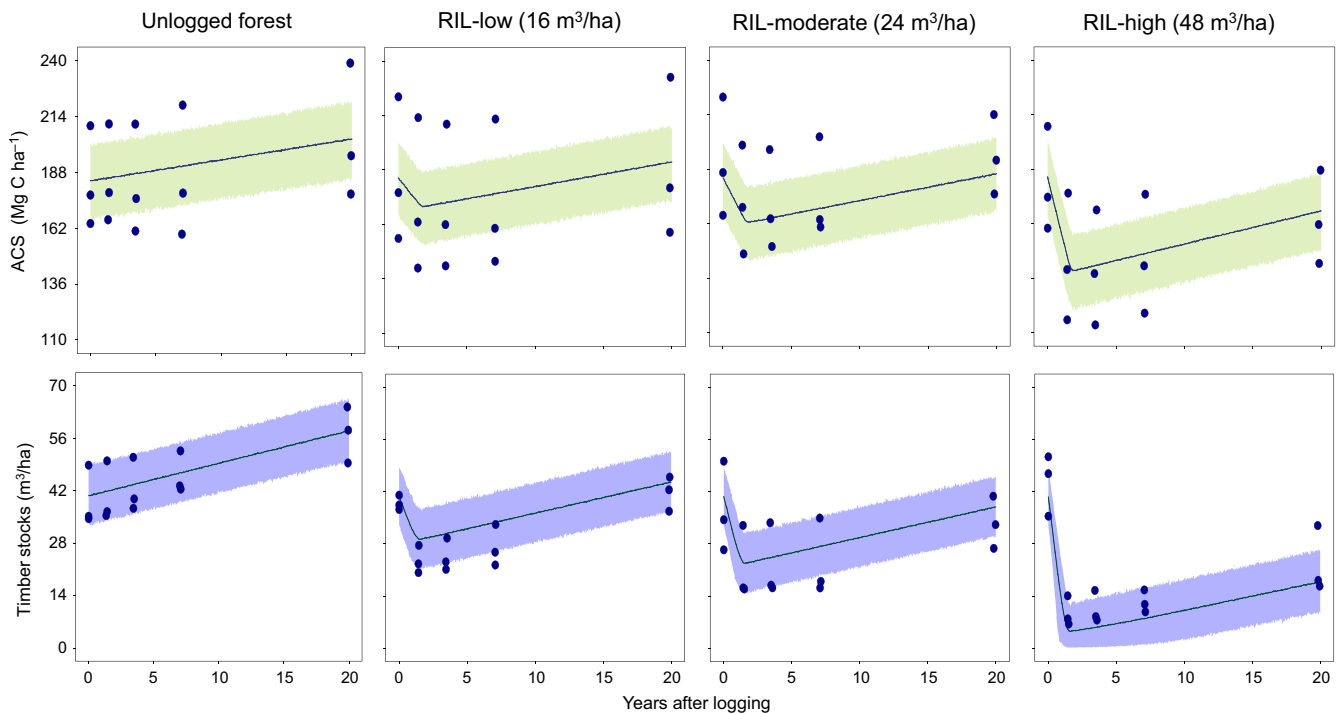


FIGURE 2 Predictions from piecewise regression models for aboveground carbon stocks (Mg C ha^{-1}) and timber stocks (m^3/ha) in unlogged forests and at different logging intensities using reduced-impact logging. Dark lines are mean predicted recovery, with 95% credible intervals indicated by the lighter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

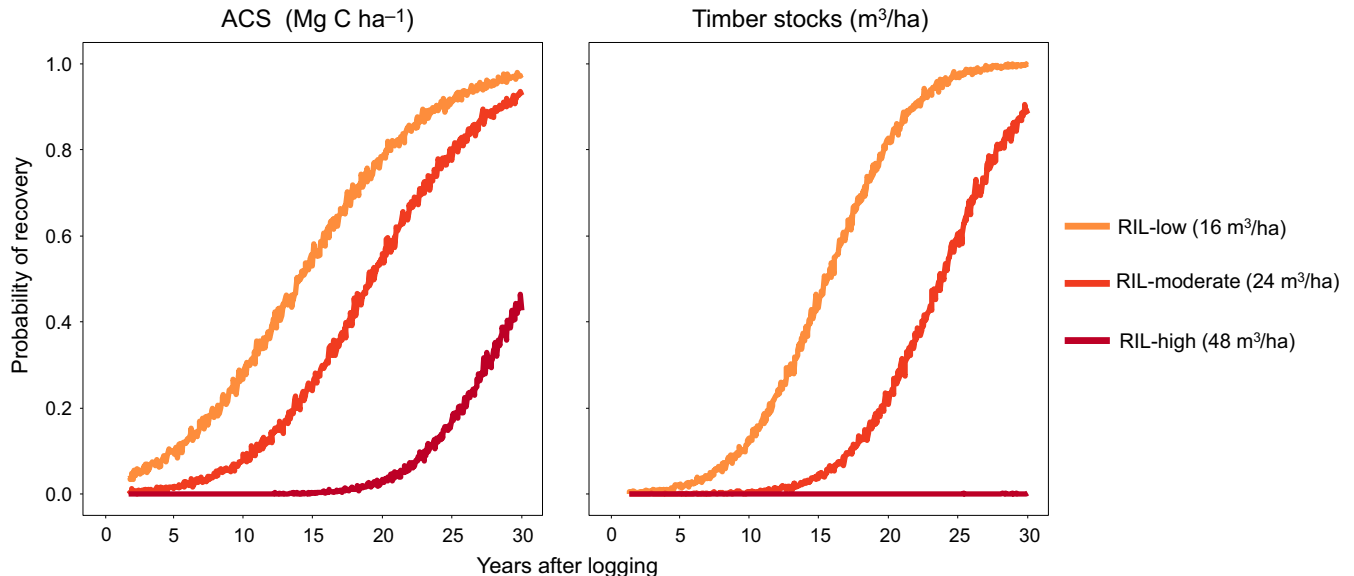


FIGURE 3 Probability of recovery of aboveground carbon stocks and harvestable timber stocks to prelogged carbon stocks (184 Mg C ha^{-1}) and harvestable timber volume ($40 \text{ m}^3/\text{ha}$) for forests logged at reduced-impact logging—low, moderate, and high intensity. Model forecasts span 30 years (10 years beyond observed data)

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 or $16 \text{ m}^3/\text{ha}$). 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.,

2015). For biodiversity benefits as well, the lowest logging intensity in our study is close to the purported threshold ($10 \text{ m}^3/\text{ha}$) above which a global meta-analysis of biodiversity impact studies revealed rapidly increasing species losses (Burivalova, Sekercioglu, & Koh, 2014).

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

	R^2 (95% CI)	RMSE (95% CI)
Piecewise models (Equation 1)		
Timber stocks	.91(0.88–0.94)	4.35 (3.72–5.00)
Aboveground carbon stocks	.92 (0.90–0.94)	8.04 (6.85–9.20)
Linear models—(excludes the α parameter and second term in Equation 1)		
Timber stocks	.00 (0.00–0.04)	16.99 (14.33–19.93)
Aboveground carbon stocks	.49 (0.33–0.63)	20.44 (17.44–23.57)

The high probability of harvestable timber volume recovery by the end of the 30 year rotation at a logging intensity of 4 trees/ha 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 trees/ha, 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 (Figueira 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 Pioniot 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).

4.2 | Intensification for timber production: timber and carbon trade-offs

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, Poels, & Van Rompaey, 1999; Peña-Claros et al., 2008). At our study site this treatment applied after RIL-moderate intensity of 8 trees/ha resulted in a four-fold 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 postlogging and 17 years after liberation, the unliberated plots were 33% below prelogged timber stocks while the liberated plots exceeded prelogged 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 noncommercial stems into the 5 cm DBH class as the logged but unliberated plots. One concern about this finding is that these noncommercial 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

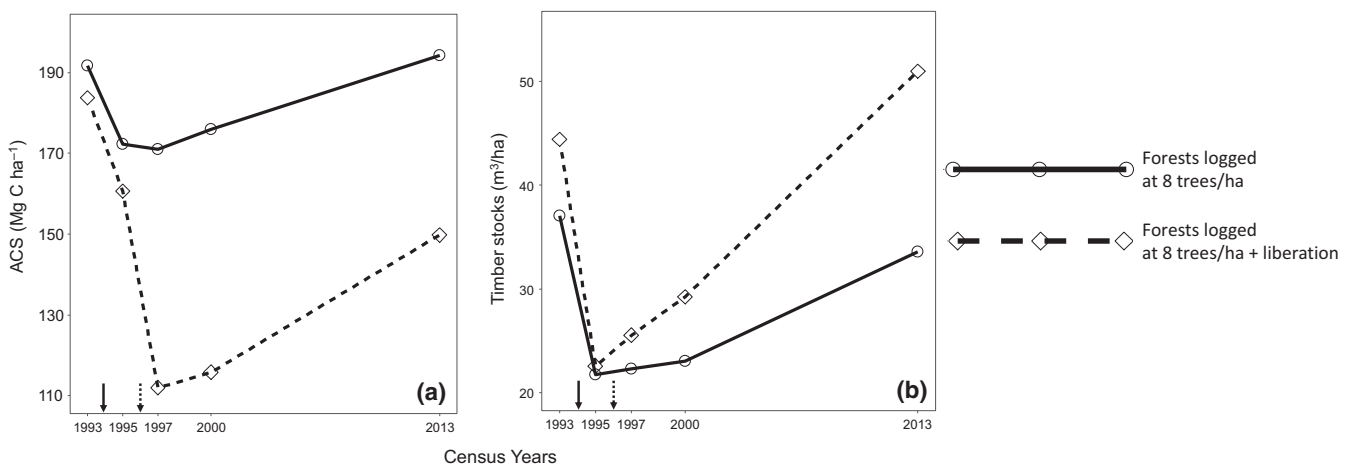


FIGURE 4 Recovery of aboveground carbon stocks (left panel—a) and harvestable timber stocks (right panel—b) for forests logged at an intermediate intensity reduced-impact logging (RIL-moderate; 8 trees/ha; solid line) and forests logged at the same intensity and subjected to liberation thinning (RIL-moderate + 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)

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 allow other, more environmentally sensitive or valuable lands to be spared from such treatments, then there could be overall landscape gains for biodiversity and other nontimber values.

4.3 | Piecewise model: accounting for demographic changes after logging

Although linear regression is often used to analyze biomass recovery after logging (e.g., Lussetti et al., 2016; Roopsind, Wortel et al., 2017; Rutishauser et al., 2015), postlogging recovery is nonlinear, 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). Modeling recovery of ACS and timber stocks as a linear response often entails dropping the prelogged 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 prelogging 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, Riera, & Dubois, 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 prelogged 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 nonlinear models will more accurately reflect postlogging 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 postlogging 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 noncommercial 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 submodels and the ability to modify and interpret source code (e.g., SYMFOR; Phillips & van Gardingen, 2001). Although the period of elevated postlogging 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).

4.4 | 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, Chheng, & Ty, 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, 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, Goodman, Burivalova, & Putz, 2017).

ACKNOWLEDGEMENTS

We would like to express our appreciation to the many field technicians who assisted in the collection of the census data over more than two decades, and especially Benedict Harry who represents an institution unto himself. We thank an anonymous reviewer who provided valuable guidance and suggestions on our model formulation. The study was supported through funding from the WWF-Guianas Program. AR was supported by a WWF-Russell E. Train Fellow and TTC was supported by NSF Grant #1415297.

ORCID

Anand Roopsind  <http://orcid.org/0000-0002-4682-1774>

Eric Arets  <http://orcid.org/0000-0001-7209-9028>

REFERENCES

- Alder, D. (1992). Simple methods for calculating minimum diameter and sustainable yield in mixed tropical forest. In F. Miller & K. Adam (Eds.), *Wise management of tropical forests. Proceedings of the oxford conference on tropical forests* (pp. 189–200). Oxford, UK: Oxford Forest Institute.
- Arevalo, B., Valladarez, J., Muschamp, S., Kay, E., Finkral, A., Roopsind, A., & Putz, F. E. (2016). Effects of reduced-impact selective logging on palm regeneration in Belize. *Forest Ecology and Management*, *369*, 155–160. <https://doi.org/10.1016/j.foreco.2016.03.040>
- Asner, G. P., Broadbent, E. N., Oliveira, P. J. C., Keller, M., Knapp, D. E., & Silva, J. N. M. (2006). Condition and fate of logged forests in the Brazilian Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 12947–12950. <https://doi.org/10.1073/pnas.0604093103>
- Asner, G. P., Keller, M., Pereira, J. R., Zweede, J. C., & Silva, J. N. M. (2004). Canopy damage and recovery after selective logging in Amazonia: Field and satellite studies. *Ecological Applications*, *14*, 280–298. <https://doi.org/10.1890/01-6019>
- de Avila, A. L., Ruschel, A. R., de Carvalho, J. O., Mazzei, L., Silva, J. N., do Carmo Lopes, J., ... Bauhus, J. (2015). Medium-term dynamics of tree species composition in response to silvicultural intervention intensities in a tropical rain forest. *Biological Conservation*, *191*, 577–586. <https://doi.org/10.1016/j.biocon.2015.08.004>
- Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., & Houghton, R. (2017). Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science*, *358*, 230–234. <https://doi.org/10.1126/science.aam5962>
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., ... Laurance, W. F. (2004b). Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *359*, 353–365. <https://doi.org/10.1098/rstb.2003.1422>
- Baker, T. R., Phillips, O., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., ... Lewis, S. L. (2004a). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, *10*, 545–562. <https://doi.org/10.1111/j.1365-2486.2004.00751.x>
- Beckage, B., Joseph, L., Belisle, P., Wolfson, D. B., & Platt, W. J. (2007). Bayesian change-point analyses in ecology. *New Phytologist*, *174*, 456–467. <https://doi.org/10.1111/j.1469-8137.2007.01991.x>
- Bicknell, J. E., Struebig, M. J., & Davies, Z. G. (2015). Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *Journal of Applied Ecology*, *52*, 379–388. <https://doi.org/10.1111/1365-2664.12391>
- Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Chave, J., & Baraloto, C. (2009). Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecological Applications: a Publication of the Ecological Society of America*, *19*, 1397–1404. <https://doi.org/10.1890/08-1572.1>
- Boltz, F., Holmes, T. P., & Carter, D. R. (2003). Economic and environmental impacts of conventional and reduced-impact logging in Tropical South America: A comparative review. *Forest Policy and Economics*, *5*, 69–81. [https://doi.org/10.1016/S1389-9341\(01\)00075-2](https://doi.org/10.1016/S1389-9341(01)00075-2)
- Bourgeois, B., Vanasse, A., Gonzalez, E., Andersen, R., Poulin, M., & Wilsey, B. (2016). Threshold dynamics in plant succession after tree planting in agricultural riparian zones. *Journal of Applied Ecology*, *53*, 1704–1713. <https://doi.org/10.1111/1365-2664.12675>
- Brunberg, B. R., & Lindgren, P. (1984). *Felling manual. Forskningsstiftelsen "Skogsarbeten"*. Stockholm, Sweden: Forest Operations Institute.
- Burivalova, Z., Sekercioglu, C., & Koh, L. (2014). Thresholds of logging intensity to maintain tropical forest biodiversity. *Current Biology*, *24*, 1893–1898. <https://doi.org/10.1016/j.cub.2014.06.065>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*, 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B., ... Henry, M. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*, 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Chave, J., Riera, B., & Dubois, M.-A. (2001). Estimation of biomass in a neotropical forest of French Guiana: Spatial and temporal variability. *Journal of Tropical Ecology*, *17*, 79–96. <https://doi.org/10.1017/S0266467401001055>
- Clark, J. S. (2005). Why environmental scientists are becoming Bayesians. *Ecology Letters*, *8*, 2–14.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., & Ni, J. (2001). Measuring net primary production in forest concepts and field methods. *Ecological Applications*, *11*, 356–370. [https://doi.org/10.1890/1051-0761\(2001\)011\[0356:MNPPIF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2)
- Condit, R., Ashton, P. S., Manokaran, N., LaFrankie, J. V., Hubbell, S. P., & Foster, R. B. (1999). Dynamics of the forest communities at Pasoh and Barro Colorado: Comparing two 50-ha plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*, 1739–1748. <https://doi.org/10.1098/rstb.1999.0517>
- Conway, S. (1982). *Logging practices: Principles of timber harvesting systems* (416 pp.). San Francisco, CA: Freeman Publications, Inc.
- Cushman, K. C., Muller-Landau, H. C., Condit, R. S., & Hubbell, S. P. (2014). Improving estimates of biomass change in buttressed trees using tree taper models. *Methods in Ecology and Evolution*, *5*, 573–582. <https://doi.org/10.1111/2041-210X.12187>
- De Graaf, N. R., Poels, R. L. H., & Van Rompaey, R. S. A. R. (1999). Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecology and Management*, *124*, 123–135. [https://doi.org/10.1016/S0378-1127\(99\)00057-2](https://doi.org/10.1016/S0378-1127(99)00057-2)
- Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., ... Loescher, H. W. (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences*, *115*, 1424–1432. <https://doi.org/10.1073/pnas.1710231115>
- Douglas, I. (1999). Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: A review. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *354*, 1725–1738. <https://doi.org/10.1098/rstb.1999.0516>
- Dykstra, D. (2001). The old and the new of reduced impact logging. *Tropical Forest Update*, *11*, 3–4.
- Dykstra, D., & Heinrich, R. (1996). *Forest codes of practice: Contributing to environmentally sound forest operations*, FAO Forest edn (eds Dykstra D, Heinrich R). Rome, Italy, 132 pp.

- Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J., ... Ota, T. (2014). Land-sharing versus land-sparing logging: Reconciling timber extraction with biodiversity conservation. *Global Change Biology*, 20, 183–191. <https://doi.org/10.1111/gcb.12353>
- Figueira, A., Miller, S. D., de Sousa, C. A. D., Menton, M. C., Maia, A. R., da Rocha, H. R., & Goulden, M. L. (2008). Effects of selective logging on tropical forest tree growth. *Journal of Geophysical Research-Bio-geosciences*, 113, G00B05. <https://doi.org/10.1029/2007JG000577>
- Ghazoul, J., & McAllister, M. (2003). Communicating complexity and uncertainty in decision making contexts: Bayesian approaches to forest research. *International Forestry Review*, 5, 9–19. <https://doi.org/10.1505/IFOR.5.1.9.17433>
- Griscom, B. W., Goodman, R. C., Burivalova, Z., & Putz, F. E. (2017). Carbon and biodiversity impacts of intensive versus extensive tropical forestry. *Conservation Letters*, 10, 160–165.
- Hammond, D. S. (2005). *Tropical forests of the Guiana shield: Ancient forests in a modern world* (528 pp.). Wallingford, UK: CABI. <https://doi.org/10.1079/9780851995366.0000>
- Hammond, D. S., & Ter Steege, H. (1998). Propensity for fire in Guianan rainforests. *Conservation Biology*, 12, 944–947. <https://doi.org/10.1046/j.1523-1739.1998.012005944.x>
- Hendrisson, J. (1990). *Damage-controlled logging in managed tropical rain forests in Suriname*. PhD thesis, Wageningen Agricultural University, Wageningen, the Netherlands, 204 pp.
- Houghton, R. A., Byers, B., & Nassikas, A. A. (2015). A role for tropical forests in stabilizing atmospheric CO₂. *Nature Climate Change*, 5, 1022–1023. <https://doi.org/10.1038/nclimate2869>
- IPCC (2003) Chapter 3. In J. Penman, M. Gytarsky, T. Krug, D. Kruger, R. Pipatti, L. Buendia, K. Miwa, T. Ngara, K. Tanabe & F. Wagner (Eds.), *Good practice guidance for land use, land-use change and forestry (GPG-LULUCF)*. Hayama, Japan: IPCC/IGES.
- Johnson, M. O., Galbraith, D., Gloor, M., De Deurwaerder, H., Guimberteau, M., Rammig, A., ... Phillips, O. L. (2016). Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: Implications for dynamic global vegetation models. *Global Change Biology*, 22, 3996–4013. <https://doi.org/10.1111/gcb.13315>
- Jonkers, W. B., & Hendrisson, J. (2011). The CELOS Management System: Concept, treatments and costs. In: M. J. A. Werger (Ed.), *Sustainable management of tropical rainforests. The CELOS Management System*. Paramaribo, Suriname: Tropenbos International.
- Lussetti, D., Axelsson, E. P., Ilstedt, U., Falck, J., & Karlsson, A. (2016). Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo. *Forest Ecology and Management*, 381, 335–346. <https://doi.org/10.1016/j.foreco.2016.09.025>
- Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., ... Killeen, T. J. (2004). The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, 10, 563–591. <https://doi.org/10.1111/j.1529-8817.2003.00778.x>
- Mazzei, L., Sist, P., Ruschel, A., Putz, F. E., Marco, P., Pena, W., & Ferreira, J. E. R. (2010). Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management*, 259, 367–373. <https://doi.org/10.1016/j.foreco.2009.10.031>
- Metcalfe, C. J. E., Clark, J. S., & Clark, D. A. (2009). Tree growth inference and prediction when the point of measurement changes: modelling around buttresses in tropical forests. *Journal of Tropical Ecology*, 25, 1. <https://doi.org/10.1017/S0266467408005646>
- Miller, S. D., Goulden, M. L., Hutryra, L. R., Keller, M., Saleska, S. R., Wofsy, S. C., ... De Camargo, P. B. (2011). Reduced impact logging minimally alters tropical rainforest carbon and energy exchange. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 19431–19435. <https://doi.org/10.1073/pnas.1105068108>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Pearson, T. R. H., Brown, S., Murray, L., & Sidman, G. (2017). Greenhouse gas emissions from tropical forest degradation: An underestimated source. *Carbon Balance and Management*, 12, 3. <https://doi.org/10.1186/s13021-017-0072-2>
- Peña-Claros, M., Fredericksen, T. S., Alarcón, A., Blate, G. M., Choque, U., Leño, C., ... Putz, F. E. (2008). Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, 256, 1458–1467. <https://doi.org/10.1016/j.foreco.2007.11.013>
- Petrokofsky, G., Sist, P., Blanc, L., Doucet, J. L., Finegan, B., Gourlet-Fleury, S., ... Putz, F. E. (2015). Comparative effectiveness of silvicultural interventions for increasing timber production and sustaining conservation values in natural tropical production forests. A systematic review protocol. *Environmental Evidence*, 4, 8. <https://doi.org/10.1186/s13750-015-0034-7>
- Phillips, P. D., & van Gardingen, P. R. (2001). The SYMFOR framework for modelling the effects of silviculture on the growth and yield of tropical forests. In: *Proceedings of IUFRO 4.11 Conference on Forest Biometry, Modelling and Information Science*, pp. 1–12.
- Pinard, M. A., & Putz, F. E. (1996). Retaining forest biomass by reducing logging damage. *Biotropica*, 28, 278–295. <https://doi.org/10.2307/2389193>
- Pinard, M. A., Putz, F. E., Tay, J., & Sullivan, T. E. (1995). Creating timber harvest guidelines for a reduced-impact logging project in Malaysia. *Journal of Forestry*, 93, 41–45.
- Piponiot, C., Sist, P., Mazzei, L., Peña-Claros, M., Putz, F. E., Rutishauser, E., ... Hérault, B. (2016). Carbon recovery dynamics following disturbance by selective logging in Amazonian forests. *eLife*, 5, e21394. <https://doi.org/10.7554/eLife.21394>
- Plummer, M. (2011). *JAGS Version 3.1. 0 user manual*. International Agency for Research on Cancer. Retrieved from http://www.stats.ox.ac.uk/~nicholls/MScMCMC15/jags_user_manual.pdf
- Putz, F. E., & Romero, C. (2014). Futures of tropical forests (sensu lato). *Biotropica*, 46, 495–505. <https://doi.org/10.1111/btp.12124>
- Putz, F. E., & Ruslandi. (2015). Intensification of tropical silviculture. *Journal of Tropical Forest Science*, 27, 285–288.
- Putz, F. E., Sist, P., Fredericksen, T., & Dykstra, D. (2008). Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management*, 256, 1427–1433. <https://doi.org/10.1016/j.foreco.2008.03.036>
- Putz, F. E., Zuidema, P. A., Synnott, T., Peña-Claros, M., Pinard, M. A., Sheil, D., ... Palmer, J. (2012). Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. *Conservation Letters*, 5, 296–303. <https://doi.org/10.1111/j.1755-263X.2012.00242.x>
- Quesada, C. A., Lloyd, J., Schwarz, M., Patino, S., Baker, T. R., Czimczik, C., ... Santos, A. J. (2010). Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, 7, 1515–1541. <https://doi.org/10.5194/bg-7-1515-2010>
- R Development Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Roopsind, A., Caughlin, T. T., Sambhu, H., Fragoso, J. M. V., & Putz, F. E. (2017). Logging and indigenous hunting impacts on persistence of large Neotropical animals. *Biotropica*, 1–11.
- Roopsind, A., Wortel, V., Hanoeman, W., & Putz, F. E. (2017). Quantifying uncertainty about forest recovery 32-years after selective logging in Suriname. *Forest Ecology and Management*, 391, 246–255. <https://doi.org/10.1016/j.foreco.2017.02.026>

- Ruslandi, Cropper, W. P., & Putz, F. E. (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. *Forest Ecology and Management*, 390, 104–118. <https://doi.org/10.1016/j.foreco.2017.01.019>
- Rutishauser, E., Hérault, B., Baraloto, C., Blanc, L., Descroix, L., Sotta, E. D., ... De Oliveira, L. C. (2015). Rapid tree carbon stock recovery in managed Amazonian forests. *Current Biology*, 25, R787–R788. <https://doi.org/10.1016/j.cub.2015.07.034>
- Rutishauser, E., Hérault, B., Petronelli, P., & Sist, P. (2016). Tree height reduction after selective logging in a tropical forest. *Biotropica*, 48, 285–289. <https://doi.org/10.1111/btp.12326>
- Sasaki, N., Chheng, K., & Ty, S. (2012). Managing production forests for timber production and carbon emission reductions under the REDD+ scheme. *Environmental Science & Policy*, 23, 35–44. <https://doi.org/10.1016/j.envsci.2012.06.009>
- Shenkin, A., Bolker, B., Peña-Claros, M., Licona, J. C., & Putz, F. E. (2015). Fates of trees damaged by logging in Amazonian Bolivia. *Forest Ecology and Management*, 357, 50–59. <https://doi.org/10.1016/j.foreco.2015.08.009>
- Sist, P. (2000). Reduced-impact logging in the tropics: Objectives, principles and impacts. *International Forestry Review*, 2, 3–10.
- Sist, P., & Nguyen-Thé, N. (2002). Logging damage and the subsequent dynamics of a dipterocarp forest in East Kalimantan (1990–1996). *Forest Ecology and Management*, 165, 85–103. [https://doi.org/10.1016/S0378-1127\(01\)00649-1](https://doi.org/10.1016/S0378-1127(01)00649-1)
- Sist, P., Rutishauser, E., Peña-Claros, M., Shenkin, A., Hérault, B., Blanc, L., ... Descroix, L. (2015). The Tropical managed forests Observatory: A research network addressing the future of tropical logged forests. *Applied Vegetation Science*, 18, 171–174. <https://doi.org/10.1111/avsc.12125>
- ter Steege, H., Boot, R. G. A., Brouwer, L. C., Caesar, J. C., Ek, R. C., Hammond, D. S., ... Zagt, R. J. (1996). *Ecology and logging in a tropical rain forest in Guyana. With recommendations for forest management* (123 pp.). Wageningen, the Netherlands: The Tropenbos Foundation.
- ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., ... Von Hildebrand, P. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, 443, 444–447. <https://doi.org/10.1038/nature05134>
- Ter Steege, H., Jetten, V., Polak, A., & Weger, M. (1993). Tropical rain forest types and soil factors in a watershed area in Guyana. *Journal of Vegetation Science*, 4, 705–716. <https://doi.org/10.2307/3236137>
- Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: A tool for identifying ecological thresholds. *Ecology*, 84, 2034–2041. <https://doi.org/10.1890/02-0472>
- Van Dam, O. (2001). *Forest filled with gaps. Effects of gap size on water and nutrient cycling in tropical rain forest. A study in Guyana*. Tropenbos-Guyana Series 10. Georgetown, Guyana: Tropenbos-Guyana Programme.
- Van der Hout, P. (1999). *Reduced impact logging in the tropical rain forest of Guyana*. Tropenbos-Guyana Series 6, 353 pp.
- Van der Hout, P. (2000). Pibiri permanent plots-objectives, design and database management. *Tropenbos-Guyana Series*, 1–73.
- Vanmechelen, E. (1994). *Vegetatiestructuur en lichtklimaat van een Greenheartbos in Guyana*. Leuven, Belgium: Katholieke Universiteit Louvain.
- Vidal, E., West, T. A. P., & Putz, F. E. (2016). Recovery of biomass and merchantable timber volumes twenty years after conventional and reduced-impact logging in Amazonian Brazil. *Forest Ecology and Management*, 376, 1–8. <https://doi.org/10.1016/j.foreco.2016.06.003>
- Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., Licona, J. C., Leñaño, C., ... Choque, U. (2009). Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. *Forest Ecology and Management*, 258, 971–977. <https://doi.org/10.1016/j.foreco.2008.10.031>
- Wadsworth, F. H., & Zweede, J. C. (2006). Liberation: Acceptable production of tropical forest timber. *Forest Ecology and Management*, 233, 45–51. <https://doi.org/10.1016/j.foreco.2006.05.072>
- Zagt, R. J., Ek, R., & Raes, N. (2003). *Logging effects on liana diversity and abundance in Central Guyana*. Wageningen, the Netherlands: Tropenbos International.
- Zarin, D. J., Schulze, M. D., Vidal, E., & Lentini, M. (2007). Beyond reaping the first harvest: Management objectives for timber production in the Brazilian Amazon. *Conservation Biology*, 21, 916–925. <https://doi.org/10.1111/j.1523-1739.2007.00670.x>
- Zimmerman, B. L., & Kormos, C. F. (2012). Prospects for sustainable logging in tropical forests. *BioScience*, 62, 479–487.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

How to cite this article: Roopsind A, Caughlin TT, van der Hout P, Arets E, Putz FE. Trade-offs between carbon stocks and timber recovery in tropical forests are mediated by logging intensity. *Glob Change Biol*. 2018;00:1–13. <https://doi.org/10.1111/gcb.14155>