



## Original Articles

# Mountain forest biomass dynamics and its drivers in southwestern China between 1979 and 2017

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## ABSTRACT

Reforested areas can act as important carbon (C) sinks. In China, extensive reforestation has been carried out in mountainous regions, with resulting C storage affected by forest age, forest type and environmental settings. Evaluations of forest C sequestration therefore require a detailed spatio-temporal analysis of C storage dynamics. Here, we used aboveground biomass (AGB) of trees as a proxy for overall forest C storage to investigate spatiotemporal patterns and changes in AGB of 136,988 individual trees distributed over 1399 permanent plots in the forests of Sichuan province, China. Mean AGB of young plantation forests increased more rapidly at  $5.25 \pm 1.15 \text{ Mg ha}^{-1} \text{ year}^{-1}$  than that of natural forest ( $2.56 \pm 0.38 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ). Forest stand age, tree species diversity and tree density were superior predictors of AGB when compared to environmental and climatic factors. Linear Mixed Effect models accounting for stand age showed significant AGB storage increases with increasing soil depth as well as with decreasing longitude and altitude. Stocks in plantation forests also increased with southerly exposition and decreasing slope steepness, while in natural forests, slope steepness showed positive correlations. Warming temperatures depressed AGB increases across all forests, while decreasing annual precipitation negatively affected AGB increases in natural forest, only. Our study highlights that, to sustain forest AGB gains into the future, management especially of forest plantations needs to promote species-rich, unevenly-aged, climate-adapted forests stands.

## 1. Introduction

Responding to widespread logging and degradation of forest ecosystems across China in the last century (Yu et al., 2011), the country initiated a series of large-scale re-forestation and afforestation projects (Brandt et al., 2018; Tong et al., 2018). Accordingly, China now hosts the world's largest area of plantation forest (Payn et al., 2015), covering ~79.54 million ha and accounting for 36.45% of China's forest area. In 2018, China's forest plantations contained a total estimated stock volume of wood of 3.39 billion  $\text{m}^3$  (Cui & Liu, 2020), with their C stocks increasing from 226.12 to 1536.56 Tg C between 1977 and 2018 (Zhao et al., 2021). Concurrently, China is protecting its naturally regrowing

secondary and remaining old-growth forests (Deng et al., 2017). Partially offsetting China's anthropogenic  $\text{CO}_2$  emission (Tong et al., 2020), these measures have created a significant temporary carbon (C) sink that is expected to increase further in the future (Deng et al., 2017).

Recent studies assessing C stock dynamics in China under climate change and anthropogenic disturbances (Fang et al., 2018; Tang et al., 2018) predict forest C storage to increase to 2.97 Pg C in 2030 under the assumption of a stable forest area. Evaluating regional impacts of forest expansion on C storage, Wang et al. (2020) demonstrate that the terrestrial C sink in southwest China has generally been underestimated. Research investigating combined effects of recent forest expansion and C density changes (Fang et al., 2014a; Li et al., 2016; Tong et al., 2020)

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furthermore highlight that recent expansions in forest area also play a major role in forest C stock increases. In line with its red line policies (Sang & Axmacher, 2016), the Chinese government is nonetheless strongly limiting any new conversions of arable land to forests, so that opportunities for future expansions of China's forest area and associated C storage gains are rapidly disappearing.

Despite positive forest biomass responses to increasing atmospheric CO<sub>2</sub> (Schimel, Stephens & Fisher, 2015), the source function at least of intact mature tropical forests has become saturated, or even shown declines in recent years (Hubau et al., 2020; Koch, Brierley & Lewis, 2021). High productivity levels were observed both in plantation forests and in highly phytodiverse natural forests (Guo & Ren, 2014). Compared with primary and plantation forests, above-ground C stocks in secondary forests were generally lower, indicating a key role for plantations and primary forests in maintaining forest C storage (Brown et al., 2020; Poulsen et al., 2020). Overall, a sound understanding of AGB stocks and their recent dynamics in natural and plantation forests is indispensable to gain an understanding of current and future C storage patterns linked to China's forests, and to estimate their climate change mitigation potential (Tong et al., 2020).

Numerous approaches can be used to quantify the dynamics of AGB stocks. Remote sensing and ecological models based on large-scale forest coverage are common, cost-effective approaches used to estimate and predict C stocks under different climate scenarios (Deng et al., 2017; Koch, Hubau, & Lewis, 2021, Tong et al., 2020; Tong et al., 2018). However, these approaches are problematic at regional and local scales especially in species-rich mountainous environments (Payn et al., 2015; Fang et al., 2018; Tang et al., 2018). Here, long-term field monitoring provides an essential alternative. Long-term monitoring also allows specific assessments of the individual impacts of key factors like forest age, tree diversity and spatial heterogeneity, on AGB stocks and dynamics.

Tree species richness (Huang et al., 2018), local environmental conditions (soil moisture, evapotranspiration) (Ratcliffe et al., 2017), climate change (García-Palacios et al., 2018) and the forest stand structure (Ouyang et al., 2019) are widely considered important contributors towards forest productivity, stability, and resulting biomass and C pools. All these factors have highly differential spatiotemporal effects on productivity and associated biomass changes in natural forest ecosystems (Qie et al., 2017; Ratcliffe et al., 2017; Trotsiuk et al., 2020). For example, the C sequestration capacity of natural forest decreased from southeastern to northwestern parts of Tibet province (Liu et al., 2021). Therefore, to understand the regional-level C dynamics, it is necessary to study each case based on local survey data.

In this study, we used aboveground biomass (AGB) of trees as a proxy for forest C storage, assessing AGB and its dynamics on 1399 permanent plots in the forested regions of Sichuan province based on four-decades long-term forest monitoring. We understand that AGB in this context only represents above-ground biomass of living trees. However, these different carbon stocks are strongly linked to overall above-ground biomass (Mokany et al., 2006). Also, compared with trees, shrubs and herbaceous plants located in the forest account for a much smaller proportion of the total forest biomass. Therefore, we regard AGB as a representative of forest C storage. We aimed to 1) quantify the change of mean annual AGB stocks separately for planted and naturally generated forests based on four decades of observation and to 2) identify environmental, forest structure-related and climatic factors explaining the observed patterns. We contextualize our findings in view of their implications for future forest management.

## 2. Materials and methods

### 2.1. Study area

Our study area is located in the transition zone between the Qinghai-Tibet high plateau and the Sichuan basin (9839'E – 10424'E, 2612'N –

3414'N) that falls into China's subtropical evergreen broadleaf forest and warm temperate deciduous broadleaf forest regions (Sichuan Vegetation Cooperation Group, 1980). With regards to its biodiversity, the area is located on the western edge of the southwest China hotspot (Myers et al., 2000). Our study region mainly covers high-mountain areas dissected by deep valleys, spanning an altitudinal range from 400 to 4460 m. The mean annual temperature at our study sites ranges from 0 °C to 16.87 °C, while the annual precipitation ranges from 200 to 1,700 mm, with precipitation maxima occurring between April and October (Sichuan Vegetation Cooperation Group, 1980). Maximum annual mean temperatures range from 23.0 °C to 35 °C, and minimum annual mean temperatures from –34.0 °C to –0.8 °C. The area was historically forested, but suffered heavy deforestation from the 1950s. In recent decades, the forested area of Sichuan Province has nonetheless increased rapidly as a result of afforestation and natural forest restoration projects, and forests now cover 40% of its total land area. By the end of 2019, Sichuan's forest area amounted to 19.26 million ha, with plantations covering ~20% of that area (Cui & Liu, 2020).

As the province with the fourth largest total forest cover and the third highest carbon density (Cui & Liu, 2020), Sichuan plays a crucial role for China's national forest cover and the associated C storage. The province's natural forests are conserved under the 'Natural Forest Protection Project' and mostly distributed in alpine valleys, where naturally regenerating forests are characteristically highly biodiverse (State Forest Administration, 2012). In contrast, the province's forest plantations, mainly created under the 'Grain for Green' programme, are characterized by a much lower diversity and more homogenous age structure (State Forest Administration, 2012).

Forests in our study region are composed of coniferous, mixed coniferous and broad-leaved, and mixed evergreen and deciduous broadleaved forests. Dominant native species accounting for >1% of tree biomass across all censuses and plots belong to the conifer genera *Abies*, *Picea*, *Pinus*, *Sabina* and *Tsuga*, and to the broadleaved genera *Acer*, *Betula*, *Davidia*, *Populus* and *Tilia*. Non-native evergreen species forming noteworthy components of the forests are *Pinus elliotii*, *P. taeda*, *Cryptomeria japonica*, *Eucalyptus globulus* and further *Eucalyptus* spp.

### 2.2. Forest inventory

Permanent and temporary sampling plots have been regularly monitored by the Sichuan provincial government since the 1960s. Nonetheless, data from some sampling plots was only estimated in the 1960s, with no forest resource surveys carried out between 1979 and 1988, either. Since then, forest resource surveys were conducted every five years. For this study, we therefore used forest inventory data from the eight distinct survey instances where reliable data was available: 1979, 1988, 1992, 1997, 2002, 2007, 2012 and 2017. Each inventory consisted of records from a combination of permanent and temporary plots distributed evenly across western Sichuan province. Each survey plot measured 0.10 ha (31.62 m\*31.62 m) prior to 2002, when the size was reduced to 0.067 ha (25.84 m × 25.84 m). Sample plots were established along a stable N-S, E-W grid system, with distances of 4 or 8 km between neighboring plots in both a N-S and E-W direction. The forest inventory plots encompass both naturally regenerated and planted forests across different successional stages, from stand initiation to mature forests (stand age >100 years, Liu et al., 2014). To ensure data comparability, we decided to exclude bamboo-dominated vegetation.

We then selected permanent plots for our study based on the following criteria: 1) known origin of forest and no occurrence of additional management like re-planting to replace dead trees or logging; 2) represented in at least two census dates; 3) no obvious measurement errors or missing data, and 4) available estimate of the overall stand age. A total of 1399 permanent plots that were also unaffected from any natural disasters linked to fire or pest mass-outbreaks, were selected for analyses. Of these, 1,248 plots were classified as 'natural forest', with their vegetation differing greatly in age, diversity and structure. The

remaining 151 plots represented the region's 'plantation' forests (Fig. 1, see Appendix S1 and S2, Table S1 and S2).

The oldest planted forests in the study area were established in the 1960s, but most forest plantations were much younger, only becoming established between 1999 and 2014 (State Forest Administration, 1999–2014, Fig. S1). Most of these forest plantations are now ~20 years old, while their tallest trees already reach heights >45 m. The historical land use at reforested sites included agricultural land, "wasteland" and clear-felled plantation forests.

We used above ground biomass (AGB) of the forest trees as a measure of their cumulative productivity. AGB is integral to multiple ecosystem services like the provisioning of wood fiber and forest C storage (Chojnacky, Heath & Jenkins, 2014). Plot-level AGB ( $\text{Mg ha}^{-1}$ ) was calculated by summing the biomass of all live trees >5 cm diameter at breast height (DBH), measured at a trunk height of 1.3 m, in each plot for each measurement. AGB of each live tree was estimated using the 'scaling-up factor continuous function' method (Fang et al., 2001) (see Appendix S1). We then calculated the AGB per unit area by adding the biomass for individual trees recorded on each sampling plot. Subsequently, we also calculated the annual net aboveground biomass change ( $\delta$  AGB,  $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) as the difference of aboveground biomass on a plot between two consecutive census dates, divided by the time between the census dates in years (Brienen et al., 2015). Where, due to measurement errors, potentially in combination with variations in water content of live tree trunks (Pastur et al., 2007), DBH for a given tree decreased between individual measurements (0.46 % of cases), we generally interpreted this pattern as a measurement error and corrected the smaller measurement by interpolating DBH values from the previous and the subsequent measurement (Phillips et al., 1998). Where data was only available for two survey periods, and we observed suspicious patterns

like data gaps, decreases in values or unrealistically high increases in DBH, tree height or volume in the data when compared to previous surveys, the data was omitted from analysis.

For the analysis, we then combined AGB data with data on forest structure, environmental settings and meteorological data. Forest structure data comprised trees density (individuals  $\text{ha}^{-1}$ ), tree species richness, canopy cover (%) and mean stand age (years), while the data providing further environmental context included soil depth (cm depth of topsoil, measured to the underlying bedrock), slope (degree), aspect (degree), latitude (degree), longitude (degree) and altitude (m). Further soil data like soil pH, density or texture was excluded due to a lack of historical data.

### 2.3. Climatic data

The two meteorological datasets we included cover total annual precipitation and mean annual temperature (MAT). All climatic data were collected from 1979 to 2017 at 65 weather stations located within our study region. These data were obtained from the Chinese National Meteorological Information Center/China Meteorological Administration (<https://data.cma.cn>). Based on data for each weather station and interpolations to a spatial resolution of  $1 \text{ km} \times 1 \text{ km}$ , climatic factors of each plot were estimated using a Kriging interpolation method for the regionalizing of our variables at different scales, with further interpolations conducted to adjust the temperature to the respective mean plot elevation (Piao et al., 2011). We used this approach to individually calculate the mean value of the mean annual temperature and annual precipitation between two consecutive censuses for each plot.

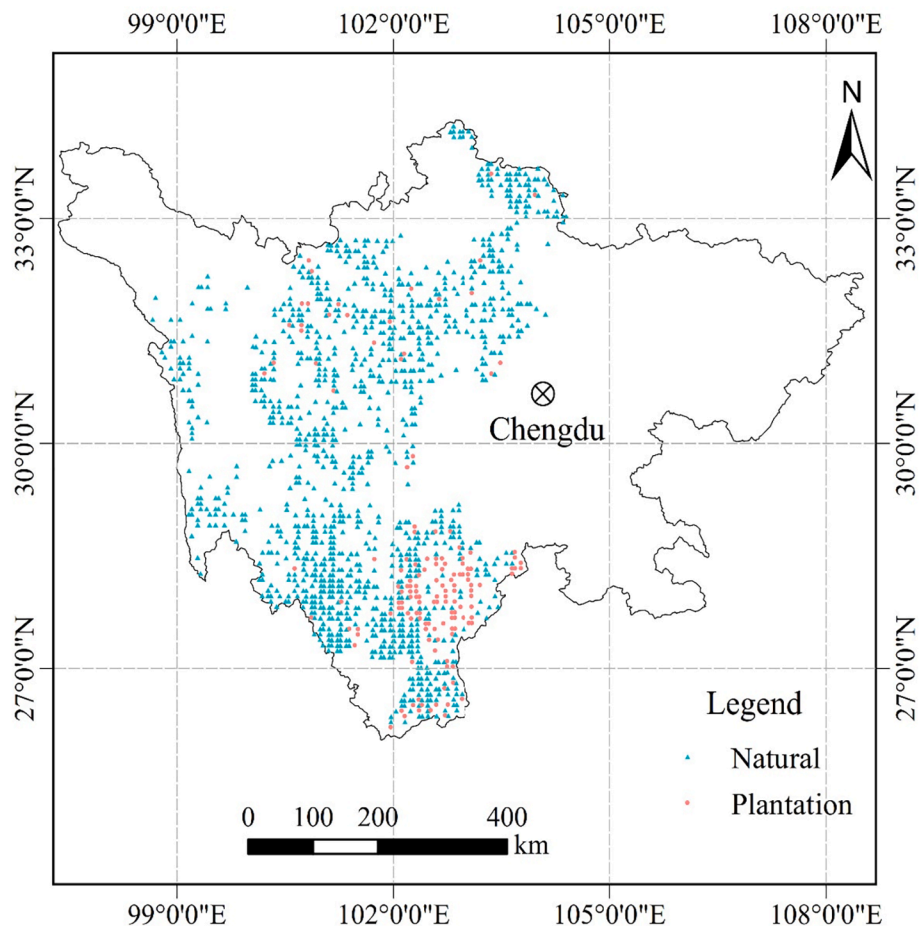


Fig. 1. Distribution of the permanent sampling plots ( $\geq 2$  censuses) in Sichuan province.

## 2.4. Data analysis

We used Linear Mixed Effect models (LMEs) to investigate spatio-temporal patterns and changes in the mean above-ground biomass (AGB) of the forest plots. Year was included as a fixed explanatory variable and “plot ID” as a random factor (Eq. (1)). The AGB was log-transformed, and a Gaussian error structure was applied in the models. Analyses were conducted separately for plantation and natural forests. To account for potential spatial dependencies in permanent sampling plots, we included a spatial autocorrelation variance factor (Dormann et al., 2007) in respective models:

$$\text{Log}_{10}(\text{AGB}_{i,j}) = \beta_0 + \beta_1 \times \text{Year}_{i,j} + \pi_i + e_{i,j} \quad (1)$$

where  $\text{Year}_{i,j}$  represents the  $i^{\text{th}}$  inventory census at the  $j^{\text{th}}$  plot;  $\beta_i$  are the coefficients to be estimated;  $\pi_i$  is a random plot effect and  $e_{ij}$  represents the random error.

Considering the important effect of stand age, we established the specific relationship between AGB and stand age. The formula was  $\log_{10}(\text{AGB}) - \log(\text{Stand.age} + 1)$ , separated into natural and planted forest. To obtain age-independent responses of AGB to environmental factors, we therefore controlled for the specific influence of forest age in the latter models. We also used LMEs to analyze the influence of forest structure, environmental and climatic factors on AGB stocks. These analyses were based on three different sets of models. Environmental models focused on specific plot characteristics and included the variables slope, soil depth, altitude, aspect, longitude and latitude as predictors. Forest stand structure models took account of the predictors tree species richness, density and canopy cover. Climate models that were only used to explore the impact of climate change on  $\delta$  AGB exclusively included both MAT and annual precipitation as main predictors. A similar model structure was used in (Blundo et al., 2021). In the following section, we firstly present information on AGB stocks (Eqs. (2) and (3)), and then on the net temporal change of AGB ( $\delta$  AGB, Eqs. (4) and (5)). In Eqs. (2) and (3), we additionally consider a temporal autocorrelation variance factor to account for general temporal trends in the data (Zuur et al., 2009). Similarly, to address potential issues associated with spatial autocorrelation, we integrate a spatial autoregressive structure based on latitude and longitude (Dormann et al., 2007) in Eqs. (4) and (5).

The overall structure of the full models used can be written as:

$$\text{Log}_{10}(\text{AGB}_{i,j}) = \beta_0 + \beta_1 \times \text{Slope}_{i,j} + \beta_2 \times \text{Soil depth}_{i,j} + \beta_3 \times \text{Altitude}_{i,j} + \beta_4 \times \text{Aspects}_{i,j} + \beta_5 \times \text{Latitude}_{i,j} + \beta_6 \times \text{Stand age}_{i,j} + \pi_i + e_{i,j} \quad (2)$$

$$\text{Log}_{10}(\text{AGB}_{i,j}) = \beta_0 + \beta_1 \times \text{Treerichness}_{i,j} + \beta_2 \times \text{Trees density}_{i,j} + \beta_3 \times \text{Canopy}_{i,j} + \beta_4 \times \text{Stand age}_{i,j} + \pi_i + e_{i,j} \quad (3)$$

$$\delta \text{AGB} = \beta_0 + \beta_1 \times \text{MAT} + \beta_2 \times \text{Pre} + \beta_3 \times \text{MEAN\_Age} + \pi_i + e_i \quad (4)$$

$$\delta \text{AGB} = \beta_0 + \beta_1 \times \text{MAT} + \beta_2 \times \text{Pre} + \beta_3 \times \text{Slope} + \beta_4 \times \text{Soil depth} + \beta_5 \times \text{Altitude} + \beta_6 \times \text{Aspects} + \beta_7 \times \text{Latitude} + \beta_8 \times \text{MEAN\_Age} + \pi_j + e_j \quad (5)$$

with models incorporating the predictor variables slope or inclination, soil depth, altitude, aspect, latitude, tree species richness/plot, tree density and canopy cover of all trees at the  $i^{\text{th}}$  census period in  $j^{\text{th}}$  plot, MAT represents the mean annual temperature for the period between the  $i^{\text{th}}$  census year and the  $i + 1$ th census date, and Pre represents the mean annual precipitation between the period  $i^{\text{th}}$  census and  $i + 1$ th census at the  $j^{\text{th}}$  plot. Stand age represents the estimated mean age of the trees on the plot at census  $i$ , forest type differentiates between natural and planted forests, and MEAN\_Age finally represents the mean age of the forest at the mid-point between census  $i$  and census  $i + 1$ .

All predictor variables were standardized using z-transformations. We fitted models with each possible combination of predictor variables and used a dredge function to screen models automatically based on AIC (Akaike's information criterion) values, focusing on averaged coefficients from models within  $\delta$  AIC < 4 units (Grueber et al., 2011). We have additionally used the BIC (Bayesian Information Criterion) and results are consistent with AIC criteria (Appendix Table S3). We therefore would like to keep the AIC results. After fitting each model, we looked at its residual diagram to establish whether the residuals of the model were evenly distributed (Chakrabarti and Ghosh, 2011). All analysis was conducted in R v4.0.2 (R Core Team, 2019). Package “nlme” (Pinheiro, 2020) were used for linear mixed models Package “spaan” (Rousset & Courtiol, 2021) was used to calculate spatial autoregressive structure; “MuMIn” package was used for the model selection and averaging (Barton, 2020). Further information about the model outcomes is presented in Appendix S1.

## 3. Results

### 3.1. Differences in forest structure, environmental factors and climate change between natural versus plantation forests

Plots representing different forest types showed some systematic differences not only in key biological factors, but also in their mean environmental settings (Fig. 2, Table S2). Compared to natural forests, planted forests were on average younger, resulting in a smaller mean DBH and canopy height. Planted forests also commonly occupied locations at lower altitude in more southerly areas of the study region on less steep slopes that furthermore experienced higher levels of precipitation, resulting in overall more favorable growth conditions. In line with our expectations, planted forests also showed a significantly lower diversity in tree species (mean and standard error of planted forest:  $1.65 \pm 0.029$ ; natural forest:  $3.45 \pm 0.012$ ,  $P < 0.001$ , Fig. 2).

### 3.2. Changes in AGB stocks

During the study period (1979–2017), the mean value (with standard error SE) of AGB stocks for natural forest was  $250 \pm 2.40 \text{ Mg ha}^{-1}$ , while plantation forests had slightly lower AGB stocks of  $215 \pm 7.62 \text{ Mg ha}^{-1}$ . AGB stocks increased significantly for both plantation and natural forests between 1979 and 2017. LME models show a mean AGB increase of  $5.25 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (95% CI: 5.18–5.32,  $t = 4.57$ ,  $P < 0.001$ ) in forest plantations and of  $2.56 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (95% CI: 2.53–2.58,  $t = 6.78$ ,  $P < 0.001$ ) in natural forests. Reflecting their greater mean age, natural forests contained a higher mean total AGB, but this difference is currently rapidly diminishing (Fig. 3).

### 3.3. Influence on AGB stocks exerted by the main environmental factors and the parameters characterizing forest structure

AGB stocks in natural forest increased significantly with greater soil depth ( $t = 7.27$ , 95% CI: 0.088–0.089,  $P < 0.0001$ ), steepness of slope ( $t = 7.05$ , 95% CI: 0.079–0.080,  $P < 0.0001$ ), as well as with decreasing longitude ( $t = -3.71$ , 95% CI: -0.049 – -0.047,  $P = 0.0002$ ) and altitude ( $t = -3.72$ , 95% CI: -0.063 – -0.061,  $P = 0.0002$ ), in models controlling for stand age and spatial and temporal autocorrelations. In contrast, AGB stocks in plantation forests increased significantly with decreasing slope steepness ( $t = -3.23$ , 95% CI: -0.088 – -0.085,  $P = 0.0012$ ), as well as with increasingly southern exposition ( $t = -2.56$ , 95% CI: -0.071 – -0.068,  $P = 0.010$ ) and, again, increasing altitude ( $t = 4.40$ , 95% CI: 0.14–0.15,  $P < 0.0001$ ) and longitude ( $t = 5.15$ , 95% CI: 0.17–0.18,  $P < 0.0001$ ). Overall, responses in planted forests were more heterogeneous when compared to natural forests (Fig. 5a, Table S4). Both forest types showed similar responses to parameters characterizing forest structure, with AGB stocks increasing strongly with increasing tree density (natural forest:  $t = 74.23$ , 95% CI: 0.745–0.748,

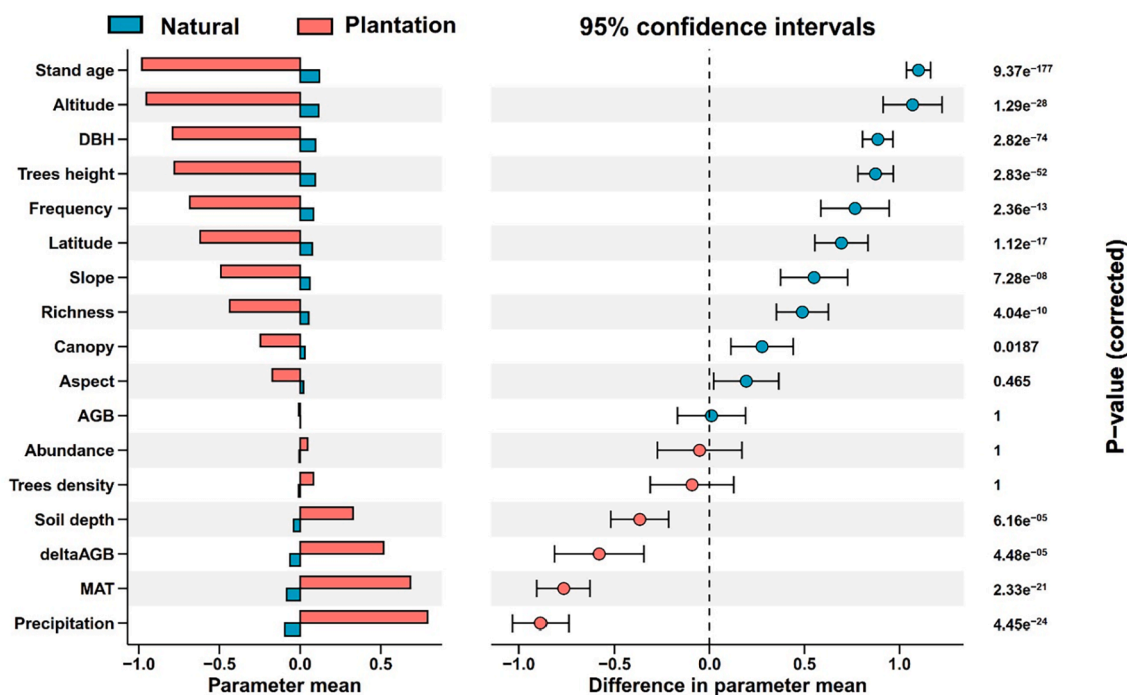


Fig. 2. Comparison of standardized explanatory parameter differences in forest above-ground biomass (AGB) between natural and plantation forests (t-tests, scaled by average values from intact forest plots), analyzed using bias-corrected 95% bootstrap confidence intervals.

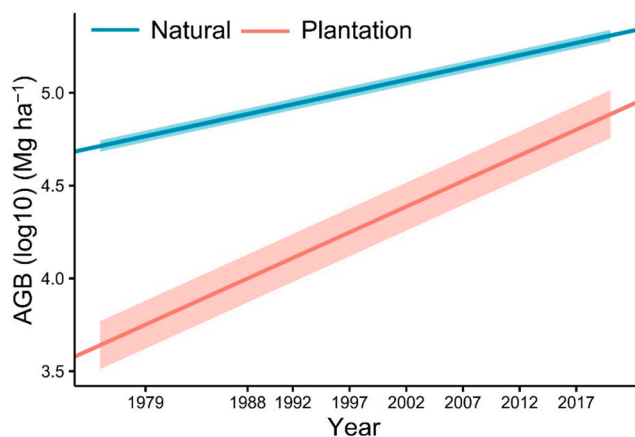


Fig. 3. Trends of AGB stocks over the last four decades. The lines and shaded areas represent estimates and 95% confidence intervals for the coefficients based on the LME models, respectively.

$P < 0.0001$ ; planted forest:  $t = 27.08$ , 95% CI:0.60–0.60,  $P < 0.0001$ ) and species richness (natural forest:  $t = 12.29$ , 95% CI:0.094–0.095,  $P < 0.0001$ ; planted forest:  $t = 7.12$ , 95%CI: 0.146–0.148,  $P < 0.0001$ ), while canopy cover showed a significant positive link to AGB stocks in natural forests ( $t = -3.68$ , 95% CI:–0.031 – –0.029,  $P = 0.0002$ ), only (Fig. 5b, Table S5). Comparing standardized coefficient for forest structure and environmental factors, the models indicate a significantly stronger effect of the former when compared to the latter set of factors (Fig. 5, Tables S4 and S5).

### 3.4. Climate change impacts on forest AGB dynamics

Long-term climatic data (1979–2017) from the study region (Fig S2) shows a gradual decrease in mean precipitation at a rate of 0.74 mm/year ( $t = -10.85$ ,  $P < 0.001$ ) and an increase in mean annual temperatures of 0.038 °C/year ( $t = 25.27$ ,  $P < 0.001$ ) over the study period.

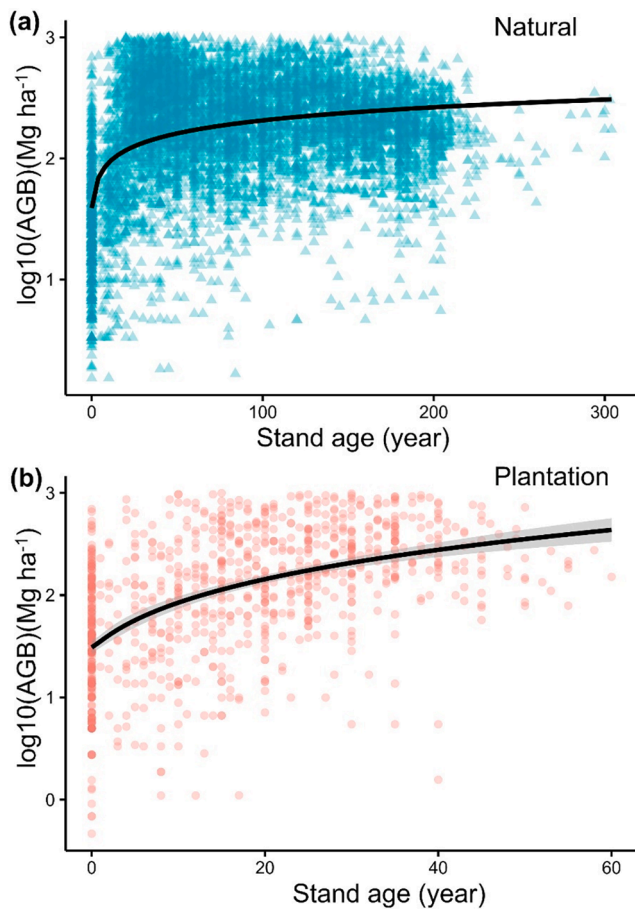
Warming temperatures depressed AGB increases in both, natural (slope = –0.15,  $t = -8.29$ , 95% CI:–0.148 – –0.146,  $P < 0.001$ ) and planted forests (slope = –0.15,  $t = -2.74$ ,  $P = 0.006$ ) in LME models accounting for forest age and spatial autocorrelations (Fig. 6). Decreasing annual precipitation had an additional, negative effect on AGB increases (slope linking precipitation with  $\delta$  AGB = 0.20,  $t = 11.46$ , 95% CI: 0.197–0.199,  $P < 0.001$ ) in natural forest, only, while no significant links were observed between precipitation and planted forest  $\delta$ AGB ( $P = 0.14$ ).

When all environmental parameters were considered jointly in LME models while controlling for the influence of forest age, changes in AGB dynamics in plantation forest were positively linked to increases in altitude ( $t = 2.48$ , 95% CI:0.062–0.070,  $P = 0.013$ ) and latitude ( $t = 2.49$ , 95% CI:0.063–0.072,  $P = 0.013$ ), while they still showed a significant negative link to MAT ( $t = 2.30$ , 95% CI: –0.099 – –0.095,  $P = 0.021$ ). Changes in natural forest AGB dynamics in contrast appeared significantly linked to increases in precipitation ( $t = 12.63$ , 95% CI:0.247–0.249,  $P < 0.0001$ ), soil depth ( $t = 2.55$ , 95% CI: 0.027–0.029,  $P = 0.011$ ), longitude ( $t = -4.23$ , 95% CI:–0.0788 – –0.0766,  $P < 0.0001$ ) and latitude ( $t = 4.33$ , 95% CI:0.136–0.139,  $P < 0.0001$ ), aspect ( $t = 2.30$ , 95% CI:0.023–0.024,  $P = 0.022$ ), with MAT ( $t = -3.35$ , 95% CI:–0.077 – –0.074,  $P = 0.00081$ ) again exerting a significant negative effect on  $\delta$  AGB (Table S6).

## 4. Discussion

### 4.1. AGB stocks in Sichuan's plantation and natural forests

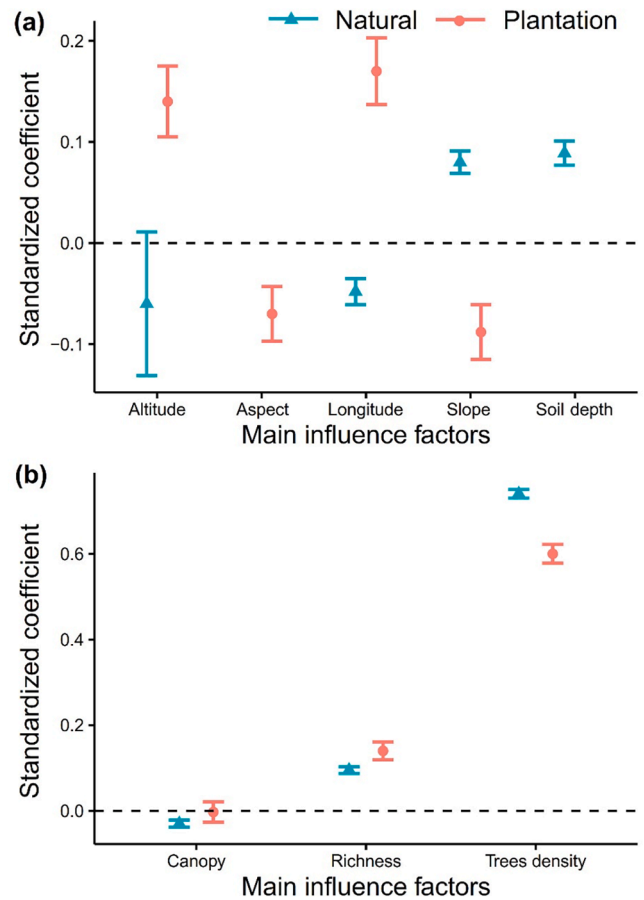
Assessing the biomass changes of over 1000 permanent plots in the forests of Sichuan province, China, between 1979 and 2017, our results indicate a significant increase in C stocks stored in both investigated forest types. This result clearly confirms the function of these forest as a C sink (Tong et al., 2020), and the values we observed exceed the average C stocks for China across all climate zones from 2007 to 2013, reported by Guo and Ren (2014; natural forest: 169 Mg ha<sup>-1</sup>, planted forest: 142 Mg ha<sup>-1</sup>). Our observation of AGB in ‘plantation’ forests increasing at twice the rate than in ‘natural’ forests again differs from



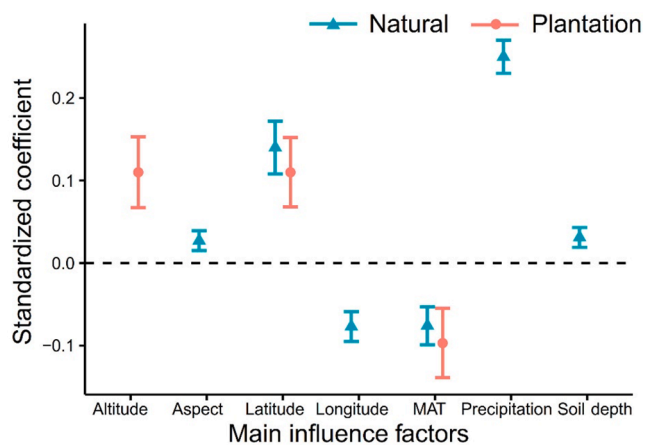
**Fig. 4.** AGB (log-transformed) in relation to stand age for plantations and natural forests. The lines and shaded areas represent estimates and their 95% confidence intervals, respectively, highlighting the strong increase in AGB in young forests, plateauing for both forest types at an age of ~50 years (Fig. 4). Stand age and AGB in natural ( $P < 0.0001$ ,  $t = 43.93$ , 95%CI: 0.15–0.16,  $R^2 = 21.15\%$ ) and planted forests ( $P < 0.0001$ ,  $t = 49.65$ , 95%CI: 0.16–0.17,  $R^2 = 23.24\%$ ).

Guo & Ren (2014)'s findings, who reported less strongly diverging productivity levels ( $17.5 \pm 3.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$  and  $10.2 \pm 4.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , respectively) for the period 2007 to 2013. Our results align with Zhao et al. (2019)'s observations that biomass C stock increases are particularly pronounced in southwestern regions. Overall, our results suggest that forest carbon storage increases over time, but productivity declines, with distinct variations in biomass C stock dynamics between forest types. Forest C storage and productivity is therefore both time-sensitive and forest type-specific, while being further modified by forest management, structure, geography and climatic conditions. A number of potential reasons can explain these highly complex patterns.

One key potential driver is the significant differences in mean environmental settings of natural and plantation forests types that were linked to differences both in AGB stocks and their dynamism. With some exceptions, forest plantations are planted at significantly lower elevation, latitude, and at areas with deeper soils on more south-exposed slopes, when compared to natural forests. In turn, planted trees will therefore experience better growth conditions than natural forests, resulting in their enhanced biomass accumulation when grown within the same broader climatic region (Schulze et al., 2014; Waring et al., 2008). A southerly exposition and a gentler slope angle in the dense, evenly aged, relatively homogenous plantation forest stands also results in a relatively homogenous in-stand temperature regime as a further positive growth determinant. As expected, AGB stocks were positively linked to deep soils across forest types – with such soils providing



**Fig. 5.** Standardized effect sizes based on conditional average models (LME,  $\delta\text{AIC} < 4$ ) for AGB stocks for both, planted and natural forests, in models accounting for stand age and temporal autocorrelation, focused on standardized coefficients of forest structure (a) and environmental factors (b). For each variable in the models, main symbols represent the standardized mean effect size and lines represent standard error. Missing predictors relate to the respective factors not being selected during the model selection procedure. We also calculated the full model, which has similar results to the final model.



**Fig. 6.** Standardized effect sizes for the conditional average models (LME,  $\delta\text{AIC} < 4$ ) for  $\delta$  AGB in planted and natural forests that accounted for mean forest age and spatial autocorrelation. For each variable in the model, main symbols represent the standardized effect size and lines represent standard error. Missing predictors in certain forest types means the relative factors were not selected during the model selection procedure. We also provided the full model, which has similar results in the final model.

enhanced access to plant-available nutrients that again benefit tree growth potential.

Forest plantations are also generally dominated by few, fast-growing tree species planted in a uniform stand-age structure (Guo & Ren, 2014), and, in the case of our study area, the plantation forests are generally young ( $17.42 \pm 11.31$  year). Observed faster AGB accumulations in plantation forests when compared to natural forests might therefore relate to the gradual degradation of annual AGB increases for all forest types as they approach a stand age of  $\sim 50$  years (see Fig. 4). This trend also indicates that the forest type-specific differences in AGB accumulation are likely to narrow significantly as plantation forests mature (Brown et al., 2020). The observed marked decline in productivity rates for older plantations does indeed indicate that most plantation forests might be approaching their saturation storage capacity already within two to three decades. That outlook differs distinctly from previous studies that reported a continuous increase of plantation forest C storage (Fang et al., 2014b).

One factor that appears to hamper AGB increases in plantation forests when compared to natural forests is forest tree diversity (see Table S2, Fig. 2 and Fig. 5b). In addition to tree density and stand age, our results reflect an important positive influence of tree species richness on AGB stocks in species-poor plantations. In contrast, the tree diversity on natural forest plots with their generally much greater species richness appears to represent a state where diversity-related differences in AGB stocks are more subtle, resulting in diversity differences exerting a much weaker overall influence on these stocks (Guo & Ren, 2014). The overall results are indicative of community-specific physiological growth patterns that can be linked to specific selection effects and mechanisms of niche complementarity (Hisano et al., 2019) in the natural forest stands, which can also explain the great variance in the richness response amongst natural forest plots. In plantation forests, however, an increase in tree diversity appears to generate general positive biomass accumulation responses that can similarly be related to mechanisms of niche complementarity, but in this instance creating a more predictable, positive impact (Ouyang et al., 2019).

#### 4.2. Climate change implications for forest biomass

While the general increase in atmospheric CO<sub>2</sub> can be assumed to positively influence AGB stocks (Fang et al., 2014b), the AGB stock increases observed in our study area appear strongly dictated by forest restoration and recovery – and by the strong positive growth trajectory underlying the young planted and naturally regenerating forest stands. Our results indicate that warming and drought negatively affected these strong positive growth trajectories. In this context, the more mature natural forests appear more sensitive and vulnerable to the current climatic change-associated trends of increasing temperature and decreasing precipitation (Chen & Luo, 2015) than the young planted forests whose C dynamics are chiefly affected by the increasing temperature, but not by the changes in precipitation.

The combination of decreasing precipitation and increasing temperature is well-established to negatively impact biomass increases in natural forest ecosystems (Walden et al., 2019). Nevertheless, links between rainfall and total productivity are highly temperature-dependent, where at least at tropical mountain rainforest sites experiencing low temperatures (16 °C), increasing rainfall exerted a negative effect on productivity (Taylor et al., 2017). In the subtropical/temperate natural forests in our study area, both decreasing precipitation and increasing temperature – that can already individually cause water shortages in the vegetation through decreasing surface and ground water resources and increased evapotranspiration, respectively – appear to combine in creating a detrimental impact on the AGB increases observed in the natural forests.

## 5. Conclusions

Our study implies that recent increases in forest C storage were largely linked to the young plantation forests, with this rapid increase diminishing as these forests age. To enhance the long-term C storage specifically in plantation forests, increasing their tree diversity, for example by targeted enrichment planting, could yield two-fold benefits. Apart from the enhanced tree diversity itself that we have shown to positively impact AGB dynamics, this strategy would also lower and heterogenize the forest age structure (Himes and Puettmann, 2020). With climate change already negatively impacting C storage in natural forests, we believe their strict future protection could similarly be accompanied by targeted enrichment planting in these forests, too. The long-term target for all regional forests should be a state where well climate-adapted long-lived late-succession tree species, which commonly store large amounts of C in their trunks (Smith and Knapp, 2003), dominate the canopy.

#### Data Availability Statement

Climate data is available through the Chinese National Metrological Information Center/China Meteorological Administration (<http://data.cma.cn>). The plant field survey data were provided by the Forestry Bureau of the Sichuan Provinces.

#### 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.

#### Data availability

The data that has been used is confidential.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109289>.

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