RESEARCH ARTICLE

WILEY

Elucidating space, climate, edaphic, and biodiversity effects on aboveground biomass in tropical forests

Arshad Ali[1] | Si-Liang Lin[1] | Jie-Kun He[1] | Fan-Mao Kong[2] | Jie-Hua Yu[1] | Hai-Sheng Jiang[1]

[1] Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou 510631 Guangdong, PR China

[2] Guangzhou Qimao Ecological Technology Co., Ltd., Guangzhou 510631 Guangdong, PR China

Correspondence
Hai-Sheng Jiang, Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou 510631, Guangdong, PR China.
Email: jhs@scnu.edu.cn

Abstract

Aim and hypothesis: This study aims to disentangle the direct and indirect roles of space, climate, edaphic, and biodiversity effects on aboveground biomass in natural tropical forests, thereby evaluating the relative effects and contribution of abiotic and biotic factors on aboveground biomass. We hypothesized that the space effect drives the longitudinal, latitudinal, and elevational patterns in climatic and edaphic factors, thereby directly and indirectly determining the relationships between biodiversity and aboveground biomass in natural tropical forests.

Methods: We used structural equation modelling for linking spatial, climatic, edaphic, and biotic factors of aboveground biomass, using data from 247,691 trees across 907 tropical forest plots (total sampling area of 145.23 ha) of Hainan Island in Southern China.

Results: Aboveground biomass increased directly with functional dominance, individual tree size inequality, and climatic water availability but decreased directly with space and edaphic effects. However, space effect increased aboveground biomass indirectly via simultaneously differential direct changes (positive, negative, and non-significant) in climatic, edaphic, and biotic factors. As such, indirect effects of mean annual temperature and climatic water availability decreased aboveground biomass through differential direct changes in biotic factors, but opposite was true for soil fertility.

Conclusions: We argue that, despite the high relative contribution of biodiversity to aboveground biomass, the direct and indirect roles of space, climatic, and edaphic effects are also important for explaining biotic factors and aboveground biomass under the predictions of several abiotic-based hypotheses. Hence, conserving biodiversity across space is important for forest management and land development under climate change.

KEYWORDS

ecosystem functioning, energy–richness, mass ratio, niche complementarity, space effect, water–energy dynamics

1 | INTRODUCTION

Conserving biodiversity and enhancing aboveground carbon stocks in tropical forests are important for mitigating global climate change (Phelps, Webb, & Adams, 2012; Van de Perre et al., 2018). World's tropical biodiversity is rapidly decreasing due to deforestation and land degradation with critical consequences for forest functioning (Bunker et al., 2005; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016). In the context of developing policies to reduce emissions from deforestation and forest degradation (REDD+), degraded forest lands in tropical areas refer to areas with less biodiversity and low carbon storage (Poorter et al., 2015; Van de Perre et al., 2018; Villa et al., 2018). Therefore, land degradation is also the change in the forest that has negative effects on the forest diversity, structure, and function so that it reduces the forest capacity to provide ecosystem services (FAO, 2014; Lohbeck et al., 2016). In this case, forest management and land development strategies that simultaneously increase biodiversity and carbon stocks represent the sustainable use of limited resources and available land under the context of both regional and global climate change (Poorter et al., 2015; Van de Perre et al., 2018; Villa et al., 2018). For this purpose, a central issue in contemporary forest ecology is to understand what maintains the relationship between biodiversity and ecosystem functioning in natural forest ecosystems (Poorter et al., 2017; Yuan, Ali, et al., 2018).

In forest ecosystems, several studies have suggested that biotic factors (i.e., biodiversity effect) may directly enhance aboveground biomass or productivity through two main ecological mechanisms (Ali & Yan, 2017b; Cavanaugh et al., 2014; Poorter et al., 2017; Yuan et al., 2016), such as the niche complementarity (Tilman et al., 2001) and mass ratio or selection effects (Grime, 1998). Although the relationship between biodiversity and aboveground biomass is generally positive, the relationship remains unclear for the simultaneous direct and indirect roles of space, climate, and edaphic effects in an integrative modelling (see Figure 1). It is generally well understood that latitudinal, longitudinal, and elevational gradients in climatic, edaphic, and biotic factors indicate important ecological mechanisms (Currie et al., 2004; Gillman et al., 2015; Weiser, Michaletz, et al., 2018; Weiser, Swenson, et al., 2018); that is, we term the 'space effect.' For example, forest productivity declines with latitudinal gradients (Gillman et al., 2015) because climatic factors influence primary productivity, and that productivity limits the number of individuals and species richness (Brown, Gillooly, Allen, Savage, & West, 2004;
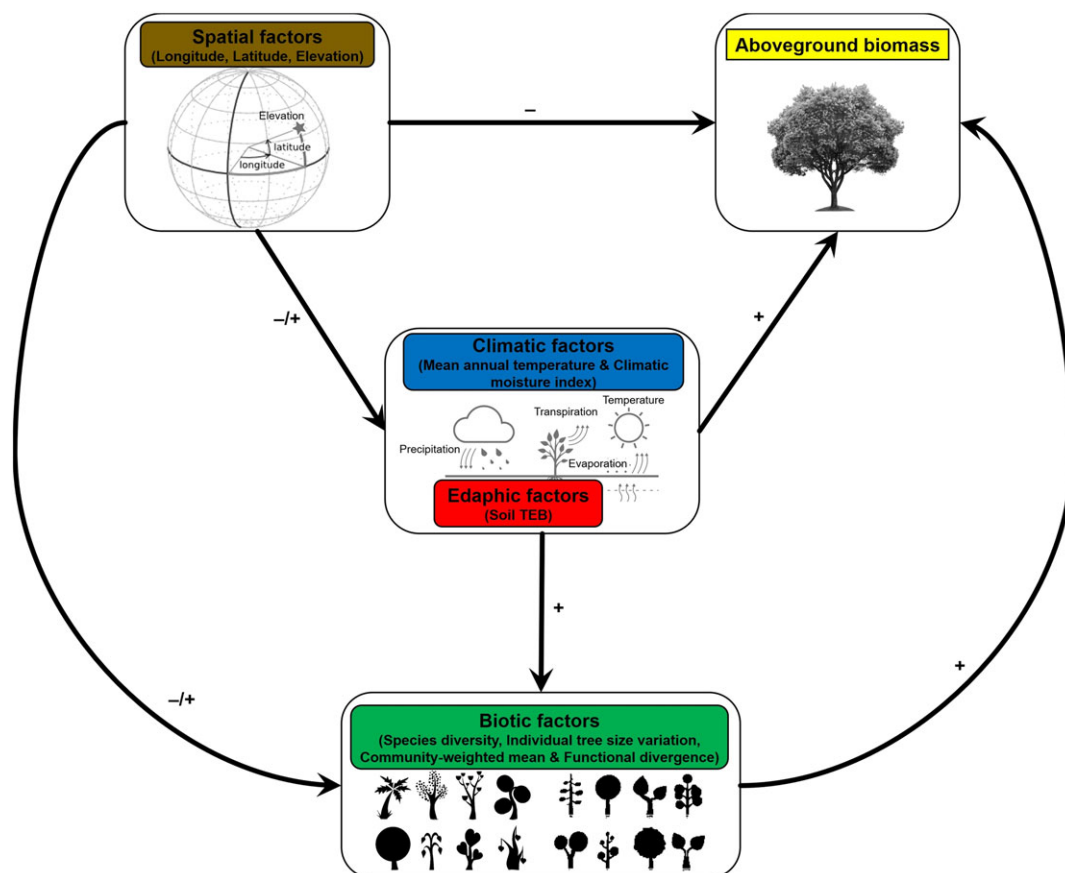

FIGURE 1 A conceptual model for elucidating the direct and indirect roles of space (i.e., longitude, latitude, and elevation), climate (mean annual temperature and climatic water availability), edaphic (soil fertility), and biodiversity (Shannon's species diversity, individual tree size inequality, and functional divergence and dominance) effects on aboveground biomass in tropical forests. Hypothesized relationships between or among variables are indicated by −, +, or −/+. TEB: total exchangeable bases [Colour figure can be viewed at wileyonlinelibrary.com]

Chu et al., 2016; Currie et al., 2004). Therefore, space effect can determine the relationships between biotic factors and aboveground biomass directly and indirectly via climatic and edaphic factors (Figure 1).

Climatic and edaphic factors can also influence aboveground biomass directly and indirectly via multiple biotic factors (Figure 1; Ali et al., 2019; Chu et al., 2016; Michaletz, Kerkhoff, & Enquist, 2018; Paquette & Messier, 2011; Poorter et al., 2017). For example, primary productivity increases with temperature and water availability along latitudinal gradients, probably due to the effect of greater energy (i.e., either solar radiation or temperature) availability, which may in turn promote more individuals and species (Currie et al., 2004; O'Brien, 2006). However, water and energy availability may promote few big-sized trees, rather than many small-sized trees, or may even decline species diversity through competition for limiting resources or vice-versa (Allen et al., 2010; Phillips et al., 2010). Therefore, it is plausible that climatic factors influence aboveground biomass or productivity directly via several metabolic processes underlying plant growth (Anderson, Allen, Gillooly, & Brown, 2006; Brown et al., 2004; Chu et al., 2016). Besides the influences of climatic factors, the soil fertility hypothesis suggests that biotic factors and aboveground biomass or productivity increase with soil nutrient availability (Quesada et al., 2012). However, many tropical forest species are often located on nutrient-poor soils (Toledo et al., 2012) and hence indirectly determining the forest diversity, structure, and functioning (Ali et al., 2019; Poorter et al., 2015).

The main objective of this study was to disentangle the direct and indirect roles of space, climate, edaphic, and biodiversity effects on aboveground biomass in natural tropical forests (Figure 1), thereby evaluating the relative effects and contribution of these abiotic and biotic factors on aboveground biomass. We mainly hypothesize that the space effect drives the longitudinal, latitudinal, and elevational patterns in climatic and edaphic factors, thereby directly and indirectly determining the relationships between biotic factors and aboveground biomass in natural tropical forests. We use a structural equation modelling (SEM) approach (Grace et al., 2016) to test hypothesized causal relationships among spatial, climatic, edaphic, and biotic factors of aboveground biomass, using data from 907 tropical forest plots in Hainan Island of Southern China. To this end, we address the following three major questions with corresponding specific hypotheses under the predictions of space-based multiple underlying ecological mechanisms in an integrative modelling (Figure 1).

First, how do longitudinal, latitudinal, and elevational gradients explain variations in climatic, edaphic, and biotic factors of aboveground biomass at regional scale (i.e., space effect)? We hypothesize that climatic, edaphic, and biotic factors of aboveground biomass vary along longitudinal, latitudinal, and elevational gradients and that aboveground biomass decreases along these spatial gradients under the general notion that forest productivity declines with latitudinal gradients (Gillman et al., 2015); that is, we term the 'space effect.' Second, how do climatic and edaphic factors drive biotic factors and aboveground biomass along longitudinal, latitudinal, and elevational gradients (i.e., climate and edaphic effects)? We hypothesize that

biotic factors and aboveground biomass increase with mean annual temperature, climatic water availability, and soil fertility under the processes of metabolic kinetics (Anderson et al., 2006), length of growing seasons (Ponce-Campos et al., 2013), and soil nutrients availability (Quesada et al., 2012), respectively. Third, how do biotic factors affect aboveground biomass along longitudinal, latitudinal, and elevational gradients (i.e. biodiversity effect)? We hypothesize that the niche complementarity effect drives the positive effects of species diversity, functional divergence, and individual tree size inequality on aboveground biomass and that functional dominance has a strong positive effect on aboveground biomass under the mass ratio effect (Conti & Díaz, 2013; Yuan, Wang, et al., 2018). We anticipate that this study may advance our understanding regarding ecosystem services, biodiversity conservation, forest management, and carbon storage under regional climate change.

2 | MATERIALS AND METHODS

2.1 | Study area, forest plots, and dataset

This study spanned a geographical area from 18°10′–20°10′N in latitude and 108°37′–111°03′E in longitude with elevation ranging between 1 and 1,819 m a.s.l. on the Hainan Island, in Southern China (Figure 2; Ali et al., 2018; Ali et al., 2019). The study area has distinct dry and wet seasons including typhoons. We collected geographical and biophysical data from 907 tropical forest plots (total sampling area of 145.23 ha). We selected those plots where trees are naturally recovered and being protected from clearcutting for more than 40 years (Lin et al., 2017; Figure 2). During April 2009–August 2017,
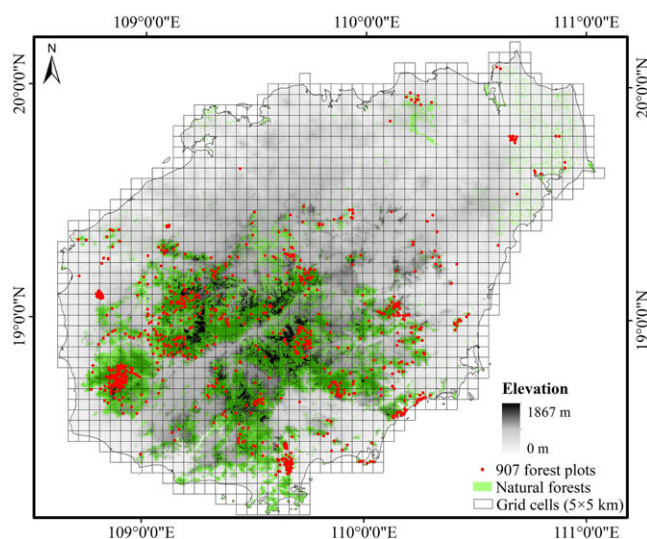

FIGURE 2 Map of vegetation cover in Hainan Island of Southern China, with the location of the 907 study plots. The intensity of the green colour indicates the amount of nature forest cover, the red dots indicate forest plots, whereas intensity of black colour indicates elevation gradients [Colour figure can be viewed at wileyonlinelibrary.com]

forest inventory was conducted. For explanation about the study area and forest plots, see Appendix SA.

2.2 | Quantification of variables

In this study, the conceptual model (Figure 1) included spatial (elevation, longitude, and latitude), climatic (water availability and temperature), edaphic (soil fertility), and biotic (species diversity, individual tree size variation, and functional divergence and dominance) factors for explaining aboveground biomass in natural large-scale tropical forests.

For each plot, latitude, longitude, and altitude (i.e., elevation) were determined by a handheld Geographic Positioning System. Using these spatial factors, climatic moisture index and mean annual temperature was derived and/or quantified to represent the overall atmospheric moisture availability and available energy or atmospheric heat stress influencing the performance of plants, respectively (Hogg, 1997; Poorter et al., 2017). As such, the average soil total exchangeable bases (i.e., indicator for soil fertility) of the topsoil and subsoil were used to quantify the nutrients available for plant growth (Ali, Lin, et al., 2018; Poorter et al., 2017).

For the quantification of biotic factors, we used four metrics of biodiversity including stand structure that were calculated for each plot, separately: Shannon's species diversity, coefficient of variation of individual tree heights (individual tree size inequality), functional dominance (i.e., community-weighted mean), and divergence (FDvar) of plant maximum height. Shannon's species diversity index was used to calculate species diversity, because this index accounts for both species richness and evenness within each plot (Ali & Yan, 2017a). For the quantification of functional divergence and dominance, plant maximum height was used (Conti & Díaz, 2013; Yuan et al., 2016), because plant maximum height may better predict the plant demographic processes such as growth, recruitment, survival, and mortality within a forest stand (Poorter et al., 2008). See Appendix SA for detailed information about the quantification of variables.

2.3 | Statistical analyses

To test the direct, indirect, and total causal effects of spatial, climatic, edaphic, and biotic factors on aboveground biomass (Figure 1), we constructed an SEM based on the following summarized hypothesized effects: (a) direct effects of spatial factors on climatic, edaphic, and biotic factors and aboveground biomass; (b) direct effects of climatic, edaphic, and biotic factors on aboveground biomass; (c) direct effects of climatic and edaphic factors on biotic factors; (d) indirect effects of spatial factors on aboveground biomass via climatic, edaphic, and biotic factors; and (e) indirect effects of climatic and edaphic factors on aboveground biomass via biotic factors. Here, we evaluated the goodness of fit of the SEM using chi-squared (χ^2) test, the goodness of fit index, the comparative fit index, and standardized root mean square residual (Hoyle, 2012). The SEM was employed using the *lavaan* package (Rosseel, 2012), which allows us to test the casual hypothesized paths among predictor (exogenous, endogenous, or mediator) variables and response variable in the conceptual model while calculating the direct, indirect, and total effects of predictor variables on response variable (Grace et al., 2016). The summary of variables used in SEM is presented in Table S1 in Appendix SB.

For the complementarity results to SEM (Poorter et al., 2017), we evaluated the simple regression relationship for each hypothesized path, as shown in Figure 1 (see Figures S1–S4; Table S2 in Appendix SB for a summary). However, the results from bivariate relationships may or may not be consistent to the results provided by SEM, probably due to the direct and indirect influences of other predictor variables (Poorter et al., 2017). We, therefore, used eight series of multiple linear regressions models by including the effects of multiple predictors on each of the eight response variables in SEM (see Figure 3), for example, (a) the multiple effects of spatial, climatic, edaphic, and biotic factors on aboveground biomass; (b) multiple effects of spatial factors on each of the climatic and edaphic factors; and (c) multiple effects of spatial, climatic, and edaphic factors on each of the biotic factors. We, then, evaluated a bivariate model's response (multiple linear regression model) against each predictor's marginal effect (i.e., while keeping all other explanatory variables remain constant), by using the *plotmo* package (Milborrow, 2015). Using the multiple linear regressions model for aboveground biomass, we evaluated the relative contribution of space, climate, edaphic, and biodiversity effects to the total explained variation in aboveground biomass through each factor and group (i.e., summation of contribution of factors within a group) analyses, using *relaimpo* package (Groemping, 2013). Pearson's correlation coefficient matrix was evaluated using *Hmisc* and *corrplot* packages (see Figure S5 in Appendix SB).

Prior to statistical analyses, all continuous numerical variables were natural-logarithm transformed and standardized for the purpose of normality and linearity. All statistical analyses were conducted in R 3.4.2 (R Development Core Team, 2017).

3 | RESULTS

The SEM had explained 58% of the variation in aboveground biomass while accounted for 60%, 31%, 31%, 20%, 18%, 10%, and 6% of the variation in mean annual temperature, functional dominance, species diversity, water availability, individual tree size inequality, functional divergence, and soil total exchangeable bases, respectively (Figure 3). Functional dominance had a strongest direct effect on aboveground biomass (β = 0.45, P < 0.001), followed by individual tree size inequality (β = 0.36, P < 0.001), longitude (β = −0.22, P < 0.001), water availability (β = 0.16, P < 0.001), elevation (β = −0.16, P < 0.001), mean annual temperature (β = −0.14, P = 0.002), soil total exchangeable bases (β = −0.07, P = 0.005), and latitude (β = −0.05, P = 0.044). As such, the relative contribution analyses showed that biodiversity effect, particularly functional dominance (20.89%) and individual tree size inequality (16.14%), had accounted for 40.77% of the explained variation in aboveground biomass (i.e., 58%), followed by climate effect (9.53%), space effect (7.29%), and edaphic effect (0.45%; Figure 4).
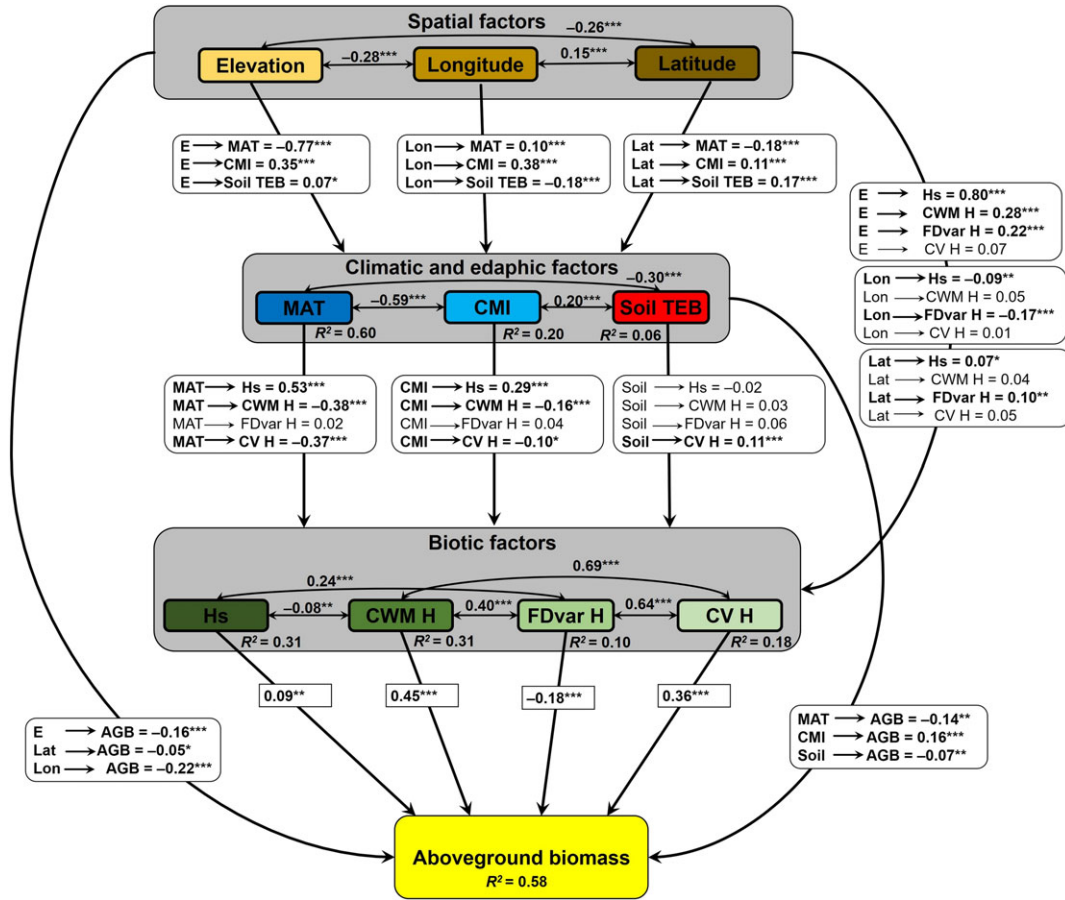
FIGURE 3 Structural equation model for linking spatial, climatic, edaphic, and biotic factors with each other and with aboveground biomass in tropical forests. The direct hypothesized paths are summarized within each box for the purpose to avoid the complexity of 45 regression paths in the model (see Table S3 for more details). For each path, the standardized regression coefficient with associated *P* value is shown (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). The significant standardized regression coefficients are indicated in bold text. Model-fit statistics: comparative fit index = 1.000; goodness of fit index = 1.000; standardized root mean square residual = 0.002; $df = 1$; χ^2 test = 0.21; $P = 0.644$; Akaike information criterion = 23828.18. E: elevation; CMI: climatic moisture index; CV H: coefficient of variation of tree height (individual tree size inequality); CWM H: community-weighted mean of pant maximum height (functional dominance); FDvar: functional divergence of plant maximum height; Hs: Shannon's species diversity; Lat: latitude; Lon: longitude; MAT: mean annual temperature; TEB: total exchangeable bases (soil fertility) [Colour figure can be viewed at wileyonlinelibrary.com]
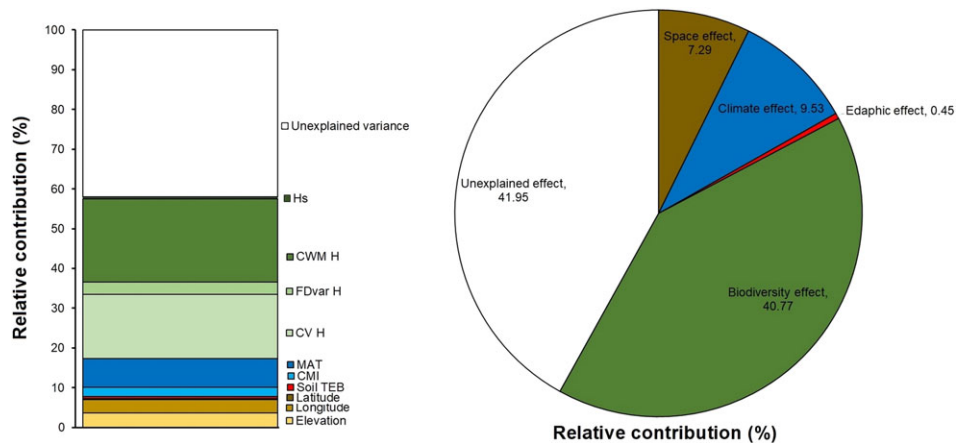

FIGURE 4 Relative contribution (in %) of each individual (stacked bar chart) and group (pie chart) factor to the explained variance in aboveground biomass of tropical forests. CMI: climatic moisture index; CV H: coefficient of variation of tree height (individual tree size inequality); CWM H: community-weighted mean of pant maximum height (functional dominance); MAT: mean annual temperature; TEB: total exchangeable bases [Colour figure can be viewed at wileyonlinelibrary.com]

Although the relative contribution of spatial, climatic, and edaphic factors was relatively less than biotic factors, these factors had influenced aboveground biomass through significant subtotal indirect effects via biotic factors (Figure 5). For example, space (i.e., longitude, latitude, and elevation) effect increased aboveground biomass indirectly via simultaneously differential direct changes (positive, negative, and non-significant) in climatic, edaphic, and biotic factors. More specifically, differential variations in mean annual temperature and climatic water availability along spatial gradients decreased aboveground biomass indirectly via two major biotic factors (i.e., functional dominance and individual tree size inequality). As such, subtotal indirect effects of mean annual temperature and climatic water availability decreased aboveground biomass through differential direct changes in biotic factors, but opposite was true for soil fertility. The total effects of longitude and temperature on aboveground biomass were significantly negative, indicating that the longitudinal gradients in temperatures shape aboveground biomass in studied tropical forests (Figure 5). We reported the specific results in Appendix SA for better understanding of ecological mechanisms linking spatial, climatic, and edaphic factors with each other and with aboveground biomass.

4 | DISCUSSION

In this study, we teased apart the direct and indirect roles of space effect, climate effect, edaphic effect, and biodiversity effect on aboveground biomass in tropical forests. We found that aboveground biomass was significantly related to the studied spatial, climatic, edaphic, and biotic factors, but biodiversity effect contributed largely to the explained variation in aboveground biomass. Although the relative contribution of spatial, climatic, and edaphic factors were relatively less, the direct and indirect roles of these factors suggest several ecological mechanisms through which biodiversity influenced aboveground biomass in large-scale tropical forests. Below, we discussed the main ecological mechanisms.

We found that aboveground biomass increased directly with increasing individual tree size inequality under the niche differentiation effect through tree sizes (Ali & Yan, 2017a; Yachi & Loreau, 2007) and that communities dominated by resource acquisition-related traits (e.g., functional dominance) rather than higher values of functional variety (e.g., functional divergence) had higher aboveground biomass as predicted by the mass ratio effect (Conti & Díaz, 2013;
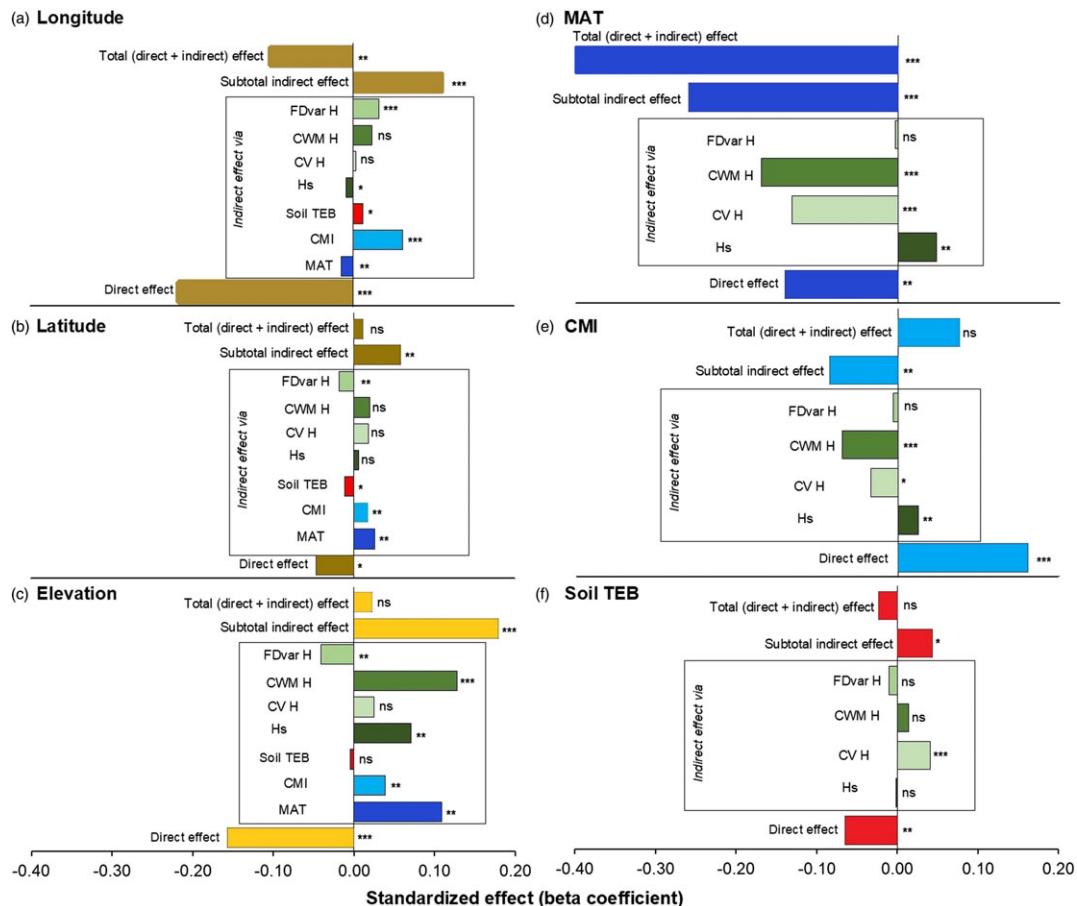

FIGURE 5 Standardized direct, indirect, and total effects of spatial (a-c), climatic (d-e), and edaphic (f) factors on aboveground biomass, based on the structural equation model in Figure 3. Climatic, edaphic and biodiversity factors were mediators for indirect effects of spatial factors on aboveground biomass (a-c), whereas only biodiversity factors were mediators for indirect effects of climatic and edaphic factors on aboveground biomass (d-f). Abbreviations of the variables are defined in Figure 3. ns: non-significant [Colour figure can be viewed at wileyonlinelibrary.com]

Yuan, Wang, et al., 2018). Not surprisingly, the observed negative direct relationship between functional divergence and aboveground biomass indicates that this negative direct effect is ultimately due to the high functional dominance of plant maximum height within diverse communities (Conti & Díaz, 2013). However, we found that Shannon's species diversity had relatively weak positive direct effect on aboveground biomass, indicating that energy–diversity (i.e., temperature) relationship controls the species coexistence because temperature affects the biotic factors and thus aboveground biomass (Currie et al., 2004; Michaletz et al., 2018). For example, we found that mean annual temperature increased species diversity but decreased functional dominance and individual tree size inequality and that mean annual temperature increased along longitudinal gradients of the studied forests. The positive diversity–energy of our studied tropical forests resulted primarily from the longitudinal gradients in temperature (Currie et al., 2004; Gillman et al., 2015; Hillebrand, 2004), showing a predominant positive relationship between diversity and productivity (Gillman et al., 2015; Liang et al., 2016).

In this study, the positive relationships of species diversity with mean annual temperature and climatic water availability are attributable to the integrated hypothesis of evolutionary rates and biotic interactions or even the metabolic theory (Brown et al., 2004; Colwell & Hurtt, 1994; Currie et al., 2004; Gillman & Wright, 2014; Rohde, 1992). However, our results also supported the tolerance–diversity, drought–mortality, and heat–mortality hypotheses because climatic water availability and mean annual temperature increased species diversity but decreased functional dominance and individual tree size inequality (Allen et al., 2010; Kalin-Arroyo, Squeo, Armesto, & Villagran, 1988; Phillips et al., 2010). Because of the spatial factors gradients, which were strongly related with mean annual temperature and climatic water availability, the results also provided strong support to the mid-domain effect as an explanation for patterns in biotic factors (Colwell & Hurtt, 1994). Furthermore, the water–energy dynamics hypothesis was also supported because all biotic factors with exception of functional divergence were simultaneously affected by climatic water availability and temperature and hence direct positive relationships of these biotic factors with aboveground biomass (O'Brien, 2006). Not surprisingly, the negative correlation between climatic water availability and mean annual temperature, which relates water and energy or drought and heat, proved to be the strongest correlate of biotic factors and aboveground biomass in the studied forests (Ali, Lin, et al., 2018; Brookshire & Weaver, 2015; Ciais et al., 2005; Gillman & Wright, 2014).

In this study, the negative direct effects of spatial factors on aboveground biomass support the general notion that forest productivity (e.g., primary productivity and leaf-litter production) declines directly with spatial factors (e.g., latitudinal) gradients (Gillman et al., 2015; Keeling & Phillips, 2007). However, the patterns of aboveground biomass or productivity are ultimately dependent on climatic, edaphic, and biotic factors across spatial gradients because plant growth is spatially controlled by climatic water, energy, or solar radiations and soil nutrients availability (Gillman et al., 2015; Kicklighter et al., 1999; Quesada et al., 2012). As such, we observed

that climatic water availability increased with all three spatial factors, whereas mean annual temperature had mixed relationships with the spatial factors in the studied region. Specifically, we found that temperature and climatic water availability decreased aboveground biomass indirectly via functional dominance and individual tree size inequality but increased via species diversity. The direct effects of climatic factors include their influences on the physiological and environmental drivers of plant growth, which are directly controlled by climatic water availability and temperature, including the kinetics of plant metabolism (Brown et al., 2004; Huxman et al., 2004; Lichstein et al., 2014). For example, heat and drought can decrease ecosystem functioning directly within a given site or region (Ciais et al., 2005), but they can also influence ecosystem functioning indirectly via species adaptions in terms of biotic factors (Michaletz et al., 2018; Poorter et al., 2017). As such, we found that high species diversity is associated with tolerance to climate change in terms of heat, whereas high functional dominance is associated with both heat and drought resistance. In addition, the observed negative relationship between soil fertility and aboveground biomass is not directly attributable to the nutrient-poor soils (Ali, Lohbeck, & Yan, 2018) but might be indirectly attributable to the high individual tree size inequality on nutrient-rich soils that increases species coexistence and hence higher aboveground biomass in the community (e.g., Ali & Yan, 2017a; Poorter et al., 2017).

This study has important implications for forest management, biodiversity conservation, and land development in the context of REDD + initiatives. Biotic factors are more than merely species richness or diversity (Poorter et al., 2017), as we show that functional dominance and individual tree size inequality had strong positive relationships with aboveground biomass, indicating that biotic factors strongly shape ecosystem functioning (Yuan, Wang, et al., 2018). For example, our studied forest plots with high variations in tree sizes (without interference from space effect but on high fertile soils) also tend to have a high aboveground biomass, indicating that areas with a high carbon storage capability also have a potential for high biodiversity conservation, land development, and ecosystem services (Ali et al., 2019; Poorter et al., 2015; Villa et al., 2018). We also show that functional dominance on high elevational forest is the strongest main biotic driver of aboveground biomass, indicating that enhancing carbon stock requires big-sized or large biomass trees (Cavanaugh et al., 2014; Lutz et al., 2018), so to speed up forest recovery in degraded forest lands, fast-growing tall stature species might be planted and encouraged (Lohbeck, Poorter, Martinez-Ramos, & Bongers, 2015; Villa et al., 2018).

5 | CONCLUSIONS

By disentangling the space, climate, edaphic, and biodiversity effects on aboveground biomass in an integrative modelling, we show that functional dominance and individual tree size inequality are the major biotic divers of aboveground biomass, accounting for more than half of the explained variation in aboveground biomass of the studied

tropical forests. These major biotic drivers of aboveground biomass are strongly influenced by mean annual temperature, climatic water availability, and soil fertility, which in turn determine aboveground biomass indirectly. As such, all these abiotic and biotic factors are strongly influenced by space effect, suggesting that the positive species–energy, diversity–biomass, and water–energy relationships of our studied tropical forests resulted primarily from longitudinal gradients. We argue that, despite biotic interactions may be playing a strong direct role in driving aboveground biomass, the direct and indirect roles of space effect on climatic and edaphic factors are also important for explaining the relationships between biotic factors and aboveground biomass under the predictions of several abiotic-based hypotheses. From the practical point of view, this study suggests that conserving biodiversity and enhancing forest functioning along latitudinal, longitudinal, and elevational gradients are important for forest land development under the context of REDD+ initiatives.

AUTHOR CONTRIBUTIONS

A. A. and H. S. J. conceived the research idea. S. L. L., J. K. H., F. M. K., J. H. Y., and H. S. J. collected the data. A. A. performed data and statistical analyses. S. L. L. created map of the study area. A. A. wrote the paper with great contributions from S. L. L., J. K. H., and H. S. J. All co-authors reviewed the paper.

DATA ACCESSIBILITY

A summary of the studies species is listed in Appendix SC. More information about dataset is available upon reasonable request to the authors.

ORCID

Arshad Ali https://orcid.org/0000-0001-9966-2917

REFERENCES

Ali, A., Lin, S.-L., He, J.-K., Kong, F.-M., Yu, J.-H., & Jiang, H.-S. (2018). Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. *Science of The Total Environment*, 647, 1211–1221. https://doi.org/10.1016/j.scitotenv.2018.08.072

Ali, A., Lin, S.-L., He, J.-K., Kong, F.-M., Yu, J.-H., & Jiang, H.-S. (2019). Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests. *Forest Ecology and Management*, 432, 823–831. https://doi.org/10.1016/j.foreco.2018.10.024

Ali, A., Lohbeck, M., & Yan, E.-R. (2018). Forest strata-dependent functional evenness explains whole-community aboveground biomass through opposing mechanisms. *Forest Ecology and Management*, 424, 439–447. https://doi.org/10.1016/j.foreco.2018.05.015

Ali, A., & Yan, E.-R. (2017a). The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest. *Forest Ecology and Management*, 401, 125–134. https://doi.org/10.1016/j.foreco.2017.06.056

Ali, A., & Yan, E.-R. (2017b). Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. *Ecological Indicators*, 83, 158–168. https://doi.org/10.1016/j.ecolind.2017.07.054

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderson, K. J., Allen, A. P., Gillooly, J. F., & Brown, J. H. (2006). Temperature-dependence of biomass accumulation rates during secondary succession. *Ecology letters*, 9, 673–682. https://doi.org/10.1111/j.1461-0248.2006.00914.x

Brookshire, E. N. J., & Weaver, T. (2015). Long-term decline in grassland productivity driven by increasing dryness. *Nature Communications*, 6, 7148. https://doi.org/10.1038/ncomms8148

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O. L., ... Naeem, S. (2005). Species loss and aboveground carbon storage in a tropical forest. *Science*, 310, 1029–1031. https://doi.org/10.1126/science.1117682

Cavanaugh, K. C., Gosnell, J. S., Davis, S. L., Ahumada, J., Boundja, P., Clark, D. B., ... Andelman, S. (2014). Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecology and Biogeography*, 23, 563–573. https://doi.org/10.1111/geb.12143

Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., & Sack, L. (2016). Does climate directly influence NPP globally? *Global change biology*, 22, 12–24. https://doi.org/10.1111/gcb.13079

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., ... Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437, 529.https://doi.org/10.1038/nature03972–533.

Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious rapoport effect. *The American Naturalist*, 144, 570–595. https://doi.org/10.1086/285695

Conti, G., & Díaz, S. (2013). Plant functional diversity and carbon storage—An empirical test in semi-arid forest ecosystems. *Journal of Ecology*, 101, 18–28. https://doi.org/10.1111/1365-2745.12012

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J.-F., Hawkins, B. A., ... Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters*, 7, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x

FAO (2014) *State of the world's forests 2014*. Enhancing the socioeconomic benefits from forests. Food and Agriculture Organization of the United Nations Statistics Division Rome.

Gillman, L. N., & Wright, S. D. (2014). Species richness and evolutionary speed: The influence of temperature, water and area. *Journal of Biogeography*, 41, 39–51. https://doi.org/10.1111/jbi.12173

Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, 24, 107–117. https://doi.org/10.1111/geb.12245

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., ... Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393. https://doi.org/10.1038/nature16524

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86, 902–910.

Groemping, U. (2013) Relative importance of regressors in linear models.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211. https://doi.org/10.1086/381004

Hogg, E. H. (1997). Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology*, 84, 115–122. https://doi.org/10.1016/s0168-1923(96)02380-5

Hoyle, R. H. (2012). *Handbook of structural equation modeling*. New York, NY, USA: Guilford Press, New York City.

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., ... Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651.https://doi.org/10.1038/nature02561–654.

Kalin-Arroyo, M. T., Squeo, F. A., Armesto, J. J., & Villagran, C. (1988). Effects of aridity on plant diversity in the Northern Chilean Andes: Results of a natural experiment. *Annals of the Missouri Botanical Garden*, 75, 55–78. https://doi.org/10.2307/2399466

Keeling, H. C., & Phillips, O. L. (2007). The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, 16, 618–631. https://doi.org/10.1111/j.1466-8238.2007.00314.x

Kicklighter, D. W., Bondeau, A., Schloss, A. L., Kaduk, J., McGuire, A. D., & Intercomparison, T.P.O.F.T.P.N.M (1999). Comparing global models of terrestrial net primary productivity (NPP): Global pattern and differentiation by major biomes. *Global Change Biology*, 5, 16–24. https://doi.org/10.1046/j.1365-2486.1999.00003.x

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., ... Reich, P. B. (2016). Positive biodiversity–productivity relationship predominant in global forests. *Science*, 354.https://doi.org/10.1126/science.aaf8957, aaf8957.

Lichstein, J. W., Golaz, N.-Z., Malyshev, S., Shevliakova, E., Zhang, T., Sheffield, J., ... Pacala, S. W. (2014). Confronting terrestrial biosphere models with forest inventory data. *Ecological Applications*, 24, 699–715. https://doi.org/10.1890/13-0600.1

Lin, S., Jiang, Y., He, J., Ma, G., Xu, Y., & Jiang, H. (2017). Changes in the spatial and temporal pattern of natural forest cover on Hainan Island from the 1950s to the 2010s: Implications for natural forest conservation and management. *PeerJ*, 5, e3320. https://doi.org/10.7717/peerj.3320

Lohbeck, M., Bongers, F., Martinez-Ramos, M., & Poorter, L. (2016). The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. *Ecology*, 97, 2772–2779. https://doi.org/10.1002/ecy.1499

Lohbeck, M., Poorter, L., Martinez-Ramos, M., & Bongers, F. (2015). Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, 96, 1242–1252. https://doi.org/10.1890/14-0472.1

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., ... Zimmerman, J. K. (2018). Global importance of large-diameter trees. *Global Ecology and Biogeography*, 27, 849–864. https://doi.org/10.1111/geb.12747

Michaletz, S. T., Kerkhoff, A. J., & Enquist, B. J. (2018). Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, 27, 166–174. https://doi.org/10.1111/geb.12685

Milborrow, S. (2015) Plot a model's response and residuals.

O'Brien, E. M. (2006). Biological relativity to water–energy dynamics. *Journal of Biogeography*, 33, 1868–1888. https://doi.org/10.1111/j.1365-2699.2006.01534.x

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, 20, 170–180. https://doi.org/10.1111/j.1466-8238.2010.00592.x

Phelps, J., Webb, E. L., & Adams, W. M. (2012). Biodiversity co-benefits of policies to reduce forest-carbon emissions. *Nature Climate Change*, 2, 497. https://doi.org/10.1038/nclimate1462

Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E., Lloyd, J., ... Vilanova, E. (2010). Drought–mortality relationships for tropical forests. *New Phytologist*, 187, 631–646. https://doi.org/10.1111/j.1469-8137.2010.03359.x

Ponce-Campos, G. E., Moran, M. S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T. E., ... Starks, P. J. (2013). Ecosystem resilience despite large-scale altered hydroclimatic conditions. *Nature*, 494, 349.https://doi.org/10.1038/nature11836–352.

Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B., Finegan, B., ... Peña-Claros, M. (2017). Biodiversity and climate determine the functioning of Neotropical forests. *Global Ecology and Biogeography*, 26, 1423–1434. https://doi.org/10.1111/geb.12668

Poorter, L., van der Sande, M. T., Thompson, J., Arets, E. J., Alarcón, A., Álvarez-Sánchez, J., ... Peña-Claros, M. (2015). Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography*, 24, 1314–1328. https://doi.org/10.1111/geb.12364

Poorter, L., Wright, S. J., Paz, H., Ackerly, D., Condit, R., Ibarra-Manríquez, G., ... Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, 89, 1908–1920. https://doi.org/10.1890/07-0207.1

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., ... Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, 9, 2203–2246. https://doi.org/10.5194/bg-9-2203-2012

R Development Core Team (2017). *R version 3.4.2. R Foundation for statistical computing*. Austria: Vienna.

Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos*, 65, 514–527. https://doi.org/10.2307/3545569

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48, 1–36. https://doi.org/10.18637/jss.v048.i02

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845. https://doi.org/10.1126/science.1060391

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., ... Poorter, L. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, 100, 253–263. https://doi.org/10.1111/j.1365-2745.2011.01890.x

Van de Perre, F., Willig, M. R., Presley, S. J., Bapeamoni Andemwana, F., Beeckman, H., Boeckx, P., ... Verheyen, E. (2018). Reconciling biodiversity and carbon stock conservation in an Afrotropical forest landscape. *Science Advances*, 4, eaar6603. https://doi.org/10.1126/sciadv.aar6603

Villa, P. M., Martins, S. V., de Oliveira Neto, S. N., Rodrigues, A. C., Martorano, L. G., Monsanto, L. D., ... Gastauer, M. (2018).

Intensification of shifting cultivation reduces forest resilience in the northern Amazon. *Forest Ecology and Management*, 430, 312–320. https://doi.org/10.1016/j.foreco.2018.08.014

Weiser, M. D., Michaletz, S. T., Buzzard, V., Deng, Y., He, Z., Shen, L., … Kaspari, M. (2018). Toward a theory for diversity gradients: The abundance–adaptation hypothesis. *Ecography*, 41, 255–264. https://doi.org/10.1111/ecog.02314

Weiser, M. D., Swenson, N. G., Enquist, B. J., Michaletz, S. T., Waide, R. B., Zhou, J., & Kaspari, M. (2018). Taxonomic decomposition of the latitudinal gradient in species diversity of North American floras. *Journal of Biogeography*, 45, 418–428. https://doi.org/10.1111/jbi.13131

Yachi, S., & Loreau, M. (2007). Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, 10, 54–62. https://doi.org/10.1111/j.1461-0248.2006.00994.x

Yuan, Z., Ali, A., Wang, S., Gazol, A., Freckleton, R., Wang, X., … Loreau, M. (2018). Abiotic and biotic determinants of coarse woody productivity in temperate mixed forests. *Science of The Total Environment*, 630, 422–431. https://doi.org/10.1016/j.scitotenv.2018.02.125

Yuan, Z., Wang, S., Ali, A., Gazol, A., Ruiz-Benito, P., Wang, X., … Loreau, M. (2018). Aboveground carbon storage is driven by functional trait composition and stand structural attributes rather than biodiversity in temperate mixed forests recovering from disturbances. *Annals of Forest Science*, 75, 67. https://doi.org/10.1007/s13595-018-0745-3

Yuan, Z., Wang, S., Gazol, A., Mellard, J., Lin, F., Ye, J., … Loreau, M. (2016). Multiple metrics of diversity have different effects on temperate forest functioning over succession. *Oecologia*, 182, 1175–1185. https://doi.org/10.1007/s00442-016-3737-8

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.