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Reduced tree density and basal area in Andean forests are associated with bamboo dominance

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ABSTRACT

Forest structure and composition play an essential role in determining the carbon storage capacity of tropical forests. Andean forests, with great potential for carbon accumulation, include large expanses of high-density woody bamboo communities. Woody bamboos can potentially alter forest structure, composition and dynamics and thus can affect carbon storage capacity; however, they are commonly excluded from forest monitoring and modelling. With the aim of documenting patterns of bamboo abundance and disentangling its association with forest structure, we carried out a bamboo census in seven 1-ha long-term forest monitoring plots situated across a large elevation gradient (1000–3600 m a.s.l.) in the Peruvian Andes. We determined that bamboo is a dominant plant group in the study area. In every plot, bamboos were the most common genera in terms of number of stems, and in two of the plots bamboo species were among those with the greatest basal area. We used a combination of Generalized linear mixed models (GLMM) and structural equation modelling (SEM) to hypothesize a causal framework and determine the direction and size of the effects of bamboo abundance (basal area) on number of individual trees, total tree basal area, mean tree basal area, mean tree growth rate and tree mortality rate. We found an overall negative association between bamboo abundance and total tree basal area driven mainly by reduced tree density (directly and indirectly mediated by an increase in tree mortality). However, the decrease in tree density and the increase in tree mortality are also associated with a small increase in tree diameter (mean tree basal area). Overall, the negative association between bamboo abundance and tree basal area suggests a lower biomass accumulation and thus a lower carbon storage capacity of trees in Andean forests where bamboo is dominant. Our results, which show the importance of bamboo in determining forest function, highlight the need for including bamboo in monitoring efforts and modeling studies.

1. Introduction

Tropical forests play an important role in regulating Earth's climate through their storage and cycling of carbon (Malhi and Grace 2000, Pan et al. 2011, Spracklen and Righelato 2014, Brienen et al. 2015). Interactions between plants, in particular, competition for aboveground and belowground resources (e.g., light and water or soil nutrients, respectively), play an important part in shaping forest structure and composition, which ultimately determines the forest's carbon storage capacity (Duran and Gianoli 2013, Poorter et al. 2015, Tymen et al. 2016). A well-documented case is competition between lianas (woody vines) and trees which results in decreased tree growth and increased tree mortality (Clark and Clark 1990, Laurance et al. 2001). This inter-guild competition can lead to a strong alteration of forest function; for example, in Panama, lianas cause a ~76% reduction of the forest's annual net aboveground carbon uptake (van der Heijden et al. 2015).

While the importance of lianas for determining the dynamics of tropical forests is increasingly appreciated (Schnitzer et al. 2015), there are other groups of plants with strong competitive potential, such as bamboo (Family Poaceae, subfamily Bambusoideae), for which the effect on tropical forest function remains understudied (Fadrique et al., 2020a).

Bamboo has previously been identified as a potential modulator of forest structure, composition and dynamics (growth, mortality, and recruitment) in several Neotropical ecosystems. Specifically, in Atlantic and semideciduous tropical forests, the presence of bamboo has been associated with increased tree mortality and decreased tree growth (Guilherme et al. 2004, Lima et al. 2012). In addition, bamboo has been shown to alter gap dynamics and reduce tree sapling richness and abundance (Campanello et al. 2007, Montti et al. 2011) and to reduce tree recruitment rates (Guilherme et al. 2004). In contrast, the presence of the bamboo *Guadua tagoara* in the Brazilian Atlantic forests is linked to higher tree recruitment rates than in nearby bamboo-free forests. In the Southwestern Amazon, the presence of *G. sarcocarpa* and *G. weberbaueri* is associated with decreased tree density and basal area (Silman et al. 2003, Griscom and Ashton 2006, Nelson, 1994, de Carvalho et al. 2013) in addition to altered functional and taxonomic composition. These two species of *Guadua* have also been found to reduce species richness and increase establishment of fast-growing pioneer tree species (Silveira 2001, Silman et al. 2003, Griscom et al. 2007), while in Argentinean Atlantic forests *Chusquea ramosissima* and *Merostachys clausenii* bamboos have been found to reduce recruitment of pioneer tree species into gaps (Campanello et al. 2007).

In summary, although the potential effects of bamboo on forests, as well as the driving mechanisms causing these effects, differ between ecosystems and species, bamboos are generally associated with lower tree density and survival and with a biased species composition. The most important mechanisms behind these effects are likely to be 1) the physical damage caused by mass loading of senescent bamboo culms (Silman et al. 2003, Griscom and Ashton 2003, 2006), 2) the modification of the microclimate (light, water, nutrients) (Griscom and Ashton 2003, Takahashi et al. 2003, Campanello et al. 2007) and, in relationship with these two, 3) the gregarious monocarpic flowering cycle (in many bamboo species), that provides a narrow window for selective regeneration of non-bamboo plants during the bamboo mortality period (González et al. 2002, Silman et al. 2003, Holz and Veblen 2006, Montti et al. 2011). Other mechanisms such as allelopathic effects (Jose et al. 2016) and soil modifications may also be important aspects of the tree-bamboo interactions, but they remain poorly documented.

There are over 130 bamboo species in the Andes (Guerreiro et al., 2013) creating unique communities (Judziewicz et al. 1999, Clark et al. 2015b). Information about their ecology remains sparse and comes primarily from studies of mid- and high-elevation forests in Chile, where several understory bamboos of the genus *Chusquea* reduce the growth and establishment of the shade-intolerant tree *Nothofagus* (Veblen 1982, González et al. 2002, Holz and Veblen 2006). Despite the abundance and widespread distribution of bamboo in the Andes, and the large contribution of Andean forests to the global carbon storage (Spracklen and Righelato 2014), we have very limited information on how dominant bamboos are in these forests and whether they are associated with alterations of forest structure that could lead to reduced forest carbon storage capabilities.

In order to increase our understanding of the roles that bamboo plays in Andean forests, we performed exhaustive bamboo censuses in seven 1-ha permanent plots along a large elevational gradient (spanning 2600 m elevation) in the Kosñipata Valley of southern Peru. Extensive research has previously been conducted in this area to understand elevational patterns of ecosystem functioning, including studies examining forest productivity, nutrient cycling, hydrology, plant composition, and tree demography along the elevation gradient (Feeley et al. 2011, Rapp et al. 2012, Asner et al. 2014, Clark et al. 2014, Girardin et al. 2014, Malhi et al., 2016). However, prior to the current study, bamboo was not included in the forest plot inventories and thus no information was

available about the distribution of bamboo in the area or the interaction between bamboo and trees. By combining our new bamboo census data with the tree census data from several of the established plots, we addressed several important questions, including: 1) Is bamboo a dominant plant group in terms of density and basal area along this elevation gradient of tropical montane forests? 2) Are there associations between bamboo abundance and variation in tree size and tree growth rate? And between bamboo abundance and total tree basal area, density, and mortality rates? In addition, we used Structural Equation Modeling to (3) contextualize the relationship between bamboo and total tree basal area considering multiple direct and indirect interactions. Understanding bamboo dominance and its relationship with forest structure and dynamics is crucial for obtaining a more-holistic view of forest functioning and to incorporate the potential effect of bamboo on tropical forest carbon dynamics.

2. Materials and methods

2.1. Study area

The focal area of research was in and around Manu National Park, in southeastern Peru. An elevational transect of permanent forest monitoring plots was established by the Andean Biodiversity Ecosystem Research Group (ABERG; http://www.andesconservation.org) (Malhi et al. 2010) along the Kosñipata Valley between 2003 and 2006. These plots have subsequently been maintained and regularly censused in collaboration with ForestPlots (https://www.forestplots.net/) and the Global Ecosystems Monitoring Network (GEM; http://gem.tropicalfore sts.ox.ac.uk/projects/aberg). All plots were established in areas with homogeneous stand structure and soil substrate and with no indications of recent human influence. In addition to the Kosñipata Valley plots, we also included a plot established at 1000 m a.s.l. in an adjacent valley (Tono valley). In total, we conducted bamboo censuses in seven 1-ha plots located between 1,000 and 3,600 m a.s.l. (Table 1, Fig. SI.1). The cloud base in the Kosñipata Valley is estimated to be around 1500 m a.s.l. (Halladay et al. 2012) and thus the 1000 m plot is in pre-montane forest and the rest of the plots are in cloud forests. The highest elevation plot is located at 3600 m a.s.l. near the tree-line ecotone. Further information on the plots can found in Table 1 and in Malhi et al. (2016).

2.2. Bamboo census

We performed the bamboo censuses of the seven study plots in July-August 2017. To carry out the bamboo censuses, we initially divided each of the 1-ha plots into 25 subplots of 20 m × 20 m. In five of the seven plots, we sampled 10–13 subplots (i.e., 40–52% of the plot area); in two plots (WAY-01 and ESP-01) we sampled all of the subplots (i.e., 100% of the plot area).

To estimate bamboo abundance, we followed the bamboo monitoring protocols of Fadrique et al. (2020a) using "Approach 2". In each of the selected subplots, we counted every mature culm belonging to a woody bamboo species able to reach at least 1 cm in diameter. During these counts, we identified each culm to species (or morphospecies) and assigned the culm to a 1-cm diameter class (e.g., 0–1.0 cm, 1.01–2.0 cm, etc.). Next, we calculated the mean diameter per bamboo species and plot using the counts and midpoints of each diameter class. We calculated bamboo culm basal area as the area of a circle corresponding to the culm diameter, regardless of whether the species had a solid or a hollow culm.

To extrapolate the subplot estimations of each bamboo species' culm density and basal to the entire 1-ha plot, we sampled 25 subplot values with replacement from the observed measurements. We reiterated this resampling procedure 1000 times to generate a mean and standard deviation per species. We used a similar procedure to estimate combined bamboo culm density and basal area for each 1-ha plot, as well as the percentage of woody basal area accounted for by bamboo (((Bamboo

Table 1
Description of the study plots.

Plot code	Latitude (S)	Longitude (W)	Elevation (m a.s.l.)	Tree Basal Area (m²/ha)	Tree density	Dominant tree genera	Bamboo species (n = 12)
ACJ-01	13° 8′ 48.84″	71° 37′ 56.28″	3,600	37.4	680	*Symplocos* *Miconia* *Clethra* *Weinmania*	*Chusquea scandens* *Chusquea sp20*
TRU-01	13° 6′ 48.96″	71° 36′ 24.84″	3,450	27.9	515	*Miconia* *Weinmania* *Symplocos*	*Chusquea scandens* *Chusquea aff.simplicissima* *Chusquea sp19*
WAY-01	13° 11′ 26.88″	71° 35′ 14.64″	3,000	34.1	994	*Weinmania* *Clusia*	*Aulonemia aff.hirtula* *Chusquea sp3* *Chusquea dombeyana*
ESP-01	13° 10′ 30.36″	71° 35′ 41.28″	2,800	28.6	720	*Weinmania* *Clusia*	*Chusquea dombeyana*
TRU-08	13° 4′ 12.72″	71° 33′ 21.24″	1,800	28.4	961	*Cyathea* *Myrcia* *Clethra*	*Chusquea sp5* *Chusquea sp21*
SPD-01	13° 2′ 51″	71° 32′ 32.28″	1,750	31.6	760	*Cyathea* *Tapirira* *Miconia*	*Chusquea sp5* *Chusquea sp22* *Chusquea sp3*
TON-02	12° 57′ 33.12″	71° 33′ 56.88″	1,000	24.9	378	*Perebea* *Virola*	*Guadua sp27*

BA/(Bamboo BA + Tree BA)) * 100) in each plot.

2.3. Tree census

We used tree data from the two most-recent plot censuses available (2013/2014 and 2017). In the plot censuses, all individual trees (including palms and tree ferns) with diameter at breast height (dbh) $>= 10$ cm are mapped, tagged, identified, and measured for dbh. Using these data, we calculated the following tree parameters at the subplot level: 1) number of individual trees (trees with multiple stems count as one individual); 2) total tree basal area per subplot (m²); 3) mean tree basal area (total basal area divided by number of trees) per subplot (m²); 4) mean tree growth rate per subplot (using individual tree growth rates calculated as the annualized change in basal area between censuses) (cm²/year); and 5) tree mortality rate per subplot (expressed as % annual mortality, estimated as $[1 - (n0 - m)/n0]^{1/y} * 100$ (%/year); where n0 is the number of individuals in the initial census, m is the number of dead individuals at the final census, and y is years between censuses (Sheil and May 1996).

2.4. Statistical analyses

2.4.1. Bamboo abundance and distribution

To investigate elevational patterns, we performed linear and two-degree polynomial regressions between the total number of bamboo culms, the bamboo basal area per plot, and the percentage of bamboo basal area per plot vs. plot elevation.

To investigate the relative abundance of bamboo species we calculated the species-rank abundance distribution for each plot based on the species' basal area per hectare. In addition, we calculated the genus-rank abundance distribution for each plot based on number of stems per genus per hectare.

2.4.2. Bamboo spatial autocorrelation

In order to confirm that the subplots could be treated as independent sampling units, we performed a Moran's I test to check for within-plot spatial autocorrelations of bamboo abundance for 1) all species combined, and 2) each species individually. Moran's I varies from -1 (negative spatial autocorrelation) to 1 (positive spatial autocorrelation) and values close to zero indicate an absence of spatial autocorrelation (Moran 1950, Fortin et al. 2002).

2.4.3. Generalized linear mixed models

In order to analyze the effects of bamboo on forest dynamics as represented by the different tree parameters, we used a Generalized linear mixed model (GLMM) approach where plot identity was included as a random factor, bamboo abundance (basal area per subplot) was the fixed effect variable and one of the tree parameters (number of trees, total tree basal area, mean tree basal area, mean tree growth rate or mortality rate – all per subplot) was the response variable. We first found the best random structure by comparing the Akaike's information criterion (AIC) value for each linear mixed model and choosing the model with the lowest AIC or the model with the fewest parameters when AIC values differed by less than 2 units. We tested three different models for each parameter: 1) plot identity as random intercept, 2) plot identity as random slope, 3) plot identity as random slope and intercept. In all cases the random intercept model had the lowest AIC values or was within 2 units of the model with lowest AIC (usually the model with random slope and intercept).

To account for non-normality, we applied generalized linear mixed models using the "Gamma" family with log link for the models with positive continuous dependent variables, and the "Poisson" family with the log link for the variable with zero value observations (mortality rate). We visually confirmed normality of the residuals of the resultant models. The family and link used in each model are specified in Table SI.4. The resultant fixed effects slopes and predicted values were back transformed from the logarithm by using the exponential function. The marginal (fixed effects) and conditional (random effects) R^2 values are based on the trigamma estimation (R package MuMIn; function r.squaredGLMM (Burnham and Anderson 2002, Nakagawa et al. 2017)).

2.4.4. Structural Equation Model

We used piecewise Structural Equation Modeling (SEM) to contextualize the indirect and direct effects of bamboo and trees on total tree basal area. SEM's are probabilistic models that combine multiple predictor and response variables into one integrated causal framework based on a priori hypotheses. Although we do not necessarily know the causal direction of the interactions between the bamboo and tree parameters, the results can support or refute the hypothesized structure and causal pathways (Lefcheck 2016). The relationships between the variables are input as a series of models that correspond to potential pathways in the final model. The paths are hypothesized causal relationships and the variables can be both predictors and responses (Shipley 2000, Lefcheck 2016). In the piecewise SEM each equation is individually evaluated. SEMs were constructed using the piecewiseSEM

package (v.2.1, Lefcheck 2016) to include the significant relationships between bamboo and trees obtained from the previous GLMM's and the expected relationships between tree parameters based on previous studies. We carried out a Shipley's test of d-separation (Shipley 2009) to assess whether there were important paths missing from the initial model and to observe the significance of the interactions between parameters in order to eliminate the non-significant ones. Thus, the final model incorporates all important paths and only significant interactions between variables. The equations supplied to the model are shown on Table SI.1. The marginal (fixed effects) and conditional (random effects) R^2 values for each of the predicted variables are based on the trigamma estimation.

The standardized coefficients could not be calculated for piecewise SEM's since the GLMMS have gamma distributions. However, in order to obtain an estimation of the magnitudes of the effects of bamboo on tree basal area, we constructed another SEM with the same relationships as the final input model but using the log-transformed data set and LMMs. In the case of tree mortality, a square-root transformation was used. We obtained a model where all but one of the relationships showed the same directionality as the SEM constructed with GLMMs. Given the circumstances of this analysis, we were not concerned about the significance of each individual predictor. We included both unstandardized and standardized coefficients in Fig. 3. We estimated path coefficients by multiplying the standardized coefficients of each link in the path.

3. Results

3.1. Bamboo abundance and distribution

We found 12 woody bamboo species (four identified to species and eight as morphospecies) from the genera *Guadua*, *Aulonemia* and *Chusquea* in the seven 1-ha forest inventory plots. Nine bamboo species were found in only one plot while three bamboo species occurred in two plots (always at adjacent elevations). We observed a maximum of three bamboo species per plot, and two of the plots (ESP-01 and TON-02) each had only one species of bamboo (Fig. 1). There was no significant relationship between bamboo density and elevation (linear - Adj. $R^2 =$ 0.26, p = 0.14), although high-elevation plots tended to have greater bamboo culm densities than the lower elevation plots (Fig. 2). Indeed, bamboo density per hectare reached a maximum of ~16,000 culms in a high elevation plot (TRU-01; 3450 m a.s.l.) and a minimum of ~700 culms in the lowest elevation plot (TON-02; 1000 m a.s.l.) (Fig. 2). On average, we observed much larger diameter culms in the low-elevation species (5.7 cm, *Guadua sp27*) than in the higher-elevation species of the genus *Chusquea* and *Aulonemia* (Chu_dom: 0.5 cm, Chu_sp20: 1 cm, Aul_hir: 1.4 cm) (Fig. 1). When density and diameter are combined to calculate bamboo basal area, we observed that the plots with highest density (TRU-01; 3450 m a.s.l.) and the plot with larger species mean diameter (TON-02; 1000 m a.s.l.) are the plots with higher bamboo basal areas (2.83 ± 0.16 and 1.91 ± 0.4 m^2 respectively) and also with the highest percentage of bamboo basal area (9.38 ± 0.8 and 8.53 ± 1.87% respectively) (Fig. 1). Nevertheless, there was no significant relationship between total bamboo basal area (polynomial - Adj.R^2 = 0.08, p = 0.38) or percentage of bamboo basal area (polynomial - Adj.R^2 = 0.20, p = 0.28) and elevation (Fig. 2).

The rank-abundance distributions show that most bamboo species are within the upper 50% of species in terms of basal area in their respective plots and were occasionally amongst the very highest-ranking groups (Fig. SI.2). In TON-02, *Guadua sp27* is the third most abundant species in basal area, in TRU-01 *Chusquea sp19* is the fourth most abundant species, and in TRU-08 *Chusquea sp21*, is the 10th most abundant species. When looking at the abundance in terms of the number of stems, even when taxa are combined at the genus level, bamboos are clearly the most abundant genus in every plot where they occur (Fig. SI.3).
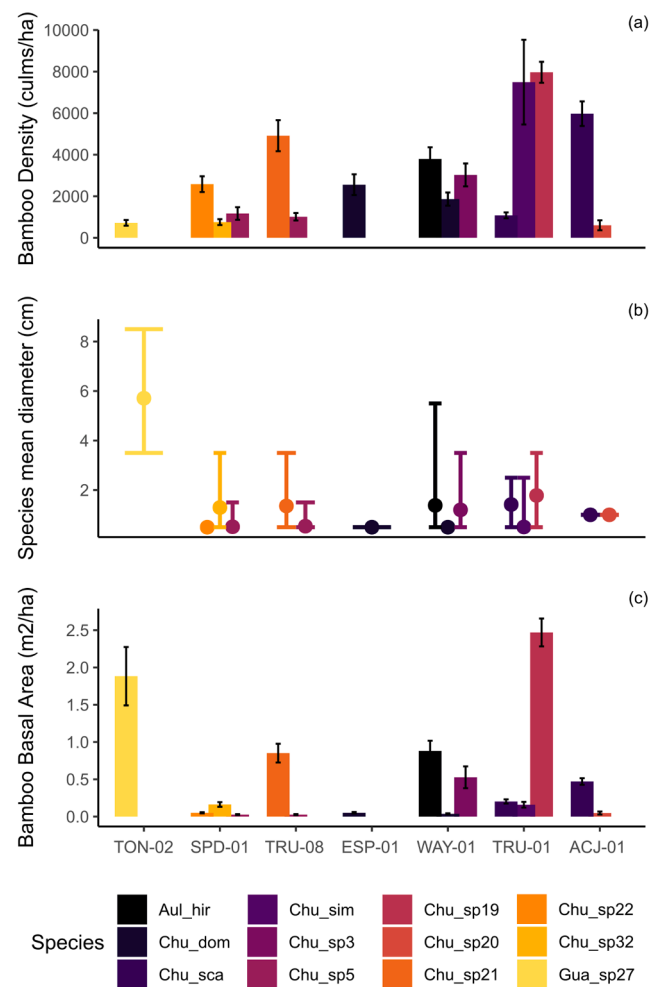

Fig. 1. Bamboo density, diameter, and basal area per species and plot. Mean density (a), mean diameter (b), and total basal area (c) of each bamboo species (or morphospecies) in each plot (plot ordered by increasing elevation). The error bars in a and c denote standard deviations and the error bars in b denote the species' minimum and maximum diameters.

3.2. Spatial autocorrelation

We performed a Moran's I test to check for spatial autocorrelation in bamboo abundance per each plot and test the independence of the subplots units. Using the sum of bamboo basal area per subplot (all species combined), we found that four of the seven plots showed significant autocorrelation, however, the autocorrelation values were close to zero (<0.081), which represents only a very minor signal of clustering (Table SI.2). When we performed the same test for each species per plot separately (Table SI.3), we found that five of the 15 combinations of species per plot showed signs of spatial autocorrelation (one species per plot did not have enough data for the test). From these results we conclude that the effect of spatial autocorrelation on bamboo basal area is generally minor and as such we did not incorporate any correction procedures into our subsequent analyses.

3.3. Generalized linear mixed models

In order to analyze whether bamboo abundance could explain variation in different tree parameters within the plots, we performed several generalized linear mixed models (GLMM) where plot identity was always included as a random intercept, bamboo basal area per subplot was
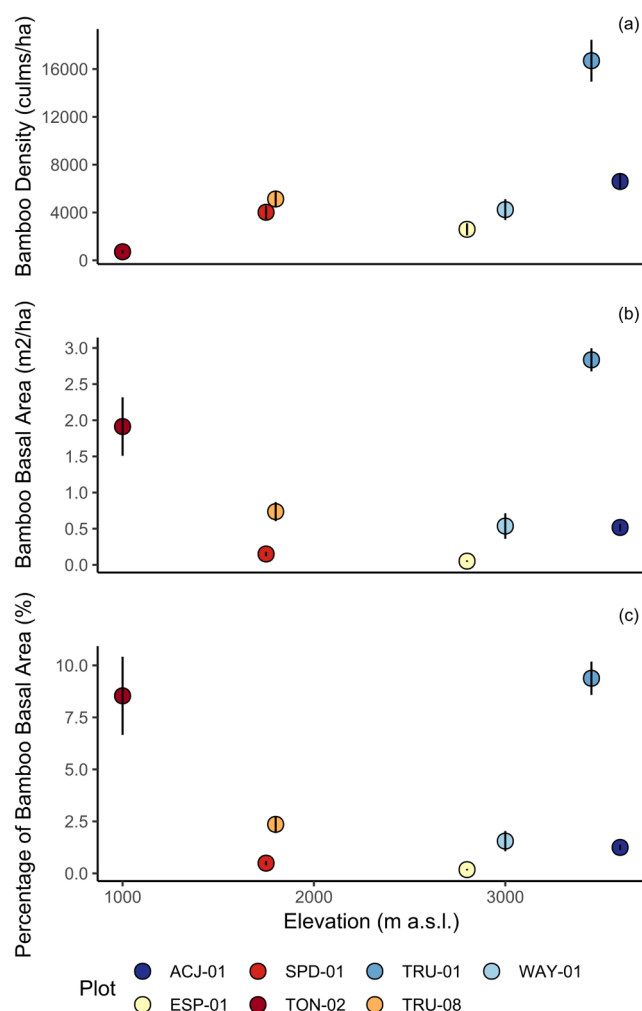
Fig. 2. Bamboo density, basal area and percentage of bamboo basal area per plot. Total bamboo density (a), total bamboo basal area (b) and percentage of plot basal area attributable to bamboo (c) for the combined bamboo species in each plot vs. plot elevation. Error bars indicate standard deviations. Dashed lines indicate non-significant relationships.

Table 2
Summary of the results from the GLMM. Bamboo basal area was the predictor variable and the effect of plot identity is included as a random intercept.

	Direction of effect	P value		R^2marginal	R^2conditional
Number of trees	Negative	0.000	***	0.137	0.304
Total tree basal area	Negative	0.000	***	0.179	0.276
Tree growth rate	Positive	0.006	**	0.085	0.223
Tree mortality rate	Positive	0.004	**	0.049	0.239
Mean tree basal area	Negative	0.247		0.018	0.211

the fixed effect and the selected tree parameter was the response variable. The distribution of bamboo per subplot is shown in Figure SI.4. The GLMM (Table 2, Table SI.4) indicated a significant negative relationship between bamboo basal area and tree density (marginal Adj.R^2 = 0.14, p < 0.001) and between bamboo basal area and total tree basal area per subplot (marginal Adj.R^2 = 0.18, p < 0.001). In addition, there was a

significant positive relationship between bamboo basal area and mean tree growth rate (marginal Adj.R^2 = 0.09, p < 0.01) and tree mortality rate (marginal Adj.R^2 = 0.04, p < 0.01). There was no significant relationship between bamboo basal area and mean tree basal area (a proxy to tree diameter) (marginal Adj.R^2 = 0.02, p = 0.25). The overall predicted values from the significant models are shown in Fig. SI.5 and the predicted values for each plot are shown in Fig. SI.6.

3.4. Structural Equation model

The results from the SEM (Fig. 3, Table SI.5) aligned with the results from the individual GLMM's. The SEM that we constructed adequately fitted the data (Fisher's C = 4.45, p = 0.82; where p > 0.05 indicates no significant lack of fit between the model and the data). The explanatory power of the fixed effects is relatively low for tree mortality rate (marginal R^2 = 0.05), moderate for number of trees, tree growth rate and mean tree basal area (marginal R^2 = 0.19, 0.17 and 0.23 respectively) and high for the total tree basal area (marginal R^2 = 0.87). The inclusion of plot identity as a random effect (conditional R^2) increased the overall fit of the models.

The final SEM supports the a priori structure of causality, such that total tree basal area has a direct negative association with bamboo basal area and positive associations with tree density and tree diameter. Bamboo basal area had a negative association with tree density and tree diameter, and a direct positive association with tree mortality rate. Tree mortality had a negative association with tree density, which had a negative relationship with mean tree diameter. Finally, tree mortality had a positive relationship with tree growth, which could affect tree diameter although this link is not supported in the model.

The standardized coefficient calculations (using the log-transformed data set and LMM's – Table SI.6) revealed an overall negative relationship between bamboo and tree basal area, where the strongest effect is through the reduction of tree density (−0.19) (Table SI.7). The other direct and indirect paths have minor roles in the overall interaction.

4. Discussion

By combining our new bamboo census data with the existing tree data from seven 1-ha plots distributed across a >2500 m elevation gradient, we were able to characterize bamboo dominance in Andean forests and the association of bamboo to a particular forest structure with less trees, lower total basal area, and altered dynamics with faster mortality and growth rates.

Bamboo represents a dominant component of Andean forests by reaching extremely high relative densities. In our study plots, bamboo genera account for a greater number of stems than any of the tree genera, or even all >10 cm dbh trees combined. Bamboo is less dominant in terms of basal area but still occupies a top position with most bamboo species being ranked in the top half of species in the abundance distributions. In the plot with the largest bamboo (TON-02) and the one with the highest bamboo density (TRU-01), bamboo species were third and fourth in basal area rankings, respectively. We found no relationship between bamboo density and basal area with elevation but there was a marked transition between the genus *Guadua* (larger diameter and basal area) which grows at low elevations and *Chusquea* (usually smaller and denser) which grows from mid to high elevations.

Although bamboo density is high on the study area, higher densities of *Guadua* and *Chusquea* have been found in other Neotropical ecosystems. For example, in Atlantic forests, *C. ramosissima* reaches >23,000 stems/ha (Campanello et al. 2007), in the Chilean Andes, *C. culeau* and *C. tenuiflora* reach >100,000 stems/ha (Veblen et al. 1980, Veblen 1982), or in *Guadua*-dominated forests in the Southwestern Amazon, *G. weberbaueri* and *G. sarcocarpa* reach densities of more than 3500 and 2000 stems/ha respectively (e.g. Griscom and Ashton 2006). Bamboo density varies along the species life cycle, becoming higher towards the more mature population stages (Dalagnol et al., 2018; Yuen et al., 2017).
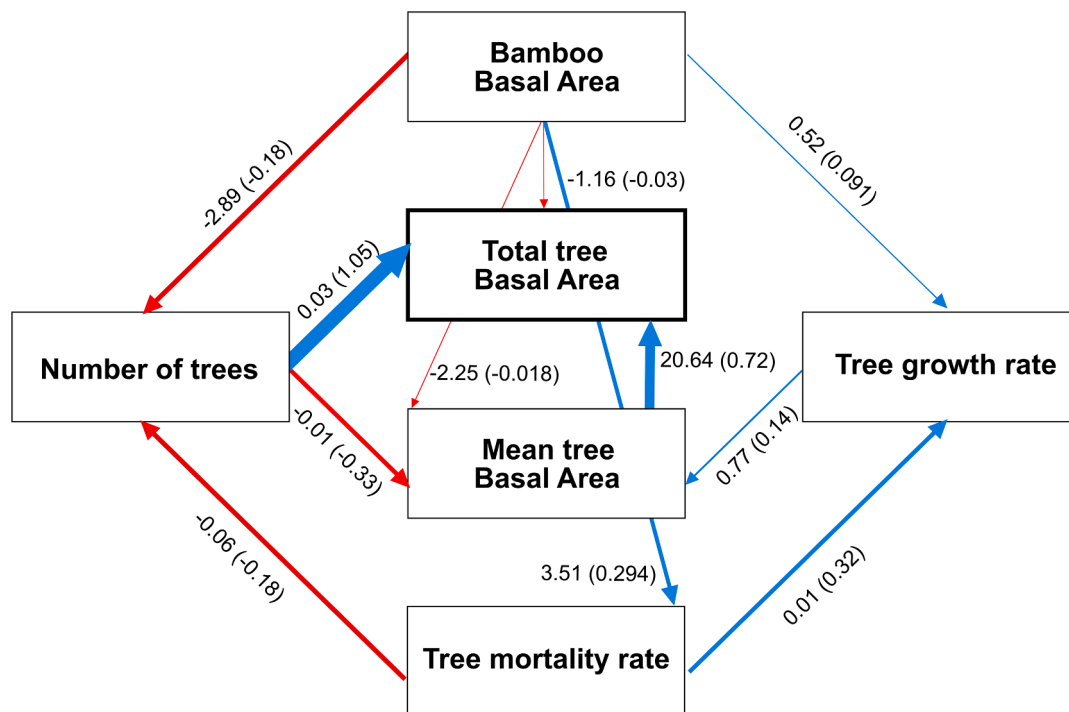
Fig. 3. Structural Equation Model (SEM) of total tree basal area. Arrows show directionality of the interactions. Blue and red arrows denote positive (+) and negative (−) relationships respectively. Coefficients represent unstandardized estimated effects (outside parenthesis) and standardized effects (in parenthesis- using the log transformed dataset for calculations). Arrow thickness is proportional to standardized coefficients. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We lack information on when the bamboo populations in our study area flowered or on what is the length of the flowering cycles in our different species. It is possible that some of the populations that we censused are "young" and show lower densities than will occur at more-mature stages.

Across the seven plots, areas with higher bamboo basal area were associated with higher mean tree growth and tree mortality rates, and with lower tree density and total tree basal area. In other words, where there was more bamboo there were fewer but larger trees and a smaller total tree basal area. The SEM integrated all the predicted relationships to highlight an overall reduction of tree basal area with increasing bamboo abundance, suggesting that the amount of aboveground biomass stored in trees in bamboo-dominated Andean forests is lower and consequently the carbon storage capacity of the trees is reduced. According to the hypothesized causal relationships used to construct the SEM, the negative effect of bamboo on tree basal area is be mainly driven by the reduction of tree density (directly and indirectly mediated by an increase in tree mortality). Conversely, there are other indirect paths that have marginal positive effects on tree basal area. First, the decrease in tree density, likely mediated through reduced competition for resources, is associated with slight increases in tree size (mean tree basal area) in bamboo-dense areas which contributes positively to total tree basal area. In addition, higher bamboo abundances and increased tree mortality may lead to higher tree growth rates and eventually to larger trees, contributing to greater total tree basal area.

The negative relationship between bamboo and tree density has been observed in previous studies and is usually attributed to a reduction of tree regeneration. Increased shading, structural damage on saplings (Silman et al. 2003, Griscom and Ashton 2006) and litter accumulation (Larpkern et al. 2011) have been proposed as explanations for the reduced tree regeneration in bamboo-dominated ecosystems such as in Amazonian *Guadua*-dominated forests (Silman et al. 2003, Griscom and

Ashton 2003, 2006) and in riverine forests of Southeastern Brazil (Oliveira-Filho et al. 1994). Several species of *Chusquea* may alter forest structure by modifying gap-phase regeneration (Campanello et al. 2007). For example, *Chusquea* suppress tree establishment in *Nothofagus* forests in the southern Andes (Veblen 1982, 1989a) and in *Quercus* forests in Costa Rica (Widmer 1998). It has been proposed that the new clearings that typically form following bamboo's gregarious flowering and mortality events may improve regeneration success of some tree species, however, previous studies have found little support for this idea. It is possible that the large amounts of dead biomass, the fast growth of the new bamboo cohort, and the colonization of mortality gaps by other plant groups (Holz and Veblen 2006, Campanello et al. 2007, Montti et al. 2011) continues to supress tree regeneration even through the mass mortality events.

Together with suppressed regeneration, another explanation for reduced tree density in bamboo-dense forests is increased tree mortality. In the *Guadua* forests of the Amazon and the Brazilian Atlantic forests, increased tree mortality rates have been associated with the bamboo-imposed physical disturbances and the higher abundance of pioneer tree species (fast growing, short lifespan) (Silveira 1999, 2001, Griscom and Ashton 2006, Lima et al. 2012). The *Chusquea* species found in our Andean forests are generally thinner and shorter and could not exert much physical stress in adult trees. As such, physical damage is a compelling explanation only for our lowest plot where the larger *Guadua sp27* occurs. Other processes that increase mortality rates in bamboo-dominated areas could include the effects of microbial communities, competition for water resources (Fadrique et al. 2020b) and/or allelopathic interactions (Jose et al. 2016).

In addition to changes in mortality, our results indicate an increase in tree growth rates in areas where bamboo is abundant. This is likely due to the lower tree density and its associated micro-environmental factors (e.g., increased light, reduced competition for water, etc.). Similar

results were found in Amazonian bamboo-dominated forest where tree growth rates were faster in the forest edge (where bamboo is more abundant) than in the forest interior (where there is less bamboo) (Medeiros et al. 2013). On the other hand, the association between tree growth rates, mortality rates and bamboo abundance could be mediated by differences in tree functional composition. Fast-growing pioneer tree species are usually associated with the disturbed and open-canopy *Guadua* forests in the Southwestern Amazon (Alves de Oliveira 2000, Silveira 2001, Griscom et al. 2007), while the shaded understory and fast colonization of gaps reduces the abundance of pioneer trees in *Chusquea*-dominated ecosystems such as in the Atlantic forest (Tabarelli and Mantovani 2000, Campanello et al. 2007) or in the southern Andes (Holz and Veblen 2006). Given that most of the bamboos in the gradient are understory *Chusquea* species, we doubt that there is a functional bias that favors fast growing tree species. Long-term monitoring of the plots, detailed bamboo species information, and analyses of the plots' composition will help to determine the contribution of bamboo to the functional strategies of coexisting trees.

Although we hypothesize a framework of causality where bamboo affects forest structure, it is still not possible to determine whether bamboo creates or thrives under these structural conditions. For instance, it is possible that bamboo does not cause increases in tree mortality and growth rates, but rather that bamboo *a posteriori* colonizes areas with low tree densities and high mortality rates, such as treefall gaps and landslides (both of which are common in Andean forests) (Veblen 1989b, Tabarelli and Mantovani 2000, Clark et al., 2015a). It is also unclear whether the bamboo biomass compensates for the decrease in tree biomass associated with high bamboo densities (Arango and Camargo, 2010). For example, the aboveground biomass of *Guadua weberbaueri* in the Brazilian Amazon was estimated to be around 10.2 Mg/ha (Torezan and Silveira, 2000). Similarly, the aboveground biomass of *Chusquea culeau* and *Chusquea tenuiflora* in mid and high elevation forests in the Chilean Andes was estimated to reach 9 Mg/ha. The lack of allometric species-specific and locally relevant equations to estimate bamboo biomass prevents our ability to answer this question. It is known, however, that bamboo biomass is highly variable and depends on species characteristics (size, woodiness) and culm densities (Veblen et al. 1980, Veblen 1982), which in turn vary widely through time and in our study area, along elevation (Yuen et al. 2017). Further work on bamboo biomass and temporal dynamics will provide a better estimation of Andean forests carbon cycle. Despite their singular structure and carbon dynamics, bamboo-dominated forests hold high conservation value due to, among others, the specialized mammals, birds and ants that inhabit these ecosystems (Davidson et al., 1998; Dunnum and Salazar-Bravo, 2004; Rother et al., 2013; Silveira et al., 2013).

A potential limitation of our study was the small number of plots and subplots. This limitation could lead to a higher influence of random events in the observed pattern. Similarly, in our study, as in many other tropical forest monitoring networks, 10 cm dbh is the minimum size for censusing trees. The inclusion of tree stems with dbh < 10 cm would provide additional insight into the dominance of bamboo and its relationship with tree recruitment and forest dynamics. In addition, although all our bamboo species grow in the understory and thus their potential mechanisms for forest structure modification are similar, our models explained only a small proportion of the variance in forest structure and dynamics. *Guadua sp27* is the only species that could have a different mechanism because of its larger size, weight, and crown area and we have therefore addressed it separately. There are many other factors excluded from the model such as light conditions, species identity, etc., that play an important part in determining tree growth, density and mortality. Despite these limitations, based on our work and the results of prior studies across many different tropical and temperate habitats, we are confident that the directionality of the association between bamboo and trees is properly characterized. Both the continuation of bamboo censuses through time and experimental work are necessary to better disentangle the bamboo-tree interaction.

5. Conclusions

Bamboo is an extremely abundant plant group in Andean forests and its presence is associated to a particular forest structure with less trees, lower total basal area, and altered dynamics with faster mortality and growth rates. The overall reduction of tree basal area with increasing bamboo abundance suggests that the carbon storage capacity of the trees in bamboo-dominated Andean forests is reduced. Our results reveal the important associations between bamboo, forest structure and carbon cycling in Andean forests and highlight the need for including bamboo in monitoring efforts and modeling studies. With the limited data currently available, we cannot predict whether the association between bamboo and lower tree density could eventually lead, through a negative feedback cycle, to the complete extirpation of trees in certain areas. However, we believe that the combination of long-term competition for resources between bamboo and trees, together with the rapid colonization of disturbed areas by bamboo, has the potential to radically change local landscapes. In addition, climate change in the Andes is hypothesized to favor species that are best able to withstand or adapt to the new conditions. Several studies point to the strong resilience and functional plasticity of bamboos (Montti et al. 2014, Yang et al. 2012), which may facilitate their growth and expansion as climate changes. Further monitoring and research (including better characterization of bamboo ecology and life history) are necessary to fully understand patterns of forest regeneration and to model long-term trajectories. Likewise, experimental manipulations of bamboo communities could provide valuable insight into the causality of the observed relationships and the mechanisms driving these patterns.

CRediT authorship contribution statement

Belen Fadrique: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **Paul Santos:** Investigation, Writing - review & editing. **William Farfan-Rios:** Project administration, Funding acquisition. **Norma Salinas:** Project administration, Funding acquisition, Writing - review & editing. **Miles Silman:** Project administration, Funding acquisition, Writing - review & editing. **Kenneth J. Feeley:** Funding acquisition, Conceptualization, Methodology, Supervision, Writing - review & editing.

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 A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118648.

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