LETTER

The impact of abiotic and biotic factors on growth, mortality and net tree C stock in mountain forest ecosystems in southwest China

Ting Li1,2,4,∗, Yang Liu5, Qi Wang6, Changhong Lai5, Yuming Qiu7, David T Tissue4, Jiangtao Xiao1, Xuhua Li8 and Li Peng1,2,∗

1 Key Laboratory of the Evaluation and Monitoring of Southwest Land Resources (Ministry of Education), Sichuan Normal University, Chengdu 610068, People’s Republic of China
2 The Faculty Geography Resource Sciences, Sichuan Normal University, Chengdu 610068, People’s Republic of China
3 Key Laboratory of Southwest Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nan Chong 637001, People’s Republic of China
4 Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia
5 Sichuan Forestry and Grassland Research and Planning Institute, Chengdu 610041, People’s Republic of China
6 Key Laboratory of Aquatic Genomics, Ministry of Agriculture, and Beijing Key Laboratory of Fishery Biotechnology, Chinese Academy of Fishery Sciences, Beijing 100141, People’s Republic of China
7 Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences, Chongqing 400000, People’s Republic of China
8 Sichuan Academy of Forestry, Chengdu 610081, People’s Republic of China
∗ Authors to whom any correspondence should be addressed.
E-mail: pengli@imde.ac.cn and liting@sicnu.edu.cn

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Abstract
Mountain forest ecosystems play an important role in global carbon sequestration and may respond differently to variations in climate. The timely and accurate assessment of the factors (abiotic and biotic) that affect forest types will improve our understanding of the ecological mechanisms underlying forest carbon stock and dynamics. Here, we used linear mixed effect models to assess the impact of abiotic and biotic factors on the rate of net tree C accumulation, growth, and mortality, over nearly four decades in 1248 permanent forest plots, in different forest types along an elevational gradient on the eastern Qinghai-Tibet Plateau in China. We found that the annual rise in net tree C stock ranged from 0.13 to 0.23 Mg C ha⁻¹ yr⁻¹, as forest growth increased from 1979 to 2017. The highest rates of growth and mortality were in coniferous broad-leaved mixed forest (CBMF), followed by deciduous broad-leaved forests (BDF), evergreen, deciduous broad-leaved mixed forest (EDBMF), and coniferous forest (CF). Mortality increased in EDBMF and CF during the study period. The most important biotic factors were tree richness and tree density, especially in BDF and CBMF. The most important abiotic factors driving these biological responses were a significant rise in monthly mean temperature (MMT) and a decline in precipitation in the growing season. The decrease in precipitation was negatively correlated with net tree C in CBMF and CF. The increase of MMT was positively correlated with growth and mortality of each forest type, and generally more important than richness and density, and overall had a positive effect on net tree C in CBMF and CF. Overall, we suggest that tree carbon stocks will continue to increase in CBMF and CF in the coming decades due to the warming.

1. Introduction

The carbon reserves in forests have increased significantly since the implementation of restoration and protective measures in Europe and China (Ceccherini et al 2020, Zhao et al 2021). To successfully achieve carbon neutrality, it is very important to promptly and accurately evaluate different forest carbon stocks. Differences among forests mainly reflect two general categories: (a) geographical and environmental background (external factors), including climate, essential resources and historical land use patterns; and
(b) processes of forest growth and recovery (endogenous factors), including community structure and composition (Fang et al. 2014). The main and interactive effects of these factors influence the carbon sequestration process, which is complex because vegetation and forest types respond differently to environmental change (Sierra et al. 2009, Pan et al. 2013, Paullick et al. 2017). For example, the cover area of temperate coniferous forests (CFs), like Pinus tabuliformis, showed expansion under RCP8.5 in Jiuzhaigou Nature Reserve, while the distribution area of cold temperate CFs, such as fir, spruce, would shrink under RCP8.5 (Liu et al. 2021). Furthermore, the geographical environment and climate affect forest species composition, species diversity, tree growth, and life span, which further affects forest carbon storage and the carbon cycle (Yu et al. 2019, Brien et al. 2020).

Forest carbon reserves reflect the processes of forest regeneration, growth and mortality. The occurrence and growth of tree seedlings are closely related to microenvironment, which is affected by tree canopy cover, solar radiation, soil humidity and temperature (Liu et al. 2022, Schmerbeck and Gupta 2022). Long-term plots have consistently shown decreases in the turnover time of living vegetation carbon, likely driven by increasing tree mortality across all major climate zones (Yu et al. 2019). Drought has a delayed effect on forest productivity, resulting in increased tree mortality and reductions in tree regeneration (Kannenberg et al. 2020). Delayed increases in tree mortality may result in immediate, but temporary, increases in forest carbon stocks. To understand the consequences of future changes in warming and drought recurrence, it is first necessary to provide a baseline of current conditions through long-term monitoring.

The effects of climate change on the spatio-temporal patterns of forest carbon storage can be mediated by community composition, structure, and distribution of species (Zhang et al. 2018). Complex terrains and rich species diversities complicate accurate assessments of carbon storage in forests, especially in mountainous ecosystems. Individuals are often classified based on shared values of specific traits, with the aim of predicting a group response to environmental change (Hooper and Vitousek 1997). However, species may respond differently to environmental change depending on their functional traits. For example, Phillips et al. (2010) found that larger trees with lower wood density had higher sensitivity to drought in tropical forests, which could greatly reduce carbon storage. Furthermore, on a global scale, biomass carbon turnover in broadleaved evergreen forests was larger than in CFs due to stand replacing disturbances (Pugh et al. 2019). Therefore, we should assess the impacts of environmental change on forest growth and mortality for different forest types at a regional scale by utilizing forest inventories data to better understand dynamic changes in forest carbon storage as a function of different abiotic and biotic factors.

Ongoing environmental change is expected to alter plant regeneration, growth, mortality, and species composition, all of which will affect plant carbon pools. There is an urgent need to understand the dynamics associated with changes in net tree C stocks and predict the impacts of environmental change on net tree C and its components in different forest types. We used the mountainous forests in the eastern Qinghai-Tibet Plateau as our study region to address two questions: (a) how have growth, morality, and net tree C stocks changed in different forest types? and (b) which abiotic and biotic factors had greater influence on changes in net tree C stocks and its components in different forest types? This study represents a comprehensive assessment of tree C budgets over a nearly four-decade period (1979–2017) and improves our understanding of the ecological mechanisms underlying forest tree biomass carbon stocks and dynamics.

2. Materials and methods

2.1. Study area and forest inventory data

The forest areas of Southwest China are the second largest forested area in China, and forest types are diverse, with high forest stock, especially in the high mountains and deep valleys in the eastern Qinghai-Tibet. Beginning in the 2000s, China initiated the Natural Forest Protection Project and the Grain for Green Programme to recover forested areas that were previously thinned and clear cut. Forest carbon storage has increased gradually following efforts to generate forest recovery (Li et al. 2022). To understand the carbon sequestration potential of forests on the eastern Qinghai-Tibet Plateau, we used a network of permanent sampling plots (PSPs) to examine the temporal dynamics in forest carbon storage. Most PSPs were restored after deforestation and located on state-owned lands. We differentiated the historical land use patterns of PSPs, including forest, farm land, barren land, economic forest, burned land, forest after clear-cut harvest, shrubland, and sparse wood. Forest land contains forest that was not subject to human activity and secondary forest recovering from previous human land use, yet the original data did not distinguish whether selective thinning occurred.

We selected PSPs that were: (a) without management since recovery or monitoring, including primary and secondary forests; and (b) represented in at least two censuses. A total of 1248 plots (total of 102.62 ha) were selected for further analysis, with 119 231 trees measured during the monitoring period from 1979 to 2017; many trees were likely to have been measured more than once. The average measurement interval was 5.15 years, with an average of
3.95 censuses taken during the study period. Each sampling plot measured 0.10 ha (20 m × 50 m) prior to 2002, when the size was changed to 0.067 ha (25.82 m × 25.82 m). The study area was mainly affected by the warm and wet monsoon climate. Mean annual temperature (0 °C–17 °C) and mean annual precipitation (200 mm to 1700 mm) were highly variable in the study area. The elevation range was 400–4460 m a.s.l., generating different forest types along this elevation gradient. We divided the forest into five different forest types: evergreen broad-leaved forest (EBF), evergreen and deciduous broad-leaved mixed forest (EDBMF), deciduous broad-leaved forest (BDF), coniferous broad-leaved mixed forest (CBMF), and CF (figure 1, table S1) (Sichuan Vegetation Cooperation Group 1980). The EBF at low altitude was most heavily influenced by human activities based on the plot selection criteria mentioned above, so it was removed during the screening. In the study, there were 152 tree species overall. In all censuses and plots, the individual tree genera which accounted for >1% of tree biomass included conifers (Abies, Picea, Pinus, Sabina, and Tsuga) and broadleaved (Acer, Betula, Davidia, Populus, and Tilia) trees.

2.2. Annual change in net carbon stock and its components
Carbon content at the plot-level was calculated by summing the carbon stocks of all above-ground biomass (AGB) and below-ground biomass (BGB) of all live trees in each plot for each measurement period. AGB of each live tree was estimated using the ‘scaling-up factor continuous function’ method (Fang et al 2001). Due to the lack of BGB data, we estimated BGB at the plot level using the empirical allometric model, i.e. BGB = 0.489 × AGB^{0.89}, of Mokany et al (2006), which has been widely used for BGB estimations for a wide range of tree species (Saatchi et al 2011, Tyukavina et al 2015, Feng et al 2021). Total forest carbon, calculated as the sum of AGB and BGB, was converted to total forest biomass carbon stocks using a conversion factor of 0.5 (Saatchi et al 2011, Zarin et al 2016). Next, we calculated the annual change in net carbon stock (ACC, Mg ha^{-1} yr^{-1}) as the difference in carbon stock between censuses divided by the time between censuses (years). The annual change in net carbon stock was composed of annual carbon gain due to the growth of surviving trees plus new recruitment trees (δ ACC_g), and subtracting the annual carbon loss due to tree mortality (δ ACC_m), calculated as the summed carbon of all dead trees between two successive censuses divided by the time between censuses (in years); this approach was similar to previous studies (Hisano and Chen 2020).

2.3. Climate
Climate data, including monthly mean temperature (MMT) and precipitation in the growing season (April to October), were collected annually from 1979 to 2017 at 65 weather stations located within our study region by the Chinese National Meteorological Information Center/China Meteorological Administration (http://data.cma.cn). According to the weather station, weather data were interpolated at a 1 km × 1 km spatial resolution for the whole study area. The climatic factors of each plot were estimated using the Kriging interpolation method for regionalizing variables at different scales, with further interpolations conducted to adjust temperature according
to the mean plot elevation (Piao et al 2011). We used this approach to calculate the change in the mean values of MMT and precipitation in the growing season between two consecutive censuses for each plot, which were seen as climate drivers affecting net C stock.

2.4. Forest structure, composition and environmental factors

The abiotic factors in the study included soil depth (depth of topsoil measured to the underlying bedrock, cm), slope (degree), aspect (degree), altitude (m), and historical land use patterns of PSPs. The biotic drivers describing forest structure and composition included tree density (individuals ha\(^{-1}\)), tree species richness, canopy cover (%), diameter at breast height (DBH in cm) and tree height (m). Stand age could not be determined in these forest types due to the lack of appropriate data.

2.5. Data analysis

We assessed whether data were normally distributed and observed that the distributions of growth and mortality were right skewed, and \(\delta\) ACC was left skewed. Thus, we used 1000 iterations to bootstrap the fitted coefficients (Hisano and Chen 2020). Linear mixed effect (LME) models were used to investigate the spatiotemporal patterns and changes in the net carbon stock (\(\delta\) ACC) of the forest plots. Investigation year was included as a fixed explanatory variable and ‘plot ID’ as a random factor (equation 1). Meanwhile, we analyzed \(\delta\) ACC due to growth and mortality in forest plots using the same method. Analyses were conducted separately for EDBMF, BDF, CBMF, and CF forest types. To account for potential spatial dependencies in PSPs, we included a spatial autocorrelation variance factor (Dormann et al 2007) in the respective models:

\[
\delta\text{ACC}, \delta\text{ACC}_g, \delta\text{ACC}_m = \beta_0 + \beta_1 \times (\text{Year}_{i+1,j} - \text{Year}_{ij}) + \pi_j + \epsilon_{ij}
\]

where \(\text{Year}_{ij}\) represents the \(i\)th inventory census value at the \(j\)th plot; \(\beta_1\) are the coefficients to be estimated; \(\pi_j\) is a random plot effect; and \(\epsilon_{ij}\) represents the random error. \(\delta\) ACC represents the mean annual difference in ACC between the \(i\)th and the \(i + 1\)th inventory censuses for each plot.

To assess the relationships between the biotic and abiotic factors before modeling, we conducted Pearson correlation analysis on forest structure, composition and environmental factors (figure S1). To determine which predictive factors had a greater effect on the dependent variables (in the following section), we integrated abiotic and biotic factors into one model, and used LMEs to present the effect of abiotic and biotic factors on the net change in ACC (\(\delta\) ACC), \(\delta\) CNC\(_g\), and \(\delta\) CNC\(_m\) using equation (2). We also considered the spatial autocorrelation (Dormann et al 2007) in equation (2).

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

\[
\delta\text{ACC}, \delta\text{ACC}_g, \delta\text{ACC}_m = \beta_0 + \beta_1 \times \text{MMT}_{ij} + \beta_2 \times \text{Precipitation}_{ij} + \beta_3 \times \text{Slope}_{ij} + \beta_4 \times \text{Soil depth}_{ij} + \beta_5 \times \text{Altitude}_{ij} + \beta_6 \times \text{Aspects}_{ij} + \beta_7 \times \text{Latitude}_{ij} + \beta_8 \times \text{Historical land use patterns} + \beta_9 \times \text{Tree richness}_{ij} + \beta_{10} \times \text{Trees density}_{ij} + \beta_{11} \times \text{Canopy}_{ij} + \beta_{12} \times \text{Tree height}_{ij} + \beta_{13} \times \text{DBH}_{ij} + \pi_j + \epsilon_{ij}
\]

All predictor variables were standardized using \(z\)-transformations. We fitted models with each possible combination of predictor variables and averaged coefficients from models within delta Akaike’s information criterion (AIC) < 4 units (Grueber et al 2011, Rusch et al 2011). All analyses were conducted in R v4.0.2 (R Core Team 2019). Package ‘nmlm’ (Pinheiro 2020) was used for linear mixed models. Package ‘spam’ (Rousset and Courtiol 2021) was used to calculate spatial autoregressive structure. Package ‘MuMin’ was used for the model selection and averaging (Barton 2020). Further information about the model outcomes is provided in appendix S1.

3. Results

3.1. Temporal trends in growth, mortality, and net change in C stocks

On average, the net change in tree carbon stock (\(\delta\) ACC) increased over time for all of the forest types, with increments ranging from 2.81 to 4.44 Mg ha\(^{-1}\) yr\(^{-1}\) (table S1 and figure S2). The mean changes in net tree C stock, growth, and mortality were generally higher in CBMF than in EDBMF, BDF, and CF (figure S2). The net change in tree C stocks in EDBMF did not vary significantly (figure 2, table S2), but increased significantly in BDF, CBMF, and CF, ranging from 0.13 to 0.23 Mg ha\(^{-1}\) yr\(^{-1}\) (BDF: slope = 0.23, \(P < 0.001\); CBMF: slope = 0.16, \(P < 0.001\); CF: slope = 0.13, \(P < 0.001\)). Mortality increased significantly in EDBMF and CF (EDBMF: slope = 0.15, \(P = 0.016\); CF: slope = 0.030, \(P = 0.0042\)), but not in BDF or CBMF (figure 2, table S2). Growth increased significantly in all four forest types, but the rate varied in the different forest types, ranging from 0.15 to 0.27 Mg ha\(^{-1}\) yr\(^{-1}\) (EDBMF: slope = 0.20, \(P = 0.0018\); BDF: slope = 0.27, \(P < 0.001\); CBMF: slope = 0.18, \(P < 0.001\); CF: slope = 0.15, \(P < 0.001\), table S2).

3.2. Potential drivers of growth, mortality and net C stock

In the past four decades, MMT increased significantly in all four forest types, but there were differences in...
Figure 2. Growth, mortality, and net change of C stocks over time in four different forest types. Evergreen and deciduous broad-leaved mixed forests (EDBMFs), deciduous broad-leaved forests (BDFs), coniferous broad-leaved mixed forests (CBMFs), and coniferous forests (CFs). Lines and shaded areas represent the estimates of slope and 95% confidence intervals of the LME, respectively. Year indicates the time interval between 1979, 1988, 1992, 1997, 2002, 2007, 2012 and 2017.

the rate of warming (figure S3): which was highest in EDBMF (slope = 0.095 °C yr⁻¹, P = 0.0065), and progressively lower in BDF (slope = 0.064 °C yr⁻¹, P < 0.001), CBMF (slope = 0.039 °C yr⁻¹, P < 0.001), and CF (slope = 0.033 °C yr⁻¹, P < 0.001). Growing season precipitation differed in the four forest types, declining significantly in CBMF and CF (slope = -2.18 mm yr⁻¹, P < 0.001; slope = -0.87 mm yr⁻¹, P = 0.040, respectively).

In EDBMF, when all influencing drivers were considered in the LME models and the influences of spatial autocorrelation were considered, we found that growth showed a positive relationship with MMT (z = 2.47, P = 0.014) (figure 3, table S3), and decreased with higher altitude (z = 2.63, P = 0.0084) and latitude (z = 2.59, P = 0.0096). Mortality increased significantly with MMT (z = 2.67, P = 0.0076) and decreased at higher elevations (z = 2.56, P = 0.011) (figure 3, table S3). There were no influencing factors that significantly correlated with net tree C stocks in EDBMF. Apart from geographical location, MMT was the most important influencing factor affecting growth and mortality in EDBMF.

In BDF, growth was positively correlated with MMT (z = 4.42, P < 0.001), precipitation (z = 3.90, P < 0.001), density (z = 11.67, P < 0.001), and richness (z = 2.54, P = 0.011), but negatively correlated with altitude (z = 3.96, P < 0.001) and canopy (z = 2.05, P = 0.041). Mortality was positively correlated with MMT (z = 3.84, P < 0.001), but negatively correlated with tree height (z = 6.56, P < 0.001). Net tree C stocks were positively related to species richness (z = 4.82, P < 0.001) and tree density (z = 2.29, P = 0.022) in BDF (figure 3, table S3). The primary factor affecting growth in BDF was tree species richness and MMT was the primary factor affecting net C stocks.

In CBMF, growth was positively correlated with MMT (z = 4.42, P < 0.001), precipitation (z = 3.90, P < 0.001), density (z = 11.67, P < 0.001), and richness (z = 2.54, P = 0.011), but negatively correlated with altitude (z = 3.96, P < 0.001) and canopy (z = 2.05, P = 0.041). Mortality was positively correlated with MMT (z = 3.84, P < 0.001), but negatively correlated with tree height (z = 6.56, P < 0.001). Net tree C stocks were positively related to species richness (z = 2.37, P = 0.018), tree density (z = 9.95, P < 0.001), MMT (z = 4.17, P < 0.001), and precipitation (z = 6.86, P < 0.001), but negatively correlated with altitude (z = 5.08, P < 0.001). Overall, tree density, precipitation, and MMT were the main factors affecting net tree C stocks in CBMF.
In CF, growth was positively correlated with degraded forest land during recovery ($z = 2.00$, $P = 0.046$), MMT ($z = 3.93$, $P < 0.001$), precipitation ($z = 2.56$, $P = 0.011$), density ($z = 8.64$, $P < 0.001$), latitude ($z = 3.74$, $P < 0.001$) and canopy ($z = 2.95$, $P = 0.0032$), but negatively correlated with height ($z = 9.34$, $P < 0.001$), altitude ($z = 2.83$, $P = 0.0047$) and longitude ($z = 5.68$, $P < 0.001$) (table S3, figure 3). Mortality was positively correlated with MMT ($z = 2.90$, $P = 0.0037$), tree height ($z = 2.59$, $P = 0.0236$) and canopy ($z = 2.37$, $P = 0.018$), but negatively correlated with density ($z = 3.34$, $P < 0.001$). Net tree C stock was positively correlated with density ($z = 13.70$, $P < 0.001$), precipitation ($z = 4.68$, $P < 0.001$) and MMT ($z = 3.62$, $P < 0.001$), but negatively correlated with tree height ($z = 9.17$, $P < 0.001$) (table S3). In CF, tree density, height, MMT and precipitation were the primary drivers of changes in net tree C stock.

4. Discussion

On average, net tree carbon stocks in all four forest types increased from 1979 to 2017, primarily due to increasing growth. Tree growth neutralized or offset carbon loss due to mortality, especially in EDBMF and CF. Annual net tree C stock ranged from 2.81 to 4.44 Mg ha$^{-1}$ yr$^{-1}$, which was lower than the mean values of annual net tree C stock of 4.99 Mg ha$^{-1}$ yr$^{-1}$ at 40–50 years of age, and 5.96 Mg ha$^{-1}$ yr$^{-1}$ at 50–60 years of age in evergreen needle forests, and 4.83 Mg ha$^{-1}$ yr$^{-1}$ in deciduous broad-leaved forests in China (Wang et al. 2011). In the present study, the increase in annual net tree C stock was lower than observed in early successional forest stages (0–100 years) (Chave et al. 2003, Gautam and Mandal 2016, Paulick et al. 2017). Nevertheless, the annual increment in net tree C stock change ranged from 0.13 to 0.23 Mg ha$^{-1}$ yr$^{-1}$, which may indicate that tree C stocks will rise due to growth. Although productivity reaches a peak in middle-aged stands and then declines (He et al. 2012), the increase in net tree carbon stock in our study showed that carbon sequestration has not been sufficient to meet the carbon neutral state (Odum 2014), which might be achieved in the later periods of forest succession.

In an earlier study, differences in carbon stocks were present among the live and dead organic matter pools in different forest types (Zhu et al. 2017). There were differences in net tree carbon stocks, growth, and mortality when comparing CBMF and CF, with intermediary changes in EDBMF and BDF (Figure S2). Differences in forest types have also been observed by Wang et al. (2011), who found that the productivity of mixed forests was higher than non-mixed forests, such as BDF and CF. In contrast to the consistent increases in growth rates, mortality increased in both EDBMF and CF in our study, which did not change significantly in BDF and CBMF. These differences in mortality may be explained by differences in environmental background, climate change, and forest composition and structure factors (Stephenson...
et al. 2011). Overall, in our study, the main factors affecting forest growth and mortality were altitude, latitude, species richness, tree density, MMT, and precipitation in the growing season.

One of main causes of differences in growth, mortality, and net tree C stocks may be differences in geographical location and climate in the four forest types (table S1) (Woodward and Williams 1987). Growth and mortality are generally higher in warmer and wetter forests, such as EDBMF, where there are warmer temperatures in the growing season (figure S3). Trees in EDBMF can obtain more resources because they occupy locations where light, water, and heat are plentiful and conducive to forest growth and carbon turnover (Schulze et al. 2014). In contrast, the net tree C stocks of CF were limited by lower temperatures and annual precipitation than the other forest types.

Differences in climate among the different forest types generated differences in net tree C stocks. Higher elevations experienced severe drought in CBMF and CF (figure S3), and future droughts associated with climate change may deliver more severe negative effects to native forest communities and carbon stocks (Kannenberg et al. 2020). Observations in this study, that warmer temperatures in the growing season generated higher tree growth, are similar to other studies that indicate that warming may increase AGB and C storage in wet and cold areas (Creutzburg et al. 2017, Finzi et al. 2020). Furthermore, warm temperatures in the growing season were also linked to increased mortality in all forest types. These findings are similar to the ‘faster growth–higher mortality–shorter carbon turnover time’ phenomenon, which has been observed at local scales, particularly in tropical forests and recently demonstrated in boreal forests (Pugh et al. 2019). Although warmer temperatures in the growing season accelerated the turnover of carbon, it still promoted the increase of net tree C stocks in CBMF and CF over the past four decades (table S3).

Tree density and richness were more strongly and positively correlated with growth than with mortality, thereby generating an increase in net tree C stocks on average. CBMF, with higher species richness than all other forest types, had both higher growth and mortality, and maintained higher net tree C stocks, which reflected the positive effect of tree diversity on net C turnover (Larjavaara and Muller-Landau 2012). Forest productivity can be enhanced using complementary strategies that increase functional characteristics and morphological diversity (Brun et al. 2019), such as niche complementation in mixed forests (Del Rio et al. 2017). For example, current low productivity in BDF could be improved if species richness could be increased through management.

In addition to tree species diversity, tree density is also important for forest productivity, especially in CBMF and CF. Higher stand densities increased forest C storage and wood production through higher canopy cover, which intercepts more light for photosynthesis (Ouyang et al. 2019). CFs have smaller canopy coverage than broad-leaved forests, so increasing tree density may increase productivity. Moreover, in CF, net tree C stocks and growth decreased because CFs are located in higher elevations with lower precipitation than other forest types (table S1), and precipitation is declining (figure S3).

5. Conclusions

Overall, tree carbon stocks in four forest types have increased significantly over the past 40 years due to higher forest growth under climate warming. The important factors affecting forest growth and mortality included geographical location (latitude and altitude), tree density, species richness, MMT, and precipitation in the growing season; however, the relative importance of each factor varied in the four forest types. In EDBMF, growth and mortality were primarily correlated with geographical location, climate background and MMT. In BDF, the primary factor affecting growth was tree species richness and MMT was the primary factor affecting net C stocks. In CBMF, tree density, precipitation, and MMT were the main factors affecting net tree C stocks. In CF, tree density, height, MMT and precipitation were the primary drivers of changes in net tree C stock. MMT in the growing season accelerated growth and mortality in all forest types, often having a greater influence than richness and tree density, and was positively correlated with net tree C in CBMF and CF. Based on this study, net tree C stocks may continue to increase in CBMF and CF, in the next few decades, due to rising monthly average temperature in the growing season. Overall, this study may provide a guideline for the restoration and protection of different forest types in montane environments.

Data availability statement

Data available from the authors upon request.

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Authors’ contributions

Ting Li and Qi Wang analyzed data and wrote the manuscript. Yang Liu, Changhong Lai, Yuming Qiu, David T Tissue, Jiangtao Xiao, Xuhua Li, Li Peng contributed to the final preparation of the manuscript.
Conflict of interest

The authors declare that there are no competing interests.

ORCID iDs

Ting Li  https://orcid.org/0000-0002-5579-0586
Li Peng  https://orcid.org/0000-0003-0016-2977

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