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Above-ground biomass storage potential in primary rain forests managed for timber production in Costa Rica

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ABSTRACT

Tropical forests play a fundamental role in mitigating climate change through storage of carbon in above- and below- ground biomass. Their mitigation potential is, however, affected by significant greenhouse gas emissions through tropical deforestation or forest degradation. Mitigating degradation caused by conventional logging is therefore an important challenge for silvicultural management, and various reduced impact logging techniques seek to reduce biomass loss and other logging impacts during forest logging activities.

Little knowledge exists about the potential of sustainable management for maintaining and restoring the climate change mitigation capacity of tropical forests. Our research contributes to knowledge about this potential, as our aim is to evaluate the above-ground biomass (AGB) stock of tropical forests managed for sustainable timber production and compare it with that of intact primary forests. We also determine the environmental and spatial factors that influence AGB.

We estimated the AGB of 141 permanent sampling plots in Costa Rican tropical forests (71 plots set up in areas managed for timber production forests and 70 plots set up in areas with intact primary forests) using data for the 2000–2015 period. We compared the AGB of timber production forests with that of primary forest using linear mixed models and examined the relationship between forest AGB and climate, soil fertility and spatial variables (PCNM eigenvalues) using variation partitioning (VARPART) and multiple linear regression in the mixed model framework.

Mean AGB was higher in forest plots set up in areas managed for timber production than in plots set up in areas with intact primary forests. In VARPART, spatial variables had the strongest effect on AGB with a small but significant effect of soil fertility. Regression showed potassium levels in the soil to be positively related to AGB. There was no significant effect of climate, probably because of the short temperature and precipitation gradients.

Sustainable forest management in these Costa Rican forests managed for timber production has enabled them to store as much carbon in biomass as primary forests, due to the low intensity logging and sustainability criteria stipulated by the country's forestry legislation. As a result, sustainable forest management, in addition to providing a sustainable timber ecosystem service, is also a natural climate solution, maintaining the mitigation potential of Costa Rica's tropical forests in the current climate context.

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1. Introduction

Tropical forests are expected to play a fundamental role in mitigating climate change and achieving the global temperature rise target set as part of the 2015 Paris Agreement. Indeed, tropical forests are crucial systems for regulating the climate and mitigating climate change (Baccini et al., 2017; Griscom et al., 2020; Sullivan et al., 2020). These forests can sequester up to 30% of anthropogenic carbon dioxide (CO_2) emissions and represent at least 59% of global carbon stocks (Yguel et al., 2019). They store approximately 470 billion tonnes of CO_2 in above and below ground biomass (Pan et al., 2011, Huntingford et al., 2013; Pugh et al., 2019). Interest in tropical forests specifically is therefore thoroughly justified since they are the ecosystems with the most potential for storing additional terrestrial carbon (Griscom et al., 2020).

On the other hand, one of the greatest sources of greenhouse gas emissions stems from the tropical deforestation (Griscom et al., 2020). These ecosystems display greater and more rapid changes in land use than any other ecosystem, as a result of anthropogenic deforestation and degradation (Chazdon et al., 2016; Poorter et al., 2016; Mitchard, 2018). Net decreases in the area of tropical forests were enormous during the decade 2010–2020, mainly in Africa (3.9 million ha) and South America (2.6 million ha) (FAO, 2020).

Deforestation leads to numerous sources of emissions as well as cryptic sources that occur more gradually and include the edge effect in fragmented forests (Maxwell et al., 2019). Newly accessible forests will be earmarked for a first selective conventional logging, which could result in substantial carbon emissions (Pearson et al., 2014; Maxwell et al., 2019). Conventional selective logging in tropical forests for timber and/or fuelwood is usually a source of forest degradation, since the loss of live biomass as a result of harvesting practices is, in general, greater than the accumulation of biomass through regrowth over many years (Pearson et al., 2014). The loss of biomass is mainly related to damage caused by the felling of harvested trees, incidental damage to neighbouring trees and damage caused by unplanned log extraction (Pearson et al., 2014).

This study, therefore, focuses on how selective logging affects the mitigation potential of tropical production forests. More specifically, we are interested in sustainable logging and its impact on biomass storage in tropical production forests.

Various improved reduced-impact logging (RIL) techniques have been developed. They seek to balance environmental protection with timber production in tropical production forests. RIL, in addition to mitigating the damage caused by log extraction reduces the loss of carbon stocks in the remaining vegetation, thereby providing a natural climate solution (Ellis et al., 2019). Natural climate solutions are made up of discrete and quantifiable actions that avoid the emission of greenhouse gases or increase carbon sequestration in forests, savannah, agricultural lands and wetlands (Griscom et al., 2020). In this context, many studies have reported that RIL in tropical forests could eventually reduce carbon emissions equivalent to 29–50% of the net emissions caused by tropical deforestation and changes in land use (Cerullo and Edwards, 2019; Sasaki et al., 2016). Moreover, the relatively small net emission of CO_2 by RIL hides the high potential for CO_2 storage in the form of biomass (Houghton et al., 2015).

Our research seeks to contribute knowledge about the potential of sustainable management for maintaining carbon storage in timber production forests. We specifically study above-ground biomass (AGB) storage in timber production forests submitted to sustainable logging techniques. Knowing more about AGB storage in timber production forests will enable sustainable logging to be promoted as a natural climate solution in the tropics, where only a small area of forest is currently subject to sustainable management (FAO, 2020). Comparing biomass stocks in recovering timber production forests with those of primary forests (forests with no known recent human intervention) makes it possible to demonstrate how logging impacts carbon storage.

The current research applies to primary rain forests in Costa Rica, where sustainable forest management and forest conservation take place on private farms within a landscape matrix that is highly fragmented (e.g. Schedlbauer et al., 2007; Morse et al., 2009). Costa Rica is one the rare, if not the only tropical country that reports a net gain of forest cover, mainly through natural regeneration. Forest cover represented 52.38% of the national territory (REDD/CCAD-GIZ Program, 2015; Hernández Sánchez et al., 2017). However, as more generally in Central American countries, between the 1950s and the 1990s, Costa Rica went through an intensive process of deforestation, during which land suitable for forestry was stripped of its forest cover, with as much as 18,000–42,000 ha reportedly deforested annually. The country reached its climax of deforestation in the 1980s. Deforestation was mainly caused by land use changes following conversion to agricultural and pastoral uses. Non sustainable logging activities were also an important degradation factor, opening up tropical primary forest and leading to deforestation.

To encourage forest recovery, from the 1990s the Costa Rican government established various incentives for natural forest management. To this end, Forestry Law No. 7575 was passed in the late 1990s to “safeguard the conservation, protection and management of natural forests as well as the production, exploitation, industrialisation and stimulation of the country’s forestry resources to that end” (Costa Rica, 1996). In Article 19, the Law establishes that in areas declared as forest, conversion to agriculture, livestock or other uses is prohibited. This prohibition discouraged deforestation. Moreover, the law introduced sustainable forest management in Article 20, with the aim of mitigating degradation from logging activities. The law therefore stipulates that natural forest can be exploited for timber production but only when there is a management plan that curbs the impact that logging may cause to the environment. Therefore, in Costa Rica, any natural forest (outside of protected areas) which is exploited for timber production is subject to forest management, with the condition that it must follow a strict legal framework focusing on forest integrity and ecological sustainability, which is defined in a detailed management plan. The management plan must be submitted and approved by the National System of Conservation Areas (Sistema Nacional de Áreas de Conservación, SINAC), an institution of the Ministry of the Environment and Energy (Ministerio de Ambiente y Energía, MINAE). The management plan will be approved if it meets sustainable management criteria, and therefore must include an assessment of the possible impact of logging, with specific reference to the impact on residual mass and soil, as well as the corresponding mitigation measures (MINAE, 1997). In this paper, the term sustainable management therefore refers to the criteria for sustainability established in Costa Rica’s forestry legislation, which include appropriate planning of trunk extraction routes, training of workers in tree fall directionality, and also a methodology for calculating felling intensity based on forest censuses.

Under this scheme, the Costa Rica Forest Ecosystems Observatory

(Observatorio de Ecosistemas Forestales de Costa Rica, OEFo) was set up, with its main aim to evaluate the status and dynamics of forest ecosystems according to their level of disturbance and to build knowledge about the ecosystem services that they provide. In pursuit of these aims, the member institutions of the OEFo network established permanent sampling plots in experimental management units of tropical primary forest, both managed for timber production (following sustainable forest management as defined by Costa Rica's forestry legislation) and intact (not subjected to any forest management plan), in various locations throughout the country.

The objective of this research was to estimate the above-ground biomass (AGB) in primary forest managed for timber production and to compare it with the AGB in intact primary forests within the experimental network of permanent sampling plots of the OEFo in Costa Rica. For this paper, the estimate was calculated from data collected for the period 2000–2015 (Appendix 1). We also examined the relationship between AGB stock and i) the spatial distribution of the plots, ii) climate variables, and iii) soil variables. To conclude, we discuss the results, focusing on the potential of sustainable management as a natural climate solution, through potential for storage of AGB in forests managed for timber production.

2. Materials and methods

2.1. Area of study

The research was carried out with data from primary and timber production forests in Costa Rica. Costa Rica is located at between latitudes 08°02′26″N and 11°13′12″N and between longitudes 82°33′48″W and 85°57′57″W, being a country situated within the tropical belt (ING, 2005). Costa Rica's mountain ranges divide the territory into five climatically defined regions, two on the Caribbean or Atlantic slope, and

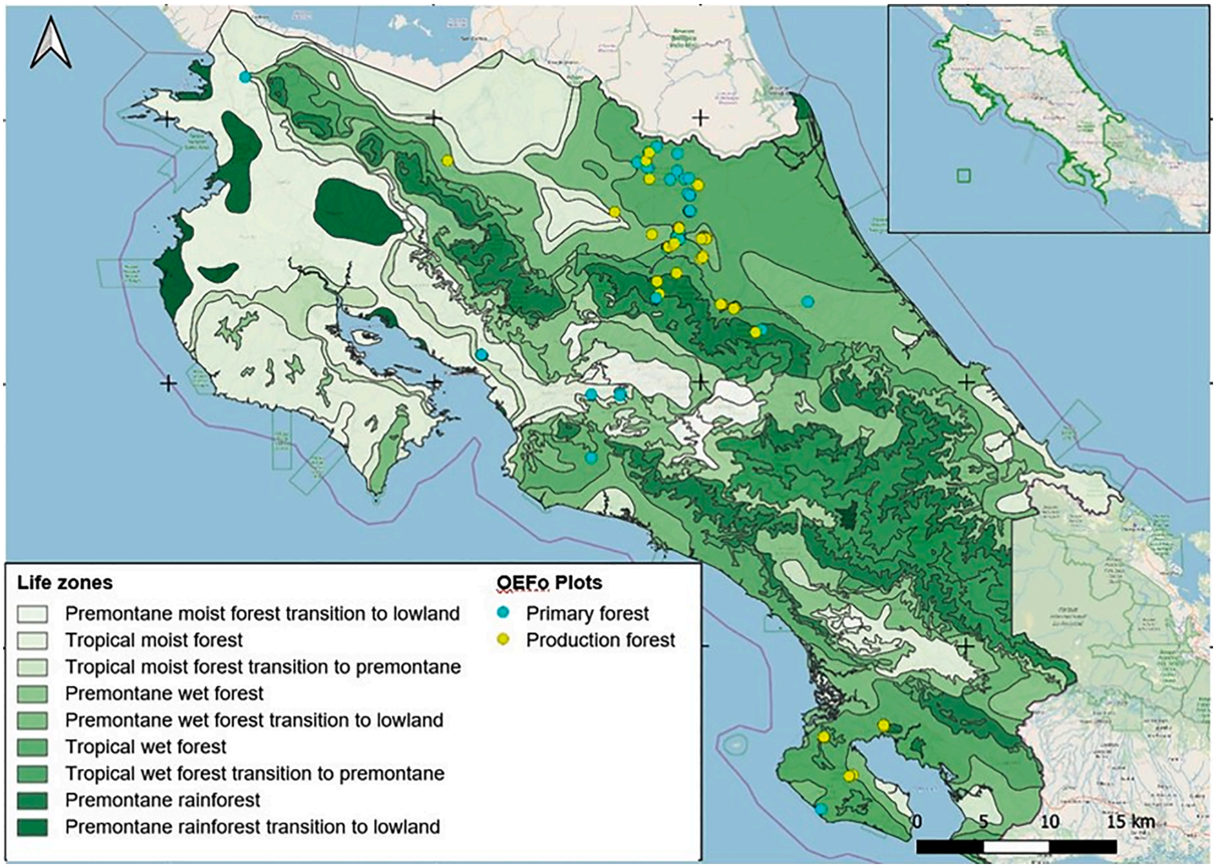

Fig. 1. Map of the distribution of the study plots across Holdridge Life Zones in Costa Rica.

three on the Pacific slope (Fig. 1). According to the bioclimatic Holdridge Life Zone System, Costa Rica is further divided into 12 life zones and 12 transition zones (Quesada, 2005).

2.2. *Experimental plots and data*

The permanent sampling plots (PSPs) selected for this research are part of the Costa Rica Forest Ecosystems Observatory (Observatorio de Ecosistemas Forestales de Costa Rica, OEFo) (Morrison Vila, 2020). For the purposes of this research, we selected 141 PSPs of primary tropical forests located on private farms (outside of protected areas). The PSPs selected were located in nine life zones and transition zones (Holdridge, 1967; Quesada, 2007) (Table 1, Fig. 1).

Among the PSPs, 70 were set up in intact primary forest and 71 were set up in forest management units managed for timber production, following strict management plans associated with the sustainability criteria set out in Forest Law No. 7575. Before implementation, each management plan was approved by the SINAC. Following Costa Rican forestry legislation, generally logging is applied to trees with a diameter at breast height (DBH) ≥ 60 cm, along with strictly respecting the sustainability criteria of the Forestry Law No. 7575, as mentioned above. In our dataset, the logging intensity varied between 33% and 100% of the trees with DBH ≥ 60 cm, with the majority of plots (66 plots out of 71) submitted to a logging intensity between 33% and 60%, and only one plot submitted to a logging intensity of 100% (see Appendix 2 for detailed information on logging intensity applied to each management unit).

The 71 plots located in areas of management for timber production were also subject to a variety of treatments. Table 2 summarises the logging intensity, sylvicultural treatment and year of logging for each management unit and by institution. Detailed information on the management applied to each plot is presented in Appendix 2.

Table 1
Distribution of primary and production forest study plots by life zone.

Life zone	Altitudinal Tier	Altitudinal Range (m.a.s.l.)	Mean annual precipitation(mm)	Mean annual temperature (°C)	No. of plots	Type of forest
Tropical moist forest	Lowland	0–700	2000–4000	24–30	8	primary
Premontane moist forest, transition to lowland	Premontane	700–1400	2000–4000	18–24	1	primary
Tropical moist forest, transition to premontane	Lowland	0–700	2000–4000	24–30	2	primary
Tropical wet forest	Premontane	700–1400	4000–8000	18–24	1	primary
Premontane wet forest, transition to lowland	Premontane	700–1400	4000–8000	18–24	18	primary (1 plot)production (17 plots)
Tropical wet forest	Lowland	0–700	4000–8000	24–30	94	primary (54 plots) production (40 plots)
Tropical wet forest, transition to premontane	Lowland	0–700	4000–8000	24–30	6	production
Premontane rainforest	Premontane	700–1400	8000 +	18–24	7	primary (3 plots) production (4 plots)
Premontane rainforest transition to lowland	Premontane	700–1400	8000 +	18–24	4	production

Table 2
Summarised information about the management and treatments applied, by institution, in the 71 timber production forest plots in our study sample.

Institution	Sustainable management	Treatment	Logging intensity (harvested trees)	year of logging
CATIE	Yes	RILRing barked	33–60%	1990–1992
CODEFORSA	Yes	RILRefinementRelease	50–100%	1991–1992
FUNDECOR	Yes	RIL	33–60%	1998–2001
TEC	Yes	RIL	33% – 60%	1992

The area of monitoring plots varied between 0.2 ha and 1 ha. In all plots, trees with a DBH of at least 10 cm at a standard height of 1.3 m were measured. Most trees were identified by genus and family and many at the level of species. The identification was carried out by qualified staff and botanists.

Palms (Arecaceae family) were excluded from the study since they were only taken into account in the monitoring of a few plots. Moreover, palm trees do not exhibit growth in their diameter so it is difficult to estimate their contribution to productivity (Goodman et al., 2013). Lianas were also excluded from the analysis since there was no consistent data relating to them.

2.3. Environmental variables

In order to characterise the relationship between climate-related factors with AGB, annual precipitation and mean temperatures in all the plots were considered. We obtained precipitation and temperature data from Chelsa (Climatologies at high resolution for the earth's land surface areas) database (Karger et al., 2017, Karger et al., 2018), through interpolation with the location coordinates of the plots, using R software (R Core Team, 2019).

In addition to temperature and rainfall, soil data were obtained from the Centre for Agricultural Research (Centro de Investigaciones Agronómicas, CIA) of the University of Costa Rica (Mata et al., 2016). This database draws on 1500 soil sampling locations distributed throughout Costa Rica. The values of soil characteristics used in the analyses were chosen according to the proximity of the CIA sampling locations to PSPs and by life zone. We used values for 0–40 cm soil depth (Sesnie et al., 2009, Santiago-García et al., 2019). The following variables were considered: pH in water, acidity, Ca, Mg, K, Zn, P, Cu, Fe, Mn, effective cation exchange capacity (ECEC), organic carbon (OC) and the percentage of sand, loam and clay in the soil. These variables are considered to be attributes of soil fertility by Mata et al. (2016).

Table 3
Descriptive statistics for AGB in primary and production forests. Standard deviation (SD) and standard error (SE).

Type of forest	No. of plots	Mean AGB(Mg ha^{-1})	SD	SE	Min	Max
primary	70	296.3	90.9	10	123.1	530.8
Production	71	329.3	75.9	9.9	160.3	496.8

2.4. Estimation of above-ground biomass

For the estimation of AGB, data collected for the selected plots covering the period 2000–2015 were used. During this period, some plots were measured only once and others up to seven times (Appendix 1).

The *BIOMASS* package (*computeAGB* function) was used to estimate the AGB (Mg ha^{-1}) of the trees (Réjou-Méchain et al., 2017), using R software (R Core Team, 2019). This function uses the pantropical equation of Chave et al. (2014), to estimate AGB using DBH, species wood density and tree height, as follows:

AGB = 0.0673 * (WD * H * D^2) ^0.976

Wood density (WD) was obtained from the *getWoodDensity* function of the *BIOMASS* package. The estimate is based on the taxonomy of the trees, or similar, using the global wood density database (Chave et al., 2009, Réjou-Méchain et al., 2017), which returns a value for each species that represents dry mass divided by dry volume (g cm^{-3}). For trees that were not identified by species, the *BIOMASS* package averages wood density values by taxonomical level (genus) or assigns mean values by sub-plot.

Tree height H was estimated using the *retrieveH* function, also from the *BIOMASS* package, which uses the general model of Chave et al. (2014). In their model, H is estimated on the basis of tree DBH and plot bioclimatic variables that include climatic water deficit as well as temperature and precipitation seasonality. The geographic coordinates of the plots were used to obtain these bioclimatic variables.

Plot AGB was obtained from the sum of the biomasses of all trees in each plot (Mg ha^{-1}). For plots with two or more enumerations, an

Table 4
Variation partitioning of above-ground biomass of 141 plots explained by spatial and environmental variables. The values for adjusted R^2, the *F* statistic and *P* value for significance are shown for all the fractions measured for space (Sp), soil (So) and Climate (Cli). The individual effect of a matrix after removal of the effects of others is indicated by the symbol '|'. Overall model R2adj was 0.44.

Variable	R^2Adj	*F*	*P*
Sp	0.35	13.98	0.001
So	0.15	7.44	0.001
Cli	0.02	2.62	0.071
All variables	0.44	10.19	0.001
Sp|So,Cli	0.28	12.29	0.001
So|Sp,Cli	0.058	4.42	0.001
Cli|Sp,So	0.004	1.49	0.239

Table 5
Values from multiple regression statistics for the explanatory variables according to the value of Mallows' C_p criterion for prediction.

Variables	*T*	Mallows' C_p	*P*
PCNM58	−4.72	33.26	<0.001
PCNM16	−4.51	31.32	<0.001
PCNM127	−3.46	23	<0.001
K	2.65	18.03	0.01
PCNM131	2.64	17.95	0.01
PCNM3	2.46	17.06	0.02
%MO	1.86	14.44	0.07
Silt	1.75	14.05	0.08
Cu	1.44	13.06	0.15
PCNM138	−1.26	12.58	0.21
Temperature	−1.25	12.55	0.21
Precipitation	1.04	12.07	0.3

average plot AGB was obtained from the set of enumerations.

2.5. Statistical analysis

In order to compare AGB between the timber production and primary forest plots, ANOVA (analysis of variance) was carried out with a linear mixed model using InfoStat software (Di Rienzo et al., 2019). The model takes differences in plot size into account, giving less weight to the AGB of the plots with the smallest area. We selected the best adjusted model using the AIC and BIC criteria. Assumptions of normality and variance homogeneity were evaluated using QQ-plots and residuals versus predicted plots respectively (Appendix 3).

2.5.1. Spatial variables: Principal coordinates of neighbour matrices (PCNM) analysis

Principal coordinates of neighbour matrices (PCNM) analysis was used to calculate spatial variables to evaluate the effect of plot spatial distribution on AGB. This was calculated by using a log transformation of the spatial coordinates of each plot, resulting in a Euclidean distance matrix of the distances between the plots. In order to detect and quantify spatial patterns, the logarithmic values were truncated to create a second matrix of eigenvalues which were submitted to a principal component analysis (PCA). The result is a set of eigenvectors known as PCNMs (Borcard and Legendre, 2002; Dray et al., 2006). These represent the spatial relationships among plots at different scales. The analysis was carried out in R software (R Core Team, 2019) using the *Vegan* library and the *PCNM* function (Oksanen et al., 2013).

2.5.2. Spatial, soil and climate variables affecting AGB

In order to evaluate the relationship of AGB to spatial and environmental variables, the climate and soil variables were standardised. A *forward selection* (R Core Team, 2019) was then carried out for each of the three matrices of explanatory variables, which selected the variables most closely associated with the response matrix (AGB) through a process of permutation using residuals from the reduced model (Blanchet et al., 2008). For the PCNM matrix the hypothesis test was based on 1,000 permutations using $\alpha = 0.01$. The hypothesis test for the soil matrix was based on 999 permutations with $\alpha = 0.05$.

In order to verify that a high correlation between the selected variables and the climate variables did not exist as a result of forward selection, Pearson's correlation coefficient was applied (Appendix 4).

2.5.3. Variation partitioning analysis

We used variation partitioning (VARPART, Jones et al., 2008) to evaluate the explanation of AGB variation by matrices of climate (annual mean temperature and precipitation), soil and spatial variables (PCNM). VARPART combines redundancy analysis and partial redundancy analysis by dividing the variation in the matrix of the response variable (AGB) into explanatory or predictive matrices. Using VARPART allowed the pure and joint effects of the three matrices to be identified, as well as the overall variance explained by the set of three matrices. For this analysis, the *varpart* function was used from the *Vegan* package (Oksanen et al., 2013).

The adjusted R^2 (R^2 adj) values indicate the proportion of variation in AGB that is explained by each explanatory matrix. The significance of fractions from the VARPART analysis ($p \leq 0.05$) was confirmed with a redundancy analysis (RDA) test.

2.5.4. Linear regressions

To establish the effect of each explanatory variable on the AGB, the variables were standardised. Linear mixed model regressions were then carried out between the dependent variable (AGB) and the explanatory variables selected for the VARPART analysis. Life zone and the institution responsible for PSPs were used as random effects to take into account variations in plot size and in the number of plots between forest types. The t-statistic value and Mallows' C_p criterion for prediction were the statistics used to identify the explanatory variables with most influence on AGB. These analyses were carried out using InfoStat software (Di Rienzo et al., 2019).

3. Results

3.1. Above-ground biomass

The above-ground biomass (AGB) of 58,661 trees from 812 taxa was estimated, distributed across 141 plots. Of these, 86% of individuals were identified to species. Mean AGB varied significantly between the two types of forest ($p < 0.0001$). Production forests stored more AGB (329.3 Mg ha^{-1} ± 90.9) than the primary forests (296.3 Mg ha^{-1} ± 75.9) (Table 3).

3.2. Influence of spatial, soil and climate variables on AGB

The variables selected for the soil matrix were potassium (K), percentage of organic matter (%OM), percentage of silt and copper (Cu). For the spatial matrix, PCNM58, PCNM16, PCNM3, PCNM138, PCNM127, PCNM131 were selected. These represent the spatial relationship between plots both at the local scale (PCNM138) and on the regional scale (PCNM3) (Appendix 4).

A Pearson correlation test verified that the regional-scale spatial relationship represented by PCNM3 was independent of climate and soils variables (Appendix 5).

VARPART showed that the combined effects soil, climate and spatial matrices explained 44% of variation in AGB (Table 4). Space, soil and climate, alone and in interaction, had Radj^2 values of 0.35 and 0.15, respectively ($p < 0.001$). Climate did not have a significant effect on AGB. The explanation in AGB variation caused by spatial distribution and soil, alone and in interaction, was significant ($p < 0.001$). The individual effect of space was highly significant and that of soil significant but small (R^2adj = 0.058).

3.3. Multiple regression analysis

Linear regression enabled the variables with most influence on variability in AGB to be identified (Table 5), according to the Mallows' C_p values obtained from the regression. The variables with higher values are those that exert a greater influence on biomass prediction. Plot spatial distribution was found to influence AGB variation strongly, and potassium was among the soil fertility variables that was also associated with AGB variation.

4. Discussion

Tropical forests play a fundamental role in changes to atmospheric carbon concentrations in the industrial era. They act as a carbon sink that varies from year to year and can revert, becoming a source of carbon in drought years or as a result of anthropic disturbances. Monitoring and evaluation of current carbon stocks in biomass in disturbed tropical forests is important for understanding their contribution to climate change mitigation. Several studies involving monitoring of field plots show large variations in carbon sequestration and storage which could be related to the degree of previous disturbance (Poorter et al., 2016, Mitchard, 2018).

The objective of our study was to characterise the AGB of Costa Rican forests, determine whether AGB in production forests is different from that in primary forest, and to determine the effects of spatial and environmental variables on AGB. We found that plot spatial distribution was the factor that best explained variability in biomass, followed by soil fertility. Climate variables were shown to have no effect. These results are based on 290,000 measurements of trees from 141 plots which were enumerated up to seven times in a period of 15 years.

The quantity of biomass in a forest determines the potential quantity of carbon (1 Mg of biomass = 0.5 Mg of carbon) (Brown and Lugo, 1992) that has been sequestered from the atmosphere and stored. On this basis, between 2000 and 2015 the intact primary forests studied in this research would have stored on average 148.15 Mg ha^{-1}C and production forests, 164.65 Mg ha^{-1}C.

4.1. Timber production forests contain greater AGB than intact primary forests

Plots in primary forests managed for timber production had higher mean AGB ha^{-1} than primary forests during the period 2000–2015. This result demonstrates the potential of sustainable management as a natural climate solution i.e. that decreases the emission of greenhouse gases or increases carbon sequestration in forests. Sustainable logging techniques are already recognised for their potential to reduce carbon emissions resulting from forest logging (Ellis and Putz, 2019). Numerous studies have demonstrated that in forests subject to reduced-impact logging (RIL) under sustainable management plans, the biomass retained was substantially greater than in forests that were conventionally logged (Putz et al., 2012; Sasaki et al., 2016; Cerullo and Edwards, 2019). Furthermore, a study in Amazonian forests demonstrated that AGB recovers more quickly after RIL than after conventional logging (Rutishauser et al., 2015). RIL can translate into a reduction of 50% or more of the impact caused by collateral damage (Putz et al., 2008; Sasaki et al., 2016; Cerullo and Edwards, 2019).

In the present study, we further present sustainable logging techniques as a natural climate solution that increases AGB stock in forest managed for timber production. Indeed, according to detailed records and data provided by the OEFo member institutions, the 141 plots considered for this research were located in primary forests. Of these, 71 plots were associated with forest management units where reduced-impact logging was carried out, as defined by Article 20 of Costa Rica's Forestry Law No. 7575 and in accordance with the sustainability criteria more generally defined by RIL (see Table 2 and Appendix 2 for logging intensity and the logging techniques applied). Sustainable management applied under 7575 allows for moderate intensity felling of "60–40%", by which 60% of trees with DAP $\geq$ 60 cm can be logged, leaving the remaining 40% of trees with DAP $\geq$ 60 cm. This represents 5–7 trees per hectare. Finegan and Camacho (1999), in a typical example, recorded the cutting of four trees per hectare for a mean volume of 10 m^3 ha^{-1} in rainforest at an experimental site in the north of the country (Tirimbina plots, CATIE with RIL, included in our research). This logging involved sustainable management criteria as established under forestry legislation, along with the corresponding measures for reducing degradation. We found a slight variability in logging intensity in each management unit (see Table 2 and Appendix 2 for logging intensity and logging techniques applied), with the majority of plots (66 plots out of 71) subjected to a logging intensity between 33% and 60%. Accounting for the variability in logging intensity, mean AGB of plots within forest areas managed for timber production was significantly higher than the AGB of plots within intact forest areas. Within our timber production sample plots, one plot was submitted to a logging intensity of 100% (all the trees with a DBH $\geq$ 60 cm). We included the plot in our study and its AGB (439.17 Mg ha^{-1}) was consistent with the mean AGB of plots in areas managed for timber production.

The plots used for monitoring managed forestry units varied in size from 1 ha to 0.3 ha. Putz et al., 2019 contend that small plots in managed logging units may be less affected by logging and therefore may lead to overestimating the biomass area of production forests. According to the authors, the small size of some plots means that it is less likely that logging will affect biomass. Factors associated with this relate to the accessibility of these small plots, steepness of slope or distance from the road. In our study, however, the management units were located in areas that were accessible for logging, since they were set up specifically for timber extraction. This reduces the probability that the small plots would not be affected by logging. Furthermore, the mean AGB ha $^{-1}$ obtained from these small plots (301.74 Mg ha^{-1}) was less than from the larger plots of a hectare (331.42 Mg ha^{-1}) (Appendix 6). Therefore, even if they had not been affected by logging due to their smaller size, their biomass was not overestimated. In any case, the government of Costa Rica prohibits logging of trees in locations where the slope is $\geq$ 60%. Moreover, our statistical model is weighted by area, with less importance given to small-sized plots.

Our study suggests that under certain circumstances, AGB in forests managed for sustainable timber production can be greater than that in primary forests. AGB resilience in neotropical secondary forests is well-studied (Poorter et al., 2016) but the potential for AGB storage in timber production forests has been less reported in the literature. The regeneration of fast-growing long-lived tree species in logging gaps could contribute more biomass to the system (Herault et al., 2010). Also, the growth of dominated individuals may be stimulated by the gap opening that results from logging, since gaps create canopy openings exposing understory trees to sunlight of increased duration and intensity (Herault et al., 2010, Edwards et al., 2014). Carbon stock enhancement after sustainable logging could be converted into carbon credits for initiatives such as REDD+ (Cerullo and Edwards, 2019).

Another possible explanation for our results is that edge effects due to forest fragmentation are in fact impacting AGB stock of primary forests, as has been shown at an Amazonian site by Laurance et al. (2006). Both timber production and primary forests in our study are located on private farms in fragmented landscapes, as documented by Morse et al. (2009) for the northern zone of the country. While pasture was for many years the main agricultural land use, agricultural intensification, for example the spread of pineapple agroindustry, is a recent trend, potentially exacerbating edge effects in the remaining forest (Shaver et al., 2015). However, Schedlbauer et al. (2007) in their study showed that AGB was not affected by proximity to forest edges in north eastern Costa Rica, where most of the sample plots of the present study are located, and changes in understorey vegetation at edges are minimal (Bouroncle and Finegan, 2011). Future studies accounting for the landscape matrix dynamics around our timber production and intact forest plots may confirm the potential impact of forest fragmentation and agricultural intensification between 2000 and 2015, when the study data were collected.

4.2. *Influence of spatial, soil and climate variables on above-ground biomass*

AGB and biomass productivity depend on environmental conditions in terms of resource availability (water, nutrients and light) and on forest attributes, in terms of quality and quantity of vegetation (Lohbeck et al., 2015, Poorter et al., 2017). Furthermore, the resilience of tropical forests to long-term and discrete disturbances is defined by various dynamic processes that in turn are shaped by different drivers that act simultaneously. Climate variation (precipitation and temperature) is one of these drivers. Indeed, numerous studies have associated climate and soil with AGB at the local and regional scale, suggesting a potential role on a global scale (Malhi et al., 2006, Slik et al., 2013). However, our study showed a null effect of climate variables on variation of AGB and demonstrated that the effect of plot spatial distribution was the most relevant factor in explaining this variability. Although our study covered four climate regions, it is probable that the range of precipitation and temperature covered by our sample plots is not as great as in other studies (Lewis et al., 2013, Poorter et al., 2015), the results of which indicate that climate-related factors have the most influence on biomass variability.

AGB stock variation in our study was more strongly explained by plot spatial distribution than by soil fertility or climate-related variables. As is the case for forest composition and species diversity (Legendre et al., 2009), the relationship between AGB stock and plot spatial distribution may be influenced by dispersal limitations and regional biogeography, if different dominant species have different potentials for accumulation of AGB due to differences in key functional traits such as maximum adult height (Finegan et al., 2015). The species composition of the forests we studied varies both within landscapes, for example in the northeast of the country (Sesnie et al., 2009) and between forests in the northeast and those of the southwest (compare Sesnie et al., 2009, with Cornejo et al., et al., 2012). Within-landscape and regional variation in species composition could generate the effects on AGB of the spatial variables PCNM 138 (within landscapes) and PCNM 3 (regionally). Chisholm et al. (2013) reported that species richness and AGB were positively related across forest sites at small spatial scales and this could be attributed to the local variation in stem density, more than to the effect of species, niche complementarity or facilitation (Chisholm et al., 2013). Therefore, forests that share geographical locations would share similar environmental conditions, potentially displaying a similar composition and structure as well as AGB stocks.

The relationship between soil and AGB stock often shows mixed and conflictive results in the literature. Frequently this is because different studies use slightly different sampling methodologies (for example, depth and intensity of the sample), which will include different nutrients and differ between each other if the sample represents the available quantity or the total quantity of these nutrients. We took soils data from a national soil database (Mata et al., 2016), in contrast to studies like Poorter et al. (2016), who used CEC from a gridded global soils database as an estimate of fertility. Therefore, different methodologies for obtaining this data could be a factor influencing results.

In our study, potassium was the soil variable with most influence on biomass variability. K was correlated with local AGB distribution in a 50 ha forest plot in central Panamá (Ledo et al., 2016) and with AGB in secondary rain forests across north eastern Costa Rica (Santiago *et al.,* 2009). Also, when added with N in a tropical moist forest fertilisation experiment, K increased tree growth rates (Wright et al., 2011). Our study complements the cited work suggesting that soil K plays a role in regulating forest AGB at multiple scales (Ledo et al., 2016). However, the differences in AGB stocks between forest managed for timber production and intact forest could not be explained by differences in soil fertility variables. Soil fertility variables between primary forest managed for timber production and intact forest did not allow differentiation by forest type (Appendix 7). This finding reflects and underscores why there are no criteria relating to soil fertility required for the submission of forest management plans in Costa Rica.

4.3. Research perspectives

The percentage of variation in AGB not explained by climate, soil and spatial variables (44%) in our research could be related to indirect effects of underlying drivers such as the structural attributes of the forests: tree diameter, tree density and specific leaf area. These attributes might vary between communities (due to disturbances) and across communities (due to environmental gradients) (Poorter et al., 2015). For example, the study by Finegan *et al.* (2015) reported that, in primary tropical forests, AGB was positively correlated with community-weighted mean adult height. Furthermore, the relationship between the richness of species and AGB may vary along environmental gradients. The richness of species could also be associated with a selection effect, where highly productive species, or species of large size which store a lot of biomass, are included in the forest (Poorter et al., 2015). It is therefore recommended that functional traits, species composition and species diversity be included in this kind of research, since functional traits play an important role in increasing carbon stocks and forest productivity, leading to a better biomass dynamic.

4.4. Climate change mitigation

The climate-related sensitivity of tropical forest carbon is a key uncertainty in predicting the global effects of climate change. Although it is known that droughts and the short-term increase in temperature affect forests, there is uncertainty as to whether these effects will translate into long-term responses (Sullivan et al., 2020). In addition to the effects of climate change on tropical forests, they are continually threatened by deforestation and degradation that are estimated to contribute to between 8 and 15% of global anthropogenic carbon emissions, which exacerbates climate change (Chazdon et al., 2016). It is in this context that sustainable tropical forest management is emerging as a mechanism in response to global efforts to mitigate carbon emissions.

Our research showed that production forests (managed in a sustainable way) under some circumstances can accumulate more biomass than primary forests. This potential for carbon sequestration and storage in production forests suggests the resilience of these forests to discrete disturbances. The latter may push these ecosystems from a stable steady-state to a state of instability which, without major disturbances, will transition back to their initial state. This displacement will depend on the type, scale, intensity, and duration of the disturbance. If it is large, frequent or novel, the return of the ecosystem to its original state is unlikely (Ghazoul et al., 2015). Therefore, these forests may function as carbon sources or sinks, depending on the type of management to which they are subjected (Piponiot et al., 2016). According to our results, production forests in Costa Rica would be acting as carbon stores and possibly sinks because of the sustainability of the logging techniques applied.

5. Conclusions

The overall objective of our research was to estimate above-ground biomass (AGB) stock in primary forests under sustainable forest management for timber production and to compare it to above-ground biomass in primary forests. Furthermore, we examined the relationship between AGB and i) the spatial distribution of the plots, ii) climate variables, and iii) soil fertility variables, to see if these had any effect on biomass storage potential. Combining analysis of all plots according to type of forest, timber production forests were, on average, those that accumulated most AGB stocks in the period 2000–2015. Furthermore, the spatial distribution of the plots was the factor that best explained the variability of biomass, followed to a lesser degree by soil fertility, while climate variables were shown to have no effect.

Although we did not find an effect of climate on AGB variation, the effect of water availability on vegetation growth resulting in the accumulation of more biomass over time is undeniable. It is probable that research on a regional or continental scale would provide evidence of the effect of climate patterns on biomass variability.

Even though it is well known that tropical forests are the richest in carbon and the most productive of the forest biomes, they are constantly under threat, which means that mechanisms need to be found to support their sustainable management and conservation. The productivity, conservation and mitigation potential of production forests make them important ecosystems that can enhance tropical forests' resilience in relation to climate change. Sustainable forest management, in addition to encouraging an important service by providing sustainable timber, could also be a natural climate solution, and a strategy for restoring the mitigation potential of tropical forests in the current climate context.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Institution	Type of Forest	xpar	Plot	Plot area (ha)	Year established	First year ofmeasurement	Last year ofmeasurement	Number ofmeasurements
CATIE	primary logged	Corinto	1	1	1988	1988	2010	14
CATIE	primary logged	Corinto	3	1	1988	1988	2010	10
CATIE	primary logged	Corinto	4	1	1988	1988	2010	14
CATIE	primary logged	Corinto	5	1	1988	1990	2010	11
CATIE	primary logged	Corinto	6	1	1988	1989	2010	10
CATIE	primary logged	Corinto	9	1	1988	1990	2010	11
CATIE	primary logged	Corinto	10	1	1988	2010	2010	1
CATIE	primary logged	Corinto	11	1	1988	2010	2010	1
CATIE	primary logged	Corinto	12	1	1988	2010	2010	1
CATIE	primary logged	Tirimbina	1	1	1988	1990	2015	10
CATIE	primary logged	Tirimbina	2	1	1988	1990	2015	12
CATIE	primary logged	Tirimbina	3	1	1988	1988	2015	14
CATIE	primary logged	Tirimbina	4	1	1988	1988	2015	14
CATIE	primary logged	Tirimbina	5	1	1988	1990	2015	11
CATIE	primary logged	Tirimbina	6	1	1988	1990	2015	6
CATIE	primary logged	Tirimbina	7	1	1988	1990	2015	8
CATIE	primary logged	Tirimbina	8	1	1988	1988	2015	14
CATIE	primary logged	Tirimbina	9	1	1988	1990	2015	12
CODEFORSA	primary logged	Hogar ancianos 029	4	0.25	1991	1991	2006	3
CODEFORSA	primary logged	Hogar ancianos 030	5	0.25	1991	1991	2006	3
CODEFORSA	primary logged	La Legua	1	1	1992	1992	2003	3
CODEFORSA	primary logged	La Legua 2	1	1	1992	1992	2007	8
CODEFORSA	primary logged	Montura	1	1	1992	1992	2005	3
CODEFORSA	primary logged	Octubre_78	1	1	1992	1992	2005	3
CODEFORSA	primary logged	Samen	1	1	1992	1992	2005	3
CODEFORSA	primary logged	San Jorge	9	0.25	1992	1992	2004	3
FUNDECOR	primary logged	Antonio Tosi	2201	0.3	1999	1999	2016	7
FUNDECOR	primary logged	Antonio Tosi	2202	0.3	1999	1999	2016	7
FUNDECOR	primary logged	Antonio Tosi	2203	0.3	1999	1999	2016	7
FUNDECOR	primary logged	Antonio Tosi	2204	0.3	1999	1999	2016	7
FUNDECOR	primary logged	Ecovida Inmobiliaria	3601	0.3	2012	2012	2018	3
FUNDECOR	primary logged	Ecovida Inmobiliaria	3602	0.3	2012	2012	2018	3
FUNDECOR	primary logged	Ecovida Inmobiliaria	3603	0.3	2012	2012	2018	3
FUNDECOR	primary logged	Ecovida Inmobiliaria	3604	0.3	2012	2012	2018	3
FUNDECOR	primary logged	Hacienda Rio Blanco	2102	0.3	1999	1999	2018	7
FUNDECOR	primary logged	Hector Hidalgo	901	0.3	1998	1998	2019	7
FUNDECOR	primary logged	Hermanos Miranda	102	0.3	1998	1998	2018	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1002	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1006	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1008	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1009	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1010	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1018	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1021	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1032	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1034	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1044	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1045	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Ind. Agrop. Asoc.	1049	0.3	1998	1998	2017	9
FUNDECOR	primary logged	Jose Luis Ferreto	2001	0.3	1999	1999	2015	7
FUNDECOR	primary logged	Jose Luis Ferreto	2002	0.3	1999	1999	2015	7
FUNDECOR	primary logged	Maderal Atlantic	1901	0.3	1999	1999	2018	8
FUNDECOR	primary logged	Maderal Atlantic	1902	0.3	1999	1999	2018	8
FUNDECOR	primary logged	Maderal Atlantic	1903	0.3	1999	1999	2018	8
FUNDECOR	primary logged	Maderal Atlantic	1904	0.3	1999	1999	2018	8
FUNDECOR	primary logged	Maderal Atlantic	3801	0.3	2012	2012	2015	2
FUNDECOR	primary logged	Maderal Atlantic	601	0.3	1998	1998	2018	8
FUNDECOR	primary logged	Maderal Atlantic	602	0.3	1998	1998	2018	8
FUNDECOR	primary logged	Maderal Atlantic	1500	1	1995	1995	2018	11
TEC	primary logged	Guerra	1	1	1990	1990	2018	10
TEC	primary logged	Guerra	2	1	1990	1990	2018	10
TEC	primary logged	Guerra	3	1	1990	1990	2018	10
TEC	primary logged	Guerra	4	1	1990	1990	2018	10
TEC	primary logged	Mogos	1	1	1990	1992	2017	11
TEC	primary logged	Mogos	2	1	1990	1992	2017	11
TEC	primary logged	Mogos	3	1	1990	1992	2017	11

(*continued*)

Institution	Type of Forest	xpar	Plot	Plot area (ha)	Year established	First year ofmeasurement	Last year ofmeasurement	Number ofmeasurements
TEC	primary logged	Mogos	4	1	1990	1992	2017	11
TEC	primary logged	Rincon	1	1	1990	1990	2017	10
TEC	primary logged	Rincon	2	1	1990	1990	2017	10
TEC	primary logged	Rincon	3	1	1990	1990	2017	10
TEC	primary logged	Rincon	4	1	1990	1990	2017	10

Year/date ofdisturbances	Number ofdisturbances	Type ofdisturbances (Logging, RIL, Fire)	Logging(disturbance) intensity	Years of monitoringbefore disturbance	Years of monitoringafter disturbance	Logging techniques	Time since logging	Type of treatments (if any)	Year/dateof treatment
1992	1	RIL	30–60%	4	9		28	ring barked	1996
1992	1	RIL	30–60%	3	6		28	ring barked	1996
1992	1	RIL	30–60%	4	9		28	ring barked	1996
1992	1	RIL	30–60%	2	8		28		
1992	1	RIL	30–60%	1	8		28		
1992	1	RIL	30–60%	1	9		28		
1992	1	RIL	30–60%	0	1		28		
1992	1	RIL	30–60%	0	1		28		
1992	1	RIL	30–60%	0	1		28		
1990	1	RIL	30–60%	0	9	sustainable	30	ring barked	1991
1990	1	RIL	30–60%	0	11	sustainable	30		1991
1990	1	RIL	30–60%	2	10	sustainable	30	ring barked	1991
1990	1	RIL	30–60%	1	11	sustainable	30		
1990	1	RIL	30–60%	0	10	sustainable	30		
1990	1	RIL	30–60%	0	5	sustainable	30		
1990	1	RIL	0	0	8	sustainable	30		1991
1990	1	RIL	0	2	10	sustainable	30		1991
1990	1	RIL	30–60%	0	11	sustainable	30		1991
1991	2	Low impact	50%	1	2	low impact	29	control	
1991	2	Low impact	50%	1	2	low impact	29	refinement	
1992	2	Low impact	50%	1	2	low impact	28		
1992	2	Low impact	50%	1	7	low impact	28	sil. treatment	
1992	2	Low impact	70%	1	2	low impact	28	sil. treatment	
1992	2	Low impact	60%	1	2	low impact	28	sil. treatment	
1992	2	Conventional	100%	1	2	low impact	28	sil. treatment	
1992	2	Low Impact	60%	1	2	low impact	28	release, refinement, control	
2001	1	RIL	30–60%	2	5	low impact	19		
2001	1	RIL	30–60%	2	5	low impact	19		
2001	1	RIL	30–60%	2	5	low impact	19		
2001	1	RIL	30–60%	2	5	low impact	19		
2005	1	RIL	30–60%	0	3	low impact	15		
2005	1	RIL	30–60%	0	3	low impact	15		
2005	1	RIL	30–60%	0	3	low impact	15		
2005	1	RIL	30–60%	0	3	low impact	15		
2002	1	RIL	30–60%	2	5	low impact	18		
1998	1	RIL	30–60%	0	7	low impact	22		
2000	1	RIL	30–60%	2	7	low impact	20		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	1	8	low impact	22		
1998	1	RIL	30–60%	0	7	low impact	22		
1998	1	RIL	30–60%	0	7	low impact	22		
2006	1	RIL	30–60%	4	4	low impact	14		
2006	1	RIL	30–60%	4	4	low impact	14		
2006	1	RIL	30–60%	4	4	low impact	14		
2006	1	RIL	30–60%	4	4	low impact	14		
1990(?) -2008	2	RIL	30–60%	0	2	low impact	30		

(continued)

Year/date ofdisturbances	Number ofdisturbances	Type ofdisturbances (Logging, RIL, Fire)	Logging(disturbance) intensity	Years of monitoringbefore disturbance	Years of monitoringafter disturbance	Logging techniques	Time since logging	Type of treatments (if any)	Year/dateof treatment
1998	1	RIL	30–60%	0	7	low impact	22		
1998	1	RIL	30–60%	0	7	low impact	22		
1990(?) – 2008	2	RIL	30–60%	7	4	low impact	30		
1992	1	RIL	33%	1	9	oxen	28	no	
1992	1	RIL	33%	1	9	caterpillar	28	no	
1992	1	Conventional	60%	1	9	conventional with tractor	28	no	
1992	1	RIL	33%	1	9	oxen and tractor	28	no	
1992	1	RIL	33%	1	10	oxen	28	no	
1992	1	RIL	33%	1	10	caterpillar	28	no	
1992	1	Conventional	60%	1	10	conventional with tractor	28	no	
1992	1	RIL	33%	1	10	oxen and tractor	28	no	
1992	1	RIL	33%	1	9	oxen	28	no	
1992	1	RIL	33%	1	9	caterpillar	28	no	
1992	1	Conventional	60%	1	9	conventional with tractor	28	no	
1992	1	RIL	33%	1	9	oxen and tractor	28	no	

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119462.

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