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ABSTRACT

Tropical forests play a fundamental role in mitigating climate change (CC) through storage of carbon in above-ground biomass. However, greenhouse gas emissions through tropical deforestation or forest degradation are sizeable. To mitigate degradation caused by conventional logging various techniques seek to reduce biomass loss in production forests. However, little knowledge exists about the potential of sustainable management for maintaining and restoring the CC mitigation capacity of tropical forests. Our research contributes to knowledge about this potential. We evaluate the above-ground biomass (AGB) of rain forests managed for sustainable production and compare production forest AGB 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 rain forests (70 plots in production forests and 71 plots in primary forests) with data for the 2000-2015 period. We compared the AGB of production forests with that of primary 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 production forests than in primary forests. In VARPART, spatial variables had the strongest effect on AGB with a small but significant effect of soil. Regression showed soil K 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 has enabled them to store as much carbon in biomass as primary forests, due to the low intensity logging stipulated by the country's forestry legislation. As a result, sustainable forest management, in addition to the sustainable timber provision ecosystem service, is also a natural climate solution, maintaining the mitigation potential of Costa Rica´s tropical forests in the current climate context.

KEYWORDS

Primary forests; sustainable forest management; climate change mitigation; permanent sampling plots, plot spatial distribution; variation partitioning; soil fertility.

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, Sullivan *et al*. 2020, Griscom *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 production forests. We specifically study above-ground biomass (AGB) storage in production forests submitted to sustainable logging techniques. Knowing more about AGB storage in 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 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). The objective of this research was to estimate the above-ground biomass (AGB) in production forests under sustainable management and to compare it with the AGB in primary forests. This estimation is made for the period 2000-2015, and used data collected from permanent sampling plots established in different areas of Costa Rica by the Costa Rica Forest Ecosystems Observatory (Observatorio de Ecosistemas Forestales de Costa Rica, OEFo). We also examined the relationship between AGB 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 production forests.

2. MATERIALS AND METHODS

2.1. Area of study

The research was carried out with data from primary and 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 three on the Pacific slope (Figure 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 selected for this research are part of the Costa Rica Forest Ecosystems Observatory (Observatorio de Ecosistemas Forestales de Costa Rica, OEFo) (Morrison 2020). The OEFo is a group of institutions with a network of over 400 permanent sampling plots

123 (PSPs). Its main objective is to evaluate the status and dynamics of forest ecosystems according to
124 their level of disturbance and to build knowledge about the ecosystem services that they provide. For
125 the purposes of this research, we selected 171 PSPs on private farms, located in nine life zones and
126 transition zones (Holdridge 1966, Quesada 2007) (Table 1, Figure 1).

Life zone	Altitudinal Tier	Altitudinal Range (masl)	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

127 Table 1 Distributions of primary and production forest study plots by life zones.

128

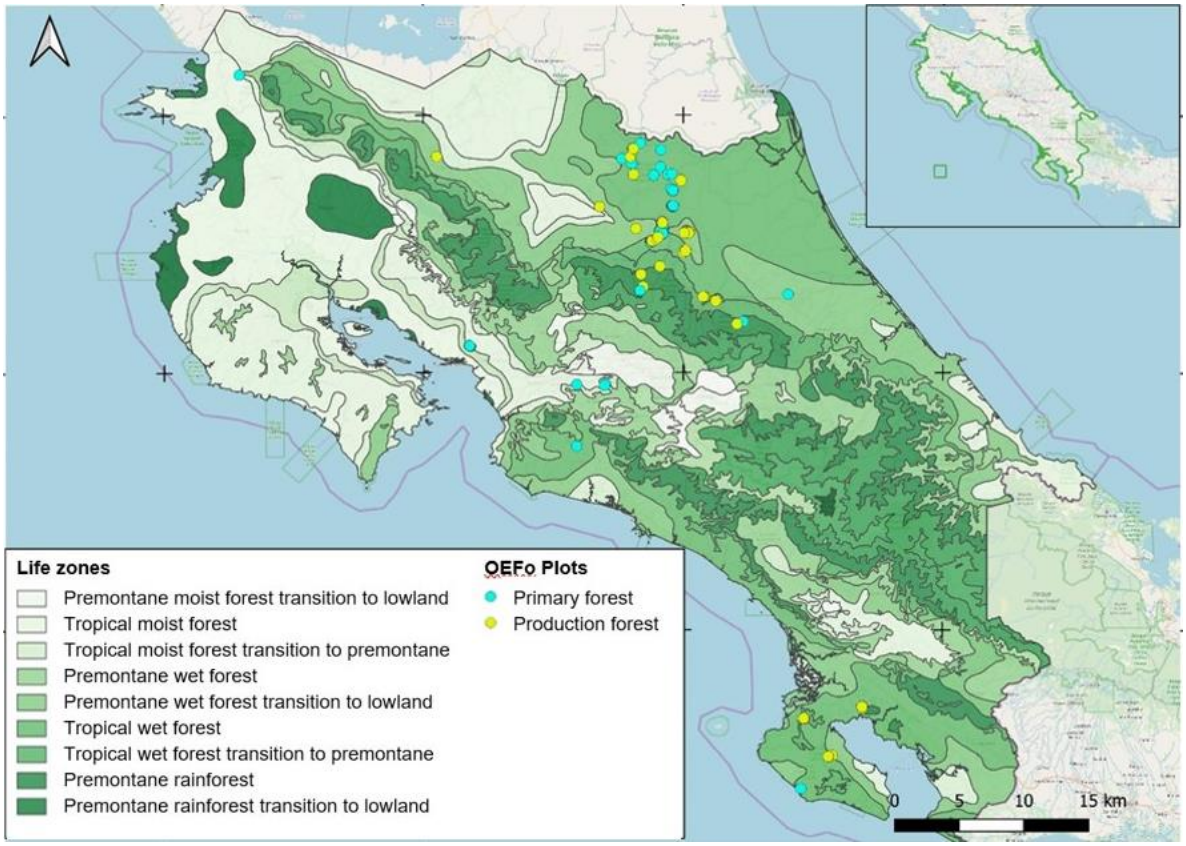

Figure 1. Map of the distribution of the study plots across Holdridge Life Zones in Costa Rica.

The area of monitoring plots varied between 0.2 ha and 1 ha. In all plots, trees with diameter at breast height (BDH, 1.3 m) were measured. Most trees were identified by genus and family and in many at the level of species. The identification was carried out by qualified staff and botanists.

Palms (family Arecaceae) 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.

140 2.3. Environmental variables

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

146 In addition to temperature and rainfall, soil data were obtained from the Centre for Agricultural
147 Research (Centro de Investigaciones Agronómicas, CIA) of the University of Costa Rica (Mata *et al*.
148 2016). This database draws on 1500 soil sampling locations distributed throughout Costa Rica. The
149 values of soils characteristics used in analyses were chosen according to the proximity of the CIA
150 sampling locations to PSPs and by life zones. We used values for 0-40 cm soil depth (Sesnie *et al*.
151 2009, Santiago-García *et al*. 2019). The following variables were taken into account: pH in water,
152 acidity, Ca, Mg, K, Zn, P, Cu, Fe, Mn, effective cation exchange capacity (ECEC), organic carbon
153 (OC) and the percentage of sand, loam and clay in the soil. These variables are considered to be
154 attributes of soil fertility by Mata *et al.* (2016).

155

156 2.4. Estimation of above-ground biomass

157 For the estimation of AGB, data were selected for the period 2000-2015 covered by the selected
158 plots. During this period, some plots were measured only once and others up to seven times (Appendix
159 1).

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

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

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 average plot AGB was obtained from the set of enumerations.

2.5. Statistical analysis

In order to compare AGB between the production and primary ANOVA (analysis of variance) was carried out with a linear mixed model using InfoStat software (Di Rienzo *et al.* 2019). The fit,of a model with no random factor was better than that of a model with plot set as the random factor according to the AIC and BIC criteria. Assumptions of normality and variance homogeneity were evaluated using QQ-plots and residuals versus predicted plots respectively (Appendix 2).

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

186 Principal coordinates of neighbour matrices (PCNM) analysis was used to calculate spatial
187 variables to evaluate the effect of plot spatial distribution on AGB. This was calculated by using a
188 log transformation of the spatial coordinates of each plot, resulting in a Euclidean distance matrix of
189 the distances between the plots. In order to detect and quantify spatial patterns, the logarithmic values
190 were truncated to create a second matrix of eigenvalues which were submitted to a principal
191 component analysis (PCA). The result is a set of eigenvectors known as PCNMs (Bocard & Legendre
192 2002, Dray *et al.* 2006). These represent the spatial relationships among plots at different scales. The
193 analysis was carried out in R software (R Core Team 2019) using the *Vegan* library and the *PCNM*
194 function (Oksanen *et al*. 2013).

195

196 *2.5.2. Spatial, soil and climate variables affecting AGB*

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

204 In order to verify that a high correlation between the selected variables and the climate variables
205 did not exist as a result of forward selection, Pearson's correlation coefficient was applied (Appendix
206 4).

207

208 *2.5.3. Variation partitioning analysis*

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

216 The adjusted R^2 (R^2 adj) values indicate the proportion of variation in AGB that is explained by
217 each explanatory matrix. The significance of fractions from the VARPART analysis ($p \leq 0{,}05$) was
218 confirmed with a redundancy analysis (RDA) test.

219 *2.5.4. Linear regressions*

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

227

228 **3. RESULTS**

229 3.1. Above-ground biomass

230 The above-ground biomass (AGB) of 58,661 trees from 812 taxa was estimated, distributed
231 across 141 plots. 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 intact primary forests (296.3 Mg ha^{-1} ± 75.9) (Table 2).

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

Table 1. Descriptive statistics for AGB in primary and production forests. Standard deviation (SD) and standard error (SE).

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

The variables selected for the soil matrix were K, %OM (organic matter), %silt and 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 3).

A Pearson correlation test verified that the regional-scale spatial relationship represented by PCNM3 was independent of climate and soils variables (Appendix 4).

VARPART showed that the combined effects soil, climate and spatial matrices explained 44% of variation in AGB (Table 3). 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 ($R^2adj=0.058$).

249

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

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

255 *3.3. Multiple regression analysis*

256 Linear regression enabled the variables with most influence on variability in AGB to be identified
257 (Table 4), according to the Mallows' C_p values obtained from the regression<n: the variables with
258 higher values are those that exert a greater influence on biomass variation. Plot spatial distribution
259 was found to influence AGB variation strongly, and potassium was among the soil fertility variables
260 that was also associated with AGB variation.

261

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

Table 3. Values from multiple regression statistics for the explanatory variables according to the value of Mallows' C_p criterion for prediction.

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 rain 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 C per hectare and production forests, 164.65 Mg C per hectare.

4.1 Production forests contain greater AGB than intact primary forests

Plots in primary production forests had higher mean AGB ha^{-1} than intact 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 *et al.*, 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 & Edwards 2019). Also, a study in Amazonian forests demonstrated that AGB recovers more quickly after RIL than after conventional logging (Rutishauser *et al.* 2015).

292 Unfortunately, records of logging intensity in the production forests we studied are not now
293 available. However, in the Costa Rican forest management context, production forests are subject to
294 RIL and a very low logging intensity under a strict forest management protocol (Alice-guier *et al*.
295 2020), in accordance with article 20 of the *Ley Forestal* (Forestry Law) No. 7575 from 1996. Finegan
296 and Camacho (1999), in a typical example, recorded the cutting of four trees per hectare for a mean
297 volume of $10m^3\ ha^{-1}$ in rain forest at an experimental site in the north of the country. RIL can be
298 translated into a reduction of 50% or more of the impact caused by collateral damage (Putz *et al.*
299 2008, Sasaki *et al.* 2016, Cerullo & Edwards 2019).

300 Our study suggests that under certain circumstances, AGB in production forests can be greater
301 than that in intact primary forests. AGB resilience in neotropical secondary forests is well-studied
302 (Poorter et al. 2016) but the potential for AGB storage in production forests has been less reported in
303 the literature. The regeneration of fast-growing long-lived tree species in logging gaps could
304 contribute more biomass to the system (Herault *et al.* 2010) though this is probably unlikely under
305 the low-intensity harvesting that typifies forest management in Costa Rica. However, carbon stock
306 enhancement after sustainable logging could be converted into carbon credits for initiatives such as
307 REDD+ (Cerullo & Edwards, 2019).

308 Another possible explanation for our results is that edge effects due to forest fragmentation are
309 in fact impacting AGB of primary forests, as has been shown at an Amazonian site by Laurance *et al.*
310 (2006). Both production and primary forests in our study are located on private farms in fragmented
311 landscapes, as documented by Morse *et al.* (2009) for the northern zone of the country. While pasture
312 was for many years the main agricultural land use, agricultural intensification, for example the spread
313 of pineapple agroindustry, is a recent trend, potentially exacerbating edge effects in the remaining
314 forest (Shaver *et al.* 2015). However, Schedlbauer *et al.* (2007) showed that AGB was not affected
315 by proximity to forest edges in north eastern Costa Rica, where most of the sample plots of the present

316 study are located, and changes in understorey vegetation at edges are minimal (Bouroncle and
317 Finegan 2012).

318 *4.2 Influence of spatial, soil and climate variables on above-ground biomass*

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

332 AGB variation in our study was more strongly explained by plot spatial distribution than by soil
333 fertility or climate-related variables. As is the case for forest composition and species diversity
334 (Legendre et al. 2009), the relationship between AGB and plot spatial distribution may be influenced
335 by dispersal limitation and regional biogeography, if different dominant species have different
336 potentials for accumulation of AGB due to differences in key functional traits such as maximum adult
337 height (Finegan *et al.* 2015). The species composition of the forests we studied varies both within
338 landscapes, for example in the northeast of the country (Sesnie *et al.* 2009) and between forests in the
339 northeast and those of the southwest (compare Sesnie *et al.* 2009 with Cornejo 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 and AGB.

The relationship between soil and AGB often shows mixed and conflictive results in the literature. Often 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 fertilization 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).

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,

388 the return of the ecosystem to its original state is unlikely (Ghazoul *et al*. 2015). Therefore, these
389 forests may function as carbon sources or sinks, depending on the type of management to which they
390 are subjected (Piponiot *et al*. 2016a). According to our results, production forests in Costa Rica would
391 be acting as carbon stores and possibly sinks because of the sustainability of the logging techniques
392 applied.

393

394 **5. CONCLUSIONS**

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

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

407 Even though it is well known that tropical forests are the richest in carbon and the most
408 productive of the forest biomes, they are constantly under threat, which means that mechanisms need
409 to be found to support their sustainable management and conservation. The productivity, conservation
410 and mitigation potential of production forests makes them important ecosystems that can enhance
411 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.

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