

# Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests

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## Funding information

China Postdoctoral Science Foundation, Grant/Award Number: 2018M643117; Wildlife Protection Bureau; Nature Reserves, Forest Farms, and Forest Bureaus

## Abstract

Large-diameter, tall-stature, and big-crown trees are the main stand structures of forests, generally contributing a large fraction of aboveground biomass, and hence play an important role in climate change mitigation strategies. Here, we hypothesized that the effects of large-diameter, tall-stature, and big-crown trees overrule the effects of species richness and remaining trees attributes on aboveground biomass in tropical forests (i.e., we term the “big-sized trees hypothesis”). Specifically, we assessed the importance of: (a) the “top 1% big-sized trees effect” relative to species richness; (b) the “99% remaining trees effect” relative to species richness; and (c) the “top 1% big-sized trees effect” relative to the “99% remaining trees effect” and species richness on aboveground biomass. Using environmental factor and forest inventory datasets from 712 tropical forest plots in Hainan Island of southern China, we tested several structural equation models for disentangling the relative effects of big-sized trees, remaining trees attributes, and species richness on aboveground biomass, while considering for the full (indirect effects only) and partial (direct and indirect effects) mediation effects of climatic and soil conditions, as well as interactions between species richness and trees attributes. We found that top 1% big-sized trees attributes strongly increased aboveground biomass (i.e., explained 55%–70% of the accounted variation) compared to species richness (2%–18%) and 99% remaining trees attributes (6%–10%). In addition, species richness increased aboveground biomass indirectly via increasing big-sized trees but via decreasing remaining trees. Hence, we show that the “big-sized trees effect” overrides the effects of remaining trees attributes and species richness on aboveground biomass in tropical forests. This study also indicates that big-sized trees may be more susceptible to atmospheric drought. We argue that the effects of big-sized trees on species richness and aboveground biomass should be tested for better understanding of the ecological mechanisms underlying forest functioning.

## KEYWORDS

big-crown trees, biodiversity, climate change, large-diameter trees, medium- and small-sized trees, soil fertility, tall-stature trees

## 1 | INTRODUCTION

Forests are major components of the global carbon cycle (Pan et al., 2011). Among them, tropical forests store 25% of global carbon but hold 34% of terrestrial primary productivity and harbor 96% of the world's tree species (Bonan, 2008; Poorter et al., 2015), and hence play an important role in climate change mitigation strategies (Boisvenue & Running, 2006). Across the globe, big-sized trees constitute a huge quantity (approximately 50%) of aboveground biomass in natural forests, thereby holding much stronger abiotic and biotic controls on forest carbon sequestration and stock (Bastin et al., 2015; Lutz et al., 2018; Stephenson et al., 2014). The contribution of a few large-diameter trees to forest diversity, structure, and functioning cannot be ignored, because big-sized trees relative to medium- and small-sized trees take many years, decades, or even centuries to occupy the canopy of the forests (Ali, Lohbeck, & Yan, 2018; Bastin et al., 2018; Lindenmayer & Laurance, 2017; Lutz et al., 2018; Slik et al., 2013). Yet, despite advances in our understanding of global consequences of large-diameter trees to aboveground biomass (Lutz et al., 2018), no strong consensus exists about the importance of big-sized trees attributes relative to species diversity and remaining trees attributes on aboveground biomass at the community level along large-scale natural forests.

The importance of big-sized trees is well addressed for forest structure, diversity, and functioning (Bastin et al., 2018; Lutz et al., 2018; Slik et al., 2013). For example, in forest ecosystems, big-sized trees relative to remaining (medium- and small-sized) trees contain a large portion of the aboveground biomass (Bastin et al., 2015), which in turn influence stand-level leaf area, understory diversity and functions, microclimate, and water use (Lutz et al., 2018; Martin et al., 2001; Stephenson et al., 2014; Yuan et al., 2012). Furthermore, big-sized trees limit light, water, and soil nutrients available to remaining trees, and hence a major driver of species diversity and biomass dynamic processes of remaining trees in natural forests (Ali, Lohbeck, et al., 2018; Messier, Parent, & Bergeron, 1998; Yuan et al., 2012). Surprisingly, the effect of big-sized trees is not clearly tested on diversity–structure–biomass relationships in forest ecosystems (e.g., Ali et al., 2019a; Ali, Lohbeck, et al., 2018; Paquette & Messier, 2011; Poorter et al., 2017). Yet, the following four main research aspects are crucial to advance our understanding in this research field: (a) effect of big-sized trees relative to species richness on aboveground biomass; (b) considering the effects of multiple attributes of big-sized trees (e.g., large-diameter, tall-stature, and big-crown trees); (c) full (indirect effects only) and partial (direct and indirect effects) mediation effects of climatic and soil conditions on aboveground biomass via big-sized trees attributes and species richness; and (d) additional evidence for the combined and independent effects of big-sized trees attributes relative to remaining trees attributes and species richness on aboveground biomass (see Figure 1 for conceptual models).

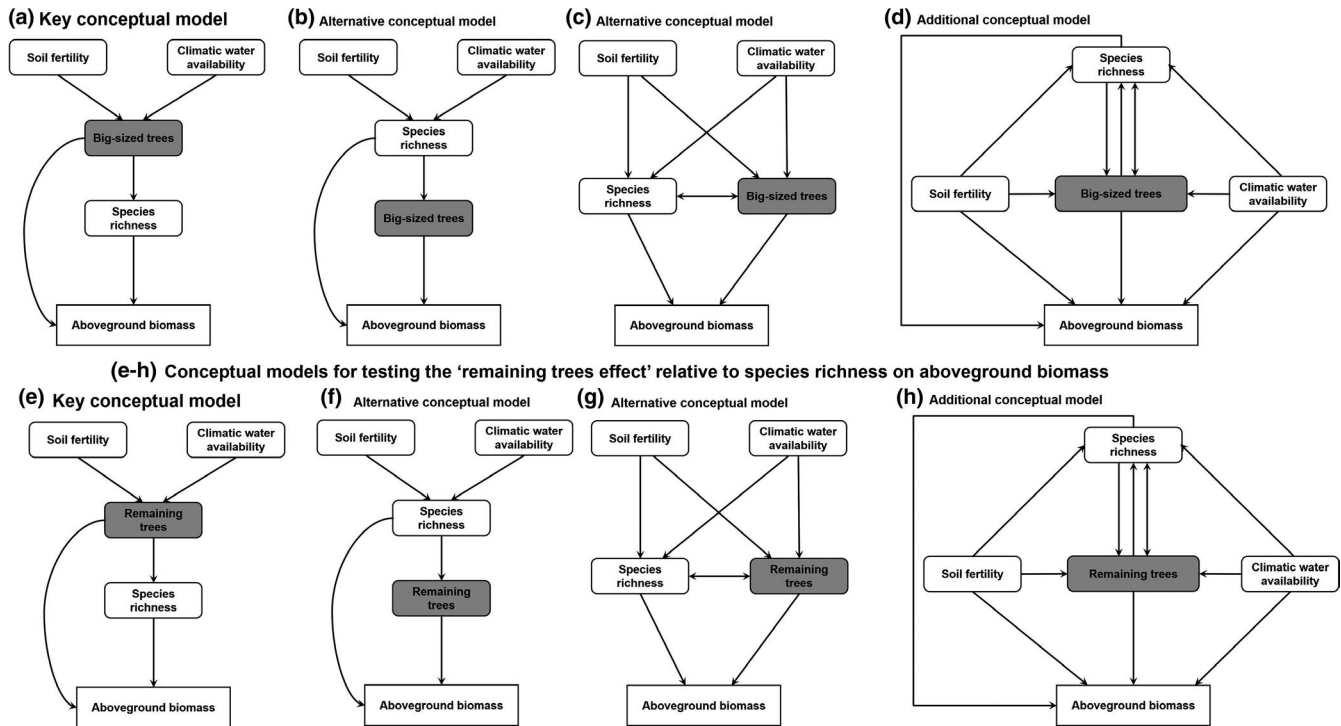
In tropical forests, stand-level aboveground biomass can be predicted from a few big-sized trees (Slik et al., 2013), and more specifically from 20 large-diameter trees per hectare (Bastin et al., 2018),

and top 5% (Bastin et al., 2015) and top 1% large-diameter trees (Lutz et al., 2018). From an ecological theoretical point of view, vegetation quantity (i.e., initial biomass stocks) compared to vegetation quality (i.e., species diversity, functional trait diversity, and trait composition) has a strong positive effect on productivity in natural forests (i.e., the “vegetation quantity hypothesis”) because steep biomass build-up during succession overrides more subtle effects of species diversity on forest functioning. (Lohbeck, Poorter, Martinez-Ramos, & Bongers, 2015; Yuan et al., 2018). Moreover, stand basal area compared to functional trait diversity promotes productivity (Paquette & Messier, 2011), and as such, the response of aboveground biomass productivity to species richness is largely mediated by stand basal area in natural forests (Vilà et al., 2013). Similarly, aboveground biomass is more strongly explained by functional dominance (i.e., community-weighted mean of maximum tree height or diameter) in tropical forests compared to functional trait diversity, probably due to the niche overlap or functional redundancy effect of the canopy trees (Cavanaugh et al., 2014; Prado-Junior et al., 2016). In this understanding, the overruling effects of stand basal area, stand density, functional dominance, and initial biomass stock on forest functioning might be attributable to the fact that top 1%–20% large-diameter trees largely explain variation in aboveground biomass at local, regional, continental, and global scales (Ali, Lohbeck, et al., 2018; Bastin et al., 2018; Lutz et al., 2018; Malhi et al., 2006; Slik et al., 2013). However, the relative contribution of big-sized trees to the stand-level aboveground biomass varies among the regions of tropical forests (Feldpausch et al., 2012), probably due to the fact that all species or individuals are not capable of reaching large-diameter threshold (e.g., diameter  $\geq$  60 cm) in many tropical forest sites (Lutz et al., 2018). In this context, we focus on the importance of top 1% large-diameter, tall-stature, and big-crown trees to aboveground biomass, proposing that few (i.e., top 1%) big-sized trees matter for explaining aboveground biomass compared to species richness and 99% remaining trees attributes of the tropical forests.

In natural forests, previous studies have suggested to include the direct and indirect effects of abiotic factors on forest diversity, structure, and functioning (Paquette & Messier, 2011; Poorter et al., 2017; Yuan et al., 2019), as well as interactions between forest diversity and structure (Ali et al., 2016). For example, climatic and soil conditions can affect forest functioning directly or indirectly via forest diversity and structure under the assumptions of several abiotic-based hypotheses or theories (Ali et al., 2019a; Condit, Engelbrecht, Pino, Pérez, & Turner, 2013; Poorter et al., 2017). The big-sized trees may suffer more than medium- and small-sized trees from climate change (e.g., a decrease in climatic water availability with an increase in temperature), because big-sized trees are directly exposed to solar radiations, wind pressure, temperature variation, and atmospheric drought (Allen et al., 2010; Bennett, Mcdowell, Allen, & Anderson-Teixeira, 2015). However, big-sized trees may impose competitive constraints on medium- to small-sized trees due to their overruling effect on soil nutrients (Ali, Lohbeck, et al., 2018; Paoli & Curran, 2007). Therefore, climatic and soil conditions might control the stand structural complexity, which in turn might maintain species

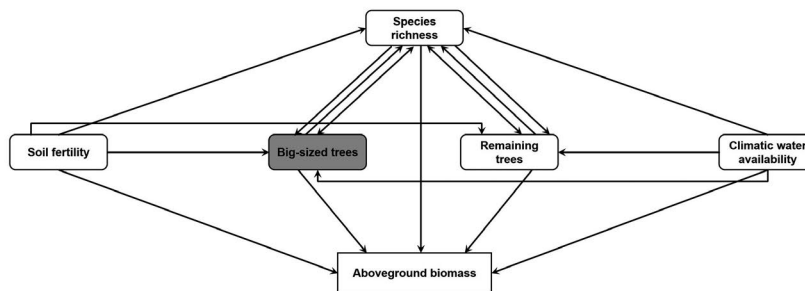
## FULL MEDIATION EFFECTS OF CLIMATIC AND SOIL CONDITIONS

(a–d) Conceptual models for testing the ‘big-sized trees effect’ relative to species richness on aboveground biomass



## PARTIAL MEDIATION EFFECTS OF CLIMATIC AND SOIL CONDITIONS

(i) Integrative conceptual model for testing the relative effects of big-sized trees, remaining trees and species richness on aboveground biomass



**FIGURE 1** Conceptual models for testing the importance of the “big-sized trees effect” relative to the effect of species richness on aboveground biomass (a–d); the “remaining trees effect” relative to the effect of species richness on aboveground biomass (e–h); and the relative importance of the “big-sized trees effect,” “remaining trees effect,” and species richness effect on aboveground biomass in tropical forests (i). In case of additional conceptual models (d and h) and integrative model (i), three models were tested using three different directions ( $\rightarrow$ ,  $\leftarrow$ , and  $\leftrightarrow$ ) of the relationship between species richness and with each of big-sized trees and remaining trees attributes

coexistence via plant–plant interactions in natural forests (Ali et al., 2019a; Yachi & Loreau, 2007). In this case, both big-sized trees attributes and species richness could influence aboveground biomass through their interactions or feedbacks along large-scale climatic and soil gradients (Figure 1).

In this study, we were particularly interested to test the “big-sized trees effect” relative to the effect of species richness on aboveground biomass while accounting for the full (see Figure 1a–c) and partial mediation (see Figure 1d) effects of climatic and soil conditions, as well as interactions between big-sized trees attributes and species richness, in natural tropical forests. Here, in addition to other variable (Figure 1), we use three attributes of the big-sized trees (i.e., top 1%

large-diameter, tall-stature, and big-crown) that control some of the main changes in aboveground biomass and nutrients over time and space (Bastin et al., 2018; Chave et al., 2014; Goodman, Phillips, & Baker, 2014; Lutz et al., 2018). Based on the hypothesized paths in the key conceptual model for the “big-sized trees effect” (Figure 1a), we address the following specific research questions. (a) How do big-sized trees affect aboveground biomass directly and indirectly via species richness? (b) How do climatic and soil conditions affect big-sized trees directly? We hypothesize that the effects of large-diameter, tall-stature, and big-crown trees overrule the effect of species richness on aboveground biomass in tropical forests (i.e., we term the “big-sized trees hypothesis”). We expect that: (a) big-sized trees promote species

richness directly; (b) climatic water availability and soil fertility promote big-sized trees directly; and (c) climatic water availability and soil fertility promote aboveground biomass indirectly via big-sized trees. In the alternative conceptual models for the “big-sized trees effect” (Figure 1b,c), we expect that: (a) big-sized trees link positive species richness and aboveground biomass, after considering for the direct effects of climatic and soil conditions on species richness only; and (b) both big-sized trees and species richness provide positive feedback for driving higher aboveground biomass, after considering for the direct effects of climatic and soil conditions on both of them. In the additional conceptual models (Figure 1d), we expect that the importance of the “big-sized trees effect” on aboveground biomass will not be changed when considering the partial mediation effects of climatic and soil conditions on species richness, big-sized trees, and aboveground biomass.

Despite our efforts for evaluating the “big-sized trees effect,” uncertainties regarding the remaining trees (i.e., the remaining 99% diameter, height, and crown area within a pot) still exist. Therefore, after providing a specific test for the “big-sized trees hypothesis,” we were then parallelly interested to clarify whether the “remaining trees effect” overrules the effect of species richness on aboveground biomass when the “big-sized trees effect” is excluded (Figure 1e–h). We hypothesize that the variations in remaining trees attributes and species richness promote aboveground biomass (i.e., we term “the remaining trees hypothesis”) through several underlying ecological mechanisms. For example, this “remaining trees hypothesis” may explain the diversity–biomass relationship under the predictions of the niche complementarity and tree crown complementarity effects, given that a variety of remaining species (i.e., 99% in our study) might have different niches and therefore they would be able to utilize the available resources more efficiently or facilitate each other, thus promoting aboveground biomass (Ali et al., 2019b; Lohbeck et al., 2015; Poorter et al., 2015; Yachi & Loreau, 2007). However, high biomass and species-rich forests may exclude weak competitors, which may lead to the negative relationships among remaining trees attributes, species richness, and aboveground biomass (i.e., the competitive exclusion effect; Ali et al., 2019a; Carroll, Cardinale, & Nisbet, 2011). As such, a by-chance inclusion of high functioning species in a species-rich community may also lead to high productivity (i.e., the selection effect; Cavanaugh et al., 2014; Lohbeck et al., 2015; Poorter et al., 2015). In this context, we were finally interested to clarify the confounding role of the “remaining trees effect” on aboveground biomass by providing additional evidence based on single integrative modeling (see Figure 1i). Here, we extend the “big-sized trees hypothesis” by proposing that the effects of large-diameter, tall-stature, and big-crown trees overrule the effects of remaining trees attributes and species richness on aboveground biomass in tropical forests.

## 2 | MATERIALS AND METHODS

### 2.1 | Available datasets

In this study, we used forest inventory and environmental factor datasets, which were collected in large-scale tropical forests covering an

environmental zone from 18°10′–20°10′N in latitude and 108°37′–111°03′E in longitude, at 1 to 1,819 m above sea level (Figure S1 in Appendix A), in Hainan Island of southern China (Ali, Lin, et al., 2018; Ali et al., 2019b). Across studied plots, mean annual precipitation ranged from 1,008 to 2,038 mm, mean annual temperature from 17 to 25°C, mean annual potential evapotranspiration from 1,125 to 1,451 mm, elevation from 1 to 1,819 m a.s.l., and the soil total exchangeable bases (TEBs) from 2.2 to 28.5 cmol/kg. The soils are classified as Acrisols, Arenosols, Alisols, Andosols, Anthrosols, Cambisols, Fluvisols, Ferralsols, Leptosols, Regosols, Nitisols, and Solonchaks in the Harmonized World Soil Database (FAO et al., 2012).

Forest inventory was conducted during April 2009–August 2017, where tree diameter at breast height (DBH), height, and crown dimensions (i.e., X–width from east to west direction and Y–width from north to south direction) for all individual trees (187,748 stems) having DBH  $\geq$  3 cm were measured or assessed across 712 plots. For the identification of species in Latin names, Chinese Flora Database (<http://foc.eflora.cn/>) was used. As recommended by previous studies (Cornelissen et al., 2003; Pakeman & Quested, 2007), we covered and identified 75%–95% of the most of the abundant and dominant species of the total community (i.e., plot) coverage across 712 forest plots, based on both the species’ relative frequency and relative basal area within each plot. The average plot size was 0.16 ha, that is, 1,600 m<sup>2</sup> (a total sampling area of 115.68 ha across 712 plots; Ali, Lin, et al., 2018; Ali et al., 2019a, 2019b).

The natural forests in the study area represent both second-growth and old-growth forests, where most of the second-growth forests are originated naturally and being protected from human intrusions for more than four decades (Ali, Lin, et al., 2018; Lin et al., 2017). Prior to the 1950s, the area occupied by forests on Hainan Island was largely natural, whereas the nonforested area was mainly farmland. However, natural forests had been subjected to both anthropogenic and natural disturbances, and hence decreased considerably with natural forest cover reached to a minimum level in the 1980s. In response to this dramatic loss of the natural forest cover due to the variable intensities of the human disturbances, the Hainan Provincial Government implemented logging ban rules in the natural forests in 1994 (Lin et al., 2017).

### 2.2 | Species richness, top 1% big-sized trees, and 99% remaining trees

Observed species richness was used to quantify the effects of biodiversity on aboveground biomass and its relationships with top 1% big-sized trees and 99% remaining trees. We showed that rarefied species richness increased with increasing observed species richness across 712 plots in the study area (Figure S2).

We used the top 1% of big-sized trees for the quantification of big-sized trees effect within each plot (Lutz et al., 2018). The top 1% big-sized trees were quantified using the 99th percentile scores for tree diameter, height, and crown area within each plot. Crown diameters (in m) for each individual tree were used to calculate the tree crown area (in m<sup>2</sup>). In this study, we considered to use the 99th percentile score of tree DBH, height, and crown area to represent

the big-sized trees attributes because of the following two main reasons: (a) Tropical forests compared to temperate forests contain many more small- and medium-sized individual trees or stems per ha with significantly higher understory species and functional trait diversity (Ali, Lohbeck, et al., 2018; Lutz et al., 2018); and (b) not all of the species or individuals are capable of reaching large-diameter threshold (e.g., DBH  $\geq$  60 cm) even in some old-growth forests, as also some constraints existed in large forest plots (Lutz et al., 2018). Hence, big-sized trees can be found in any region or sampling plot, but different abiotic and biotic factors may limit their large-diameter threshold (Bastin et al., 2018; Feldpausch et al., 2012). Therefore, in this study, the “big-sized trees effect” may be equally important in both secondary and old-growth forests where top 1% large-diameter, tall-stature, and big-crown trees are highly expected (but having different trees' size threshold and tree age) in naturally heterogeneous, species-rich, and structurally complex large-scale tropical forests. Therefore, in this study, to elucidate the ecological mechanisms and importance of big-sized trees relative to species richness on aboveground biomass at the scale of community did not require big-sized sample plots (e.g.,  $\geq$ 1 ha) and also did not require big-sized old trees (i.e., a specific diameter threshold, e.g., DBH  $\geq$  60 cm) or old-growth forests. For example, as one of the suggested approaches for large-diameter trees (Lutz et al., 2018), the top 1% of the big-sized trees within each plot can simply and better explain the influences of big-sized trees on species richness and aboveground biomass in naturally heterogeneous, species-rich, and structurally complex large-scale tropical forests.

For the quantification of 99% remaining trees, we calculated several remaining percentiles (95th, 90th, 75th, 50th, 25th, 10th, and 5th) scores for the diameter, height, and crown area of the remaining trees within each plot. So, there is no single index to quantify the remaining trees attributes within each plot, because of the presence of several classes of trees' size as compared to top 1% big-sized trees. We, therefore, used coefficient of variation (CV) to quantify the trees' size variation in order to capture the individual trees' size variation among remaining big-sized trees (i.e., 95th–90th or in other words, top 5%–10% big-sized trees), medium-sized trees (i.e., 75th–50th), and small-sized trees (i.e., 25th, 10th, and 5th). We used the CV index (in %) for the quantification of 99% remaining trees because it may well match with the approach used for the top 1% big-sized trees. Moreover, CV (a measure of relative variability) of trees' size classes, the ratio of the standard deviation of all trees' size measurements to the mean trees' size within a plot, can better represent the niche differentiation among different remaining-sized trees within a community (Ali, Lin, et al., 2018). A summary of the percentile scores used for the calculation of CV of the remaining trees' attributes is provided in Table S1 (Appendix A).

### 2.3 | Aboveground biomass

The aboveground biomass of each tree was estimated using the tree DBH, height ( $H$ ), and species' wood density ( $\rho$ ) in a

best-fit pantropical allometric equation for world's tropical forests,  $AGB = 0.0673 \times (\rho \times DBH^2 \times H)^{0.976}$  (Chave et al., 2014). The wood density databases were searched for the collection of species' wood density (Reyes, Brown, Chapman, & Lugo, 1992; Zanne et al., 2009).

### 2.4 | Climatic water availability and soil fertility

To assess the influences of climatic and soil conditions on big-sized trees, remaining trees, species richness, and aboveground biomass, we recorded the geographic coordinates (latitude and longitude) and elevation of each plot. We, then, extracted mean annual precipitation and mean annual potential evapotranspiration for each plot from a global climate dataset (<http://www.worldclim.org/>) using spatial geographic coordinates (latitude, longitude, and elevation). Climatic moisture index (CMI; mean annual precipitation – mean annual potential evapotranspiration) was used as an indicator for climatic water availability (Ali, Lin, et al., 2018; Poorter et al., 2017), where higher values of CMI represent higher water availability for plants (Hogg, 1997).

To assess the influences of edaphic factors on big-sized trees, remaining trees, species richness, and aboveground biomass, we obtained soil TEB (the sum of base cations  $Ca^{2+}$ ,  $Mg^{2+}$ ,  $K^+$ , and  $Na^+$ , in cmol/kg) of the topsoil (0–30 cm) and subsoil (30–100 cm) from the Harmonized World Soil Database (FAO et al., 2012). We used a mean value of soil TEBs of the topsoil and subsoil as an indicator of soil fertility for each plot to better represent the available soil nutrients for plant growth (Ali, Lin, et al., 2018; Poorter et al., 2017).

### 2.5 | Statistical analyses

We tested several structural equation models (SEMs) based on our conceptual models for testing the “big-sized trees hypothesis” (Figure 1a–d), “remaining trees hypothesis” (Figure 1e–h), and integrative modeling (Figure 1i) in large-scale tropical forests. We used a latent variable in our SEMs for defining the “top 1% big-sized trees effect,” which incorporated correlated variables including top 1% large-diameter, tall-stature, and big-crown, which we used to test the “big-sized trees effect” on species richness and aboveground biomass. As such, we used a latent variable in our SEMs for defining the “99% remaining trees effect,” which incorporated correlated variables including 99% remaining diameter, stature, and crown, which we used to test the “remaining trees effect” on species richness and aboveground biomass.

Model fit for SEM was assessed using three different indices: the standardized root mean square residual (SRMR), the comparative fit index (CFI), and the goodness-of-fit index (GFI; Hoyle, 2012). The SRMR is an absolute measure of fit that determines the average difference between the observed correlation and the model predicted correlation, and hence, SRMR  $<$ 0.08 represents reasonable model fit to the data. The CFI is an incremental fit index that measures the relative improvement in the model fit of the SEM over a null model; for example, CFI ranges from 0 (poor fit) to 1 (perfect fit), considered

satisfactory when CFI > 0.90. The GFI is a measure of fit between the hypothesized model and the observed covariance matrix, which is affected by the number of indicators of each latent variable, and theoretically ranges from 0 (poor fit) to 1 (perfect fit), with a GFI value of over 0.90 generally indicating acceptable model fit. In addition to the assessment of model-fit indices, the significance of each hypothesized pathway in the SEM was evaluated with the Wald statistic ( $p < 0.05$ ). We used a robust maximum likelihood estimator with standard errors and scaled statistics to estimate coefficients. Bias in direct, indirect, and total effect coefficients due to deviation from multivariate normality was evaluated by estimating standardized coefficients. Residuals and modification indices were also evaluated to determine the obvious discrepancies in the SEM data in order to evaluate which variable should be excluded or any extra path should be added, but we preferred to follow our conceptual models. However, we used two latent variables for testing the effects of big-sized trees and remaining trees in one integrative model, which might not lead to the perfect model fit probably due to the confounding effects of extra or remaining paths in the SEM. In this case, we further tested several integrative identical SEMs (i.e., path analyses) based on all possible combinations of the big-sized trees and remaining trees attributes (i.e., 27 models), in order to validate the main findings from the main integrative SEMs and to show the most optimal model as evidence. After testing the SEMs, we calculated the relative contribution of each predictor to the explained variance in aboveground biomass, following Ali et al. (2019b). For the calculations of relative contributions, we used partial mediation SEMs because those models allowed us to test the direct and indirect effects of climatic and soil conditions on aboveground

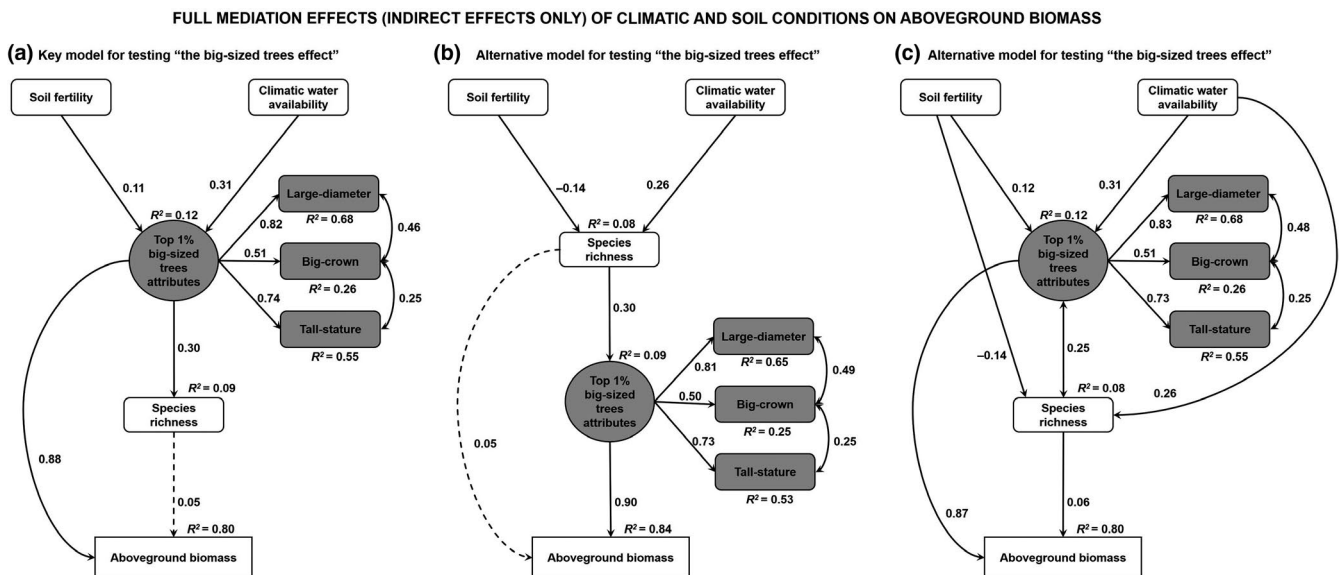
biomass. The SEMs were employed using the *lavaan* package (Rosseel, 2012) in R 3.4.2 (R Development Core Team, 2017).

Prior to all steps of statistical analyses, all tested variables were natural-logarithm-transformed and standardized for meeting normality and linearity. We also assessed the bivariate relationships among the tested variables used in the SEMs, using simple regression models and Pearson's correlations. The summary (i.e., mean, standard error, maximum, and minimum) of variables used in this study is accessible in Table S1.

### 3 | RESULTS

#### 3.1 | Big-sized trees overrule species richness on aboveground biomass: Models without considering 99% remaining trees attributes

The key SEM for testing the “big-sized trees hypothesis” showed that aboveground biomass increased strongly with a direct effect of top 1% big-sized trees attributes, followed by indirect positive effects of climatic water availability and soil fertility via big-sized trees. The direct effect of species richness on aboveground biomass was nonsignificant. Although big-sized trees increased species richness, an indirect effect of big-sized trees on aboveground biomass via species richness was relatively weak in the effect size. Big-sized trees increased with increasing climatic water availability and soil fertility. This result suggested that big-sized trees rather than species richness increased aboveground biomass under high availability of soil fertility and climatic water (Figure 2a; Table S2).



**FIGURE 2** Key and alternative structural equation models for testing the relative effect of top 1% big-sized trees attributes (a latent variable incorporating top 1% large-diameter, tall-stature, and big-crown area trees) and species richness on aboveground biomass while considering for the full mediation effects of climatic and soil conditions, as well as interrelationships between big-sized trees attributes and species richness, in tropical forests. Black color arrows represent direct effect, while gray color arrows represent the indirect effects. Solid arrows represent significant paths ( $p < 0.05$ ), while dashed arrows represent nonsignificant paths ( $p > 0.05$ ). For each path, the standardized regression coefficient is shown (see Tables S2–S4 for statistics). Model-fit statistics for key model (a), comparative fit index (CFI) = 0.912, goodness-of-fit index (GFI) = 0.919, and standardized root mean square residual (SRMR) = 0.069; alternative model (b), CFI = 0.901, GFI = 0.913, and SRMR = 0.120; and alternative model (c), CFI = 0.935, GFI = 0.939, and SRMR = 0.056

An alternative SEM (Figure 2b) for testing the “big-sized trees effect” showed that big-sized trees had a strong positive direct effect on aboveground biomass, followed by a positive indirect effect of species richness via big-sized trees. Species richness had a positive direct effect on big-sized trees but a nonsignificant direct effect on aboveground biomass. Species richness increased directly with climatic water availability but decreased directly with soil fertility. Unlike in the key SEM for testing the big-sized effect (Figure 2a), climatic water availability and soil fertility did not influence aboveground biomass indirectly via species richness. It was noted that the “big-sized trees effect” on aboveground biomass increased slightly, perhaps due to the promoting effect of species richness on big-sized trees (Figure 2b; Table S3). Similarly, another alternative SEM (Figure 2c) showed that aboveground biomass increased strongly with a direct effect of top 1% big-sized trees attributes, followed by indirect positive effects of climatic water availability and soil fertility via big-sized trees (Table S3). These findings suggested that species richness and big-sized trees are simultaneously maintaining each other for enhanced aboveground biomass (Figure 2b,c).

As expected, additional SEMs (Figure 3) showed that the importance of big-sized trees effect on aboveground biomass did not change, but improved when considered for the partial mediation effects of climatic water availability and soil fertility. As such, the nonsignificant effect of species richness on aboveground biomass and the positive relationship between species richness and big-sized trees remained unchanged (Figure 3) as suggested by the key and alternative SEMs for the “big-sized trees effect” (Figure 2). Moreover, climatic water availability and soil fertility determined aboveground biomass indirectly via big-sized trees but not via species richness (Figure 3; Tables S5–S7). These results from additional SEMs suggested that big-sized trees rather than species richness increased aboveground biomass under high availability of soil fertility and climatic water, and remained unchanged when considering for the additional direct and indirect multiple pathways (Figure 3). We also showed that big-sized trees explained 52%–75% of the accounted variation in aboveground biomass (Figure 3d). Bivariate relationships between the exogenous and endogenous variables used in the SEMs for testing the “big-sized trees hypothesis” are shown in Figure S3 (see Table S8 for the detailed statistics).

### 3.2 | Remaining trees and species richness promote aboveground biomass: Models without considering top 1% big-sized trees attributes

The key SEM for testing the “remaining trees hypothesis” showed that aboveground biomass increased with a direct effect of the 99% remaining trees attributes, followed by species richness and the indirect positive effects of climatic water availability and soil fertility via remaining trees (Figure 4a; Table S9). Remaining trees did not influence species richness, and hence, an indirect effect of remaining trees on aboveground biomass via species richness was nonsignificant. Remaining trees increased with increasing climatic water availability and soil fertility (Figure 4a; Table S9). As such, alternative

SEMs (Figure 4b,c; Tables S10 and S11) for testing the “remaining trees effect” showed the similar results as suggested by key SEM (Figure 4a). Species richness increased directly with climatic water availability but decreased directly with soil fertility (Figure 4b). These findings suggested that species richness and 99% remaining trees attributes did not maintain each other, and hence promoted aboveground biomass directly and independently under high availability of soil fertility and climatic water (Figure 4).

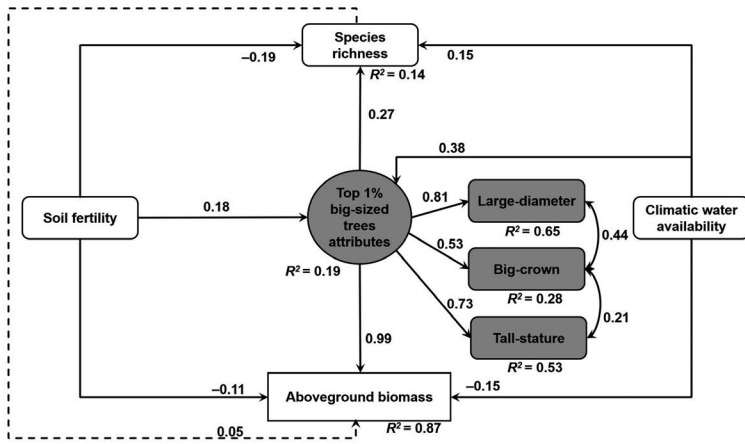
As expected, additional SEMs (Figure 5), for testing the “remaining trees hypothesis,” showed that the importance of remaining trees and species richness on aboveground biomass did not change, but improved when considered for the partial mediation effects of climatic water availability and soil fertility. As such, the nonsignificant relationship between species richness and remaining trees attributes remained unchanged (Figure 5) as suggested by the key and alternative SEMs for the remaining trees effect (Figure 4). Moreover, climatic water availability and soil fertility determined aboveground biomass indirectly via remaining trees and species richness (Figure 5; Tables S12–S14). These results from additional SEMs suggested that remaining trees and species richness increased aboveground biomass directly and independently when considering the additional direct and indirect multiple pathways (Figure 5). We also showed that 99% remaining trees attributes and species richness explained 55% and 22% of the accounted variation in aboveground biomass, respectively (Figure 5d). Bivariate relationships between the exogenous and endogenous variables used in the SEMs for testing the “remaining trees hypothesis” are shown in Figure S4 (see Table S15 for the detailed statistics).

### 3.3 | Big-sized trees overrule remaining trees and species richness on aboveground biomass: Models considering both top 1% big-sized and 99% remaining trees attributes

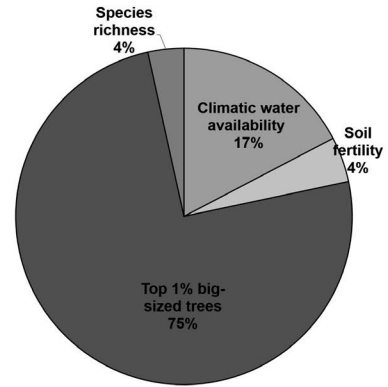
The integrative SEMs for testing the relative importance of “big-sized trees effect,” “remaining trees effect,” and species richness on aboveground biomass showed that the strong effect of top 1% big-sized trees attributes on aboveground biomass did not change dramatically. More specifically, big-sized trees attributes overruled the effects of remaining trees attributes and species richness on aboveground biomass (Figure 6; Tables S16–S18), which were observed in the specific models for the “remaining trees hypothesis” (Figures 4 and 5). We also showed that top 1% big-sized trees explained most of the accounted variation (55%–70%) in aboveground biomass as compared to 99% remaining trees (6%–10%) and species richness (2%–18%) (Figure 6d). Top 1% of big-sized trees and 99% remaining trees increased with increasing climatic water availability and soil fertility, whereas species richness decreased with soil fertility but increased with climatic water availability. As such, climatic water availability and soil fertility determined aboveground biomass directly and indirectly via the strong influence of big-sized trees (in most cases) as compared to remaining trees and species richness (Figure 6; Tables S16–S18).

PARTIAL MEDIATION EFFECTS (DIRECT AND INDIRECT EFFECTS) OF CLIMATIC AND SOIL CONDITIONS ON ABOVEGROUND BIOMASS

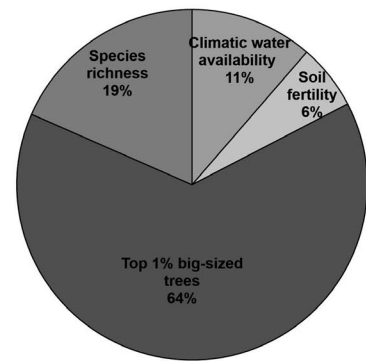
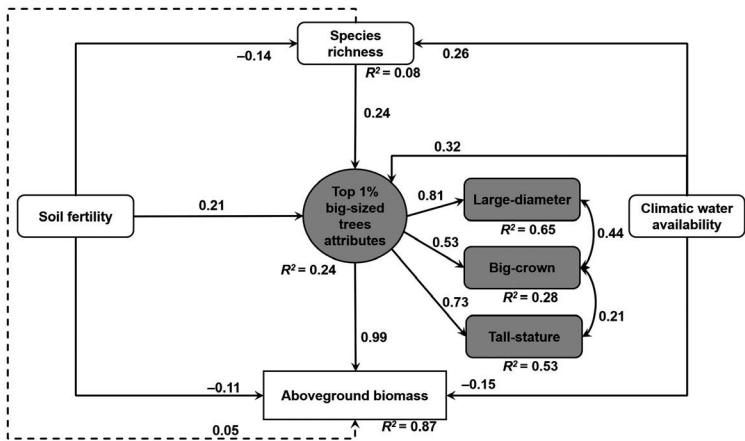
(a) Additional model for testing “the big-sized trees effect” (effect of big-sized trees on species richness)



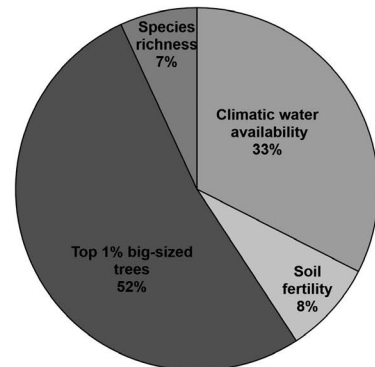
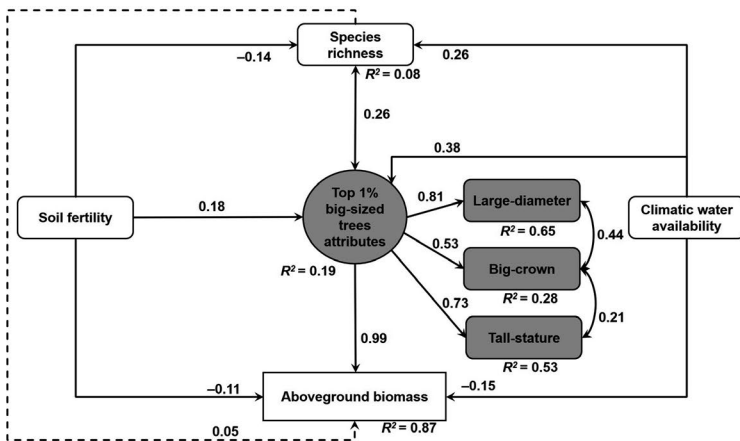
(d) Relative contribution (%)



(b) Additional model for testing “the big-sized trees effect” (effect of species richness on big-sized trees)

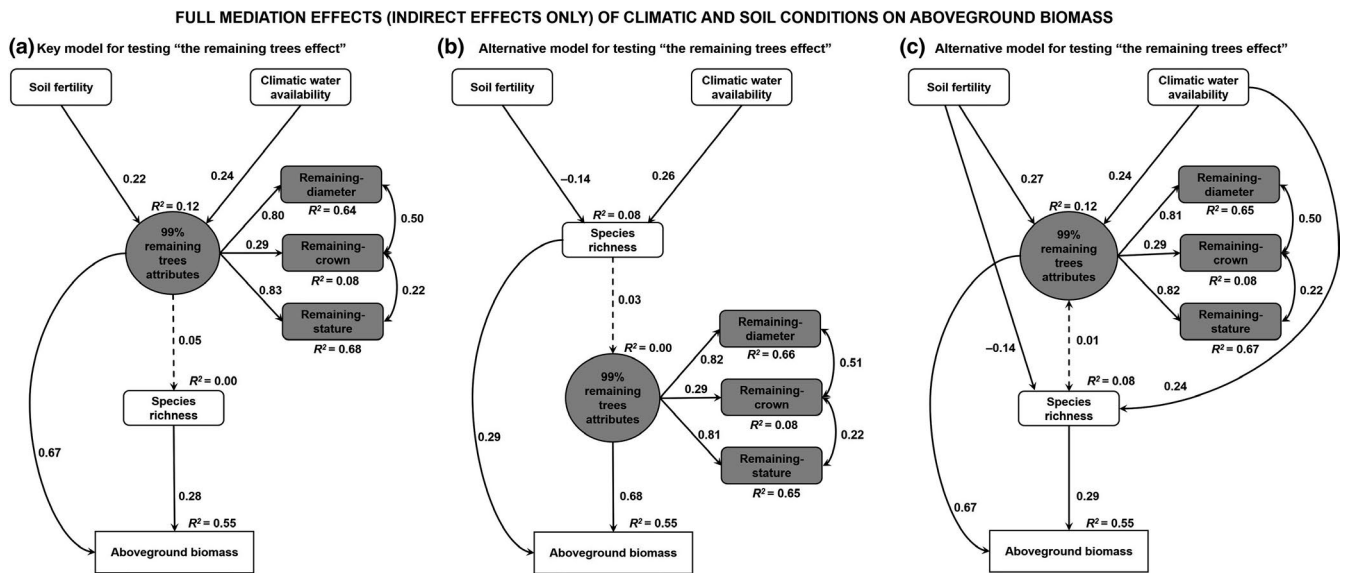


(c) Additional model for testing “the big-sized trees effect” (feedback between species richness and big-sized trees)



**FIGURE 3** Additional structural equation models (a, b, and c) for testing the relative effect of top 1% big-sized trees attributes (a latent variable incorporating top 1% large-diameter, tall-stature, and big-crown area trees) and species richness on aboveground biomass while considering for the partial mediation effects of climatic and soil conditions, as well as interrelationships between big-sized trees attributes and species richness, in tropical forests. Solid arrows represent significant paths ( $p < 0.05$ ), while dashed arrows represent nonsignificant paths ( $p > 0.05$ ). For each path, the standardized regression coefficient is shown (see Tables S5–S7 for statistics). (d) Pie chart shows the relative contribution, based on total or direct (if there is no indirect path) effect, of predictors to the accounted variation in aboveground biomass in each SEM. All three models had the similar fit to the data, that is, comparative fit index = 0.957, goodness-of-fit index = 0.959, and standardized root mean square residual = 0.043





**FIGURE 4** Key and alternative structural equation models for testing the relative effect of 99% remaining trees attributes (a latent variable incorporating 99% remaining diameter, stature, and crown area) and species richness on aboveground biomass while considering for the full mediation effects of climatic and soil conditions, as well as interrelationships between remaining trees attributes and species richness, in tropical forests. Black color arrows represent direct effect, while gray color arrows represent the indirect effects. Solid arrows represent significant paths ( $p < 0.05$ ), while dashed arrows represent nonsignificant paths ( $p > 0.05$ ). For each path, the standardized regression coefficient is shown (see Tables S9–S11 for statistics). Model-fit statistics for key model (a), comparative fit index (CFI) = 0.915, goodness-of-fit index (GFI) = 0.935, and standardized root mean square residual (SRMR) = 0.066; alternative model (b), CFI = 0.901, GFI = 0.934, and SRMR = 0.101; and alternative model (c), CFI = 0.959, GFI = 0.968, and SRMR = 0.040

This result suggested that top 1% big-sized trees attributes, rather than 99% remaining trees attributes and species richness, increased aboveground biomass under high availability of soil fertility and climatic water (Figure 6). Moreover, the additional integrative SEMs showed that the individual direct effect (i.e., without considering a latent variable) of top 1% large-diameter, tall-stature, and big-crown trees overruled the individual direct effect of 99% remaining diameter, stature and crown, and species richness on aboveground biomass (Figures S5–S7). These additional integrative SEMs, particularly best-fit models based on the combination of either top 1% tall-stature or large-diameter with 99% remaining crown area (partlabels e, g in Figures S5–S7), provided a strong support to the general notion of main integrative SEMs (Figure 6). Pearson's correlations between the pairs of the tested variables in integrative SEMs are shown in Figure S8.

## 4 | DISCUSSION

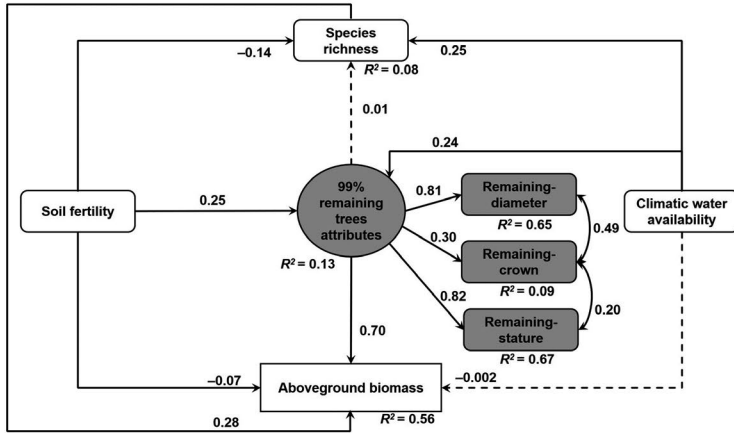
In this study, we assessed the importance of: (a) the “top 1% big-sized trees effect” relative to the effect of species richness; (b) the “99% remaining trees effect” relative to the effect of species richness; and (c) the “top 1% big-sized trees effect” and effect of species richness on aboveground biomass in large-scale tropical forests. By testing several SEMs, for either “top 1% big-sized trees effect” or “99% remaining trees effect,” and then testing integrative SEMs, we found strong support for the “big-sized trees hypothesis.” Top 1% large-diameter, tall-stature, and

big-crown attributes were the main drivers of aboveground biomass, while species richness and 99% remaining trees attributes were only of additional importance for promoting aboveground biomass. As such, generally, species richness was also crucial for promoting aboveground biomass indirectly via increasing the “big-sized trees effect” but via decreasing the “99% remaining trees effect,” even though the specific combinations of species richness with a single attribute of either big-sized or remaining trees showed differential results in some cases.

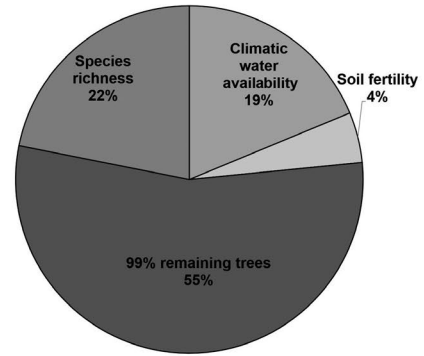
Our results support the general notion that vegetation quantity (i.e., initial biomass stocks) overrules the effect of vegetation quality (i.e., species diversity, functional trait diversity, and composition) in explaining ecosystem functions (Lohbeck et al., 2015; Yuan et al., 2018), and hence, the attributes of the big-sized trees contribute much to the aboveground biomass of forests (Ali, Lohbeck, et al., 2018; Lutz et al., 2018; Stephenson et al., 2014). The strongest positive effect of big-sized trees on aboveground biomass suggests that forests can store large fractions of aboveground carbon when there is the presence of large-diameter, tall-stature, and big-crown trees, despite the species richness of forests (Bastin et al., 2018; Feldpausch et al., 2012; Lutz et al., 2018; Slik et al., 2013; Stephenson et al., 2014). Our “big-sized trees effect” and integrative models explained 80%–87% and 80%–85% of the variation in aboveground biomass, respectively, where a latent variable of top 1% big-sized trees was the only biotic factor contributing largely to biomass, supporting the “big-sized trees hypothesis.” Although species richness was not strongly related to aboveground biomass, it had a potentially strong indirect positive effect on aboveground biomass via big-sized trees effect. This result

PARTIAL MEDIATION EFFECTS (DIRECT AND INDIRECT EFFECTS) OF CLIMATIC AND SOIL CONDITIONS ON ABOVEGROUND BIOMASS

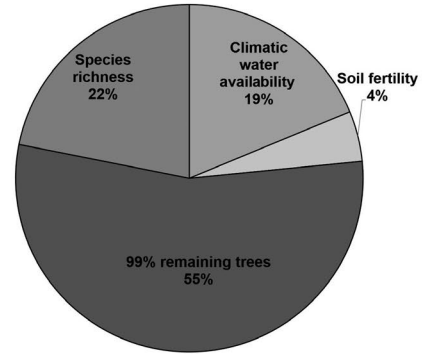
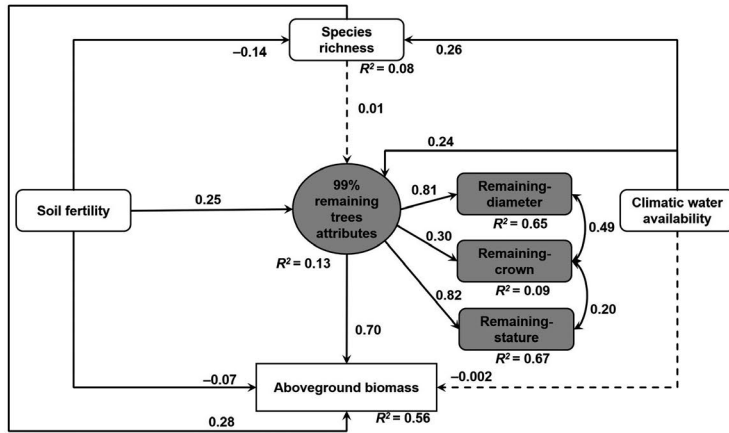
(a) Additional model for testing “the remaining trees effect” (effect of remaining trees on species richness)



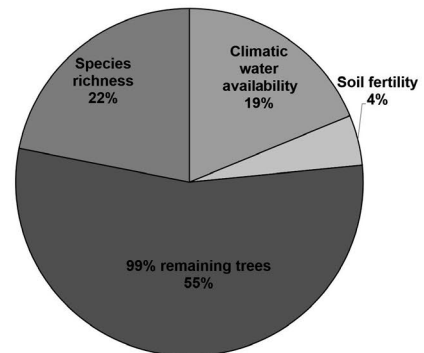
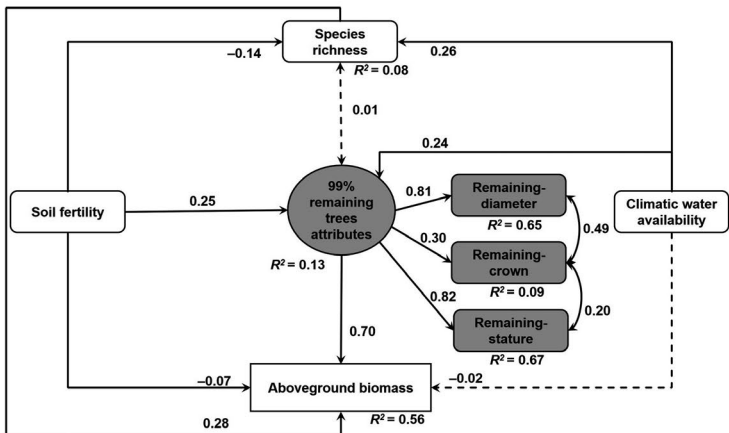
(d) Relative contribution (%)



(b) Additional model for testing “the remaining trees effect” (effect of species richness on remaining trees)



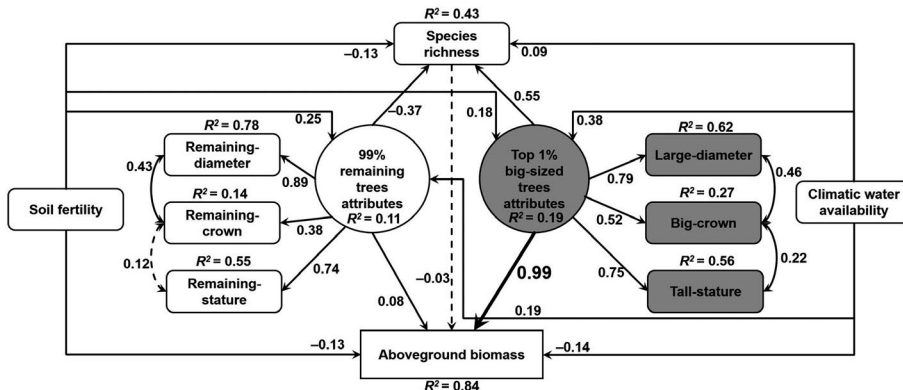
(c) Additional model for testing “the remaining trees effect” (feedback between species richness and remaining trees)



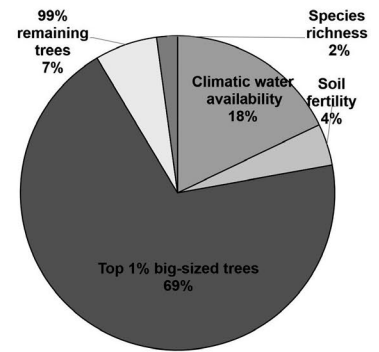
**FIGURE 5** Additional structural equation models (a, b, and c) for testing the relative effect of 99% remaining trees attributes (a latent variable incorporating 99% remaining diameter, stature, and crown area) and species richness on aboveground biomass while considering for the partial mediation effects of climatic and soil conditions, as well as interrelationships between remaining trees attributes and species richness, in tropical forests. Solid arrows represent significant paths ( $p < 0.05$ ), while dashed arrows represent nonsignificant paths ( $p > 0.05$ ). For each path, the standardized regression coefficient is shown (see Tables S12–S14 for statistics). (d) Pie chart shows the relative contribution, based on total or direct (if there is no indirect path) effect, of predictors to the accounted variation in aboveground biomass in each SEM. All three models had the similar fit to the data, that is, comparative fit index = 0.962, goodness-of-fit index = 0.972, and standardized root mean square residual = 0.038

PARTIAL MEDIATION EFFECTS (DIRECT AND INDIRECT EFFECTS) OF CLIMATIC AND SOIL CONDITIONS ON ABOVEGROUND BIOMASS

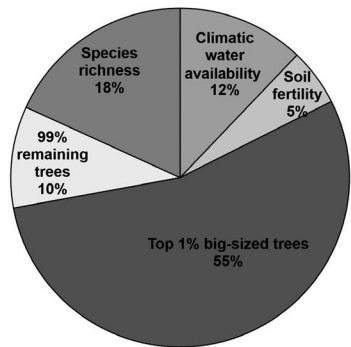
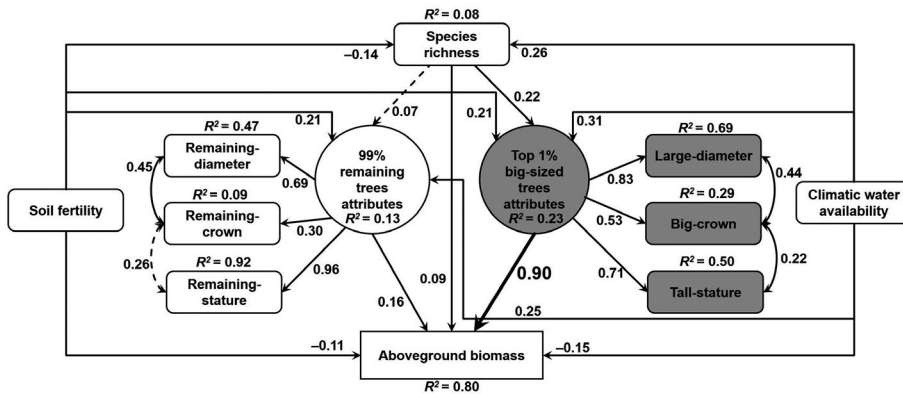
(a) Integrative model for the effects of big-sized trees, remaining trees, and species richness on aboveground biomass (effects of big-sized trees and remaining trees on species richness)



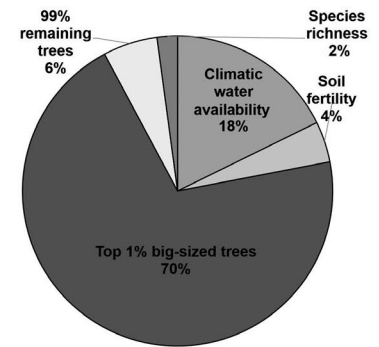
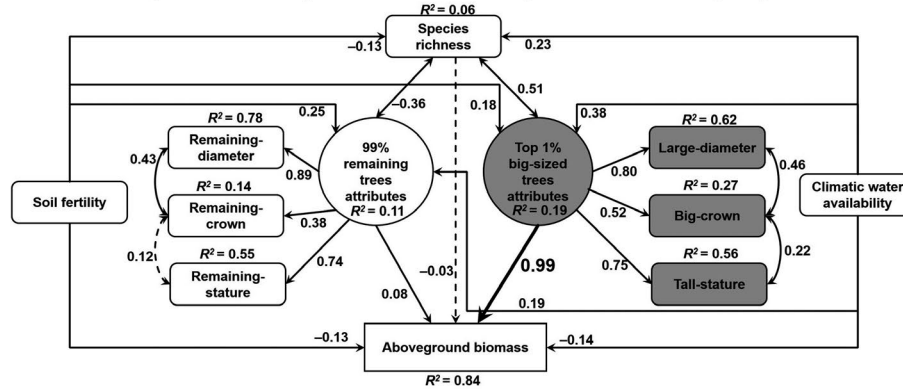
(d) Relative contribution (%)



(b) Integrative model for the effects of big-sized trees, remaining trees, and species richness on aboveground biomass (effects of species richness on big-sized trees and remaining trees)



(c) Integrative model for the effects of big-sized trees, remaining trees, and species richness on aboveground biomass (Feedback between species richness and each of big-sized trees and remaining trees)



**FIGURE 6** Integrative structural equation models (a, b, and c) for testing the relative effect of top 1% big-sized trees attributes (a latent variable incorporating top 1% large-diameter, tall-stature, and big-crown area trees), 99% remaining trees attributes (a latent variable incorporating 99% remaining diameter, stature, and crown area), and species richness on aboveground biomass while considering for the partial mediation effects of climatic and soil conditions, as well as interrelationships between species richness and each of big-sized trees and remaining trees attributes, in tropical forests. Black color arrows represent direct effect, while gray color arrows represent the indirect effects. Solid arrows represent significant paths ( $p < 0.05$ ), while dashed arrows represent nonsignificant paths ( $p > 0.05$ ). For each path, the standardized regression coefficient is shown (see Tables S16–S18 for statistics). (d) Pie chart shows the relative contribution, based on total or direct (if there is no indirect path) effect, of predictors to the accounted variation in aboveground biomass in each SEM. Model-fit statistics for model (a), comparative fit index (CFI) = 0.711, goodness-of-fit index (GFI) = 0.783, and standardized root mean square residual (SRMR) = 0.219; model (b), CFI = 0.702, GFI = 0.780, and SRMR = 0.194; and model (c), CFI = 0.711, GFI = 0.783, and SRMR = 0.219. Specific integrative SEMs based on different combinations of big-sized and remaining attributes are shown in Figures S5–S7, for the purpose to highlight the most optimal (best-fit) integrative SEMs and to provide additional evidence to the main SEMs

again confirms the “big-sized trees hypothesis” as a linking mechanism for positive species richness and aboveground biomass in species-rich and structurally complex tropical forests. Furthermore, this result suggests that, as natural forests increase in tree diameter, height, and crown area, their vegetation quantity (i.e., initial biomass stocks) also increases, which in turn may promote absolute annual biomass gain (Lohbeck et al., 2015; Lutz et al., 2018; Yuan et al., 2018). For example, the average size of the tree diameter, height, and crown area increases with increasing individual tree growth (Stephenson et al., 2014), which could be one of the underlying ecological mechanisms within a community (Lohbeck et al., 2015; Poorter et al., 2016; Yuan et al., 2018). Moreover, such type of a positive relationship between vegetation quantity (i.e., initial biomass stocks, stand basal area, mean DBH) and aboveground biomass productivity has been widely reported for old-growth and secondary natural forests across the globe (Jucker et al., 2016; Lohbeck et al., 2015; Paquette & Messier, 2011; Vilà et al., 2013; Yuan et al., 2019, 2018).

In this study, the observed patterns are almost similar to previous studies where the effect of stand basal area overrules the effect of species diversity on aboveground biomass productivity in natural forests (Paquette & Messier, 2011; Vilà et al., 2013), given that it is reasonable that big-sized trees contribute much to the stand basal area. For example, many small- and medium-sized trees cannot contribute comparable stand basal area and aboveground biomass to a few big-sized trees (Lutz et al., 2018), although remaining trees can contribute substantially to biodiversity and soil carbon cycling (Ali, Lohbeck, et al., 2018; Chapin & Stuart, 1983; Meakem et al., 2018). Therefore, the strongest positive effect of the top 1% big-sized trees on aboveground biomass at the scale of community supports the importance of large-diameter, tall-stature, and big-crown individual trees to carbon sequestration and productivity (Lutz et al., 2018; Stephenson et al., 2014). For example, the scaling theory suggests that large-diameter trees are usually tall statures having big crowns, and occupy most of the growing space at the top of the canopy not available to small- and medium-sized trees in natural forests (Van Pelt, Sillett, Kruse, Freund, & Kramer, 2016; West, Enquist, & Brown, 2009). Under the predictions of the scaling theory, we found that large-diameter, tall-stature, and big-crown individual trees were positively correlated, thereby increasing species richness and aboveground biomass in the studied forests. Alternatively, variations in stand structural attributes among and within species (i.e., both big-sized and small-sized trees) increase species diversity and aboveground biomass under the predictions of the tree crown complementarity, niche differentiation, and resource heterogeneity mechanisms in species-rich and structurally complex natural forests (Ali et al., 2019b, 2016; Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017; Yachi & Loreau, 2007).

In this study, the “99% remaining trees” models showed that remaining trees and species richness increased aboveground biomass when the “big-sized trees effect” on species richness and aboveground biomass is excluded. These results further confirm that the “big-sized trees effect” overrules the effects of tree crown complementarity and niche differentiation of the remaining trees on

aboveground biomass. Our results also support the general notion that functional dominance (i.e., community-weighted mean of few tall-stature or large-diameter trees) or functional redundancy matters more for tropical forest functioning compared to species richness and functional trait diversity (Ali, Lohbeck, et al., 2018; Cavanaugh et al., 2014; Prado-Junior et al., 2016). In addition, the negative relationships between species richness and the 99% remaining trees attributes might be attributable to the fact that high biomass stand excludes weak competitors (Ali et al., 2016), because 99% remaining trees still contain top 10%–25% remaining big-sized trees (Bastin et al., 2015). Although it was not the main focus of this study, we observed such confounding effects during our analyses when testing several SEMs which generally suggested that the effect of top 1% big-sized trees overruled the remaining top 10%–25% trees, which in turn overrule the effect of remaining 75%–90% trees as shown by the strong overruling effect of top 1% big-sized trees. In this case, it is understandable that the intra- and interspecific competition of the 99% remaining trees lead to the community assembly processes, which in turn might impose differential effects on forest functioning probably due to the differential functional strategies (i.e., fast-growing acquisitive and slow-growing conservative) of the component species and interacting individuals within a community (Ali, Lohbeck, et al., 2018; Lohbeck et al., 2015; Reich, 2014; Yuan et al., 2019).

We found that the top 1% of big-sized trees attributes, 99% remaining trees attributes, and species richness increased with increasing climatic water availability, but high climatic water availability increased aboveground biomass indirectly via big-sized trees effect compared to remaining trees and species richness, suggesting greater length of growing season is required for the performance of big-sized trees for higher forest functioning (Ali, Lin, et al., 2018; Poorter et al., 2017). It is therefore plausible that tall-stature trees are vulnerable to sapwood cavitation and are also exposed to high solar radiations (Allen et al., 2010), but large-diameter trees are still storing higher amount of carbon than small-sized trees (Stephenson et al., 2014) and hence contributing large portion of aboveground biomass at the community level across different biomes (Bastin et al., 2015; Lutz et al., 2018). Our results also warned that increasing atmospheric drought may increase the mortality of both big-sized and remaining trees in species-rich forest communities, but confirming that big-sized trees suffer most during a drought in the world's forests (Bennett et al., 2015). However, previous studies have also shown that climatic water availability increased aboveground biomass indirectly via forest diversity, functional traits, and stand structure in large-scale tropical forests (Ali et al., 2019a, 2019b; Poorter et al., 2017), indicating that all individual trees within each plot are susceptible to atmospheric drought (Phillips et al., 2010). However, a recent global study has shown that tropical big-sized trees are more resilience to climate change probably due to the highest absolute large-diameter tree richness and stand structural complexity (Lutz et al., 2018). In addition, we found the negative or nonsignificant effects of soil nutrients on species richness and aboveground biomass, suggesting the nutrient imbalance and adaptation of certain species to the surrounding environments (Ali et al., 2019a; Poorter et al., 2017;

Prado-Junior et al., 2016). The observed negligible or negative relationships might be further attributable to the species longevity, aboveground biomass retention, and the buildup of a larger biomass pool at the stand level (Baker et al., 2009; Poorter et al., 2015). For example, we also found that both big-sized and remaining trees increased with greater availability of soil nutrients, but soil nutrients increased aboveground biomass indirectly via big-sized trees, indicating the dominant role of big-sized trees compared to remaining trees on available resources (Ali, Lohbeck, et al., 2018).

Lastly, we anticipate that our study might encourage further studies regarding the effects of big-sized trees, remaining trees attributes, and multiple metrics of species diversity (e.g., taxonomic, phylogenetic, and functional trait diversity and composition) on forest multifunctionality (e.g., biomass productivity, litterfall production, seed production, belowground functions) and stability across space and time. For example, it would be very interesting to explore the underlying ecological mechanisms (in one integrative SEM) for the “big-sized trees effect” on initial biomass stock, and then on biomass growth, recruitment, and mortality (or considering net biomass change only), while accounting for the effects of abiotic factors as well as multiple metrics of species diversity and stand structure (Poorter et al., 2017; Rozendaal et al., 2017; Yuan et al., 2019). Nevertheless, we show that the “big-sized trees effect” overrides the effects of remaining trees and species richness on aboveground biomass in large-scale tropical forests. We also show that the top 1% of big-sized trees increase with climatic water availability, indicating that large-diameter, tall-stature, and big-crown trees may be more susceptible to atmospheric drought or drought-related mortality effects. We argue that the effects of top 1% large-diameter, tall-stature, and big-crown trees on species richness and aboveground biomass should be tested for better understanding the underlying mechanisms by which forest diversity and stand structure affect forest functioning.

## ACKNOWLEDGEMENTS

This study is supported by China Postdoctoral Science Foundation (Grant No. 2018M643117), the Wildlife Protection Bureau, the Nature Reserves, Forest Farms, and Forest Bureaus in Hainan Island. We thank Qing Chen, Huanqiang Chen, Shuo Sun, Yiwen Liang, Chundong Wang, Lin Fang, Yanni Mo, Hua Zhu, and Qiang Xie for their help and support during the fieldwork.

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## AUTHORS' CONTRIBUTION

AA and HSJ designed the conceptual idea. SLL, JKH, FMK, JHY, and HSJ collected field data. AA compiled and analyzed the data and wrote the manuscript with the help from SLL, JKH, and HSJ through multiple rounds of revision. All authors gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Variables across 712 plots used in the analysis are provided in Appendix B.

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**How to cite this article:** Ali A, Lin S-L, He J-K, Kong F-M, Yu J-H, Jiang H-S. Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. *Glob Change Biol.* 2019;00:1–15. <https://doi.org/10.1111/gcb.14707>