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Species *α*-diversity promotes but *β*-diversity restricts aboveground biomass in tropical forests, depending on stand structure and environmental factors

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Abstract Forest plays a vital role in the global biogeochemical cycles through a high rate of carbon sequestration and harboring biodiversity. However, local species diversity is declining while also becoming increasingly homogenized across communities. Although effects of local biotic processes (e.g., species *α*-diversity and stand structural heterogeneity) and environmental factors on aboveground biomass (AGB) have been widely tested, there is a huge knowledge gap for the effect of regional biotic processes (i.e., taxonomic and functional *β*-diversity) in forests. Here, we hypothesized that regional and local environmental factors along with biotic processes jointly regulate AGB through species shifts in tropical forests. Using piecewise structural equation modeling (pSEM), we linked climatic water availability, soil fertility, stand structural heterogeneity (either tree DBH inequality, height inequality, or stand density), species *α*-diversity, taxonomic or functional *β*-diversity (and its two components; *β*-turnover and *β*-richness), and AGB across 189 inventory plots in tropical forests of Sri Lanka. Soil fertility and climatic water availability shaped local and regional biotic processes. Stand structural heterogeneity promoted species *α*-diversity but declined *β*-diversity (but increased *β*-taxonomic turnover). Species *α*-diversity and stand structural heterogeneity promoted AGB whereas taxonomic and functional *β*-diversity declined (but *β*-taxonomic turnover increased) AGB. The relationships of AGB with species *α*-diversity and *β*-diversity varied from significant to nonsignificant positive depending on the specific combinations of stand structural heterogeneity metrics used. This study shows that local biotic processes could increase AGB due to the local and regional niche complementarity effect whereas the regional biotic processes could restrict

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AGB due to the regional selection or functional redundancy effect under favorable environmental conditions. We argue that biotic homogenization, as well as drought conditions, may have strong divergent impacts on forest functions and that the impacts of tree diversity loss may greatly reduce carbon sequestration.

Introduction

Forest is the main component of terrestrial ecosystems and plays a vital role in the global biogeochemical cycles through a high rate of carbon sequestration and harboring biodiversity (Pan et al. 2011; Boisvenue and Running 2006). Among different forest ecosystems, tropical forests store a large amount of carbon due to hyperdiverse and complex vegetation structure as well as longer growing seasons (Poorter et al. 2017; Cavanaugh et al. 2014; ter Steege et al. 2013). This situation is further complicated by multiple metrics of biodiversity and stand structural heterogeneity which could also explain aboveground biomass (AGB) differently in forest ecosystems (van der Plas 2019; Ali 2019). However, most of the previous studies have shown that climate and soil can also control the relationships of AGB with stand structural complexity and biodiversity in forest ecosystems (Poorter et al. 2017; Ali et al. 2019; Ratcliffe et al. 2017; Jucker et al. 2016). Although the effects of local biotic processes, such as taxonomic α-diversity (i.e., species richness within a forest plot) and stand structural heterogeneity (i.e., tree size inequality within a plot) on AGB have been evaluated across several forest ecosystems, few studies have attempted to explore the effects of regional biotic patterns, such as species β-diversity (i.e., species turnover and richness differences from species pool) in forests (Mori et al. 2018; van der Plas 2019).

An increasing number of studies have shown how local biotic processes can help to increase AGB in forest ecosystems (van der Plas 2019; Liang et al. 2016), and such understanding is much more important to recognize the influence of biodiversity loss in the context of global climate change (Naeem 2002). Three main ecological mechanisms have received great attention in explaining the observed higher AGB due to the local biotic processes in forests: the complementarity effect, the mass ratio effect, and the selection or sampling effect (van der Plas 2019; Ali 2019). The complementarity effect occurs when a highly biodiverse and structurally complex forest is better equipped to use limited resources more efficiently due to the variety of complementary traits of coexisting species (Lasky et al. 2014; Poorter et al. 2017; Ali et al. 2019). The mass ratio effect occurs

when traits of the dominant species regulate AGB in forests due to the functional dominance or species-specific functional strategy, i.e., conservative or acquisitive (Prado-Junior et al. 2016). The selection or sampling effect occurs when a highly productive or functioning species is introduced into a community from a regional species pool that could be able to make use of the resources available in highly biodiverse and complex stand structural forests (Morin et al. 2011). Yet, much debate has been circled on the roles and functions of species α-diversity and stand structural heterogeneity in maintaining AGB in forests (van der Plas 2019; Ali 2019), but so far, relatively less debate has been focused on the roles and functions of β-diversity (but see van der Plas et al. 2016; Silva Pedro et al. 2016). For example, abiotic heterogeneity is typically higher at a large scale as compared to a small scale, and thus, different species under different abiotic conditions may shape AGB through different ecological mechanisms (Chu et al. 2019; Loreau et al. 2001; Poorter et al. 2017). The taxonomic and functional β-diversity could enhance our understanding of the ecological mechanisms driving variations in biodiversity and their influences on AGB (Mori et al. 2018). Focusing on regional biotic processes could be especially important in highly biodiverse and complex stand structural tropical forest communities that are probably subjected to regional environmental fluctuations and local stand structural heterogeneity (Ehbrecht et al. 2021; ter Steege et al. 2013).

Regional biotic patterns (e.g., taxonomic and functional β-diversity) are usually dependent on local and regional environmental factors which are controlled by the spatial scale and extent (Mori et al. 2018). However, regional environmental factors (e.g., climate) not only determine the regional-scale patterns of species distribution (i.e., β-diversity) but also affect the local-scale i.e., α-diversity patterns (van der Plas et al. 2016). In addition, local environmental factors (e.g., availability of soil fertility) and stand structural heterogeneity can shape β-diversity because patterns of α-diversity are usually controlled by local-scale community assembly processes (Villa et al. 2021; Ali 2019; van der Plas et al. 2016). However, β-diversity can be partitioned into two distinct components, i.e., (1) turnover which reflects species replacement between sites along the environmental gradients; and (2) richness or nestedness which reflects species loss or gain by triggering the biota of species-poor sites to become biota's subsets at species-rich sites (Legendre 2014; Mori et al. 2018). On the one hand, it is usually expected that dominant species are contributing to the β-richness across communities, thereby shaping forest functions (e.g., AGB) due to the selection effect (i.e., the mass ratio effect) at larger spatial scales (Mori et al. 2018). On the other hand, different species are contributing to β-turnover under different environmental conditions by complementing each other for the efficient utilization of

the available resources, and as a result, increasing the number of niche spaces occupied across communities (Hautier et al. 2018). Therefore, *β*-turnover can be attributed to the niche complementarity effect for shaping forest functions at larger spatial scales (Mori et al. 2018). However, functionally dominant species may also vary across communities, and hence, *β*-turnover may shape AGB due to the selection or mass ratio effect rather than the niche complementarity effect at smaller spatial scales (Hector and Bagchi 2007). In other words, local and regional environmental factors can cause local and regional biotic heterogeneity within and across communities. Therefore, the by chance inclusion of highly functioning or productive species may increase AGB due to the selection effect, or a wide range of species having different functional traits can increase AGB because of the niche complementarity effect at both larger and smaller spatial scales (Hector and Bagchi 2007; Mori et al. 2018; van der Plas 2019).

Environmental factors and stand structural heterogeneity can influence AGB not only directly but also through induced changes in local biotic processes (Poorter et al. 2017; Ali et al. 2019). While the majority of previous studies reported the direct positive effects of stand structural heterogeneity on AGB and productivity, some have also found negative or non-significant effects (Ali 2019). However, an increasing number of studies showed that high inequality in stand density and tree-size dimension can increase AGB directly or indirectly via taxonomic *α*-diversity due to the high canopy packing, which allows interactions between component species and their individuals in a community to capture and use light efficiently (Ali et al. 2020; Jucker et al. 2016; Chiang et al. 2016). This ecological mechanism provides additional support to the species complementarity processes, i.e., forest communities having higher levels of tree stratification and canopy packing can enhance the functioning of forests due to the efficient and complementarity uses of limited resources (Yachi and Loreau 2007; Williams et al. 2017; Ali 2019). As such, a growing body of evidence showed that climatic water availability increases AGB directly as well as through induced changes in local biotic processes, whereas several inconsistencies existed across studies on the influence of soil fertility (Poorter et al. 2017; Ali et al. 2019; Bordin et al. 2021; Chiang et al. 2016; Yuan et al. 2019). Nevertheless, the general understanding is that AGB increases with the greater climatic water availability due to the longer growing season length, i.e., favorable climatic condition for plant growth, because it is plausible that drought condition increases tree mortality and shapes species distribution patterns (Toledo et al. 2012; Engelbrecht et al. 2007). Also, the general notion is that soil fertility increases AGB due to the higher availability of soil resources that are important for plant growth, but it can also induce higher mortality rates due to strong interspecific

(a) Local and regional biotic processes
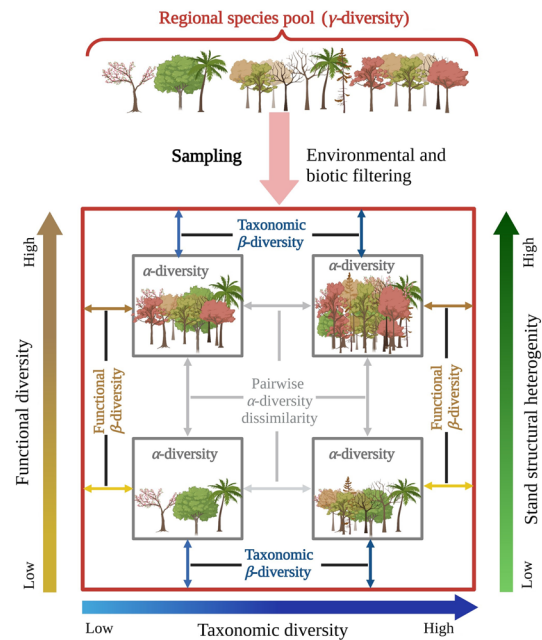
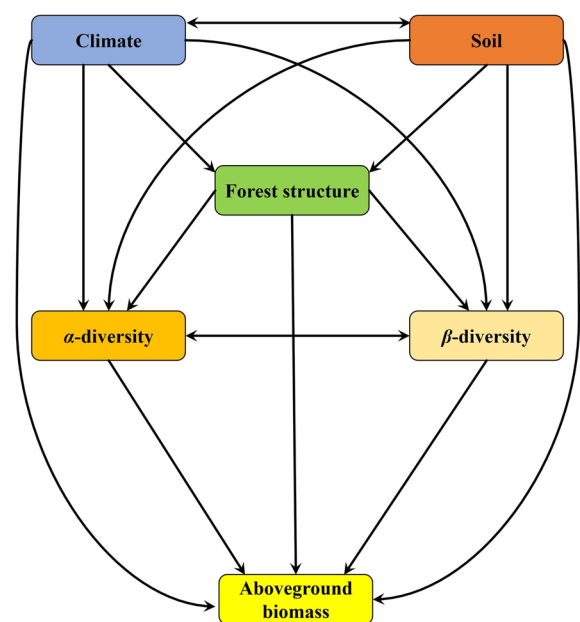

(b) Conceptual model

Fig. 1 Schematic presentation for local and regional biotic processes **a** and conceptual model **b**. **a** A theoretical graphical concept for explaining the community assembly processes, and for the quantification of taxonomic *α*-diversity (i.e., rarefied species richness in a plot), stand structural heterogeneity (i.e., stand density and tree size inequality in a plot), and importantly for taxonomic and functional *β*-diversity (for each plot) through pairwise dissimilarity from a regional species pool (i.e., *γ*-diversity; pooled 189 forest plots data in our case). **b** A conceptual model is developed based on ecological mechanisms for linking environmental factors, local and regional biotic processes, and aboveground biomass (AGB) in tropical forests

competition for acquiring similar resources (Yuan et al. 2019; Quesada et al. 2012). Our understanding, however, is limited to the effects of regional and local environmental factors on local biotic processes and then on AGB as compared to the regional biotic processes.

In this study, we aim to tease apart the combined effects of environmental conditions, stand structural heterogeneity, taxonomic α-diversity, and (either taxonomic or functional) β-diversity (and its associated components) on AGB in tropical forests (Fig. 1). Using the forest inventory datasets across 189 inventory plots, along with environmental factors in the tropical forest of Sri Lanka, we address the following research questions and hypothesis through the use of piecewise structural equation modeling (pSEM; see a conceptual model in Fig. 1b). (1) How do local (i.e., soil fertility) and regional (i.e., climatic water availability) environmental factors influence local (stand structural heterogeneity and species α-diversity) and regional (β-diversity) biotic patterns, and AGB? (2) How does stand structural heterogeneity through changes in tree-size dimension inequity and stand density control the relationships of AGB with local and regional biotic processes? (3) How do regional biotic processes through changes in taxonomic and functional β-diversity and their two associated components influence the relationships of AGB with local biotic processes? and (4) What is the main biotic driver or processes—local (i.e., α-diversity and stand structural heterogeneity) or regional (β-diversity)—of AGB? We hypothesize that regional and local environmental factors along with biotic processes jointly regulate AGB through species shifts in tropical forests.

Materials and methods

Study area and forest plots

This study was carried out across the central and southern regions of Sri Lanka, covering major climatic zones, i.e., dry, intermediate, and wet. Sri Lanka's climate is influenced by two major tropical monsoon spells, i.e., the first from May to September and the second from December to February. Vegetation in the studied region mainly comprises dry to wet tropical forests, with a mean annual temperature and precipitation ranging from $15\,°C - 28\,°C$ and $1250 - 5100$ mm, respectively, depending upon the regional topography. The soil in the region is generally primarily acidic with a pH ranging from 4.7–6.4 (Mattsson et al. 2016; Ali et al. 2020).

Forest inventory datasets across 189 forest plots were collected by stratified randomly selecting forest plots while covering possible gradients in both local and regional environmental factors (Fig. S1). To do so, we considered different forest types based on the topography and climatic water availability. Forests in the studied region have been disturbed previously by natural and anthropogenic activities, resulting in undisturbed, degraded, and secondary forests. To cater for heterogeneity in present forest quality, we excluded severely deteriorated forest plots, and hence, considered those plots with limited observations of current disturbances or with secondary preserved status. Tree individuals with a diameter at breast height (DBH) ≥ 3 cm were measured within each plot (which varies between 0.0225 and 0.2000 ha). By doing so, we measured tree height, DBH, and name of the tree species, and tried our best to identify the major part of the tree individuals (i.e., approximately 90%) within each plot by following standard forest inventory research protocols (Cornelissen et al. 2003). In total, 15,451 stems of 354 species have been measured during inventory across 189 forest plots.

Environmental factors—climatic water availability and soil fertility

In this study, we used climatic moisture index (CMI, mm yr^{-1}) and soil cation exchange capacity (CEC: cmol kg^{-1}) as the best indicators of climate (regional) and soil (local) conditions, respectively. Most of the previous studies in tropical regions including Sri Lankan forests have suggested that CMI and soil CEC are the best predictors of forest diversity, structure, and functions (Poorter et al. 2017; Ali et al. 2020; O'Brien et al. 2000). We retrieved mean annual potential evapotranspiration and precipitation data at a spatial resolution of the 30 s for each forest plot using the Global ET0 Climate database v2 (Trabucco and Zomer 2019) and the WorldClim database (Fick and Hijmans 2017). We, then, quantified CMI by subtracting mean annual potential evapotranspiration from mean annual precipitation to constitute the climatic water availability. Higher values of CMI indicate higher plant water availability (Hogg 1997). For soil CEC, Regridded Harmonized World Soil Database v1.2 was used to extract the values at two soil depths, i.e., $0 - 30$ and $30 - 100$ cm, at 0.05-degree spatial resolution, and then, the mean CEC value was used for each forest plot (Wieder 2014). We extracted and processed CMI and CEC values using the *rgdal*, *raster*, *sp*, and *ncdf4* packages in R statistical software.

Stand structural heterogeneity, tree species α-diversity, β-diversity, and AGB

Stand structural heterogeneity was quantified based on three simple indices, i.e., stand density (SD), tree height inequality (CVH), and DBH inequality (CVD). Stand density was defined as the number of tree individuals per hectare (i.e., SD ha^{-1}). We quantified plot-wise individual tree height and DBH inequality through the coefficient of variance

(i.e., CV = standard deviation divided by mean multiplied by 100, i.e., represented in percentage) as a proxy for tree-size dimension inequality representing the realized tree-sizes differences. We used stand density, tree height inequality, and DBH inequality as the measures of stand structural heterogeneity because these indices have been recognized as the potential predictors of AGB through canopy packing and niche differentiation mechanisms in forests (Ali 2019; Chiang et al. 2016; Clark 2010; Yachi and Loreau 2007). Species *α*-diversity was quantified based on species rarefaction curves instead of counting the observed species because rarefaction counts species richness based on the structure of rarefaction curves. Also, the rarefied species index solves the multicollinearity issues, particularly by addressing the confounding influences of stand density and plot size on species diversity patterns (Poorter et al. 2017).

The species taxonomic and functional *β*-diversity indices were calculated based on species abundance and standardized functional trait values by computing the pairwise differences between a specific forest plot and the regional species pool (i.e., the pooled data representing gamma diversity; *γ*-diversity; see Fig. 1a), through the Jaccard index, using the *beta* function from the BAT package (Cardoso et al. 2015). The functional *β*-diversity was quantified using the mean trait values of two important plant functional traits (i.e., plant maximum height and wood density) representing species growth strategies. The *beta* function results in two distance metrics for each taxonomic and functional *β*-diversity pattern i.e., partitioning of *β*-diversity into species turnover (β_{Tover}) and species richness (β_{Rich}), whereas *β*-diversity in total (β_{Tot}) is the sum of β_{Tover} and β_{Rich}. The beta turnover reflects species replacement in a specific plot, whereas *β*-richness or *β*-nestedness reflects species loss or gain (richness differences) by a specific plot as a result of biotic or environmental filtering (Cardoso et al. 2014; Podani and Schmera 2011; Legendre 2014; Mori et al. 2018). Therefore, partitioning of the total *β*-diversity into *β*-turnover and *β*-richness is much important for understanding the influences of regional biotic processes on AGB (Mori et al. 2018).

The AGB of an individual tree was quantified using the broadly-used pantropical allometric equation (Eq. 1):

$$\text{AGB} = 0.0673 \times (\rho \times \text{DBH}^2 \times \text{H})^{0.976} \quad (1)$$

that uses tree DBH, height (H), and species' wood density (ρ) as the model input parameters (Chave et al. 2014). We used the total AGB of all individual trees present within each forest plot as the response variable (i.e., AGB in megagram per hectare; Mg ha^{-1}) because it best indicates the total aboveground carbon stock in the woody parts of forests. The species' wood densities were retrieved from the renowned

worldwide wood density databases (Reyes et al. 1992; Zanne et al. 2009).

Statistical analyses

We used pSEM to test the hypothesized paths and related ecological theories to answer the research questions and hypothesis in a single model, by combined effects of environmental conditions, stand structural heterogeneity, species *α*- and *β*-diversity patterns (either taxonomic or functional) on AGB. However, we used boxplots to assess the differences in variables between plot sizes. In doing so, we grouped plot sizes into small (i.e., ranging between 0.0225 and 0.0625 ha; 72 plots) and large (i.e., 0.09 to 0.20 ha; 117 plots) plots. After this, we tested two types of pSEMs, i.e., with and without plot size as a random effect, for the purpose to explore the confounding effects of plot size on ecological mechanisms, drivers, and effects. Considering the fixed conceptual model (Fig. 1b), we tested a total of 36 pSEMs with (18 pSEMs) and without (18 pSEMs) plot size as a random effect using different combinations of three indices of stand structural heterogeneity (i.e., either stand density or tree height inequality or DBH inequality) with each of three indices of either taxonomic or functional *β*-diversity (i.e., either β_{Tot} or β_{Rich} or β_{Tover}), while considering the consistent fixed effects of CMI, CEC and species *α*-diversity.

For the assessment of model fit to the data, we used two important statistical parameters, i.e., Fisher's C statistic and *P*-value of the pSEM (i.e., $P > 0.05$ suggests that the fit of pSEM is reasonable). We excluded correlations between CMI and soil CEC as well as correlations between *α*- and *β*-diversity across all models to improve the model fit and to avoid the statured or over-fitted models. However, we evaluated the confounding effects of excluding and including some paths between variables using the directional separation test, but we did not find any strong change in the fit of pSEM. We used the multiple linear (mixed-effect) regression models to construct the pSEM using the *piece-wiseSEM* package (Lefcheck 2016). For each dependent or endogenous variable in pSEM, we calculated the variance explained by fixed predictors (i.e., R^2_m), as well as variance explained by both fixed and random factors (i.e., R^2_c; for pSEMs with plot size as a random effect). Additionally, we quantified the relative contribution of CMI, CEC, stand structural heterogeneity, and taxonomic *α*- and *β*-diversity to AGB within each tested pSEM model, and then, the relative contributions of predictors to AGB were visually compared using pie charts.

To complement the results from pSEMs, we also quantified principal component analysis (PCA) to graphically explain the gradients of local and regional environmental factors as well as local and regional biotic processes, and

their correlations with AGB, by using the *factoextra* and *FactoMineR* packages (Husson et al. 2016). In addition, we assessed the bivariate relationships between predictors and AGB using Pearson's correlations and simple linear regression models. Before statistical analyses (except boxplots and PCA), all continuous variables were transformed by natural logarithm and then standardized at a mean of 0 and standard deviation of 1 to improve linearity and normality as well as to compare the effect sizes of predictors on AGB in each and across pSEMs (Zuur et al. 2009). All ecological and statistical analyses were conducted in R 3.6.0 and RStudio (R Development Core Team 2019).

Results

The pSEMs (with plot size as a random effect) showed that tree height inequality and stand density rather than DBH inequality were positively controlled by CMI (effect size = 0.00 to 0.35), but negatively controlled by soil CEC (effect size = 0.01 to −0.18; Figs. 2, 3, S3 and S4). Species α-diversity was positively controlled by both CMI (effect size = 0.28 to 0.49) and soil CEC (effect size = 0.37 to 0.42) in all tested pSEMs (Figs. 2, 3, S3 and S4). The effects of CMI and CEC on taxonomic and functional β-diversity indices (i.e., total, richness and turnover) were dependent

on the combination of stand structural heterogeneity index (Figs. 2, 3, S3 and S4). In addition, species α-diversity was positively controlled by stand density (effect size = 0.31) and tree height inequality (effect size = 0.22) but not significantly controlled by tree DBH inequality (Figs. 2, 3, S3 and S4). In contrast, both taxonomic and functional β-diversity indices were negatively controlled by stand structural heterogeneity (effect size = −0.25 to −0.82; Figs. 2, 3, S3−f, S4a−f), but taxonomic β-turnover was positively (effect size = 0.23 to 0.65) controlled in all tested pSEMs (Figs. S3a-c).

The pSEMs (with plot size as a random effect) showed that AGB increased directly with increasing CMI (effect size = 0.15 to 0.39) and stand structural heterogeneity indices (effect size = 0.42 to 0.60). Importantly, taxonomic β-diversity and β-richness decreased but taxonomic β-turnover increased AGB directly (Figs. 2, 4 and S3), whereas functional β-diversity indices possessed direct negative effects on AGB (Figs. 3, 4 and S4). However, species α-diversity increased AGB (effect size = 0.12 to 0.18) directly in the pSEMs when it was included in combinations with tree DBH inequality and either taxonomic or functional β-diversity (Figs. 2a, 3a, S3a, S3d, S4a, and S4d). Moreover, species α-diversity did not significantly increase AGB (effect size = 0.03 to 0.12) directly in the pSEMs when it was included in combinations with either tree height inequality or stand density as well as with either taxonomic
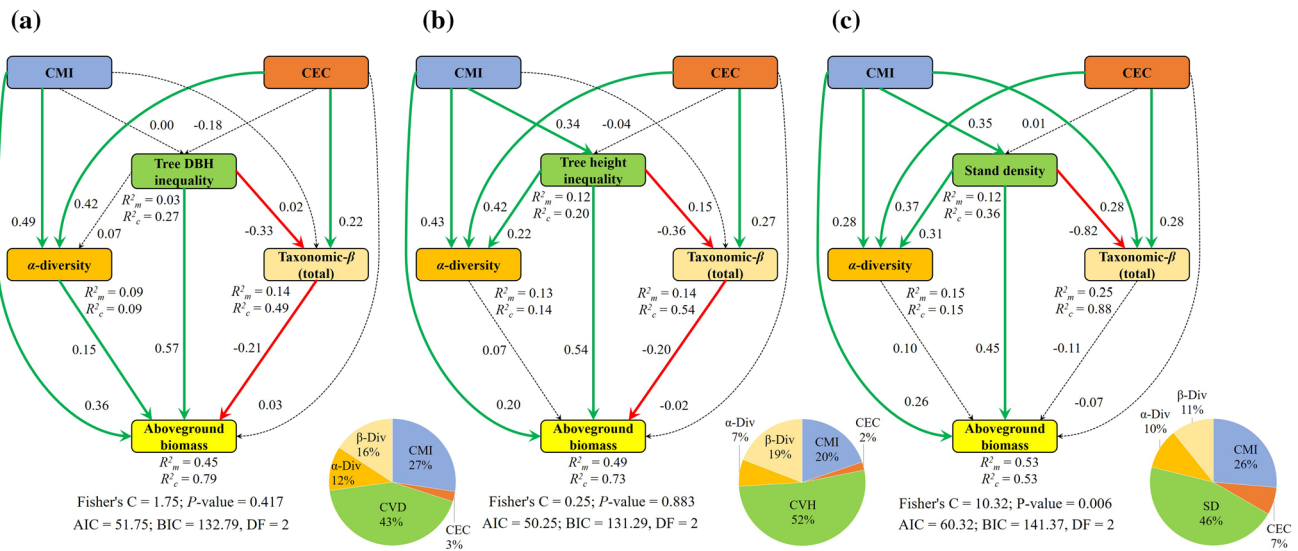

Fig. 2 Piecewise structural equation models (pSEMs) for the effects of local and regional environmental factors on local (taxonomic α-diversity and stand structural heterogeneity) and regional biotic (based on total taxonomic β-diversity) processes, and then their joint effects on aboveground biomass (AGB), while considering plot size as a random effect on both predictors and response variables, in tropical forests of Sri Lanka. Linking climatic water availability (CMI; climatic moisture index), soil fertility (CEC; cation exchange capacity), stand structural heterogeneity index, i.e., either tree DBH inequality **a** or tree height inequality **b** or stand density **c**, taxonomic α-diversity

(Tax α-Div), taxonomic β-diversity (Tax $\beta_{(Tot)}$), and AGB. Green and red solid arrows represent significantly ($P < 0.05$) direct positive and negative effects, respectively, whereas black dashed arrows represent nonsignificant ($P > 0.05$) direct effects. Standardized effect size values are presented near each arrow, whereas R^2 represents the explained variance in response variable by predictor/s. Model fit statistics are presented for each pSEM in the figure (see Tables S2, S3, and S4 for the summary of pSEMs). Pie charts show the relative contributions (in %) of predictors to AGB
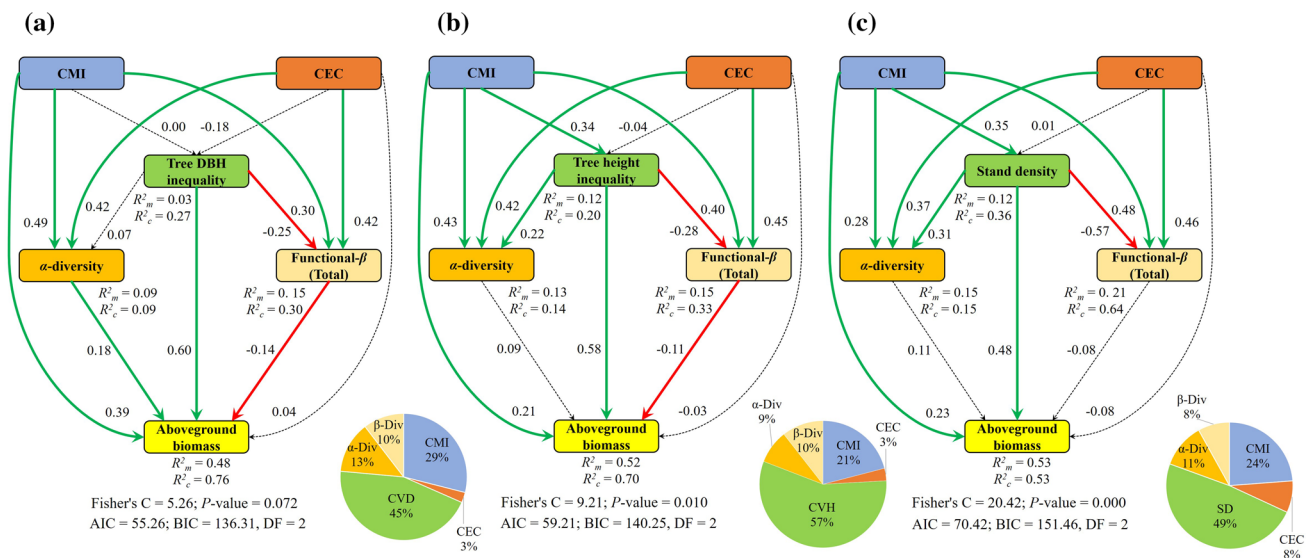
Fig. 3 Piecewise structural equation models (pSEMs) for the effects of local and regional environmental factors on local (taxonomic *α*-diversity and stand structural heterogeneity) and regional biotic (based on total functional *β*-diversity) processes, and then their joint effects on AGB, while considering plot size as a random effect on both predictors and response variables, in tropical forests of Sri Lanka. Linking climatic water availability, soil fertility, stand struc-

tural heterogeneity index, i.e., either tree DBH inequality **a** or tree height inequality **b** or stand density **c**, taxonomic *α*-diversity, functional *β*-diversity, and AGB. Model fit statistics are presented for each pSEM in the figure (see Tables S5, S6, and S7 for the summary of pSEMs). Pie charts show the relative contributions (in %) of predictors to AGB

or functional *β*-diversity (Figs. 2 b, c, 3 b, c, 4, S3b,c,e,f, and S4b,c,e). Soil CEC did not significantly influence AGB (effect size = − 0.09–0.05) directly in all tested pSEMs (Figs. 2, 3, 4, S3 and S4; Tables S2 − S19).

The relative contributions (see pie charts in Figs. 2, 3, S3 and S4) indicated that CMI was the main limiting abiotic factor (relative contribution = 14% to 29%) whereas stand structural heterogeneity (either stand density or tree DBH inequality or height inequality) was the main influencing biotic factor (relative contribution = 41% to 57%) of AGB. Although taxonomic (i.e., 8% to 30%) and functional *β*-diversity (i.e., 8% to 18%) increased AGB, the contribution was relatively less as compared to CMI and stand structural heterogeneity. In addition, PCA results showed that AGB was controlled by both local and regional biotic processes along the PC1 axis whereas it was oppositely controlled by CMI (positively) and CEC (negatively) along the PC2 axis. Although the random effect of plot size was relatively less, we noted that local and regional biotic processes, as well as environmental factors, were distributed at two opposite extremes along the PCA axis (Fig. 5).

In addition, the boxplot analysis showed that there were significant differences for most of the tested variables between small and large plots, but apparent differences were noted in a few variables only (Fig. S2). As such, the tested pSEMs (with plot size as a random effect) showed that most of the variance in predictors and response variables was explained by fixed effect (i.e., pathways) as compared to

the random effect (Figs. 2, 3, 4, S3 and S4). Likewise, the comparison of direct effects of predictors on AGB based on pSEMs with (Figs. 2, 3, 4, S3 and S4) and without (Figs. S6 − S10; Tables S20 − 37) plot size as a random effect showed that plot size as a random effect had no strong role in modulating the ecological mechanisms, even though explained variance varied a little bit in some cases (Fig. S5). The bivariate relationships and Pearson's correlation matrix for supporting the results from pSEMs are provided in Figs. S11 − S12 and Fig. S13, respectively.

Discussion

In this study, we found that environmental factors shaped both local (i.e., taxonomic *α*-diversity and stand structural heterogeneity) as well as regional biotic processes, mainly through changes in functional and taxonomic *β*-diversity patterns. Moreover, we found that stand structural heterogeneity controlled local as well as regional biotic processes, mainly through changes in both taxonomic and functional *β*-diversity. Interestingly, local biotic processes (particularly stand structural heterogeneity) and climatic water availability rather than soil fertility increased AGB but regional biotic processes declined AGB in studied tropical forests. It is noteworthy that taxonomic *β*-turnover increased but taxonomic *β*-richness declined AGB whereas both functional *β*-turnover and *β*-richness declined AGB in studied tropical
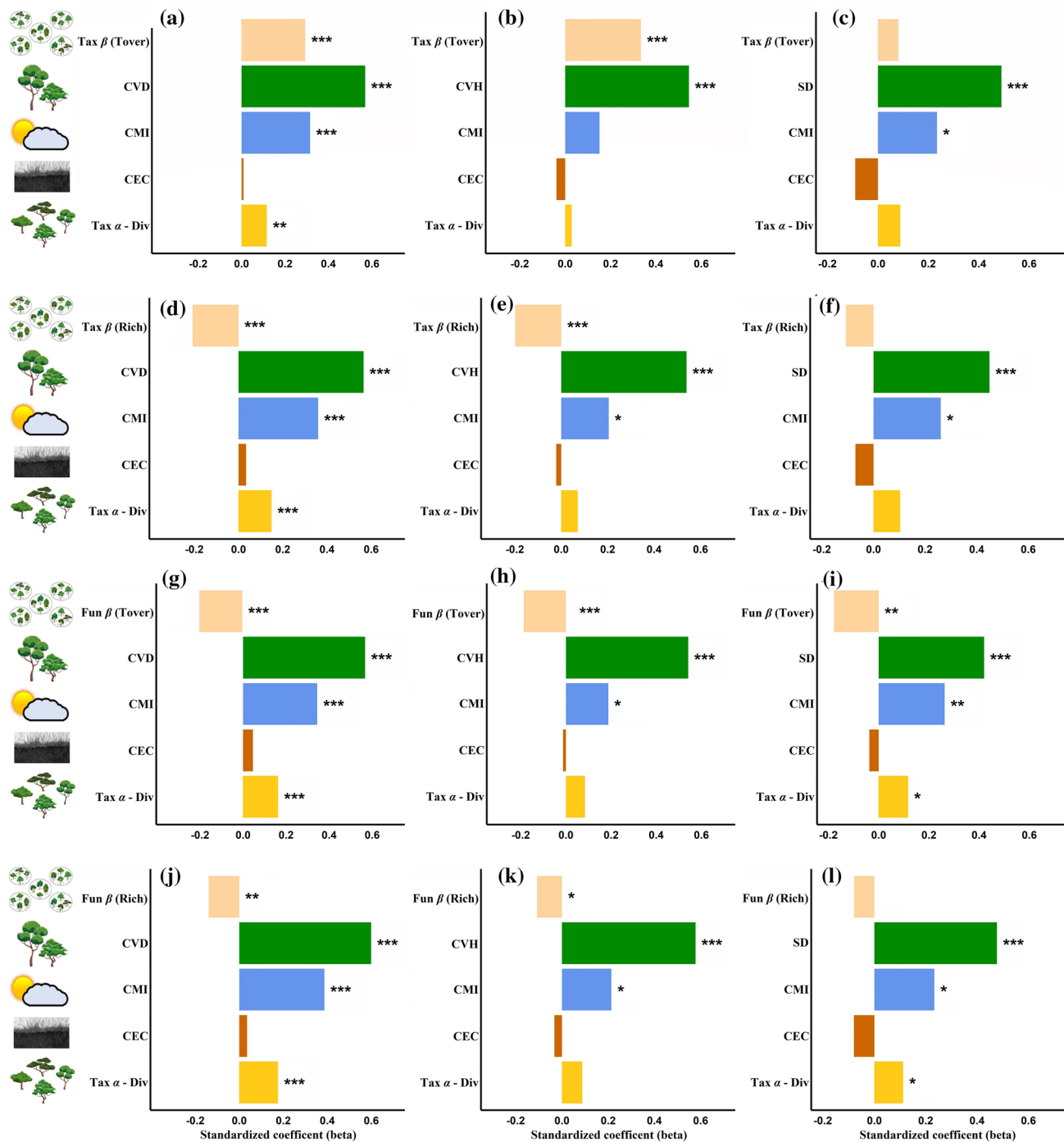
Fig. 4 Bar charts showing the direct effects (based on pSEMs) of local and regional environmental factors as well as local (α-diversity and stand structural heterogeneity) and regional biotic (based on the two components of either taxonomic or functional β-diversity) processes on AGB in tropical forests of Sri Lanka. Linking climatic water availability, soil fertility, stand structural heterogeneity index, i.e., either tree DBH inequality (**a**, **d**, **g**, **j**) or tree height inequality (**b**, **e**, **h**, **k**) or stand density (**c**, **f**, **i**, **l**), taxonomic α-diversity, either taxonomic β-turnover (**a**, **b**, **c**) or β-richness (**d**, **e**, **f**), or functional β-turnover (**g**, **h**, **i**) or β-richness (j, k, l) and AGB. Full pSEMs are provided in Figs. S3 – S4 (see Tables S8-S19 for the summary of pSEMs). Significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Abbreviations to variables are explained in Table S1

Fig. 5 Principal component analysis (PCA) for assessing the gradients of environmental factors and biotic processes in relation to aboveground biomass (AGB). Abbreviations: CMI, climatic moisture index; CEC, soil cation exchange capacity; CVD, tree DBH inequality; CVH, tree height inequality, SD, stand density; Tax α-Div, taxonomic α-diversity; Tax $\beta_{(Tot)}$, taxonomic β-diversity, Tax $\beta_{(Tover)}$, taxonomic β-turnover; Tax $\beta_{(Rich)}$, taxonomic β-richness; Fun $\beta_{(Tot)}$ functional β-diversity; Fun $\beta_{(Tover)}$, functional β-turnover; Fun $\beta_{(Rich)}$, functional β-richness. See Table S1 for details
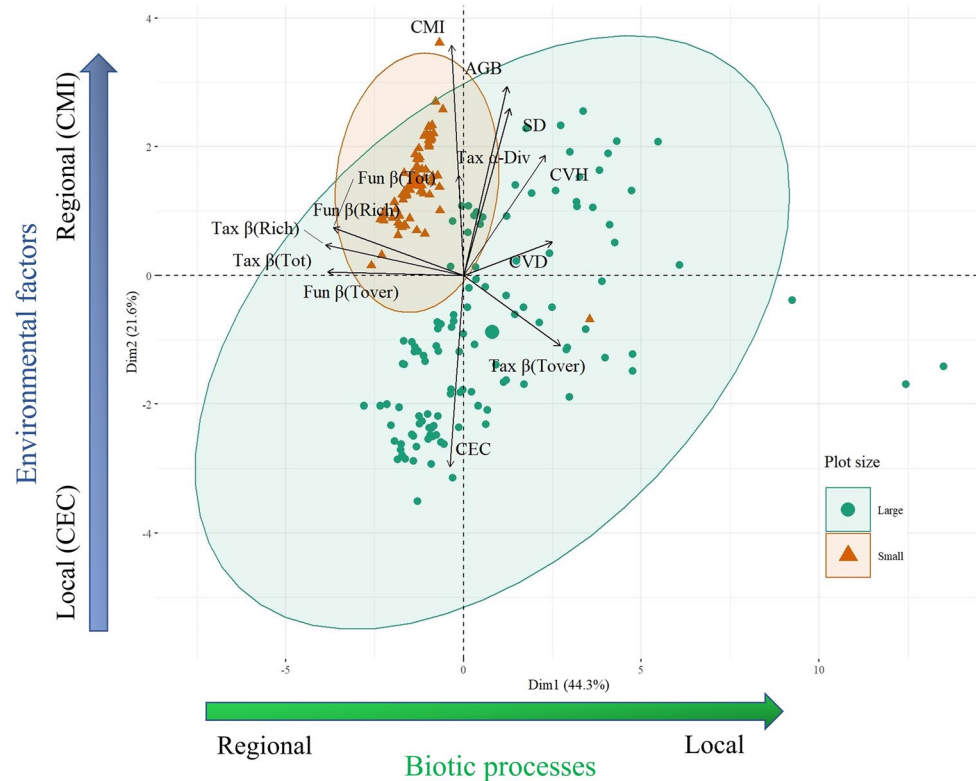
forests. However, the fact could be that functional β-turnover as compared to β-richness across studied plots showed less variation in data values (see Fig. S2 and Table S1), indicating that functional β-richness is the important component for explaining the negative effects of functional β-diversity on AGB due to the regional selection effect and functional redundancy effect along climate and soil gradients in the studied tropical forests. Thus, our study significantly contributes to the current less debated topic on the influences of local and regional biotic processes on forest functions, i.e., AGB in our study (Mori et al. 2018; van der Plas et al. 2016).

We found that species α-diversity increased with increasing climatic water availability and soil fertility in all tested pSEMs, indicating that local biotic processes are positively controlled by species-energy relationship and resource availability which might be due to the longer growing season's length and soil nutrient availability (Toledo et al. 2012; Poorter et al. 2017; Currie 1991). Local species interactions increase in a positive way when coexisting species are using the available limited resources through local biotic complementarity ways by enhancing niche differentiation and facilitation (Mori et al. 2018; Yachi and Loreau 2007). However, the observed significant positive effects of climatic water availability and soil fertility on functional β-diversity as compared to taxonomic β-diversity might be attributable to the reason that variations in functional traits could shape community assembly processes better

than taxonomic identification (Kraft et al. 2008; MacArthur and Levins 1964; Tilman 2004). In addition, we found that climatic water availability increased stand density and tree height inequality but soil fertility possessed negligible influences, indicating that a longer growing season length or less drought conditions increase stand structural heterogeneity in tropical forests (Corlett 2016; Phillips et al. 2010). However, stand structural heterogeneity could control local species complementarity through canopy packing and inequality in tree-size dimensions because different-sized trees have different requirements for light, water, and soil resources (Ali 2019; Clark 2010). As such, we found positive relationships of species α-diversity with tree height inequality and stand density which might be attributable to the local niche differentiation effect, i.e., higher stand density through the coexistence of shade-tolerant and light-demanded species (Williams et al. 2017; Kunz et al. 2019). Interestingly, we found that taxonomic and functional β-diversity (including β-richness) decreased but only taxonomic β-turnover increased with increasing tree-size dimension inequality and stand density. This overall result might support the selection effect or functional redundancy effect in shaping regional biotic processes whereas support the niche complementarity effect in shaping local biotic processes along climate and soil gradients.

In this study, we statistically found that local rather than regional taxonomic species turnover processes increased

AGB through the niche complementarity effect, and that, the effect of species α-diversity was significantly positive when tree DBH inequality was included in the model (Ali et al. 2019; van der Plas 2019). However, tree DBH inequality did not influence species α-diversity as compared to tree height inequality and stand density, indicating that local species complementarity is greatly dependent on the measured index of stand structural heterogeneity (Clark 2010; Ali 2019). Interestingly, tree DBH inequality, tree height inequality, and stand density increased AGB, and their effect sizes were nearly equal but relatively stronger than species α-diversity. This result suggests that greater canopy packing increases AGB and is strongly dependent on big trees, i.e., plots having large trees with high DBH inequality (Lutz et al. 2018; Ali et al. 2020), through complementarity ways of light capture and use by co-occurring species and their interacting individuals in tropical forests (Williams et al. 2017; Chiang et al. 2016). However, in contrast to our expectations, we found that taxonomic and functional β-diversity (with exception of taxonomic β-turnover) declined AGB, indicating that forest functions might be also controlled by regional selection effects which are often negative with increasing species diversity or seldom positive with increasing dominant species only (Yachi and Loreau 2007; Mori et al. 2018). In addition, we found that AGB was directly and strongly (positively) controlled by climatic water availability rather than soil fertility. This observed mechanism might be related to the reason that regional environmental factors matter in shaping forest functions through direct influences on metabolic processes within and across communities (Chu et al. 2016; Wang and Ali 2021). However, in contrast to our results, a previous study has found that the relationships of landscape-scale forest multifunctionality with β-diversity were always positive but negative to positive with species α-diversity (van der Plas et al. 2016). This situation highlights that the influence of local and regional biotic processes on forest functions might be context-dependent or function-dependent or diversity-dependent (Mori et al. 2018; van der Plas 2019; Ali 2019).

It is important to consider that plot size as a random effect (in pSEMs) explained some portion of the variance in stand density, tree DBH inequality, and tree height inequality. However, boxplots show that only stand density, as well as climatic water availability, declined with increasing plot size probably due to the presence of big trees which are sensitive to drought conditions and subjected to anthropogenic disturbances around the world (Lutz et al. 2018; Bennett et al. 2015; Bordin et al. 2021). By considering all consequences through an integrative approach, our results suggest the strongest role of big trees in shaping AGB, and as such, we have previously reported that topmost trees rather than foremost species enhance AGB

in studied forests (Ali et al. 2020). Nevertheless, the comparison of pSEMs, based on with and without plot size as a random effect, show that plot size explained some portion of the variance in stand structural heterogeneity attribute, but the effect size (e.g., on AGB) did not change dramatically. This result agrees with a global study where they found negligible influences of plot size on biodiversity and productivity in global forests (Liang et al. 2016). However, the variance explained by plot size as a random effect might be attributable to the presence of big trees, which are dependent on environmental conditions, and as such, we found some change in the effect sizes of CMI and soil fertility on AGB in pSEMs with and without plot size as a random effect. Through this understanding, it is important to consider the effects of big trees on forest diversity, structure, and functions for a better understanding of ecological mechanisms (Lutz et al. 2018; Bennett et al. 2015; Bordin et al. 2021).

Conclusion

In the present study, we found that local biotic processes increase AGB due to the local and regional niche complementarity effects, whereas the regional biotic processes declined AGB due to the regional selection effect or functional redundancy effect under favorable environmental conditions. These favorable environmental processes (particularly climatic water availability effects) shape AGB indirectly via two opposing mechanisms, i.e., promoting indirect effects via local biotic processes whereas suppressing indirect effects via regional biotic processes. We, therefore, argue that both local and regional biotic homogenization, as well as drought conditions, may have strong divergent impacts on forest functions and that the impacts of tree diversity loss may greatly reduce carbon sequestration.

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