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Supplementary material for this article is available [online](#)

Abstract

Around 30 Mm³ of sawlogs are extracted annually by selective logging of natural production forests in Amazonia, Earth's most extensive tropical forest. Decisions concerning the management of these production forests will be of major importance for Amazonian forests' fate. To date, no regional assessment of selective logging sustainability supports decision-making. Based on data from 3500 ha of forest inventory plots, our modelling results show that the average periodic harvests of 20 m³ ha⁻¹ will not recover by the end of a standard 30 year cutting cycle. Timber recovery within a cutting cycle is enhanced by commercial acceptance of more species and with the adoption of longer cutting cycles and lower logging intensities. Recovery rates are faster in Western Amazonia than on the Guiana Shield. Our simulations suggest that regardless of cutting cycle duration and logging intensities, selectively logged forests are unlikely to meet timber demands over the long term as timber stocks are predicted to steadily decline. There is thus an urgent need to develop an integrated forest resource management policy that combines active management of production forests with the restoration of degraded and secondary forests for timber production. Without better management, reduced timber harvests and continued timber production declines are unavoidable.

Introduction

In Amazonia, 108 Mha of forest (20% of the total forest area) are currently exploited for timber production, typically by selective harvest of a few merchantable trees per hectare followed by regrowth until the next logging event [1]. In addition to providing income and employment [2], selectively logged forests retain most of the carbon stocks and biodiversity of old-growth forests [3]. Implementing techniques of reduced-impact logging can further reduce logging damage and thus enhance the environmental value of logged forests [4]. Forest management of selective logged forests is thus often seen as a tool for Amazonian forest conservation [5].

Numerous countries have enacted logging regulations that set maximum logging intensities ($\text{m}^3 \text{ha}^{-1}$) and cutting cycles, i.e. minimum time intervals between harvests [2] to avoid depletion of timber stocks. Typically, the minimum cutting cycles over which timber stocks are assumed to recover to pre-harvesting levels are 20–35 years despite substantial evidence that without strong limits on logging intensities, these cycles are too short to sustain yields [3, 6]. Moreover, shortfalls in timber are likely to be exacerbated further in Amazonia by ongoing climate changes [7], including increased frequency and severity of droughts and wildfire events due to drier and hotter conditions [8]. A consequence of these changes is increased tree mortality, especially of large trees (loggers' main target) that are particularly sensitive to intense droughts [9].

Timber stocks are thus likely decreasing in Amazonian production forests even when loggers comply with official regulations. This calls for a revaluation of current forest rules. Regional studies are thus needed to support decision-making, but today most studies that assess the sustainability of selective logging focus on local case studies [3].

Here we investigate the potential for timber recovery across Amazonian production forests using a volume dynamics with differential equations (VDDE) model [10]. The VDDE model was calibrated at the Amazon Basin scale in a Bayesian framework with data from 3500 ha of forest plots, among which 845 ha are from 15 sites monitored for as long as 30 years after being subjected to selective logging [11].

First, we estimate for each experimental site the volume recovery of locally harvested species after one cutting cycle, and relate it to the logging intensity, the cutting cycle length and the abundance of locally harvested species (figure 2), with average harvest rates ranging $0.02\text{--}1.6 \text{ m}^3 \text{ha}^{-1} \text{yr}^{-1}$. We next explore potential timber recovery at the Amazon scale (figure 3), using an extended pool of all potential commercial timber species (50%–100% of the total volume). Additionally, we evaluate whether Amazonian production forests could support the commercial demand for sawlogs, assessed as the sawlog consumption from the Amazon region

[12], by simulating the long-term trajectory of potential timber stocks for varying logging intensities and cutting cycles (figure 4). Finally, we test the effect of increased annual mortality rates and increased disturbances (i.e. discrete events like fires cause pulses of elevated mortality and therefore reduce forest maturity) on timber stocks and recovery (figure 5), to assess the potential effects of climate change on timber provision from Amazonian production forests.

Methods

Data sources

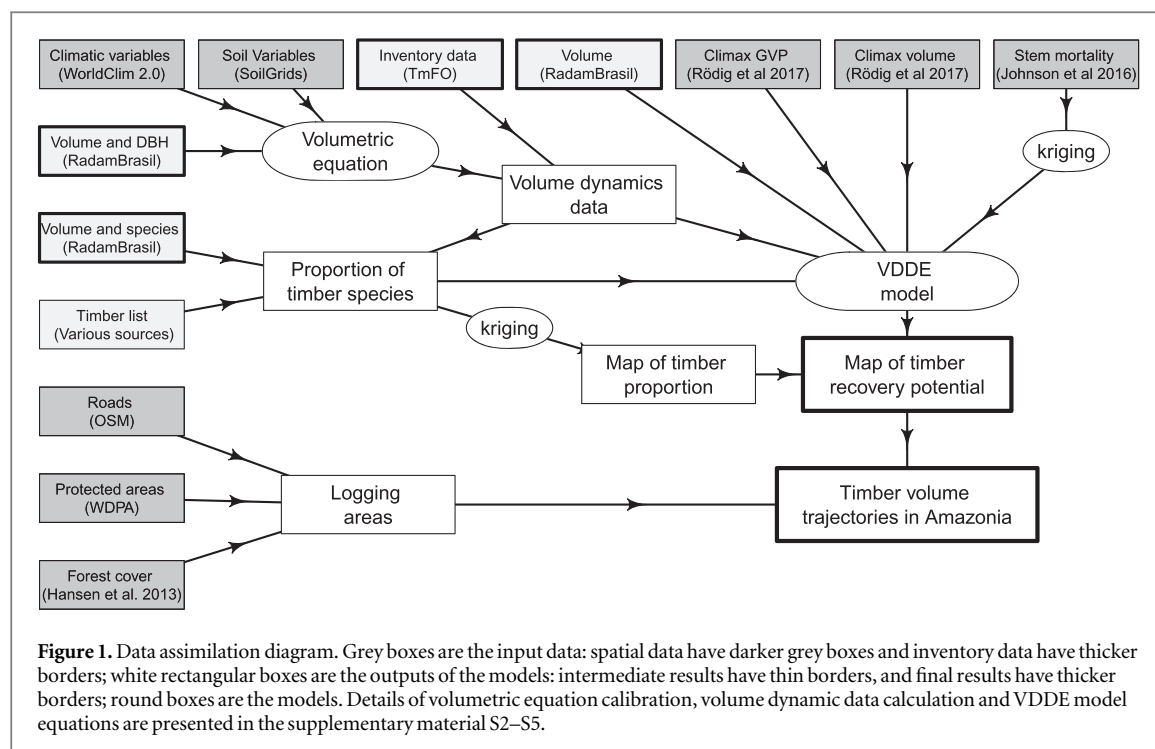
Inventory data

Our study includes data from 15 long-term (8–30 year) experimental forest sites (845 ha total) in the Amazon Basin and on the Guiana Shield (figure S1(a) is available online at stacks.iop.org/ERL/14/064014/mmedia) that are part of the TmFO network [11]. Plots were subjected to conventional logging (8% of plots), reduced-impact logging techniques (e.g. skid-trail planning and directional felling; 33%), post-logging liberation thinning (37%), and control plots with no logging (22%). All sites are located in *terra firme* forests with mean annual precipitation ≥ 1000 mm, experienced different logging intensities, and have at least one pre-logging census and two post-logging censuses. In each plot, all stems with diameter at breast height (DBH) ≥ 50 cm were measured; 82% of trees were identified to species and 15% to genus. For sites with plots ≤ 1 ha, data from those with the same treatment were aggregated to mitigate the small plot effect on the variation in density of large trees. Additionally, single measurement plot data from the RadamBrasil project [13] were made available by the Brazilian Institute of Geography and Statistics [14]. We used 2646 1 ha forest inventory plots from across the Brazilian Amazon (figure S1(b)) in which all trees ≥ 33 cm DBH were measured and identified to species between 1973 and 1982.

Spatial data

Environmental data for both study plots and Amazon-scale extrapolation were extracted from WorldClim 2.0 [15] (precipitation, seasonality of precipitation and solar radiation) and SoilGrids [16] (bulk density, CEC, soil depth, proportion of clay, of sand and of coarse fragment) at a 1 km resolution. When extrapolating to make regional predictions, spatial data was aggregated to a 1° grid by averaging values of all 1 km pixels inside areas available for logging in each 1° cell.

Annual stem mortality rates (as a proportion of live stems), estimated with the metadata from Johnson and colleagues [17], were extracted from the Forest-Plots database [18] and interpolated with the R package *gstat* [19] on a 1° resolution grid. The climax volume, and the gross volume productivity at climax were estimated with the individual-tree-based gap model FORMIND [20]. Climax volume was calculated



as the volume of all trees ≥ 50 cm DBH (per ha) in an old-growth forest; climax gross volume productivity (GVP in figure 1) was calculated as the gross volume gain from photosynthesis (before accounting for respiration losses) of trees ≥ 50 cm DBH in an old-growth forest. Raster maps of climax volume and climax gross volume productivity were created at 1 km² resolution, and values were then aggregated to a 1° resolution grid.

The map of areas available for logging (figure S4) was constructed as the intersection of 3 maps: a buffer of 25 km around all roads and motorable tracks from the OpenStreetMap database [21]; the map of areas outside of protected areas from the World Database on Protected Areas [22] (except the category VI of the IUCN classification, i.e. areas with sustainable use of natural resources that are included in the analysis); and pixels with $>90\%$ forest cover from the map developed by Hansen and colleagues [23].

Proportion of timber species

The locally-defined pool of harvested species (used in figure 2) is the per site list of timber species actually harvested. At larger scales though, timber species preferences are subject to much variation in both time and space. We thus decided to use an extended pool of all species that have been recorded as commercial at least once anywhere in Amazonia. The list was derived from (i) a working list of commercial timbers [24]; (ii) commercial species lists provided by national forest services [25–27]; and, (iii) timber species identified by TmFO site principal investigators (personal communications). The potential timber species list is provided in the supplementary material S6. The proportions of potential timber volume in the total

forest volume were then interpolated from the 2646 RadamBrasil plots and the pre-logging in TmFO plots. We used the R package *gstat* [19] to produce an Amazonian map of (pre-logging) timber proportion on a 1° resolution grid (figure S3).

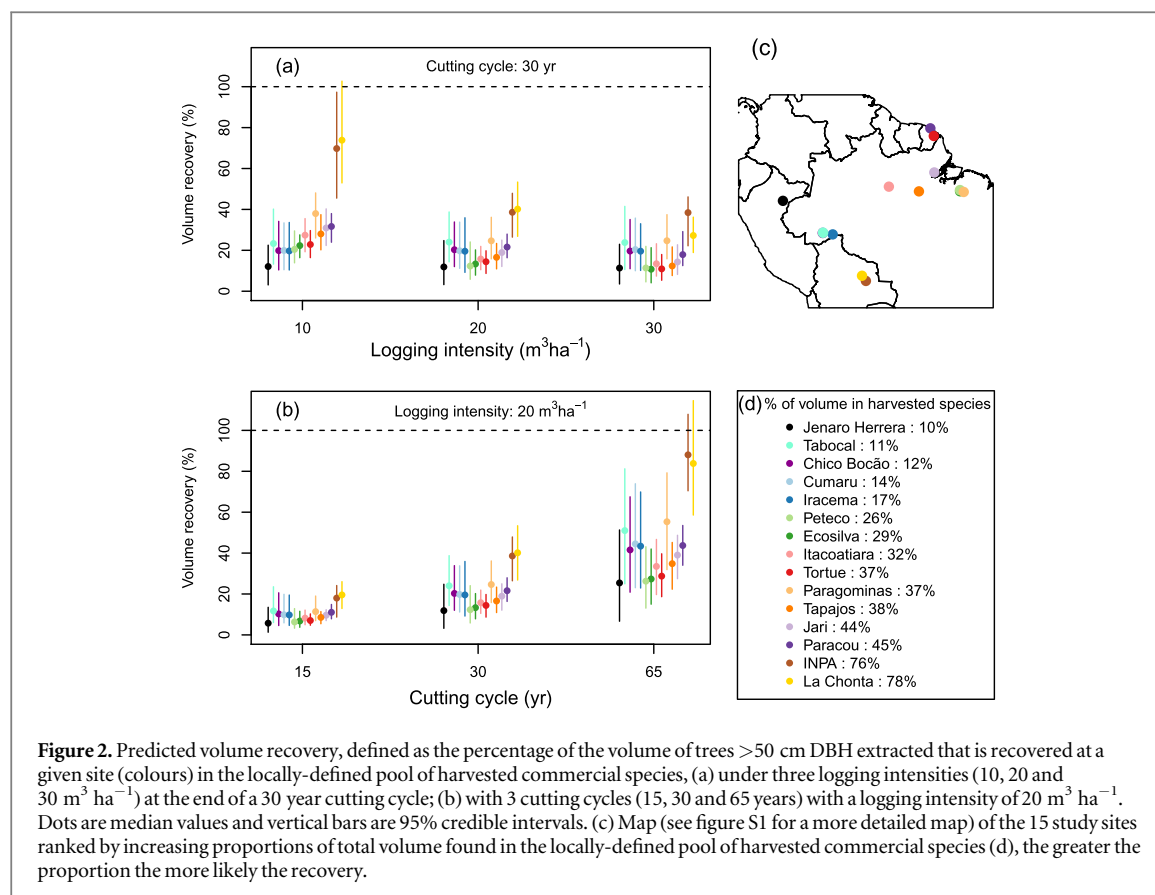
Model calibration

The VDDE model

The VDDE model [10] focuses on the volume of live trees with DBH ≥ 50 cm (the standard minimum cutting size in the Amazon Basin), hereinafter referred to simply as volume. The model was calibrated with volume dynamics data (volumes, volume gain, volume mortality, post-logging volume loss; supplementary material S3) from permanent sample plots. Calibration was carried out using an adapted form of the Hamiltonian Monte Carlo using Stan's programming language [28], and was developed in R [29] (table S1 provides parameters prior and posterior; and presents a convergence diagnostic of the Markov chains).

Three parameters of the VDDE model were expressed as a function of spatially-explicit variables: (i) the climax gross volume productivity α_G , i.e. the annual gross volume increment from trees >50 cm DBH (without volume losses from respiration and mortality) in an old-growth forest; (ii) the potential volume v_{max} (i.e. the maximum volume that an old-growth forest could reach), and (iii) the pre-logging forest maturity τ_0 , which is reflective of the site's pre-logging disturbance level [30]. Other model parameters (β_G , β_M and θ : see supplementary material S5 for a description of the VDDE model [10]) were assumed to be constant across Amazonia.

The climax gross volume productivity α_G and the climax volume V_{climax} were extracted from the map



obtained with FORMIND [20] (see paragraph ‘Spatial data’). Because the potential volume v_{max} is expected to vary with soil and topography, we allowed it to vary between plots among and within site. The potential volume of plot p in site s was modelled as:

$$v_{max_{p,s}} \sim \mathcal{N}(Vclimax_s, \sigma_{vmax}), \quad (1)$$

where σ_{vmax} is the standard deviation, and $Vclimax_s$ is the climax volume predicted with FORMIND [20] at site s .

The pre-logging maturity $\tau_{0,s}$ in site s , was modelled as:

$$\tau_{0,s} = \left(\frac{1}{mort_s} \right)^\lambda \cdot (1 - \delta i_s), \quad (2)$$

where $mort_s$ is the annual stem turnover rate (%) [17], and $\lambda > 0$ is a power parameter to the relationship between the maturity and the stem turnover rate. In our study area, Western Amazonian forests grow on nutrient-rich but unstable soils [31] and are thus more prone to natural disturbances like big blow-downs [32] than northeastern Amazonian forests. Frequent disturbances and high resource availability favour fast-growing species with high turnover rates. For this reason we chose the stem turnover rate as a proxy of the disturbance regime. Because in some sites there were human disturbances prior to the logging experiment, we added a parameter δi_s that represents the gap between the estimated and the expected pre-logging maturity at site s (table S1 provides parameters prior and posterior).

Accounting for defective stems

A significant part of large trees in natural forests have hollows or other defects that make them unsuitable for timber uses [33]. The proportion of commercial volume with defects unacceptable for sawmills ranges 20%–50% in the Brazilian Amazon [34–36]; an extensive data collection in forest concessions in French Guiana reported that on average 20% of harvestable stems had hollows and were not harvested (ONF: personal communication; [26]). We thus multiplied all timber volumes in our simulations by a factor $(1 - Pdef)$, with $Pdef$ the proportion of defective volume modelled as:

$$Pdef \sim \text{Beta}(6, 14), \quad (3)$$

where $\text{Beta}(6, 14)$ is the beta distribution of shape parameters $\alpha = 6$ and $\beta = 14$. The mean value of $Pdef$ is 30%; to reflect the uncertainty on this value, we chose a distribution with a large 95% credible interval (16%–49%).

Simulations of timber recovery

Simulations were carried for every pixel of a 1° grid. We simulated five scenarios: (1) standard logging rules (logging intensity $Vext = 20 \text{ m}^3 \text{ ha}^{-1}$, cutting cycle 30 years); (2) low logging intensity ($10 \text{ m}^3 \text{ ha}^{-1}$) with a standard cutting cycle (30 years); (3) high logging intensity ($30 \text{ m}^3 \text{ ha}^{-1}$) with a standard cutting cycle; (4) short cutting cycle (15 years) with a standard logging intensity ($20 \text{ m}^3 \text{ ha}^{-1}$); (5) long cutting cycle (65 years) with a standard logging intensity ($20 \text{ m}^3 \text{ ha}^{-1}$).

In each scenario, we consider that, each year, $\frac{1}{trot}$ of the area available for logging is actually logged (where *trot* is the cutting cycle), so that an area is logged every *trot* years and the total area logged each year is constant. Due mostly to slope restrictions and riparian reserves, but also heavy forest degradation in some parts of the Amazon, the area logged typically represent 60% of the total area allocated for logging [37, 38]. We multiplied the annual harvested area by a coefficient $\pi \sim \text{Beta}(8.2, 5.9)$, where $\text{Beta}(8.2, 5.9)$ is the beta distribution calibrated with data from logging concessions in French Guiana (reported in figure S11).

To propagate errors on results, the following steps were repeatedly taken:

1. At each location, map values (α_G , V_{climax} , and $mort$ in equations (1), (2)) are drawn from their distribution (error estimation is described in supplementary material S4).
2. At each location, model parameters are drawn from their posterior distribution (see table S1).
*Timber volumes (per ha) are calculated as:

$$V_{t,pix,l} = Vol(\tau_{t,pix,l}) \cdot \omega_{t,pix,l} \cdot (1 - Pdef), \quad (4)$$

where $V_{t,pix,l}$ is the predicted timber volume t years after the first harvest in pixel *pix* in scenario l , $\tau_{t,pix,l}$ is the predicted maturity, $Vol(\tau_{t,pix,l})$ is the volume of all trees ≥ 50 cm DBH according to equation (15), $\omega_{t,pix,l}$ is the proportion of timber volume and $Pdef$ is the proportion of defective volume;

3. For each pixel, each time step $t \in [1, 300]$ and each scenario $1 \leq l \leq 5$, the total timber volume is calculated as:

$$V_{tot,t,l} = \sum_{pix} [(V_{t,pix,l}) \cdot area_{pix} \cdot \pi], \quad (5)$$

where $V_{t,pix,l}$ is the timber volume (per ha) t years after the first harvest in pixel *pix* in scenario l ; and $area_{pix} \cdot \pi$ is the area (ha) inside pixel *pix* that is available for logging.

4. The real extracted volume (per ha) from each pixel *pix* is calculated as the minimum between the extracted volume in scenario l (i.e. the timber volume expected to be harvested) and the available timber volume at the time of logging. The total extracted volume at year t is the sum of the actual extracted volume from areas logged at t .
5. Potential timber volume recovery (%) is calculated as the increase in potential timber volume over the first cutting cycle, divided by the total extracted volume (figure 3). The annual timber recovery is calculated as the increase in potential timber volume between two consecutive years (figure 4).

Steps 1–4 were repeated 100 times and summary statistics were calculated. Timber recovery and timber extraction were compared to the current and future demand for sawlogs. Current demand was assessed as the production of sawlogs in the Amazon region in 2004, 31 Mm³ according to the Imazon [12]. Future increase in demand was assumed to follow the trend of increase in sawnwood consumption in South America as projected with the Global Forest Products Model [39]. We thus computed the proportional increase predicted between 2006 and 2060 for four Inter-governmental Panel on Climate Change Scenarios (A1B, A2, B2 and A1B-Low Fuelwood) [39] and multiplied the current demand for sawlogs by this increase to get the future demand for sawlogs (figure 4).

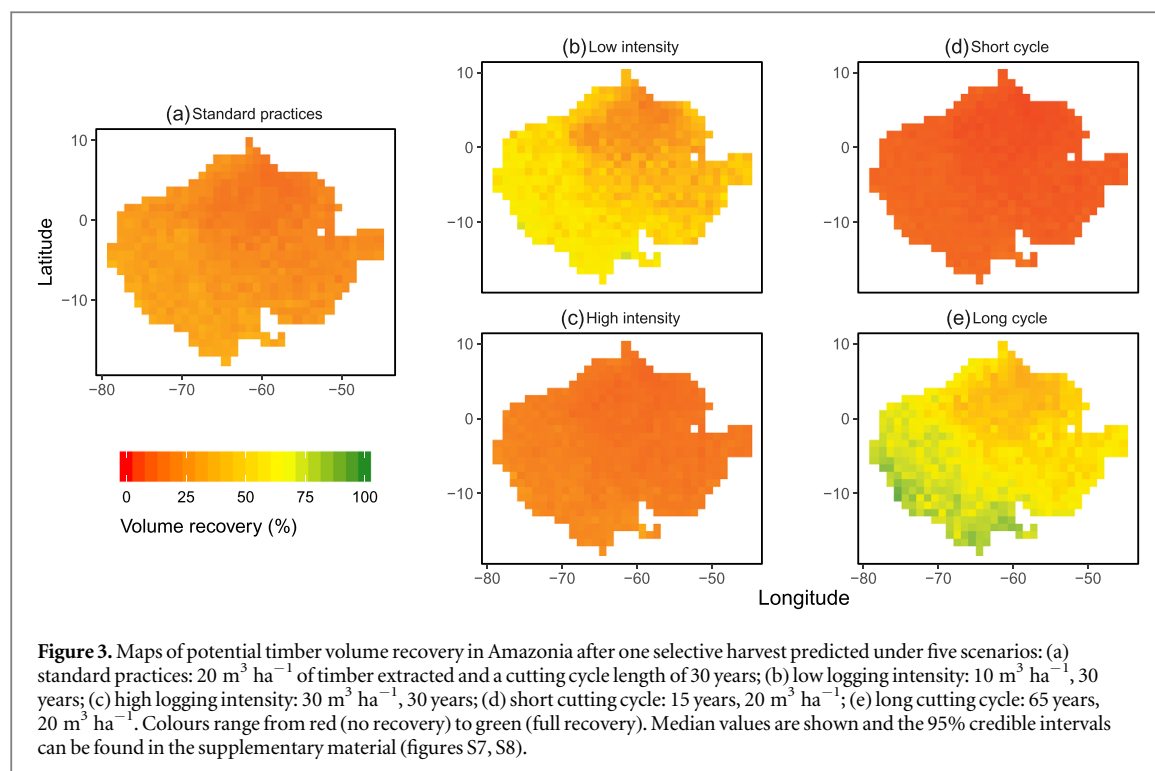
Results and discussion

What affects timber recovery?

Recovery of harvested species volume by the end of the first cutting cycle varied threefold across the experimental sites (figure 2(a)) and increased with the pre-logging proportion of the total volume shared by the local pool of harvested commercial species (Pearson coefficient $\rho = 0.58$). At the sites with the largest abundance of locally harvested species (INPA and La Chonta with $>70\%$ of stems ≥ 50 cm DBH), timber volumes are predicted to recover faster, because there is less competition with non-commercial species. This finding highlights the importance of expanding the local pool of species harvested in order to maintain timber stocks over time.

Regional variation in the rate of timber volume recovery of all potential timber species were consistent across logging intensities and cutting cycle lengths (figures 3(a)–(e)). Median timber recovery was highest in Western Amazonia (0.30 [0.18, 0.40] m³ ha^{−1} yr^{−1}—numbers in [] represent the 95% credible interval) and lowest in the Guiana Shield (0.26 [0.16, 0.34] m³ ha^{−1} yr^{−1}). These results resemble those from studies in old-growth forests that revealed higher rates of both wood production and forest demographic rates in western Amazonia than in the northeast [17, 31]. This pattern is potentially due to more frequent natural disturbances [32], or to spatial differences in seasonality and soil properties [31]. This result means that logging regulations need to reflect regional differences.

Lesser known Amazonian timber species compose a small share of the global tropical timber market, which remains heavily dominated by a few over-exploited species [40, 41]. Selective logging in Amazonia usually targets a few high-value species such as mahogany (*Swietenia macrophylla*) and ipê (*Handroanthus* spp) [40] that typically represent $<20\%$ of the total volume in a particular site [41, 42]. When overexploited, these species' volume recovery is compromised within a typical 30 year cutting cycle [40]. Due to low recovery rates of prized timber species,



what is available for second harvests is often species with low timber market values compared to the costs of extraction and transport [43].

Even if volume recovery scenarios include all the 348 lesser-known timber species, our simulations indicated that with a logging intensity of $20 \text{ m}^3 \text{ ha}^{-1}$ logged forests recover at most 70% of their pre-logging timber volumes (figure 3) within a typical 30 year cutting cycle. This result is consistent with a variety of local studies reporting that standard 30–40 year cutting cycles are insufficient for full recovery of timber stocks [3, 40]. This means that even with a substantial increase in the number of merchantable species, timber stocks will continue to decline in Amazonian production forests if current logging practices (extraction of around $20 \text{ m}^3 \text{ ha}^{-1}$ every 30 years) persist (figure 4).

Slow recovery and rising pressure on production forests

Independently of logging intensity and cutting cycle length, median timber recovery from forest regrowth was $<30 \text{ Mm}^3 \text{ yr}^{-1}$ (figure 4(c)). This over-harvesting results in a reduction in Amazon-wide timber stocks in all scenarios (figure 4(a)), meaning that natural forest regrowth will be insufficient to supply the commercial demand in the long-term. Moreover, the actual sawlog extraction could be higher than official numbers suggest: illegal logging is ubiquitous in the region, and is estimated to produce a volume of wood equivalent to 20%–60% of the legal timber markets [44, 45], further decreasing the likelihood of a sustainable timber supply from Amazonian production forests.

We stress that our model estimates are based on optimal scenarios of the recovery potential of Amazonian production forests. (i) Our plots showed no signs of having suffered severe recent human disturbance prior to logging (e.g. fire, uncontrolled logging, or fragmentation) whereas this is not the case for an estimated one-third of Amazonian forests [46]. Such disturbances might reduce forest resilience to logging [47]. (ii) Reduced-impact logging techniques were employed in most of our experimental sites [11], but these recommended logging practices are seldom implemented in the tropics [4]. (iii) Not harvesting big defective stems and keeping them in the forest will increase their proportion in the next harvests. (iv) Our scenarios do not account for post-logging degradation (e.g. fires and illegal logging [48]) or deforestation [49], which are fairly ubiquitous in the region [47, 50]. Therefore, our results represent the maximum potential volume recovery of Amazonian production forests, which is unlikely to be attained in the real world.

While the fate of Amazonian production forests remains uncertain, several studies call attention to the rising impacts of human activities on the functioning and provision of ecosystem services [8, 51, 52]. Deforestation, forest degradation, and climate change will continue to affect the resilience of Amazonian forests to future disturbances including their ability to recover timber stocks after logging [47, 53]. Moreover, future trends in deforestation can be substantially affected by political choices (e.g. road building [48], law enforcement, agricultural subsidies, access to credit [54], and corruption [55]), which were not considered in our conservative scenarios with no deforestation. Climate change is also expected to decrease

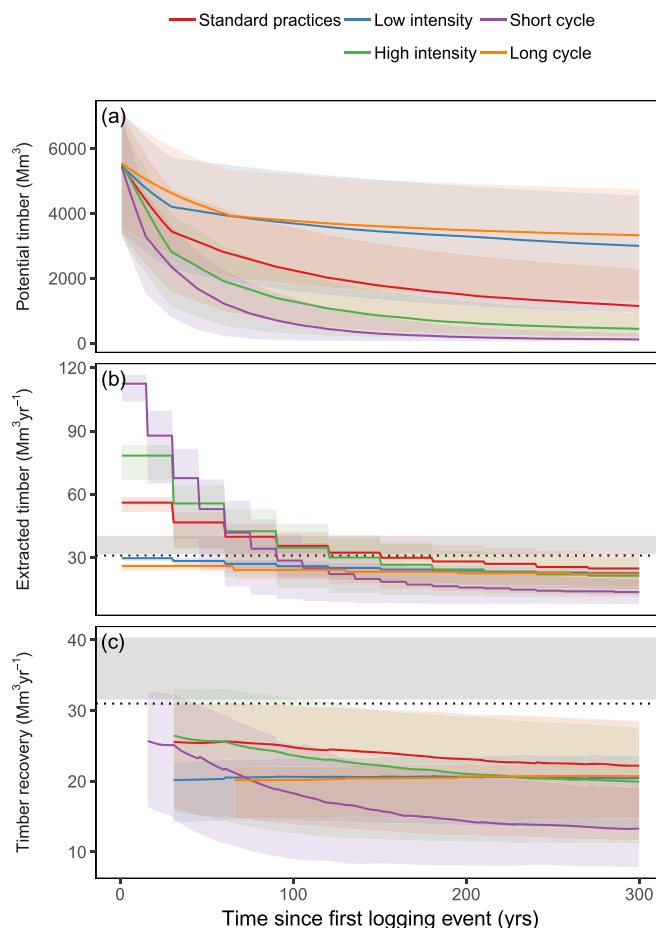


Figure 4. Predicted volume trajectories (x-axis: time since first logging, in years) of (a) total potential timber, (b) potential timber extracted annually and (c) annual potential timber recovery over 300 years in Amazonian forests under five scenarios: standard logging rules ($20 \text{ m}^3 \text{ ha}^{-1}$, 30 years, red), low intensity ($10 \text{ m}^3 \text{ ha}^{-1}$, 30 years, blue), high intensity ($30 \text{ m}^3 \text{ ha}^{-1}$, 30 years, green), short cutting cycle ($20 \text{ m}^3 \text{ ha}^{-1}$, 15 years, purple), long cutting cycle ($20 \text{ m}^3 \text{ ha}^{-1}$, 65 years, orange). The area available for logging in every pixel of the map (figure S4) was divided into as many annual units as the length of the cutting cycle (15, 30 or 65), so that one unit is logged each year and each unit is logged again at the end of the cutting cycle. Solid lines are the median predictions, and shaded areas are the 95% credible intervals. The dotted lines (panels (b) and (c)) correspond to the demand for sawlogs in the Amazon biome [12]. The grey area is the range of projected sawlog demand in 2060, based on changes in sawnwood consumption in South America estimated with the Global Forest Products Model [39]. The four extreme trajectories (high or low intensities with long or short cycles) are provided in figure S9.

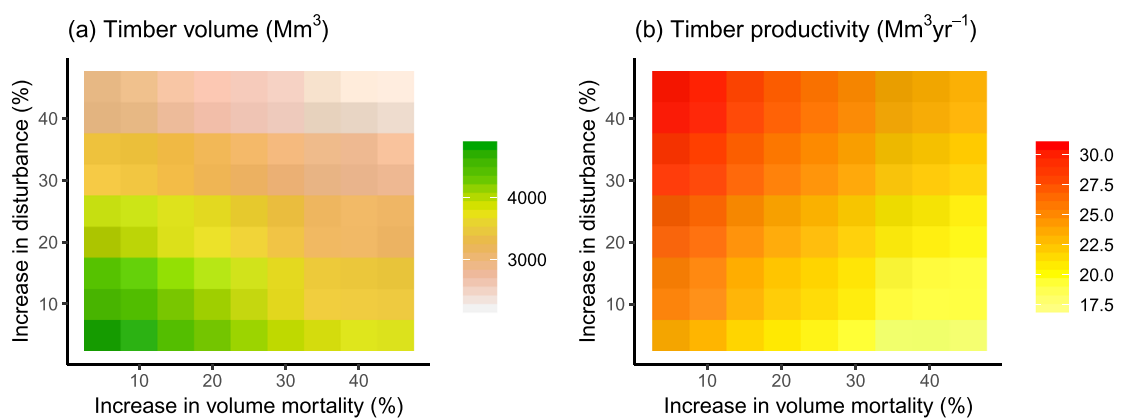


Figure 5. Predicted effect of increase in future disturbance regime (y axis) and annual mortality (x axis) on (a) potential timber volume and (b) annual volume productivity in all Amazonian areas available for logging. Increasing the disturbance regime (e.g. more frequent fires) decreases the proportion of old-growth stands and reduces the overall maturity of forests, while increasing the annual mortality (e.g. in a drier and hotter climate) decreases the long-term volume potential of forests. The effects of increased disturbance regime and annual mortality are illustrated in figure S10.

timber stocks and productivity through drier and hotter climate leading to higher mortality of large trees, which have longer hydraulic path, higher leaf area and crown exposure [56] (figure 5(a)). Increased frequency and intensity of disturbances are expected to decrease potential timber stocks while timber productivity is enhanced due to the decreased proportion of less productive old-growth forests (figure 5(b)).

Future timber production in integrated forest landscapes

Our results show that with current cutting cycles and logging intensities, forest regrowth is too slow to recover timber stocks (figures 3, 4), highlighting the need to decrease the pressure on natural production forests by adopting longer cutting cycles, and reducing logging intensities and incidental damage to the stand through reduced-impact techniques [4]. Silvicultural interventions applied to increase the stocking, growth, and commercial yields from merchantable species (e.g. liana cutting, future crop tree liberation, and enrichment planting) could also help turning the tide of forest depletion, as well as providing several other benefits such as increased carbon storage and employment [57].

Enforcing longer cutting cycles, lower intensities, reduced-impact techniques or post-logging interventions will likely increase long-term forest recovery but decrease the short-term financial benefits from legal selective logging. Moreover, restricting legal timber extraction could potentially lead to an increase in illegal logging and forest conversion [58]. This means that parallel to adopting stronger logging regulations, additional efforts on law and forest tenure enforcement will be needed. These policies should include regional coordination to avoid illegal trade and leakages effects [58, 59]. Economic viability of tropical forest management will also increase with timber prices, which are currently low compared to production costs [43], and with sawmill efficiency, currently around 35% [60]. Efforts should also be done to change consumer preferences both in terms of species and size of logs, e.g. the potential use of branches (and not only trunks) could increase timber production without additional damage to the forest. Another opportunity to increase financial revenues is to develop economic mechanisms to value other goods and services provided by the forest such as carbon storage (e.g. REDD+), hydrology, biodiversity, ecotourism, and non-timber forest product management [61].

Changing logging practices may not be enough to meet rising demands for wood products. Additional sources of timber could come from various restoration systems: plantations of exotic or native species, enriched secondary or degraded forests [62], integrated crop-livestock-forestry systems and other agroforestry systems [63]. Increasing the area of timber plantations could significantly reduce the pressure on Amazonian

natural forests [64]. Tree plantations have the potential to produce large quantities of timber on relatively small areas: timber plantations in Brazil, mostly fast-growing eucalyptus and pine, can produce 200–400 m³ ha⁻¹ of roundwood on 10–15 year cycles [65]. Such exotic species produce low-grade timber that is not directly equivalent to high-value wood currently extracted from Amazonian natural forests, but there is a potential to develop plantations of high-value native species [66, 67], even though technical alternatives are still scarce in Amazonia [67]. Moreover, it is likely that with ongoing technological advances, future high-grade timber demand will be gradually substituted by less-valuable fast-growing timbers transformed into highly-resistant materials [68].

The rising interest in tropical forest restoration, initiated by the Bonn challenge in 2011 [69], has led Brazil to commit to restore 12 Mha of forest by 2030 [70], and has motivated an initiative to restore 30 000 ha of forests in the Brazilian Amazon by 2023 [71]. These initiatives can provide opportunities to combine efforts to restore environmental values (e.g. carbon, biodiversity, and water cycle) including timber production [62], and fund applied research for both ecological restoration and timber production [72].

Conclusion

Selective logging in Amazonian forests cannot provide enough timber to meet even the current regional demand over the long term. The ‘light’ scenarios (low intensity and long cutting cycles) do not provide enough timber and the ‘heavy’ scenarios are not sustainable, insofar as they do not allow volume recovery during a cutting cycle (figure 4); moreover, future deforestation, forest degradation and climate change will likely worsen the picture. These results call for a re-evaluation of the strategy for future timber provision in Amazonia. We are in a period of transition that requires important forest policy decisions that promote diversification of timber sources and a substantial shift in the objectives of Amazonian production forest management.

Data and code availability

The data used in the analyses are available at <https://figshare.com/s/336dcbff400a812a56ea>.

Associated computer codes are available at <https://figshare.com/s/9873edea9c1e8fe98993>.

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Competing Interests

The authors declare that they have no competing financial interests.

Authors' contribution

Data Acquisition: all authors. Conception and design: CP, BH. Model Development: CP, BH, ERo. Data analysis and interpretation: CP, BH. Writing the manuscript: CP, ERo, FEP, ERu, PS, LB, BH. Manuscript revision: all authors.

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