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Effects of bamboo invasion on forest structures and diameter–height allometries

Ming Ouyang [a,b], Anwar Eziz [c], Shuli Xiao [a], Wenjing Fang [a], Qiong Cai [a], Suhui Ma [a], Jiangling Zhu [b], Qingpei Yang [d], Jinming Hu [a], Zhiyao Tang [b], Jingyun Fang [b,*]

[a] School of Ecology and Environmental Science, and Ministry of Education Key Laboratory for Transboundary Ecosecurity of Southwest, Yunnan University, Kunming, China

[b] Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

[c] State Key Laboratory of Desert and Oasis Ecology, Key Laboratory of Ecological Safety and Sustainable Development in Arid Lands, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China

[d] Jiangxi Provincial Key Laboratory for Bamboo Germplasm Resources and Utilization, and College of Forestry, Jiangxi Agricultural University, Nanchang, China

A R T I C L E I N F O

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A B S T R A C T

Forest structure is fundamental in determining ecosystem function, yet the impact of bamboo invasion on these structural characteristics remains unclear. We investigated 219 invasion transects at 41 sites across the distribution areas of Moso bamboo (*Phyllostachys edulis*) in China to explore the effects of bamboo invasion on forest structural attributes and diameter–height allometries by comparing paired plots of bamboo, mixed bamboo-tree, and non-bamboo forests along the transects. We found that bamboo invasion decreased the mean and maximum diameter at breast height, maximum height, and total basal area, but increased the mean height, stem density, and scaling exponent for stands. Bamboo also had a higher scaling exponent than tree, particularly in mixed forests, suggesting a greater allocation of biomass to height growth. As invasion intensity increased, bamboo allometry became more plastic and decreased significantly, whereas tree allometry was indirectly promoted by increasing stem density. Additionally, a humid climate may favour the scaling exponents for both bamboo and tree, with only minor contributions from topsoil moisture and nitrogen content. The inherent superiority of diameter–height allometry allows bamboo to outcompete tree and contributes to its invasive success. Our findings provide a theoretical basis for understanding the causes and consequences of bamboo invasion.

1. Introduction

Bamboos, species from the subfamily Bambusoideae of the grass family Poaceae, are known for their rapid growth and versatility (Liese and Köhl, 2015). They provide important non-timber forest products and cover approximately 50 million hectares worldwide (INBAR, 2024). The growing global bamboo industry supports 2.5 billion livelihoods and is projected to reach a value of $100 billion by 2025 (www.grandviewresearch.com/industry-analysis/bamboos-market). Despite their social and economic importance, bamboos also pose a significant threat to native ecosystems due to their invasive nature (Ouyang et al., 2022; Xu et al., 2020; Yang et al., 2015). Currently, bamboo invasion has been widely observed in Asia (e.g., China, Japan, and India), North America, South America (e.g., Brazil and Peru), and Africa (Luan et al., 2021; Ouyang et al., 2022; Pagad, 2016). The global invasion of bamboo is mainly related to their biological features, including rapid growth and strong rhizome systems (Xu et al., 2020; Yang et al., 2015). Monopodial ('running') bamboo species, particularly those belonging to the genus *Phyllostachys*, which are mostly found in subtropical and temperate regions, are highly invasive and responsible for the majority of severe invasion cases (Pagad, 2016).

Moso bamboo (*Phyllostachys edulis*) is a native, large-running bamboo species widely distributed in subtropical China, covering approximately 5.28 million hectares, which accounts for approximately 70% of all bamboo forests in the country (Feng and Li, 2023). The culm elongation stage of *P. edulis* lasts approximately 60 days, with a maximum growth rate of 166 cm·day^{-1} during the rapid growth phase (Ouyang, 2021). This bamboo species also shows extreme population overgrowth through

* Corresponding author. Department of Ecology, Peking University, Beijing, 100871, China.
E-mail address: jyfang@urban.pku.edu.cn (J. Fang).

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clonal recruitment by extensive rhizome systems (Ge et al., 2022). Due to its inherent superiority, *P. edulis* is known to be invasive and capable of invading adjacent communities, particularly derived forests (Okutomi et al., 1996). The invasion of *P. edulis* in both its native and introduced habitats has been widely reported in recent decades (Ouyang et al., 2022). This aggressive invasion has led to numerous negative ecological impacts on forest ecosystems, such as the inhibition of tree growth (Yang et al., 2015), loss of local biodiversity (Bai et al., 2013; Ouyang et al., 2016), reduction in ecosystem carbon stock (Yang et al., 2011), and disruption of nitrogen cycling (Song et al., 2017). However, the mechanisms underlying invasion-induced changes in ecosystem processes and functions remain poorly understood.

Forest structure refers to the spatial arrangement of various plant community components that sustain ecosystem functioning (McElhinny et al., 2005). Notably, complex and structurally diverse forests are essential for providing better ecosystem services than monoculture stands (Ali, 2019; Feng et al., 2022). Stand structure is commonly defined in terms of structural attributes and complexity (McElhinny et al., 2005). The appropriate set of structural attributes includes the mean and maximum individual size (diameter at breast height (DBH), height), stem density (density of individuals), and total basal area (TBA) of individuals (Chen et al., 2022; Fang et al., 2012a, 2012b). These measurements are used to capture the variety of structural and functional components that occur in forests. For example, mean DBH and TBA are indicative of stand volume and biomass and have been tested to characterise forest ecosystem dynamics (McElhinny et al., 2005). Plant invasion is an emerging driver of global change that can affect structural attributes by displacing native species and individuals within the community, potentially further influencing ecosystem function (Levine et al., 2003; Wiser et al., 1998).

The allometric relationship between DBH and height reflects the balance between vertical and lateral growth strategies that influence forest structure and dynamics (Liu et al., 2017). Allometry, characterised by the slope of the DBH (D) vs height (H) regression line on a log-log scale: $\log H \propto \alpha \log D$, where the scaling exponent (α) is typically different from 1 (McMahon, 1973; Niklas, 1995). The parameter α is of particular interest when investigating diameter–height allometry across forest types and species. First, the numerical values of α vary among plant species and life forms (Chen, 2018; Fang et al., 2020; O'Brien et al., 1995). Second, stand density can affect α primarily by altering the local light environment (Fang et al., 1993). In crowded conditions, trees are expected to allocate biomass preferentially to height growth over diameter growth (Henry and Aarssen, 1999; Uhl et al., 2015). Given that bamboo invasion often leads to an increase in stem density (Ouyang et al., 2016, 2022), it may indirectly influence plant allometry by increasing density. Third, the variation in α is partly explained by climate on a large scale (Fang et al., 2020; Liu et al., 2017; Xu et al., 2022). Trees typically exhibit vertical growth in humid areas but tend to grow radially in arid areas (Wang et al., 2006). Fourth, soil properties such as moisture and nitrogen content may affect the α-value among species by disproportionately altering plant diameter and height growth (Cramer, 2012; Chen et al., 2024).

Despite some plot studies exist (Ge et al., 2022; Okutomi et al., 1996), systematic assessments of forest structural dynamics and the interactive effects of invasion, climate, and soil on diameter–height allometry across broad spatial scales are limited. To fill this knowledge gap, we conducted a large-scale survey of invasion transects across bamboo forests in subtropical China. Specifically, we address the following two questions: (1) How do forest structural attributes respond to bamboo invasion? and (2) Which key factors drive these allometries at the stand and species level?

2. Materials and methods

2.1. Study region

We conducted field surveys during 2017–2018 at 41 sites in 13 provinces of China, spanning Fujian, Jiangxi, Zhejiang, Hunan, Anhui, Hubei, Henan, Jiangsu, Guangdong, Guangxi, Guizhou, Sichuan, and Yunnan. Our study region covered the major distribution areas of bamboo forests in China, extending from 22.26° to 31.86° N and 99.44°–121.25° E, with altitudes ranging from 85 to 2,038 m (Fig. S1). Mean annual temperature and precipitation range from 12.07 °C to 20.51 °C and from 982 to 2,059 mm, respectively.

2.2. Vegetation investigation

We established a paired invasion control system to assess the impact of bamboo invasion on the structural characteristics of forests. At each site, we selected more than three bamboo-invaded transects and established paired plots of bamboo forest (10 m × 10 m), mixed bamboo-tree forest (10 m × 15 m), and non-bamboo forest (10 m × 15 m) along the direction of bamboo invasion (Fig. S2).

Using classical community methods for vegetation surveys (Fang et al., 2009), we first recorded the latitude, longitude, elevation, aspect, slope, and canopy coverage for each invasion transect. Second, we measured the species name, DBH (breast height = 1.3 m), and height of all individual stems with a DBH ≥3 cm in the entire plot. Third, in the shrub and herb layers, we recorded the species name, mean coverage and height of the dominant plant species. Fourth, we collected five replicate topsoil samples from the 0–10 cm layer and mixed them to produce one sample for each plot.

We investigated 602 plots from 219 invaded bamboo-tree transects, of which 55 had only two paired stands. This included 201 bamboo, 218 mixed bamboo-tree, and 183 non-bamboo plots. The bamboo forest plots had an important value (IV) of bamboo greater than 75%. In each plot, the IV for bamboo was calculated using the TBA of bamboo as a percentage of the TBA.

2.3. Soil moisture and nitrogen measurements

The soil samples were air-dried to a constant weight, sieved (2 mm), and cleared of roots and stones. The moisture content of each sample was measured using the oven-drying method. Soil nitrogen content was determined using the Dumas combustion method and an elemental analyser (Elementar Vario EL III; Elementar, Hanau, Germany).

2.4. Climate data

Mean annual precipitation (MAP) data were obtained from WorldClim (http://www.worldclim.org). Mean annual potential evapotranspiration (PET) data were obtained from CGIAR (https://cgiarcsi.community/data/global-aridity-and-pet-database/) using the Hargreaves formula (Trabucco and Zomer, 2009). The wetness index (P/PET, the ratio of precipitation to potential evapotranspiration), derived from the ratio of MAP to PET, was used as a proxy variable to capture the combined influence of climate on allometry.

2.5. Statistical analyses

For each plot, we calculated the following structural variables: mean DBH (cm), maximum DBH, mean height (m), maximum height, stem density (stems·ha^{-1}), and TBA (m^2·ha^{-1}). We used reduced major axis (RMA) regression to estimate the scaling exponents of DBH vs height for stands and species (i.e., bamboo and tree) in a plot. The allometry was determined after log-transforming the data as follows: $\log H = \log \beta + \alpha \log D$, where α represents the scaling exponent.

One-way ANOVA and Tukey's HSD tests were performed to examine the significant differences in structural variables and stand scaling exponent (α_S) among forest types. A paired *t*-test was used to evaluate differences in the scaling exponent among species and paired plots. Ordinary least squares regression was employed to analyse the dependence of structural variables, α_S, and the scaling exponent for bamboo and tree

(α_B and α_T) on bamboo invasion intensity (IV of bamboo).

Structural equation modelling (SEM) was used to explore the effects of invasion intensity, climate (wetness index), and soil (moisture and nitrogen content) on α_B and α_T. SEM analysis was conducted using IBM SPSS Amos 21 (Amos Development Corporation, Wexford, PA, USA) and was based on the χ^2 test for non-significance ($P > 0.05$), a high comparative fit index (CFI > 0.85), and a low root mean square error approximation index (RMSEA < 0.05) to assess the goodness-of-fit of the model (Schermelleh-Engel et al., 2003). Statistical analyses and mapping were performed using R version 4.3.0.

3. Results

3.1. Effects of bamboo invasion on forest structures

The mean DBH, maximum DBH, maximum height, and TBA all decreased, while the mean height and stem density increased during bamboo invasion (Table 1). Mean DBH and maximum DBH decreased from 16.4 ± 4.3 and 35.8 ± 12.0 cm in the non-bamboo forest to 9.8 ± 1.4 and 13.7 ± 2.7 cm in the bamboo forest, respectively. The maximum height of the non-bamboo forest (19.6 ± 4.7 m) and mixed bamboo and tree forest (19.1 ± 3.2 m) was higher than that of the bamboo forest (17.0 ± 1.5 m). Mean TBA also decreased from 39.6 $m^2 \cdot ha^{-1}$ in the non-bamboo forest to 30.0 $m^2 \cdot ha^{-1}$ in the bamboo forest.

However, the mean height increased from 12.4 ± 2.7 m in the non-bamboo forest to 13.6 ± 1.8 m in the bamboo forest. The stem density of the bamboo forest was the largest (3,897 ± 1,558 ha^{-1}), followed by the mixed bamboo and tree forest (2,930 ± 1,128 ha^{-1}) and non-bamboo forest (1,609 ± 706 ha^{-1}).

Consistent with the above results, invasion intensity correlated negatively with mean DBH, maximum DBH, maximum height, and TBA, but positively with mean height and stem density (Fig. 1).

3.2. Effects of bamboo invasion on diameter–height relationships

At the stand level, the mean α_S value increased from 0.74 ± 0.23 in non-bamboo forests, to 0.81 ± 0.31 in mixed bamboo-tree forests, and then to 0.91 ± 0.27 in bamboo forests (Fig. 2; Table S1). For all plots, the α_S also increased with intensity of bamboo invasion (Fig. 2d).

While at the species level, the mean α value of bamboo was higher than that of tree (0.89 ± 0.22 vs 0.76 ± 0.23) (Fig. 3; Table S2). Moreover, invasion-induced changes in α differed among species. For bamboo, α_B decreased from 0.93 ± 0.24 in the mixed bamboo-tree forest to 0.85 ± 0.20 in the bamboo forest and was negatively correlated with invasion intensity. For tree, α_T was not significantly different between mixed bamboo-tree forest and non-bamboo forest (0.77 vs 0.74) but was positively correlated with invasion intensity.

3.3. Effects of bamboo invasion, climate, and soil on the diameter–height scaling

The SEM showed that α_B was negatively influenced by invasion intensity and soil nitrogen, and positively influenced by the wetness index and density (Fig. 4). Apart from the direct effect on α_B, bamboo invasion and the wetness index also impact α_B indirectly by affecting stem density and soil properties, respectively. Wetness index contributed the largest to the α_B value ($r_\partial = 0.35$, $P < 0.001$), followed by invasion intensity ($r_\partial = -0.25$, $P < 0.001$), soil nitrogen content, and density.

The α_T was directly promoted by stem density ($r_\partial = 0.22$, $P < 0.001$) and the wetness index ($r_\partial = 0.26$, $P < 0.001$). There was a strong positive relationship between bamboo invasion intensity and stem density, suggesting that invasion indirectly increased α_T values by increasing density.

Table 1
Overall statistics of structural measurements for stands across Moso bamboo invasion gradients.

Variable	Forest type	*n*	Mean	Range	SD
Mean DBH (cm)	Bamboos	201	9.8 c	6.9–12.2	1.4
	Mixed bamboo & Trees	218	11.9 b	8.1–16.9	2.4
	Non-bamboo	183	16.4 a	8.7–25.2	4.3
Maximum DBH (cm)	Bamboos	201	13.7 c	10.0–22.0	2.7
	Mixed bamboo & Trees	218	30.7 b	15.4–56.7	11.0
	Non-bamboo	183	35.8 a	19.1–63.9	12.0
Mean height (m)	Bamboos	201	13.6 a	10.4–16.7	1.8
	Mixed bamboo & Trees	218	13.0 b	9.3–16.9	1.9
	Non-bamboo	183	12.4 c	7.6–18.4	2.7
Maximum height (m)	Bamboos	201	17.0 b	14.0–20.0	1.5
	Mixed bamboo & Trees	218	19.1 a	15.0–26.0	3.2
	Non-bamboo	183	19.6 a	11.6–28.0	4.7
Stem density (ha^{-1})	Bamboos	201	3897 a	1600–7400	1558
	Mixed bamboo & Trees	218	2930 b	1281–5658	1128
	Non-bamboo	183	1609 c	580–3127	706
Total basal area ($m^2 \cdot ha^{-1}$)	Bamboos	201	30.0 b	10.6–53.3	12.0
	Mixed bamboo & Trees	218	39.1 a	15.4–72.4	15.3
	Non-bamboo	183	39.6 a	14.1–73.3	16.7

Notes: *n*, number of plots; SD, standard deviation. The range of each variable is calculated as its 2.5% and 97.5% quantiles. Lowercase letters indicate significant differences among forest types based on ANOVA and Tukey's HSD tests ($P < 0.05$).

4. Discussion

4.1. Bamboo invasion altered forest structures

Our results showed that bamboo invasion decreased the mean and maximum DBH, as well as the maximum height (Table 1; Fig. 1a, b, d). Bamboo culms do not increase in diameter with age because there is no significant accumulation of secondary tissue. New culms can grow up to 20 cm in diameter and over 20 m in height through clonal reproduction (Wang and Chris, 2006). The individual sizes of most young or mature trees far exceed the growth limits of individual bamboo plants. Consequently, bamboo invasion leads to tree mortality, particularly of larger trees (Ouyang et al., 2016), reducing the mean and maximum DBH and maximum height of the stands.

Interestingly, bamboo invasion increased the mean stand height (Table 1; Fig. 1c), which contrasts with the common perception that bamboo forests are typically shorter than non-bamboo tree forests. In the subtropical forests of China, particularly in evergreen broadleaf forests, extensive areas of primary forests have degraded into secondary forests (Ren et al., 2007; Song et al., 2005). In our study, the mean DBH and height in non-bamboo forest plots were 16.4 ± 4.3 cm and 12.4 ± 2.7 m, respectively (Table 1). Considering the relationship between DBH and the age of subtropical tree species, these secondary forests are estimated to be approximately 30–50 years old (Chi et al., 2017; Xing et al., 2012). Therefore, bamboo forests are taller than most adjacent secondary forests, which enhances their ability to effectively compete for light. This may explain why bamboo rarely invades primary forests, while evergreen broadleaf forests are the zonal vegetation in the subtropics in terms of progressive succession.

Although bamboo invasion increased stem density, it reduced TBA (Fig. 1e and f; Table 1). The invasion of bamboo into neighbouring forests displaces trees over time and eventually establishes dominance within

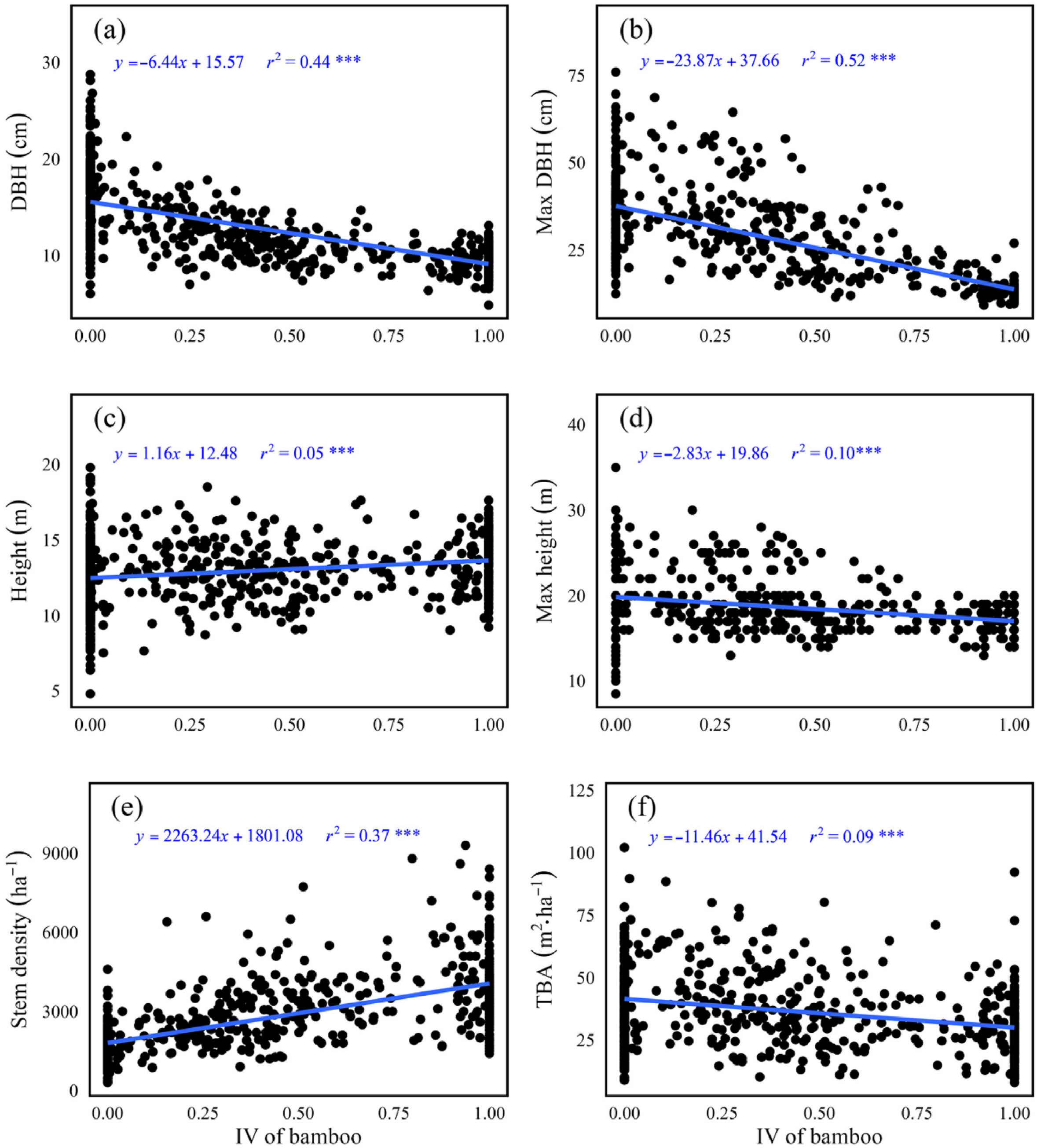

Fig. 1. Relationship between bamboo invasion intensity and structural measurements. Mean DBH **(a)**, maximum DBH **(b)**, mean height **(c)**, maximum height **(d)**, stem density **(e)** and total basal area (TBA, **f**). IV, important value.

the community. This phenomenon has direct consequences, including an increase in the number of individual culms and a decrease in the number of individual trees. Meanwhile, because culm diameters are generally smaller than those of trees, TBA gradually declines with increasing bamboo invasion intensity. Our findings are also supported by plot studies on other bamboo species. For instance, following the invasion of *Guadua sarcocarpa*, tree density decreased from 616 to 83 stems·ha^{-1}, and tree TBA decreased from 37.9 to 4.8 m^2·ha^{-1} (Griscom and Ashton, 2006).

The transformation of forest structure measurements above, owing to bamboo invasion, can be attributed to the phenotypic differences between bamboo and tree. Bamboo, characterised by a smaller size compared to mature individual trees (Liese and Köhl, 2015), influences forest structural attributes differently. Our findings indicate that bamboo predominantly invades secondary forests and rapidly alters their structural characteristics across subtropical China.

4.2. Bamboo invasion increased the scaling exponents of stand diameter vs height

Our data indicate that the scaling exponent of DBH with respect to height for stands (α_S) increased during bamboo invasion (Fig. 2; Table S1). This can be attributed to allometric differences between bamboo and tree. For example, despite significant within-species variation in exponents, bamboo consistently exhibited a higher mean exponent compared to tree across subtropical regions (0.89 vs 0.76) (Fig. 3a and c; Table S2). These results suggest that bamboo achieves greater vertical growth per unit increase in diameter than trees, thereby enhancing its competitive ability through morphological plasticity. Unlike trees, bamboo regulates its diameter–height growth strategy by

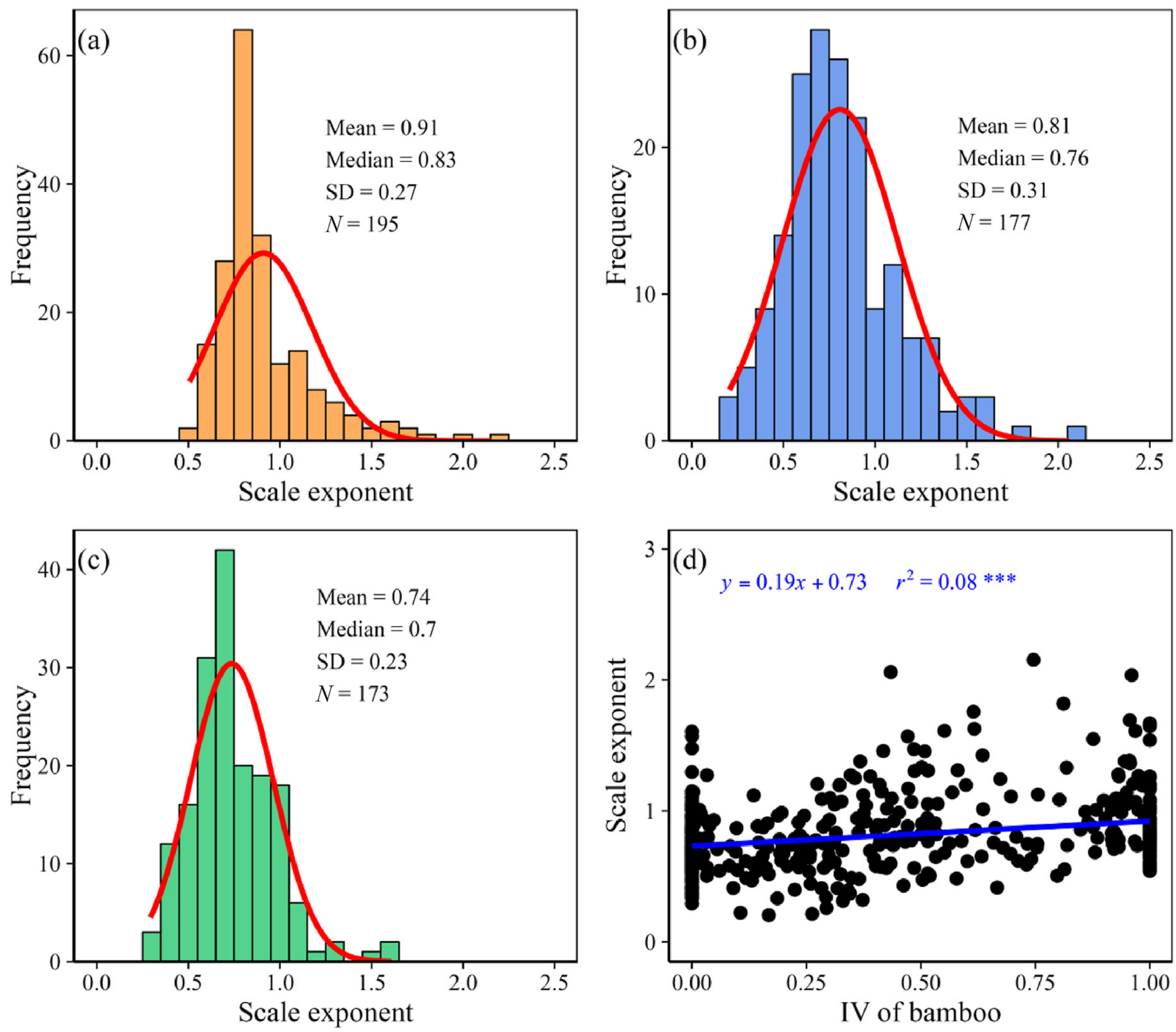

Fig. 2. Effect of bamboo invasion on the scaling exponent (α_S) of DBH–height allometry for the stand. Frequency distribution of the scaling exponents in the bamboo forest **(a)**, mixed bamboo-tree forest **(b)**, and non-bamboo forest **(c)**; Relationship between the scaling exponents and bamboo invasion intensity from all plots **(d)**. IV, important value. All regression slopes were significant ($P < 0.05$).

producing new culms each year (Liese and Köhl, 2015), continuously contributing to its successful invasion into forest ecosystems.

Biomechanical models predict that tree height should scale as 1/2, 2/3, or 1 power of stem diameter (King and Loucks, 1978; McMahon, 1973; McMahon and Kronauer, 1976). However, numerous studies indicate that no universal constant exponent for height at the stand scale (Chen, 2018; Fang et al., 2020; Pretzsch et al., 2013). First, the scaling exponent differs among forest types: it was highest in bamboo forests (0.91; Fig. 2a), followed by temperate coniferous forests (0.86) (Fang et al., 2020), mixed bamboo and tree forests (0.81; Fig. 2b), subtropical non-bamboo forests (0.74; Fig. 2c), and tropical lowland rainforests (0.66) (King et al., 2009). Second, the scaling exponent depends on forest development. Niklas (1995) found the exponent was greater than 1 for small and young trees, which decreased to 2/3 and then 1/2 as the size and age of *Robinia pseudoacacia* increased. Subsequent more evidence suggests that the scaling exponent gradually decreases during plant development (Henry and Aarssen, 1999; Sterck and Bongers, 1998; Zhang et al., 2020). Some ecologists argued growth and hydraulic constraints, rather than mechanical constraints, govern plant size-dependent allometry (Niklas and Spatz, 2004). This variation may also stem from the life-history optimisation of diameter–height growth trajectories (Hulshof et al., 2015; McMahon, 1973; Niklas, 1995).

4.3. *Drivers of the diameter vs height scaling exponents for bamboo and tree*

Although bamboo invasion increased α_B through an indirect high-density effect, the direct contribution of bamboo intensity to α_B surpassed that of stand density, resulting in an apparent negative relationship between bamboo invasion and α_B (Figs. 3b and 4). The decrease in α_B can be attributed to changes in the bamboo diameter–height growth strategy during invasion. For instance, the mean α_B of the mixed bamboo and tree forest was 0.93 ± 0.24, which is higher than that of the bamboo forest (0.85 ± 0.20) (Table S2). This suggests that invading bamboo tends to have greater culm height than post-invasion bamboo of the same diameter. Our findings are consistent with the universal understanding that bamboos may possess a competitive advantage over trees owing to their greater phenotypic plasticity (Shi et al., 2014; Yang et al., 2015).

Generally, α_T values are positively correlated with stand density, aligning with what are arguably traditional ecological expectations (Henry and Aarssen, 1999; Zhang et al., 2019). In sparse conditions, trees tend to allocate more biomass to diameter growth rather than height growth (Zhang et al., 2019). Conversely, in closed-canopy stands, trees often grow taller than open-grown trees of the same diameter, a phenomenon commonly observed in forest surveys (Xu et al., 2019; Wu et al., 2015). Nevertheless, bamboo invasion contributed relatively little to the increase in α_T (Fig. 3d and 4), because there was no significant difference

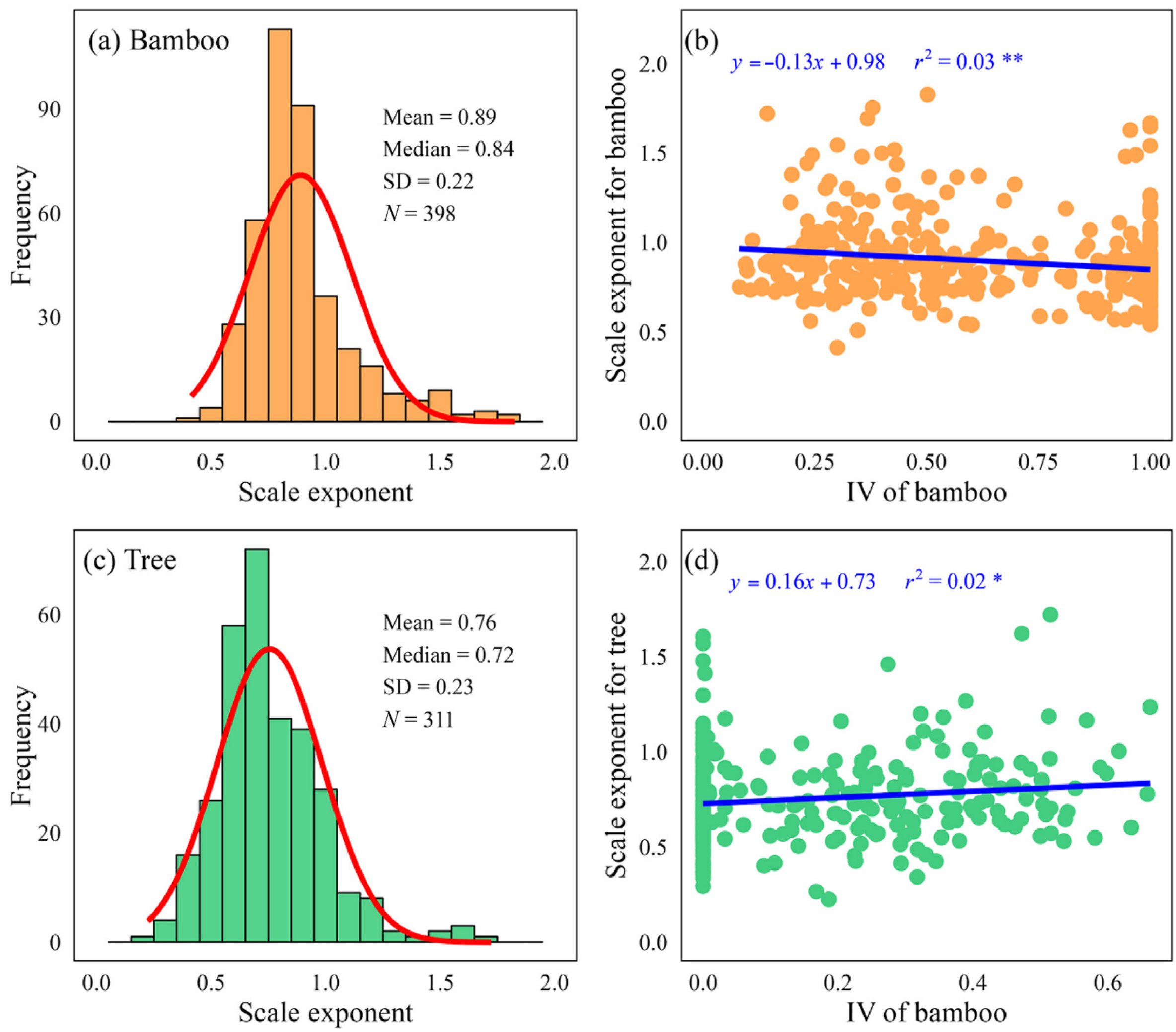

Fig. 3. Influence of bamboo invasion on the scaling exponent (α) of DBH–height allometry for species. Frequency distribution of the scaling exponents for bamboo **(a)** and tree **(c)**; Relationship between bamboo invasion intensity and the scaling exponents of bamboo **(b)** and tree **(d)**. IV, important value. All regression slopes were significant ($P < 0.05$).

in α_T between mixed bamboo-tree forest and non-bamboo forest (0.77 vs 0.74) (Table S2). Additionally, bamboo had a greater mean exponent than that of trees in the mixed bamboo and tree forest (0.93 vs 0.77) (Table S2), indicating that a greater proportion of biomass was allocated to height growth. Collectively, the plasticity in diameter–height allometry is a major cause of bamboo invasion into adjacent forests.

In addition to the impact of bamboo invasion on species-specific scaling exponents, a high wetness index was found to directly promote both α_B and α_T (Fig. 4). Trees are known to increase their height (for a given diameter) under warm and humid conditions (Fang et al., 2020; Hulshof et al., 2015). Li et al. (2011) demonstrated a positive correlation between MAP and potential tree height in temperate coniferous forests. Tao et al. (2016) found forest canopy height exhibited a hump-shaped curve with water availability: it initially increased, then peaked at approximately 680 mm of P−PET, and finally declined. In contrast to our finding, Liu et al. (2017) observed no significant effect of MAP on the α_T values of larch forests in China, possibly due to relatively favourable water conditions. Therefore, the relationship between diameter–height allometry and water availability depends largely on water constraints. Our finding suggests that plants in subtropical forests are limited by water availability and tend to grow stouter under future drought conditions.

Furthermore, the wetness index indirectly influences α_B by affecting soil moisture and nitrogen content but does not indirectly affect α_T (Fig. 4). This difference may be attributed to the high morphological plasticity of bamboo, which renders its allometry more sensitive to variations in soil characteristics (Shi et al., 2014). The negative correlation between soil nitrogen content and α_B indicates that bamboo likely allocates more culm biomass to diameter growth than to height growth at nitrogen-rich sites. However, the contribution of soil properties to this allocation pattern is relatively minor.

5. Conclusions

We quantified patterns of forest structure and identified the underlying drivers of bamboo and tree allometry in response to bamboo invasion across subtropical forests in China. Our data show that invasion gradients significantly alter stand structural characteristics and interact with climatic and soil factors to modulate these allometries. Generally, invasion led to reductions in mean and maximum DBH, maximum height, and TBA, alongside elevations in mean height, stem density, and scaling exponent of the stand. Bamboo also exhibited a higher mean scaling exponent than that of tree, indicating a competitive advantage for light. Importantly, the direction and magnitude of the effect of bamboo invasion on allometry varied between bamboo and tree. Invasion significantly reduced the scaling exponent of bamboo, but indirectly increased the scaling exponent of tree by increasing stem density. A high wetness index promoted the scaling exponents for both bamboo and tree, with only

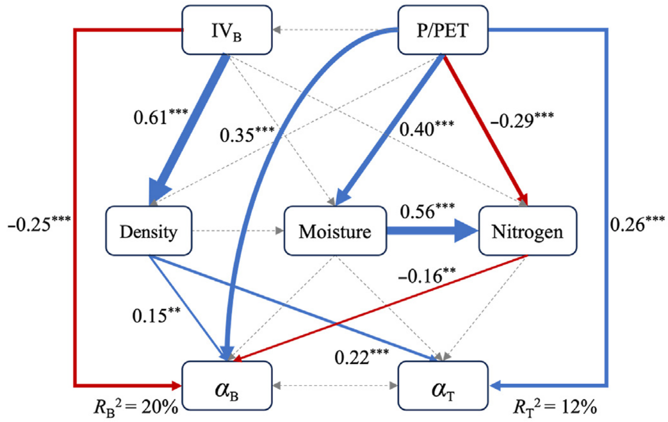

Fig. 4. Combined effects of bamboo invasion, climate, and soil on the scaling exponents of DBH–height allometries for bamboo and tree. Blue and red arrows indicate significant positive and negative correlations, respectively; the arrow width indicates the strength of the relationship. The numbers adjacent to the arrows are the standardized path coefficients indicating the effect size of the relationship. IV_B: important value of bamboo; P/PET: wetness index (the ratio of precipitation to potential evapotranspiration); α_B: the scaling exponent for bamboo from plots; α_T: the scaling exponent for tree from plots. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; grey dashed arrows indicate non-significant relationships ($P > 0.05$). R_B^2 and R_T^2 denote the proportions of variance explained by the response variables α_B and α_T, respectively. Statistics on model goodness-of-fit are shown directly below (χ^2, df-degrees of freedom, P values, CFI-comparative fit index, and RMSEA-root-mean-square error of the fit index). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

minor contributions from topsoil water and N content. Our findings suggest that the inherent superiority of bamboo diameter–height allometry may play a pivotal role in its successful invasion of secondary forests. Given that the community structure controls ecosystem functioning, future studies need to determine the consequences of bamboo invasion from a structure–function perspective.

Data availability

Data will be made available on request.

CRediT authorship contribution statement

Ming Ouyang: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anwar Eziz:** Writing – review & editing, Visualization. **Shuli Xiao:** Writing – review & editing, Validation. **Wenjing Fang:** Writing – review & editing, Project administration. **Qiong Cai:** Writing – review & editing. **Suhui Ma:** Writing – review & editing. **Jiangling Zhu:** Supervision, Project administration. **Qingpei Yang:** Writing – review & editing. **Jinming Hu:** Writing – review & editing. **Zhiyao Tang:** Writing – review & editing. **Jingyun Fang:** Writing – review & editing, Validation, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100256.

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