

RESEARCH ARTICLE

Demographic and net primary productivity dynamics of primary and secondary tropical forests in Southwest China under a changing climate

Sai Tun Tun Oo^{1,2}  | Shankar Panthi¹  | Ze-Xin Fan¹  | Xiao-Yang Song¹ |
 Huanyuan Zhang-Zheng³  | Zaw Zaw¹ | Hua-Zheng Lu^{1,4} | Hui Chen¹ |
 Yun Deng^{1,4} | Rong Zhao^{1,4} | Hua Lin¹ | Pei-Li Fu¹ 

¹CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, China

²University of Chinese Academy of Sciences, Beijing, China

³Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

⁴Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, China

Correspondence

Ze-Xin Fan and Pei-Li Fu, CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China.
 Email: fanzexin@xtbg.org.cn and fpl@xtbg.org.cn

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Abstract

Tropical forests are major carbon sinks on the Earth's land surface. However, our understanding of how the demographic rate and carbon sink capacities of tropical forests respond to climate change remains limited. In this study, we investigated the impacts of environmental drivers on forest growth, mortality, recruitment, and stem net primary productivity (NPP_{stem}) over 16 years at five tropical forest plots in Xishuangbanna, Southwest China. These plots are along a successional gradient spanning three tropical secondary forests (tropical secondary forest-1 [TSF-1], tropical secondary forest-2 [TSF-2], and tropical secondary forest-3 [TSF-3]) and two primary forests (tropical rainforest [TRF] and tropical karst forest [TKF]). Our results showed that early successional secondary forests (TSF-2 and TSF-3) had higher diameter growth rates and relative mortality rates. An extreme drought event during 2009–2010 reduced the growth rate, relative recruitment rate, and NPP_{stem} for most plots while increasing mortality in early successional forest plots. We observed significant negative effects of maximum temperature (T_{max}) on NPP_{stem} and diameter growth rate across all plots. Additionally, we found that precipitation had significant positive effects on diameter growth rate across all plots. Furthermore, tree mortality increased with rising T_{max} , whereas precipitation significantly enhanced tree recruitment. Our findings highlight the vulnerability of tree growth, mortality, recruitment, and productivity in tropical forests to extreme drought events in Southwest China. Continued climate warming and more frequent droughts will induce higher mortality rates and impede growth, thus reducing the carbon sink capacity of tropical forests, especially in early successional stage tropical secondary forests.

KEYWORDS

climate change, growth rate, mortality and recruitment, stem net primary productivity (NPP_{stem}), successional stages, tropical forests

Plain language summary

Tropical forests are vital components of the global carbon cycle and play an important role in mitigating climate change. However, the

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effects of climate change on the dynamics of these ecosystems are not fully understood. In this study, we explored how different types of tropical forests in Southwest China responded to climate change from 2004 to 2020. By tracking forest growth, mortality, regeneration, and productivity, we found that secondary forests, especially those at early successional (younger) stages, are more vulnerable to extreme climatic events like droughts and heat waves. These events reduced tree growth and regeneration, increased tree mortality, and impacted the forests' ability to fix carbon. Climate change, including rising temperatures and more frequent droughts, may decrease tropical forest growth, recruitment, and carbon sequestration while increasing tree mortality in the future.

1 | INTRODUCTION

Tropical forests serve as crucial carbon sinks and carbon pools (Bonan, 2008; Pan et al., 2011). However, their carbon sink capacity faces challenges due to climate change (Corlett, 2016; Cramer et al., 2004). Global climate change significantly impacts tropical ecosystem dynamics through increasing temperatures, changes in precipitation patterns, and more frequent and intense droughts (Corlett, 2016). Specifically, these impacts extend to reducing long-term tree growth (Lewis et al., 2009; Lewis, 2006; Malhi & Phillips, 2004), increasing tree mortality (Calvo-Rodriguez et al., 2021; Chen et al., 2021), and altering plant community composition, structure, and overall ecosystem functioning (Deb et al., 2018; Mina et al., 2018). Tropical forests in different successional stages respond uniquely to regional climate change (Lewis et al., 2004). However, our understanding of the responses of tropical forests at different successional stages to regional climate change remains limited (Sheldon, 2019).

Dynamic shifts in demographic patterns (growth, mortality, and recruitment) within tropical forests along successional gradients are influenced by anthropogenic activity and global changes, posing significant challenges for conservation and management (Wright, 2005). Primary forests are typically characterized by stable demographic rates and a diverse mix of mature trees, saplings, and seedlings (Gibson et al., 2011). In contrast, secondary forests exhibit significant demographic variations characterized by rapid expansion of pioneer species and high mortality rates (Wright, 2005). Despite these differences, secondary forests harbor substantial conservation potential as carbon sinks (Heinrich et al., 2023; Pugh et al., 2019), attributed to increasing resource availability and potentially influenced by rising atmospheric CO₂ concentrations (Lewis et al., 2009). The area of secondary tropical forests is expanding globally (Brown & Lugo, 1990), while the total forest area has declined (Keenan et al., 2015). The expansion of secondary forests offers an opportunity for tree restoration and carbon sequestration, especially with essential information available on the demographic patterns of secondary forests under environmental change (Harris et al., 2006; Peng

Practitioner points

- Secondary tropical forests demonstrate superior growth rates. Policymakers and forest managers should prioritize these forests alongside primary forests for conservation and restoration efforts.
- Early successional tropical secondary forests are more vulnerable to hot-dry climate. Forest managers should focus on the scientific and sustainable management of these forests to mitigate the effects of temperature extremes and drought.
- Climate warming threatens tropical tree growth, recruitment, and tropical forest carbon sink capacity. Experts need to develop proactive management practices and climate-resilient strategies to address these challenges.

et al., 2010). Understanding the demographic rates between primary and secondary forests is critically important because there is potential for an additional 0.9 billion ha of continuous secondary forest cover (Bastin et al., 2019).

Stem net primary productivity (NPP_{stem}) serves as a critical metric in assessing the collective biomass production and carbon dynamics within a defined area of a forest ecosystem (Ohtsuka et al., 2005). Estimating carbon accumulation over time is crucial for carbon budgeting and assessing ecosystem dynamics (Baishya & Barik, 2011). Tropical secondary forests demonstrate higher carbon uptake, with an approximate accumulation rate of 3 Mg C ha⁻¹ year⁻¹ (Chazdon et al., 2016; Poorter et al., 2016), surpassing by an order of magnitude the levels observed in mature and old-growth primary tropical forests, which typically exhibit rates around 0.5 Mg C ha⁻¹ year⁻¹ (Mitchard, 2018). Climate warming is associated with reduced carbon sink potential on the global scale (von Buttlar et al., 2018). However, regional studies, such as one conducted in China, have shown increased carbon sink capacity under a warming

climate (Gao et al., 2004), indicating that the effects of climate change on carbon sinks can vary by location. Within the scope of carbon-related studies, remote sensing-based monitoring is gaining attention, but it often includes biased estimations of forest carbon budget and productivity. Periodical biometric measurements, such as tree diameter, provide a more accurate approach to estimating forest carbon dynamics (Zhao et al., 2018). Most studies have focused on short-term local climate and forest productivity using ground-based measurement estimations (Köhl et al., 2015; Phillips et al., 2009). However, comprehensive, decadal-scale monitoring of climate and forest productivity remains rare (Kovács & Gulácsi, 2019), especially for forests in tropical regions at different successional stages.

In this study, we used forest inventory data collected over 16 years from five tropical forest plots in Southwest China, each representing different successional stages (i.e., early, late, and mature stages). Our study aims to address the following questions: (i) What are the trends in long-term demographic rates and NPP_{stem} across tropical forests at different successional stages? (ii) Do demographic rates and NPP_{stem} differ among the five tropical forest plots? (iii) What environmental variables drive tree demography patterns and NPP_{stem} across tropical forests at different successional stages? We hypothesize that growth and NPP_{stem} will decrease, while mortality will increase with climate warming. We expect to observe higher demographic rates and NPP_{stem} in early successional secondary forests compared to primary mature forests and the secondary forest in the late successional stage. Furthermore, we anticipate that maximum temperature will have the most substantial negative effect on tree growth and NPP_{stem} , while precipitation/moisture availability will be the limiting factor for growth rate and tree recruitment across different forest plots.

2 | MATERIALS AND METHODS

2.1 | Site descriptions and climate

The study sites are located within the Xishuangbanna National Nature Reserve, Yunnan, Southwest China.

We selected five permanent tropical forest plots, each representing different successional statuses and forest types (Table 1 and Supporting Information: Table S7). TKF exhibited the highest tree density, whereas TRF had the highest number of tree species and the greatest canopy height (Table 1 and Supporting Information: Table S7). The basal area was highest in TKF and lowest in TSF-2. Among the top 10 dominant species in each plot, TSF-3 and TSF-2 had the highest number of pioneer species (Supporting Information: Table S7). Human disturbances in the studied forest plots are minimal, primarily involving light interventions by local communities for the collection of wild vegetables and tourism activities. Moreover, there is no artificial felling of forest trees within the five forest plots.

The Xishuangbanna region is characterized by a typical tropical monsoon climate with distinct dry and wet seasons. The dry season lasts from November to April, while the wet season occurs from May to October. The wet season is marked by heavy summer monsoon rainfall, which accounts for over 80% of the total annual precipitation (Cao et al., 2006; Supporting Information: Figure S2). Interannual variations in mean annual temperature are mild, ranging between 21.6°C and 23°C. In contrast, total annual precipitation varies greatly from year to year, ranging between 947 mm and 1799 mm from 2004 to 2020 (Figure 1e). The annual precipitation and relative humidity have been decreasing significantly, while maximum temperatures have shown a significant increase in recent decades (Figure 1a–c). In 2010, a historical drought event occurred in the study area (Figure 1d,f) (Li et al., 2019).

2.2 | Forest inventory survey

A series of forest inventory surveys were conducted within the five forest plots from 2004 to 2020. Surveys were conducted annually before 2010, with a transition to a 5-year interval implemented thereafter. During each survey, all individual trees with a minimum DBH (diameter at breast height at 1.3 m above ground) of at least 2 cm were assessed. The survey recorded species names, tree height, and DBH, assigned unique identification tags to newly recruited individuals, and noted any dead trees.

TABLE 1 Plot size, elevation, forest type, successional stage, tree density, number of tree species, as well as the basal area of the five study plots.

Plot name	Plot size (m ²)	Elevation (m. asl)	Forest type	Successional Stage	Tree density (ha ⁻¹) (DBH ≥ 2 cm)	No. of species	Basal area (m ² ha ⁻¹)
TRF	100 × 100	750	Primary	Climax	2104	185	22.49
TKF	50 × 50	640	Primary	Climax	2520	29	25.31
TSF-1	50 × 100	560	Secondary	Late succession	991	81	23.77
TSF-2	50 × 50	630	Secondary	Early succession	1484	70	10.66
TSF-3	50 × 50	820	Secondary	Early succession	2208	70	21.98

Abbreviations: DBH, diameter at breast height; TKF, tropical karst forest; TRF, tropical rainforest; TSF, tropical secondary forest.

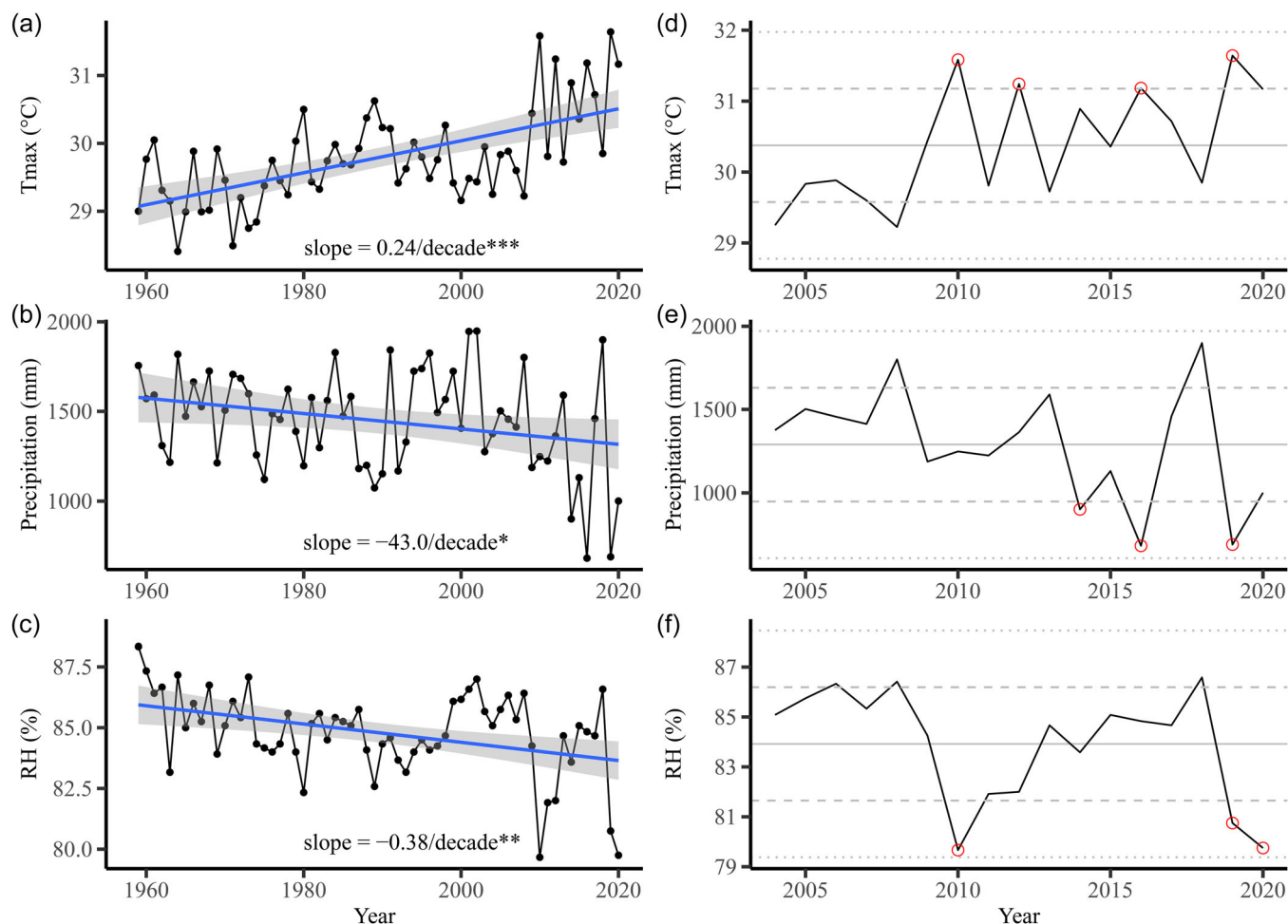


FIGURE 1 Climate conditions for the study area. Long-term trends of maximum temperature (a; Tmax), precipitation (b), and relative humidity (c; RH) for the period 1959–2020. The black line with solid circles represents annual values, the blue solid straight line corresponds to the linear trend over time, and the gray shaded area represents the 95% confidence interval for the linear trend. Interannual variations of climate factors (d–f) are shown for the study period from 2004 to 2020. The solid horizontal gray line represents the 16-year mean value, while the dashed and dotted gray lines represent ± 1 and ± 2 standard deviations from the mean, respectively. The open red circles indicate extreme climatic years.

2.3 | Environmental conditions

All the tropical forest plots studied in this research share the same climatic conditions as they are located near each other within the same valley (within ~15 km distance). Therefore, we used the same climate data from the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRFES) for all plots. The climate station of XSTRFES is situated within the Xishuangbanna Tropical Botanical Garden (21°54' N, 101°46' E, 580 m a.s.l.), and all five forest plots are within 10 km of this climate station. Soil water content (SWC) across the plots varies due to differences in topo-geology and forest successional history. SWC was measured at a depth of 20 cm using gravimetric methods. SWC measurements have been conducted every 2 months (Jan, Mar, May, Jul, Sep, and Nov) each year since 2006 by staff from XSTRFES. However, SWC data for the tropical secondary forest-3 (TSF-3) plot only covers 2017–2020; hence, we excluded SWC data from this

plot for further analysis. During the study periods, the tropical secondary forest-1 (TSF-1) and tropical secondary forest-2 (TSF-2) plots showed higher SWC than other plots (Supporting Information: Figure S1). Monthly climate and SWC data were averaged for further analysis according to the yearly forest inventory survey period (census interval) rather than on an annual basis.

2.4 | Demographic rates

To measure the raw changes in radial growth rates, we used the absolute diameter growth rate (Kambach et al., 2022). Depending on factors such as drought years, survey periods, or inaccuracies in the measurement point of DBH in each census, the radial growth rates of some trees may be negative. Trees exhibiting a reduction in DBH greater than 25% relative to the initial survey or those demonstrating raw DBH changes exceeding 5 cm compared to the initial survey were considered outliers

and omitted from the analysis (Oktavia & Jin, 2019). The absolute diameter growth rate (DGR, mm yr⁻¹) for each tree and cumulative growth rates for each census of each forest plot were calculated as follows:

$$\text{DGR (mm yr}^{-1}\text{)} = \frac{\text{DBH}_t - \text{DBH}_i}{\Delta t}. \quad (1)$$

The calculation involved stem diameter measurements at two censuses, denoted as DBH_t (diameter at the second census) and DBH_i (diameter at the first census). The difference was then divided by the time interval (Δt).

The relative mortality rate (RMR, % yr⁻¹) for each forest plot was calculated as:

$$\text{RMR (\% yr}^{-1}\text{)} = \left(\frac{D}{N\Delta t} \right) \times 100, \quad (2)$$

where D is the number of individuals that died within the time period between two consecutive surveys; N is the count of individuals that were alive at the beginning of that specific period; Δt is the time difference, which represents the duration between the two surveys (Zhou et al., 2013).

The relative recruitment rate (RRR, % yr⁻¹) for each forest plot was calculated as:

$$\text{RRR (\% yr}^{-1}\text{)} = \left(\frac{R}{N\Delta t} \right) \times 100, \quad (3)$$

where R is the number of newly recruited individuals at the end of a given time period; N is the number of individuals existing at the beginning of the census period; Δt is the time difference, which represents the duration between the two surveys (Zhou et al., 2013).

2.5 | Net primary productivity (NPP_{stem})

Tree height plays a key role in calculating above-ground biomass, but accurate measurements are often rare, and tree height can change from year to year only due to measurement errors (Réjou-Méchain et al., 2017). Therefore, the year with the highest number of maximum height records was chosen to construct the local diameter-height relationship. The modeled height was extrapolated for all trees in each census based on their diameter at breast height (DBH) values. The process was conducted separately for each plot. Correct taxonomic information for each species in all forest plots was compiled, and their wood density data were downloaded from the global wood density (GWD) database (Chave et al., 2009; Zanne, 2009). The “Biomass” R-package was used to download wood density data by matching each specific species' taxonomy with the GWD database (Réjou-Méchain et al., 2017). Then, the allometric equations were applied to estimate

above-ground biomass for each individual following Chave et al. (2005):

$$\text{AGB}_{\text{dry}} = 0.112 \times (WD \times ((D)^2) \times H)^{0.916}, \quad (4)$$

$$\text{AGB}_{\text{wet}} = 0.0776 \times (WD \times ((D)^2) \times H)^{0.940}, \quad (5)$$

where, AGB_{dry} and AGB_{wet} represent above-ground biomass for dry and wet forest types, respectively. WD is Wood density, D is tree diameter at breast height (DBH), and H is the model predicted height. Due to the unique characteristics of karst landscapes, which are characterized by an underground network of sinkholes, sinking streams, and caves, and soil availability is lower in these areas. Moreover, the proportion of deciduous tree species in karst habitats is higher than in the other four forests. Thus, only TKF was considered the drier forest type in this study.

NPP_{stem} for each tree was calculated as the change in biomass between the exact dates of two successive surveys (Malhi, Aragao, et al., 2009; Malhi, Saatchi, et al., 2009). NPP_{stem} was calculated for each tree that presented in both surveys. This calculation involves above-ground biomass at two censuses for each tree, denoted as Biomass_t (biomass at the second census) and Biomass_i (biomass at the first census). This difference was then divided by the time difference. Uncertainty for plot scale NPP_{stem} is provided by the “Biomass” R-package. Then NPP_{stem} for the plot between the two censuses was calculated as a sum of all individual tree NPP_{stem}.

$$\text{NPP}_{\text{stem}} = \frac{\text{Biomass}_t - \text{Biomass}_i}{\text{time difference}}. \quad (6)$$

2.6 | Statistical analyses

We employed linear mixed-effects models (LMMs) to investigate and compare the demographic rates and NPP_{stem} across five forest plots utilizing the “lme4” package (Douglas et al., 2015) in R (R Core Team, 2022). Forest plots were treated as fixed effects and years of forest inventory survey were treated as random effects (Equation 7). We performed Dunnett's post hoc test on each specific model for group comparisons using the “emmeans” package in R (Lenth, 2023). Additionally, LMMs were constructed to analyze 16-year trends in forest demographic rates and NPP_{stem}, treating years of forest inventory survey as a fixed effect and forest plots as random effects (Equation 8).

$$\begin{aligned} \text{Demographic rates or NPP}_{\text{stem}} &\sim \text{Plots} \\ &+ (1|\text{Year}), \end{aligned} \quad (7)$$

$$\begin{aligned} \text{Demographic rates or NPP}_{\text{stem}} &\sim \text{Year} \\ &+ (1|\text{Plots}). \end{aligned} \quad (8)$$

We further constructed LMMs to evaluate the effects of environmental variables on diameter growth rates (DGR) across the five forest plots. We used maximum temperature (T_{\max}), precipitation, and soil water content (SWC) as the environmental variables for each set of models in this study. Individual sets of LMMs were constructed for each forest plot, considering diameter growth rates as the response variables, individual tree-tag (ID) as random effects, and environmental variables as fixed effects (Equation 9). Then, manipulation on NPP_{stem} was performed by aggregating all NPP_{stem} values from each forest plot into a single linear mixed-effects model, considering combined plot-level NPP_{stem} as the response variable, environmental variables as fixed effects, and forest plots as random effects. The raw data of NPP_{stem} were log-transformed to meet the model assumption for normalization (Equation 10).

$$\text{Diameter growth rate (DGR)} \sim T_{\max} + \text{Precipitation} + \text{SWC} + (1|\text{ID}), \quad (9)$$

$$NPP_{\text{stem}} \sim T_{\max} + \text{Precipitation} + \text{SWC} + (1|\text{Plot}). \quad (10)$$

For the analysis of environmental effects on tree mortality and recruitment, generalized linear mixed-effects models (GLMMs) was utilized, as these response variables do not follow the Gaussian distribution. Separate sets of GLMMs were constructed for each plot, following a binomial probability distribution for tree mortality (i.e., dead/survive), and a Poisson distribution for tree recruitment (i.e., count of recruited individuals). In each set of GLMMs, environmental variables were considered fixed effects, and species were treated as random effects for both tree mortality and recruitment (Equations 11, 12).

$$\text{Mortality} \sim T_{\max} + \text{Precipitation} + \text{SWC} + (1|\text{Species}), \text{ family} = \text{binomial}, \text{ link} = \text{"logit"}, \quad (11)$$

$$\text{Recruitment} \sim T_{\max} + \text{Precipitation} + \text{SWC} + (1|\text{Species}), \text{ family} = \text{Poisson}, \text{ link} = \text{"log"}. \quad (12)$$

We considered all the assumptions of GLMMs and LMMs (Zuur et al., 2010), all the variables were scaled to converge models, and the standard estimates of effects were compared. Furthermore, before constructing LMMs and GLMMs, we checked for multicollinearity of environmental variables using the R-package "car" (Fox et al., 2007). Multicollinearity was determined by evaluating the Variance Inflation Factor (VIF). All of our statistical models (LMMs and GLMMs) showed VIF values ≤ 5.0 for T_{\max} , Precipitation, and SWC.

3 | RESULTS

3.1 | Demographics rates and NPP_{stem}

Secondary forest plots in early successional stages showed faster growth rates compared to

late-successional and climax forest plots. The highest diameter growth rate (DGR, mm yr^{-1}) was observed in TSF-3, while the lowest DGR occurred in TKF (Figure 2a). Similarly, relative mortality rates (RMR, $\% \text{ yr}^{-1}$) were higher in early successional secondary forest plots (TSF-2 and TSF-3) than in late successional (TSF-1) and primary forests plots (TKF and TRF) (Figure 2b). TSF-3 showed the highest relative recruitment rates (RRR, $\% \text{ yr}^{-1}$), whereas TKF exhibited the lowest RRR among the five forest plots (Figure 2c). The highest stem net primary productivity (NPP_{stem}) was observed in TSF-3 ($2.218 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), with lowest NPP_{stem} in TSF-2 ($0.874 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) (Figure 2d).

The overall temporal dynamics of NPP_{stem} ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$) and demographic rates revealed notable adverse effects of drought during 2009–2010 (Figure 3a–d). We recorded the lowest diameter growth rate, as well as lower relative recruitment rate and NPP_{stem} for most tropical forest plots during this period (Figure 3a,c,d). Similarly, relative mortality rates in 2010 were distinctly higher for early successional secondary forest plots compared to primary forest plots (Figure 3b), indicating that early successional secondary forests are more vulnerable to extreme drought and warming climates. LMMs showed significant declining trends in diameter growth rate and relative recruitment rate across the five tropical forest plots over the past 16 years (Supporting Information: Table S6). NPP_{stem} also showed a declining trend, although the trend was marginally significant (Supporting Information: Table S6). Conversely, we observed a marginally significant increasing trend over time for relative mortality rate (Supporting Information: Table S6).

3.2 | Effects of environmental variables on forest demography and productivity

We observed a significant negative effect of maximum temperature (T_{\max}) and a positive effect of precipitation on DGR (mm yr^{-1}) across all five forest plots (Figure 4 and Supporting Information: Table S1). GLMMs showed a significant positive effect of T_{\max} on tree mortality in all five forest plots (Figure 4 and Supporting Information: Table S2), while the negative effect of precipitation on tree mortality was only significant for the primary forest-TRF and late successional secondary forests (TSF-1; Figure 4 and Supporting Information: Table S2). Tree recruitment was mainly driven by precipitation except for the TSF 3 plot (Figure 4 and Supporting Information: Table S3). However, T_{\max} showed

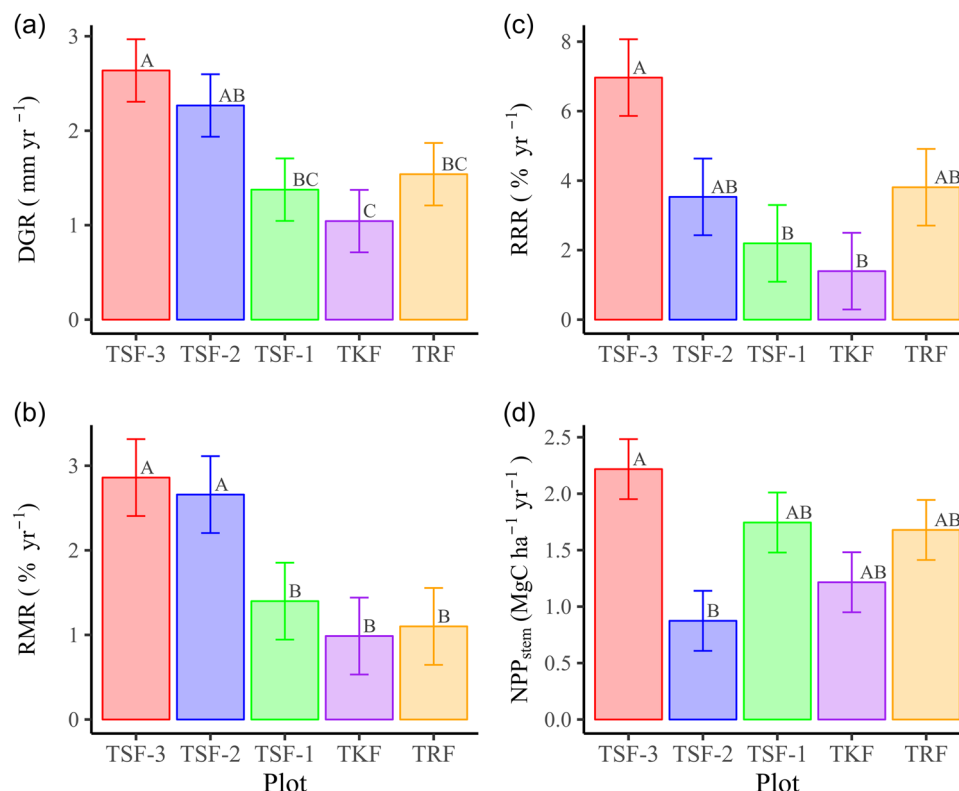


FIGURE 2 Plot-level estimated marginal means of diameter growth rate (a; DGR, mm yr⁻¹), relative mortality rate (b; RMR, % yr⁻¹), relative recruitment rate (c; RRR, % yr⁻¹), and stem net primary productivity (d; NPP_{stem}, Mg C ha⁻¹ yr⁻¹) across five tropical forest plots. Different letters represent significant differences ($p < .05$) among the forest plots. TKF and TRF are primary forests. TSF-1 is a secondary forest at late successional, while TSF-2 and TSF-3 are secondary forests at early successional. TKF, tropical karst forest; TRF, tropical rainforest; TSF, tropical secondary forest.

significantly a negative effect on tree recruitment in TRF and TSF-1, and a positive effect in TSF-3 (Figure 4 and Supporting Information: Table S3). Soil water content (SWC) was significantly and negatively linked to DGR (mm yr⁻¹) in TKF, TRF, TSF-1, and TSF-2 (Figure 4 and Supporting Information: Table S1). SWC also showed a negative effect on tree mortality in TKF, TRF, and TSF-2, but a positive effect in TSF-1 (Figure 4 and Supporting Information: Table S2). Furthermore, SWC was negatively associated solely with tree recruitment in TSF-2 (Figure 4 and Supporting Information: Table S3).

Results from the linear mixed-effects model further indicated significant negative effects of Tmax on NPP_{stem} across all five tropical plots (Figure 5a and Supporting Information: Table S4). However, the effects of SWC and precipitation on NPP_{stem} were not statistically significant.

4 | DISCUSSION

4.1 | Long-term variation in forest demographic rates and productivity

We observed that early successional secondary forest plots (TSF-2 and TSF-3) typically showed higher diameter growth rates than primary forest plots (TKF and TRF) and the late successional secondary forest plot (TSF-1) (Figure 2a). Generally,

the early successional vegetation in tropical forests shows rapid growth rates due to the availability of soil nutrients and light competition (Matsuo et al., 2024). In addition, secondary forests in tropical regions experience rapid initial growth dominated by pioneer species (Supporting Information: Table S7), leading to higher short-term growth rates compared to primary forests (Van Breugel et al., 2007). However, as these forests progress through successional stages, growth rates may decrease due to factors such as increased competition and resource-use efficiency (Küppers, 1992). Similarly, early successional forest plots also had higher relative mortality rates (TSF-2 and TSF-3) (Figure 2b). The mortality rate in secondary forests generally depends on their competitive strategy, as pioneer tree species in secondary forests tend to invest more in rapid growth but are less resilient to environmental stress (Brown & Lugo, 1990; Guariguata & Ostertag, 2001). The TSF-3 plot featured the highest relative recruitment rate among the studied forest plots (Figure 2c). The higher relative recruitment rate in TSF-3 is likely related to its high relative mortality rate, as low survival is commonly associated with high recruitment (Kambach et al., 2022). Generally, tree mortality shapes forest dynamics by influencing recruitment processes (Lutz et al., 2014). Mortality reduces competition among established trees, making more resources such as light, water, and nutrients available

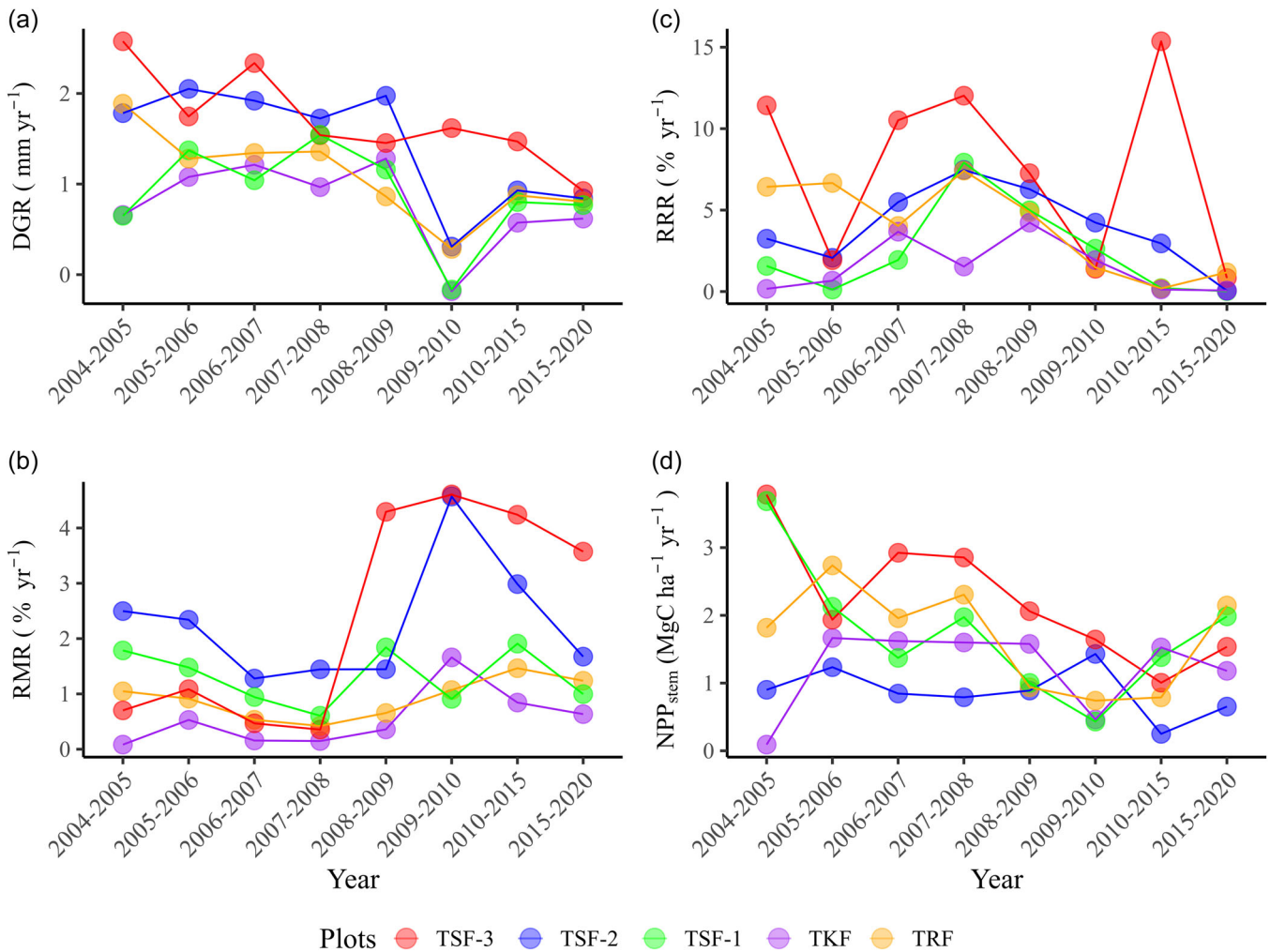


FIGURE 3 Interannual variations of plot-level means of diameter growth rate (a; DGR, mm yr⁻¹), relative mortality rate (b; RMR, % yr⁻¹), relative recruitment rate (c; RRR, % yr⁻¹), and stem net primary productivity (d; NPP_{stem}, MgC ha⁻¹ yr⁻¹) across five tropical forest plots during the period from 2004 to 2020. Note that extreme drought occurred in 2009–2010. TKF and TRF are primary forests. TSF-1 is a secondary forest at late successional, while TSF-2 and TSF-3 are secondary forests at early successional. TKF, tropical karst forest; TRF, tropical rainforest; TSF, tropical secondary forest.

for regeneration (Gessler et al., 2017). When trees die, they create gaps in the canopy, allowing increased sunlight penetration to the forest floor, which stimulates the growth of understory plants and new tree establishment (Pedersen & Howard, 2004). Additionally, decomposing trees release nutrients into the soil, enhancing fertility and supporting the growth of young trees (Ludovici & Kress, 2006). Furthermore, the results revealed that among the early successional forest plots, TSF-3 exhibited the highest NPP_{stem}, whereas TSF-2, within the same successional stage, displayed the lowest NPP_{stem} (Figure 2d). Secondary forests, undergoing regeneration after disturbances, have been recognized as significant for carbon sequestration (Heinrich et al., 2021; Kenzo et al., 2010; Medlyn et al., 2000; Taylor et al., 2014), which aligns with the highest NPP_{stem} observed in TSF-3. TSF-2 consists of a lower proportion of bigger trees (Supporting Information: Figure S4), thus contributing to lower basal area (Table 1), which may result in lower biomass (Supporting Information: Figure S3) and lower productivity (Figure 2d).

Our study also detected a decline in diameter growth rates during the extreme drought period (2009–2010 census) across the studied forest plots, except TSF-3 (Figure 3a). In 2010, an extreme drought event occurred in Southwest China, leading to a significant reduction in vegetation growth (Li et al., 2019). The period after 2010, characterized by several extremely dry and hot years (Figures 1d–f), resulted in lower diameter growth rates compared to the pre-drought period, especially in primary and late successional secondary forest plots (Figure 3a). This suggests that early successional secondary forest plots (TSF-2 and TSF-3) can recover faster after drought than other plots. We also found that during the hot-dry year of 2010, both TSF-2 and TSF-3 showed higher relative mortality rates compared to other forest plots (Figure 3b), suggesting that trees in early successional forest types are more susceptible to drought. This susceptibility may result from the faster growth rate characteristic of TSF-2 and TSF-3, which is often associated with lower wood density trees, rendering them more vulnerable to drought conditions (Phillips et al., 2010). A uniform decline in

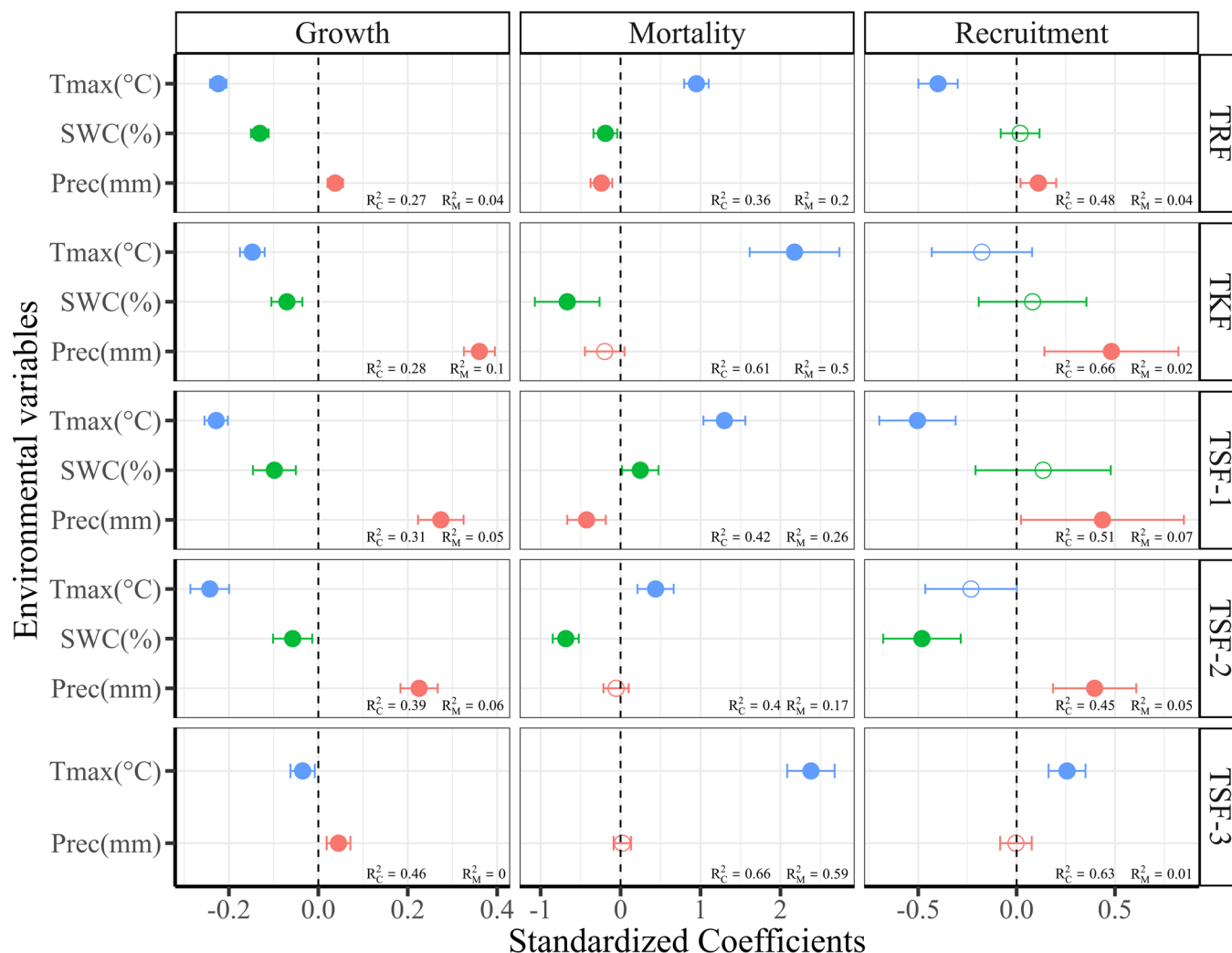


FIGURE 4 Standardized coefficients showing the effects of environmental variables on tree demography across five tropical forest plots. Solid and open circles indicate the relationship is statistically significant and nonsignificant, respectively. Error bars represent the standard error associated with each estimate at a 95% confidence interval. Note the difference in the x-axis scale for the different demographic processes. Prec, precipitation; SWC, soil water content; TKF, tropical karst forest; Tmax, maximum temperature; TRF, tropical rainforest; TSF, tropical secondary forest.

relative recruitment rates was observed during the hot-dry period of the 2009–2010 census (Figure 3c). Similarly, NPP_{stem} also declined during that hot-dry period across all forest plots, except TSF-2 (Figure 3d). Thus, the carbon sink of tropical forest ecosystems might be greatly impacted by climate warming and the increasing frequency of extreme drought events (Frank et al., 2015).

4.2 | Environmental influences on tropical tree demography and productivity

Our investigation revealed that diameter growth rates were negatively affected by Tmax and positively influenced by precipitation, indicating that the diameter growth rates among studied forest plots were primarily moisture-limited (Figure 4). This finding is consistent with other studies highlighting the adverse impact of high temperatures and drought on tropical forest growth (Altman et al., 2017; Hájek et al., 2021; Liang et al., 2023;

Walker & Johnstone, 2014; Zuidema et al., 2022), as well as the significant positive association between precipitation and tree growth (Brienen & Zuidema, 2005; Wagner et al., 2014). High temperatures pose a significant threat to plant growth primarily by inducing heat stress (Wahid et al., 2007), which can reduce growth rates by disrupting photosynthesis and elevating respiration rates (Bita & Gerats, 2013). Additionally, higher temperatures exacerbate water stress and impede nutrient uptake and metabolism (Krasensky & Jonak, 2012). We expect that the growth rate of trees in tropical forests is likely to decrease due to climate warming and frequent extreme drought. Indeed, our study showed a significant decline in the 16-year trend of diameter growth rates across our five forest plots (Supporting Information: Table S6). Therefore, assuming the continuation of current climate trends (Figure 1a–c), it is expected that the growth of tropical trees will decline in the coming years.

Furthermore, we found that Tmax is a substantial driver impacting tree mortality across all

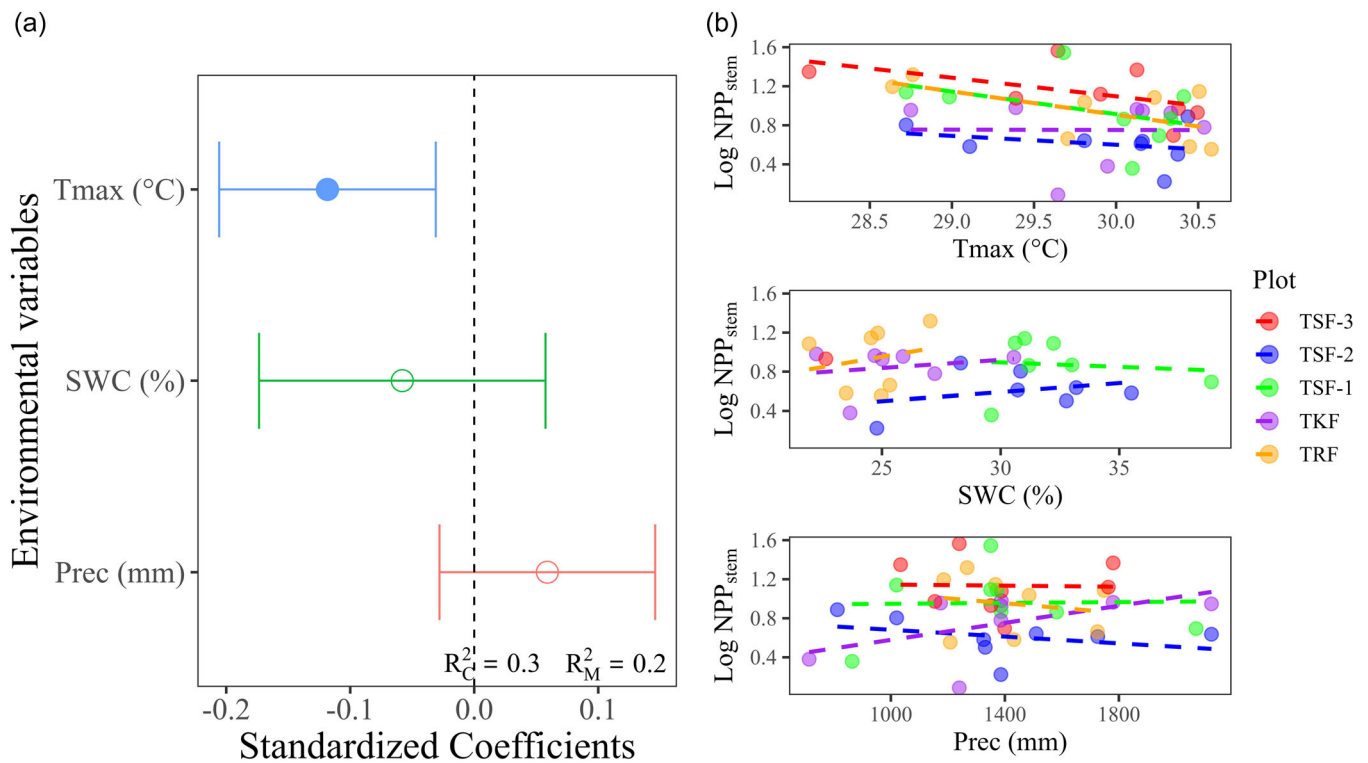


FIGURE 5 (a) Standardized coefficients showing the effects of environmental variables on log-transformed stem net primary productivity (NPP_{stem}). Error bars represent the standard error associated with each estimate at a 95% confidence interval. The filled (solid) and open circles in (a) indicate the relationship is statistically significant and nonsignificant, respectively; (b) Relationships between plot-level log-transformed NPP_{stem} and environmental variables for the period 2004–2020. The dashed lines in (b) indicated nonsignificant linear regression for each plot. TKF, tropical karst forest; TRF, tropical rainforest; TSF, tropical secondary forest.

studied plots (Figure 4). Previous studies found that rising temperatures lead to increased mortality rates in moist tropical forests (Adams et al., 2009; McDowell et al., 2018). Park Williams et al. (2013) and Vlam et al. (2014) further highlighted the negative effect of temperature on tree growth and forest vigor, supporting the link between high temperatures and tree mortality. These universal relationships underscore the importance of temperature dynamics in understanding and predicting tree mortality patterns. Additionally, precipitation showed a negative effect on tree mortality in TRF and TSF-1. Consistent with the effect of precipitation, SWC also showed a significant negative effect on tree mortality in TKF, TRF, and TSF-2 (Figure 4). These results align with previous studies indicating that the probability of mortality increases substantially with decreasing soil water availability (Caspersen & Kobe, 2001). However, TSF-1 exhibited a notable positive effect of SWC on tree mortality (Figure 4). This plot also had the highest soil water content among the five forest plots (Supporting Information: Figure S1), suggesting that soil water deficit might not be a limiting factor for tree mortality in this plot. Instead, the impact of Tmax on tree mortality is more evident (Figure 4). We anticipate a substantial rise in tree mortality within these forest plots in the future, with early successional secondary forests likely to experience the greatest impact.

The results revealed that higher precipitation can enhance the likelihood of tree recruitment in all forest plots except for TSF-3 (Figure 4). These findings are consistent with previous studies that emphasize the key role of precipitation in natural regeneration processes. For instance, precipitation has been shown to enhance seed availability and establishment (Vieira & Scariot, 2006), and increase species diversity (Rito et al., 2017). Furthermore, we observed a significant negative relationship between Tmax and tree recruitment in TRF and TSF-1 forest plots (Figure 4). Consistent with our results, previous studies also found that higher temperatures were associated with decreased growth and recruitment rates in tropical trees (Rehm & Feeley, 2015; Vlam et al., 2014). An unexpected positive relationship between Tmax and tree recruitment was observed in the TSF-3 plot (Figure 4). We propose that higher recruitment in TSF-3 is associated with its higher mortality driven by high T_{max} , which further increases recruitment due to more open canopy and higher light availability for understory seedlings. The results also revealed that SWC had an adverse effect on tree recruitment in TSF-2 (Figure 4). We suggest that relying solely on soil water content as an edaphic factor may not adequately to explain tree recruitment because the recruitment of tropical tree species may be more closely associated with soil nutrients rather than soil water content alone (Holste & Kobe, 2017). Generally, tree recruitment is

intricately tied to competitive interactions, seed dispersal mechanisms, soil nutrients, and light availability (Davis et al., 1999; Ibáñez & McCarthy-Neumann, 2014; Kraaij & Ward, 2006).

We observed a strong inverse relationship between T_{\max} and NPP_{stem} , highlighting temperature extremes as a critical issue for carbon sink capacity in the study area (Figure 5a). While Linger et al. (2020) observed a positive correlation between seasonal precipitation and NPP in tropical seasonal rainforests (TRF), our study did not detect a significant effect of precipitation on NPP_{stem} . This discrepancy could be attributed to the fact that our analysis did not account for seasonal differentiation, potentially weakening the signal of precipitation on NPP_{stem} . Pau et al. (2018) proved that Gross Primary Productivity (GPP) was highly sensitive to temperature, which might ultimately impact NPP through its effects on photosynthesis and respiration. Additionally, previous studies have reported temperature as a critical predictor for NPP (Churkina et al., 1999; Ouyang et al., 2014; Reich et al., 2014; Vilanova et al., 2018), which were consistent with our findings. Based on the observed climate changes within the study area (Figure 1a–c), we anticipate a reduction in the carbon sink capacity of tropical forests in the future. Early successional forests are expected to face greater risks due to higher mortality rates (Figure 2b), which will impact net primary productivity (Searle et al., 2022). Our study focused solely on NPP_{stem} and did not account for litterfall production. The carbon allocated to wood can be sustained longer than carbon allocated to leaves or reproductive tissues, thus making NPP_{stem} the most important component of total forest NPP (Carvalhais et al., 2014).

4.3 | Implications for forest conservation and restoration

The investigation revealed that T_{\max} exerts a substantial negative influence on tree growth and productivity, and a positive influence on tree mortality across five forest plots, with early successional forests exhibiting the highest susceptibility due to their higher mortality rates. Furthermore, secondary forest plots generally showed high carbon sink capacity (Figure 2d) and have great potential for biodiversity conservation, climate change mitigation, and landscape restoration (Poorter et al., 2021). We anticipate that the prevalence of frequent drought events and rising temperatures in the study area will exacerbate challenges, leading to reduced tree growth, decreased recruitment, and increased mortality, ultimately impacting carbon accumulation within forest ecosystems. We advocate for effective conservation strategies that prioritize enhancing ecosystem restoration in secondary forests through measures such as promoting climate-tolerant species diversity and restoring

natural hydrological regimes. These secondary forests are expanding rapidly in areas across the globe, driven by both anthropogenic activities and natural processes (Bongers et al., 2015). Leveraging the adaptive capacities of secondary forests while conserving the unique characteristics of primary forests is essential for fostering the restoration of forest landscapes amidst ongoing climate change.

5 | CONCLUSIONS

Our results revealed that secondary forests overall exhibited higher diameter growth rates and relative mortality rates compared to primary forests. The hot-dry event in 2009–2010 had an adverse impact on tropical forests in the study region, which led to higher mortality, reduced growth, recruitment, and NPP_{stem} . Specifically, early successional secondary forests experienced greater disturbance in terms of mortality. Moreover, the results demonstrated that maximum temperature had a significant negative effect on tree growth and NPP_{stem} , and a significant positive effect on mortality. Precipitation/moisture emerged as a key factor influencing tropical tree growth and recruitment. Consequently, the impacts of climate warming are expected to reduce tree growth and recruitment, thereby diminishing carbon sink capacity, and increasing tree mortality. This study provides valuable insights into the long-term demographic and productivity dynamics of tropical primary and secondary forests at different successional stages in Southwest China.

AUTHOR CONTRIBUTIONS

Sai Tun Tun Oo: Data curation; formal analysis; methodology; software; visualization; writing—original draft. **Shankar Panthi:** Formal analysis; methodology; software; writing—review & editing. **Ze-Xin Fan:** Supervision; writing—review & editing. **Xiao-Yang Song:** Formal analysis; writing—review & editing. **Huanyuan Zhang-Zheng:** Formal analysis; methodology; writing—review & editing. **Zaw Zaw:** Writing—review & editing. **Hua-Zheng Lu:** Data curation; writing—review & editing. **Hui Chen:** Data curation; writing—review & editing. **Yun Deng:** Data curation; writing—review & editing. **Rong Zhao:** Data curation; writing—review & editing. **Hua Lin:** Writing—review & editing. **Pei-Li Fu:** Conceptualization; supervision; writing—review & editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT


The data that support the findings of this study are available from the corresponding authors upon reasonable request.

ORCID

Sai Tun Tun Oo  <http://orcid.org/0009-0004-4576-1011>

Shankar Panthi  <http://orcid.org/0000-0002-3522-5555>

Ze-Xin Fan  <http://orcid.org/0000-0003-4623-6783>

Huanyuan Zhang-Zheng  <http://orcid.org/0000-0003-4801-8771>

Pei-Li Fu  <http://orcid.org/0000-0001-9092-284X>

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