https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Biogeosciences Discussions

Large-diameter trees control forest structure and function in successional temperate forests

Chang-Bae Lee[1], Arshad Ali[2], Zuoqiang Yuan[3], James A. Lutz[4], Jens-Christian Svenning[5], and Min-Ki Lee[6]

[1]Department of Forestry, Environment and Systems, Kookmin University, 77 Jeongneungro, Seongbukgu, Seoul 02707, Republic of Korea
[2]Forest Ecology Research Group, College of Life Sciences, Hebei University, Baoding, 071002, Hebei, China
[3]CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China
[4]Department of Wildland Resources, Utah State University, Logan, UT 84322, USA
[5]Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) & Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, 8000 Aarhus C, Denmark
[6]Department of Forest Resources, Kookmin University, 77 Jeongneungro, Seongbukgu, Seoul 02707, Republic of Korea

Correspondence to: Chang-Bae Lee (kecolee@kookmin.ac.kr)

Abstract. Large-diameter trees regulate forest diversity, structure and aboveground biomass (AGB), but the mechanisms whereby they control forest processes remain understudied, especially in early successional forests. We used 1,956 0.16 ha plots from the Korean National Forest Inventory from mostly 20–50 years old stands (biomass accumulation phase) in closed-canopy temperate forests, with 236 species of woody plants and 391,543 individual stems ≥ 6 cm diameter at breast height. Based hereon, we analyzed the effects of large-diameter trees on aboveground biomass (AGB) in the overstory, understory, and the two combined (total vegetation). We also considered the effects of species and functional diversity, functional dominance of traits, stem density, and abiotic drivers (i.e., topographic, climatic and edaphic variables) interacting with large-diameter trees on AGB. We performed model averaging approaches with backward stepwise regressions and piecewise structural equation modeling to quantify and compare the effects of large trees vs. other biotic and abiotic drivers. Overall, large-diameter trees had a dominant effect on AGB compared with remaining tree attributes and abiotic drivers for both the overstory and whole community; however, they did not strongly influence the understory. Large-diameter trees also modulated the strength of the direct effects of abiotic drivers, particularly soil fertility, on AGB, as well as indirect effects via regulating the attributes of smaller-diameter trees. Our study provides new insights into the mechanisms associated with self-thinning and resource availability whereby large-diameter trees drive high AGB in succession forests. We also show that the effect of large-diameter trees is forest stratum-dependent across different types of temperate forests. This study emphasizes the importance of large-diameter trees in determining the structure and function in early successional forests, and the need for conservation and management actions to protect and promote these keystone organisms.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Biogeosciences Discussions

1 Introduction

Large-diameter trees dominate the biomass of old-growth forests worldwide (Luyssaert et al., 2008; Lindenmayer et al., 2012; Lutz et al., 2018), but to the extent to which this phenomenon arises earlier in forest succession has not been explored. Furthermore, the mechanisms of biomass dominance in younger forests may control which trees persist as large-diameter individuals in older forests (e.g., self-thinning process dominated by asymmetric competition among trees; Weiner, 1990; West et al., 2009; Lin et al., 2016). How carbon sequestration is distributed and controlled in younger forests becomes increasingly important as countries undertake more active carbon mitigation efforts via reforestation (Poorter et al., 2016; Pugh et al., 2019), as carbon sequestration in younger forests is strongly affected by conservation and management policies (Heinrich et al., 2021). Forests store approximately 44% of the global carbon pool in the world's terrestrial ecosystems (Pan et al., 2011) and have important potential for climate change mitigation (Cook-Patton et al., 2020) as well as contribute to ecological stability and regulation of the biogeochemical cycles of carbon, water, and nutrients (van der Plas, 2019).

In natural forests, aboveground biomass (AGB) is generally regulated by abiotic and biotic factors (Conti and Díaz, 2013; Prado-Junior et al., 2016; Chun et al., 2020). Abiotic factors include environmental conditions such as climate (e.g., mean annual temperature, mean annual precipitation, and aridity), topography (e.g., elevation and slope), and soils (e.g., cation exchange capacity), as well as forest development-related (e.g., stand age), disturbance-related or succession-related factors (Slik et al., 2013; Jucker et al., 2014; Poorter et al., 2017). Abiotic factors directly or indirectly affect AGB by influencing biotic factors (Chu et al., 2019; Chun et al., 2020; Ali and Wang, 2021). The effects of biotic factors on AGB have been attributed to concepts of the niche complementarity and mass ratio effects (Prado-Junior et al., 2016; Poorter et al., 2017; Chun et al., 2020). The niche complementarity effect is related to species co-occurring through niche partitioning, which suggests that higher taxonomic, structural, and functional diversity could lead to higher AGB (Tilman et al., 1997; Zhang et al., 2012). The mass ratio effect states that AGB is primarily driven by the functional traits of dominant species measured using the community-weighted mean (CWM) of trait values (Grime, 1998; Fotis et al., 2018). Stand structural attributes, such as stem density, tree diameters, and height distributions at stand levels, can also directly or indirectly affect AGB via species richness and functional diversity (Ali and Yan, 2017; Fotis et al., 2018).

Recently, studies have shown that a small number of large-diameter trees drive variation in AGB (Slik et al., 2013; Stephenson et al., 2014; Lutz et al., 2018), and that the effects of large-diameter trees on AGB override the effects of medium- and small-diameter tree attributes, species richness and abiotic factors (Ali et al., 2019a; Ali et al., 2020; Bordin et al., 2021). Generally, large-diameter trees are acquisitive and limit available resources, such as light, water, and soil nutrients, to medium- and small-diameter trees (Stephenson et al., 2014; Ali et al., 2019a). Thus, the growth and fitness of the smaller-statured trees may largely depend on the ecological behavior of the relatively few large-diameter trees in a stand (Lindenmayer and Laurance, 2017). Climatic factors and soil fertility affect large-diameter trees (e.g., Slik et al., 2013). Climatic factors are often predominant drivers of large-diameter tree occurrence as well as species diversity, structure and AGB in forests (Chu et al., 2019; Ali and Wang, 2021). Large-diameter trees can be more sensitive to drought than medium- or small-sized trees as they

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

are exposed to extreme atmospheric drought, wind pressure, solar radiation, and temperature variation (Allen et al., 2010; Bennett et al., 2015). Moreover, soil fertility (e.g., cation exchange capacity and total exchangeable bases) increases the stand density and size of large-diameter trees (Slik et al., 2013; Ali et al., 2019b). In general, large-diameter trees are recognized as the major biotic drivers of forest diversity, structure, and biomass dynamics through environmental filtering and their competitive abilities in forest communities (Ali et al., 2019a; Yuan et al., 2021).

Although earlier studies have related large-diameter trees effect to species diversity, functional diversity, and stand structure, most have involved primary forests or older secondary forests (Slik et al., 2013; Lutz et al., 2018; Ali et al., 2019a; Yuan et al., 2021). In contrast, the potentially differing influences of large-diameter trees on early successional forests and the strata within them are poorly unknown. Using a data set of 1,956 plots distributed throughout the forested regions of South Korea, we sought to examine the interactions of topographic, climatic, edaphic, and stand structural attributes with large-diameter trees, and also the effects of large-diameter trees, and other biotic and abiotic factors on the AGB of other forest strata (Figure 1). To do so, we addressed the following questions and related predictions: 1) Are there any differences in the explanatory power of models with and without the inclusion of a large-diameter tree metric? Our expectation was that the AGB models including large-diameter trees as a predictor would have higher explanatory power based on their known dominance of stand biomass (Ali et al., 2019b), and that the explanatory power of models including a large-diameter tree metric would be higher for the overstory stratum and the whole community compared to the understory stratum. 2) Does the effect of large-diameter trees on forest AGB overwhelm the effects of other biotic and abiotic factors on the AGBs of other forest strata? We expect that the effect of large-diameter trees on AGB will surpass the effects of other biotic and abiotic factors for the overstory and whole community level, but not in the understory. 3) Which abiotic factors primarily influence the size (i.e., diameter at breast height) of large-diameter trees and AGB? We expect that climatic factors (i.e., MAT, MAP, and aridity) will be the primary drivers for large-diameter trees and AGB in the overstory and whole community, as large-diameter trees are disproportionately sensitive to drought stress (Phillips et al., 2010; Bennett et al., 2015). We also expected that edaphic factors would be important predictors for understory AGB because of intense competition between understory individuals for scarce resources caused by overstory trees (Ali and Yan, 2017; Ali et al., 2019b).

2 Materials and methods

2.1 Study area, data, and calculating AGB

Temperate forests occupy 64% of the total land area in South Korea (Korea Forest Service, 2019). All principal types of the temperate forests are represented; broad-leaved (38.4%), coniferous (31.8%), and mixed (27.2%). The most abundant tree species belong to Pinaeae and Fagaceae, namely the pines *Pinus densiflora* Siebold and Zucc. and *P. thunbergii* Parl, and the oaks *Quercus mongolica* Fisch. Ex Ledeh., *Q. serrata* Murray, and *Q. variabilis* Blume. Almost all forests in South Korea are early-successional forests with ages between 20–50 years old (Figure S1). Many forest sites were extensively logged during

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

the Japanese occupation (1910–1945), the period of the Korean War (1950–1953), and the immediate post-war period, which together degraded forests to a stocking of 11.2 m^3/ha by 1973.

Reforestation was prioritized from 1973–1987, and current conditions (146 m^3/ha in 2019) primarily reflect the legacies of these efforts. As a result, most South Korean forests are closed-canopy forests 40–50 years old (Figure S1) in the developmental phase of biomass accumulation (*sensu* Franklin et al., 2002).

We used data from the sixth National Forest Inventory (NFI) survey collected between 2010 and 2015. The NFI protocol has been designed and implemented to monitor changes in forest resources and forest cover considering forest quality, quantity, and function (Korea Forest Research Institute, 2011). Plots are located on a systematic sampling grid of 4 km × 4 km oriented to the cardinal directions. A sampling plot with four circular subplots was placed at the intersection of each 4 × 4 km grid line. Each circular subplot had an area of 0.04 ha (diameter of 22.6 m) for a total of 0.16 ha. All free-standing stems of woody species with a diameter at breast height (DBH) of ≥ 6 cm were identified, and DBH and height were measured for all plots (Korea Forest Research Institute 2011). From the NFI data, we extracted 2,067 sampling plots in natural forests (from the total of 3,938 plots) and selected 1,956 plots with full complements of biotic and abiotic data (Figure S2). The final dataset included 236 species of woody plants and 391,543 individual stems. Finally, we analyzed 1,955 and 1,885 plots for overstory and understory structure, respectively, after excluding plots with zero values for biomass or missing biotic variables (e.g., functional dispersion (FDis)) for either forest stratum.

The AGB of each tree was calculated according to the methods of Son et al. (2014) which are based on stem volume, wood density, and a biomass expansion factor relating whole-tree biomass to stem biomass. Stem volume is provided as basic NFI data. Wood density and biomass expansion factors for tree species reflect national means from the National Institute of Forest Science, Korea Forest Service (Son et al., 2014). To investigate the impact of forest strata on AGB, we divided all stems into overstory and understory individuals based on crown classes assigned to individual trees in each plot (i.e., dominant, codominant, intermediate, and suppressed) provided by the NFI. We categorized dominant and codominant trees as overstory and intermediate and suppressed trees as understory. All analyses were performed at the overstory, understory, and whole community levels.

2.2 Biotic factors – large-diameter trees, diversity, CWM, and stand structural variables

The definition of large-diameter trees should incorporate species, forest type, and topographic position, such as latitude, longitude, elevation, and slope (Lindenmayer and Laurance, 2017; Lutz et al., 2018; Ali et al., 2020; Ali and Wang, 2021). For cold sites, such as alpine or subalpine forests, a large-diameter tree may have a DBH of < 20 cm (e.g., Baltzer et al., 2014), whereas at warmer sites in South Korea trees can exceed 60 cm DBH. Similarly, maximum diameters in younger forests are inherently limited when species-specific diameter maxima may not be reached for several centuries. Thus, large-diameter trees are present in all forests and regions, but different abiotic and biotic attributes may limit the large diameter threshold (Bastin et al., 2018). Owing to the range of conditions and successional status throughout South Korea (Table S1), we defined large-diameter trees as the largest 1% by diameter in each plot (*sensu* Lutz et al., 2018; Ali et al., 2019a). The 99th percentile DBH

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Biogeosciences Discussions Open Access EGU

value was considered as the large-diameter threshold and was used as the large-diameter tree attribute in this study (defined as 1% large-diameter tree DBH). Within the 1,956 plots, the large-diameter threshold varied from 12 cm to 91.5 cm (Table S2). For analysis, we considered four tree categories (Figure S3): the 1% large-diameter trees, the 99% remaining trees except for the 1% large-diameter trees in whole community (defined as 99% remaining trees), the remaining trees except for 1% large-diameter trees in overstory (defined as overstory remaining trees), and understory trees.

We used taxonomic, stand structural and functional trait attributes to quantify niche complementarity and mass ratio effects (Fotis et al., 2018; Chun et al., 2020). Taxonomic diversity at the species level was evaluated using species richness (SR), Shannon H (species diversity, SD), and species evenness (SE). To describe stand structural attributes, we selected stem density because stem density at the stand level can incorporate vegetation quantity and niche complementarity effects (e.g., in general, the higher the stem density, the higher the species richness, because more species are usually observed in denser forest stands; Fotis et al., 2018; Ali et al., 2019b). To calculate functional diversity and CWM indices, we used four functional traits recognized as key characteristics for the survival and growth of plant species and ecosystem functions and services (Prado-Junior et al., 2016; Poorter et al., 2017; Ali et al., 2019a, 2019b; Chun et al., 2020). The traits were maximum height (H), leaf size (LS; leaf length multiplied by leaf width), and seed mass (SM). Functional traits were obtained from published literature and open databases (Table S3). To quantify functional diversity, we calculated single and multivariate FDis values for three traits (Laliberté and Legendre, 2010). FDis and CWM were calculated using the *FD* packages in R. The CWMs for these traits were quantified by weighting the mean trait value in each plot by the relative basal area of each tree species. Other biotic drivers (excluding the large-diameter trees) were calculated for the 99% remaining trees, overstory remaining trees, and understory trees. See Tables S1 and S2 for summary statistics.

2.3 Abiotic factors – topographic, climatic, and edaphic variables

To characterize each plot, we used eight abiotic variables (four topographic, three climatic, and one edaphic) calculated from the NFT plot locations. Topographic variables were latitude, longitude, elevation, and slope. Climatic variables were mean annual temperature (MAT; °C) and mean annual precipitation (MAP; mm) from WorldClim (www.worldclim.org), and aridity from the Global Aridity Index and Potential Evapotranspiration Climate Database (cgiarcsi.community). The edaphic variable was median cation exchange capacity (CEC; cmolc/kg) calculated based on six soil horizons between 0 and 100 cm, which were extracted from the SoilGrids database (https://soilgrids.org). To minimize covariation and redundancy within abiotic data, we used Principal Component Analysis (PCA) to reduce the dimensionality of the topographic and climatic variables separately (Table S4). The first PCA axis for each factor was used as a new explanatory variable (i.e., $PC1_{topo}$ and PC_{clim} for topographic and climatic factors, respectively) in the further analyses. The summary statistics of abiotic drivers are provided in Table S1.

2.4 Statistical analyses

We used generalized least squares models to examine spatial autocorrelation within biotic and abiotic drivers (Legendre and Legendre, 1998). Spatial models (including latitude and longitude) and nonspatial models (without latitude and longitude)

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

were examined for each plot. Spatial and nonspatial model suitability was evaluated using lower Akaike Information Criterion (AIC) values. There was no evidence for spatial autocorrelation because AIC values for nonspatial models were lower than those for spatial models (Yuan et al., 2019; Chun et al., 2020). All biotic and abiotic AGB variables were standardized using log or square root transformations to improve normality and linearity before analyses. MAP, aridity, DBH threshold for 1% large-diameter trees, and FDisMUL were log-transformed, whereas AGB, elevation, CEC, SR, SE, FDisLS, CWMLS, CWMSM, and stem density were square root transformed. The latitude, longitude, slope, MAT, FDisH and CWMH were not transformed because non-transformed values performed better.

To evaluate whether the large-diameter tree effects prevailed over the effects of biotic (i.e., species and functional diversity, functional dominance, and stand structure) and abiotic (i.e., topographic factors, climate and soil fertility) factors, we developed five competing models for each forest stratum (overstory, understory, and the whole community): 1) "complementary diversity (CD)" models (abiotic factors + 1% large-diameter tree DBH + three taxonomic and four functional diversity indices), 2) "functional dominance (FD)" models (abiotic factors + 1% large-diameter tree DBH + three CWM indices), 3) "stand structure (SS)" models (abiotic factors + 1% large-diameter tree DBH + stem density), 4) "combined" models (including each CD, FD, and SS factor and one abiotic factor with the highest standardization coefficient from each of the CD, FD, and SS model + 1% large-diameter tree DBH), and 5) "full" models (including all biotic and abiotic factors). Before implementing these competing models, we removed highly correlated variables ($r \geq 0.7$), such as SD and FDisSM in the overstory, understory, and whole community (Figure S4). We also computed variance inflation factors (VIFs) to assess multicollinearity among the explanatory variables (Graham, 2003). All VIF values were lower than 5, indicating that multicollinearity among factors should not affect our results (Chun et al., 2020). Furthermore, we examined the quadratic relationships of biotic and abiotic factors with AGB, but found no obvious quadratic relationships. We implemented a backward stepwise multiple regression procedure to select the best models for minimizing the AIC using the *stepAIC* function from the *MASS* package in R. For the second step, the best model of the five competing models was subjected to model-averaging approaches based on the corrected AIC (AIC_c) selection ($\Delta AIC_c < 2$) to determine the best predictors using the *dredge* function from the *MuMIn* package in R. We repeated these steps for the five competing models across the entire data set for the overstory, understory, and whole community without separating the large-diameter trees term to determine any differences in explanatory power for AGBs based on large-diameter trees. The CD, FD, and SS models, except for the combined and full models, are shown in Figures S4 and S5.

We also performed piecewise structural equation modeling (pSEM; Lefcheck, 2020) using the *piecewiseSEM* package in R to assess the direct, indirect, and mediation effects of large-diameter trees on AGBs and differences in the relative importance of large-diameter trees from the overstory, understory, and whole community. To minimize model complexity, we used the biotic and abiotic factors defined from the most parsimonious model (i.e., combined model) among the five competing models as factors for pSEM (Figure 1). All statistical analyses were implemented with R version 4.1.2 (R Development Core Team, 2021).

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

3 Results

The model-averaging approaches show that the inclusion of large-diameter tree DBH improved explanatory power for overstory and whole-community AGB for all combined and full models, with large-diameter tree DBH explaining the highest proportion of variance in both overstory and whole community AGB (Figures 2 and 3). In contrast, stem density had the greatest effect on understory AGB for all models, showing that large-diameter trees are not the primary driver of understory AGB (Figures 2, 3 and S7).

For the pSEM results, overstory AGB strongly increased via the direct effect of large-diameter tree DBH (Figure 4a). Furthermore, CEC showed large and indirect positive effects via large-diameter trees more than direct effects. Large-diameter tree DBH also negatively and indirectly affected FDisH, CWMH, and stem density of overstory remaining trees for overstory AGB. For attributes in overstory remaining trees, stem density showed the largest effect on AGB, while FDisH and CWMH effects remained small. Finally, FDisH showed negative correlations with CWMH and stem density of overstory remaining trees, and CWMH was positively correlated with stem density. The importance of large-diameter tree DBH for AGB was much lower for the understory compared to the overstory (Figures 4b, S8 and S9). Instead, stem density of understory trees showed the greatest effect on understory AGB, supporting the results of model-averaging approaches.

The results for the whole tree community were similar to those of the overstory (Figures 4c). The indirect effect of CEC via the large-diameter tree DBH on total AGB was larger than the direct effects. Unlike the overstory, the SE and stem density for 99% remaining trees indirectly affected the large-diameter tree DBH. However, the direct effect of large-diameter tree DBH on AGB was much larger than the indirect effects. Stem density had the largest effect on total AGB for 99% remaining trees among the three potential drivers.

4 Discussion

Large-diameter trees affect the AGB of the forest overstory and understory differently because of the different ecological processes acting across forest strata. Large-diameter tree size (DBH) was the primary driver of AGB of the overstory and the entire community whereas stem density was the primary driver for AGB in understory. Whole community and overstory AGB responded similarly to biotic and abiotic predictors because of the major contribution of overstory AGB to whole community AGB (Ali et al., 2019b). Generally, the attributes of large-diameter trees contribute more to forest AGB than smaller-sized trees in subtropical, tropical and temperate forests (Slik et al., 2013; Lutz et al., 2018; Ali et al., 2019a; Ali et al., 2020). A large number of small-diameter trees cannot equal the AGB of large-diameter trees, most likely due to the increased height and bole volume of large diameter trees (Lutz et al., 2018) although smaller-diameter trees can contribute to carbon cycling and productivity dynamics (Meakem et al., 2018). According to the metabolic scaling hypothesis (Enquist et al., 1999; Sheil et al., 2017), large-diameter trees are taller, have larger crowns, and/or are occupying growing spaces and resources which are not available to smaller trees under the closed canopy (West et al., 2009). Therefore, the unique attributes of large-diameter trees on whole community and overstory AGBs in this study suggest that the conservation and management of these trees is

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Biogeosciences Discussions

important for increasing forest carbon sequestration and productivity (Stephenson et al., 2014; Lutz et al., 2018; Ali and Wang, 2021). Furthermore, our results show that the impact of vegetation quantity (e.g., stand biomass, stand density, and vegetation coverage), particularly stem density, on overstory, understory and whole community AGBs in the studied early successional temperate forests is more important than vegetation quality (e.g., SR, species composition, and functional trait diversity) in explaining ecosystem function (Lohbeck et al., 2015; Ali et al., 2019a). These positive relationships between vegetation quantity and AGB have been widely documented in natural forests, including temperate forests across the world (Lohbeck et al., 2015; Yuan et al., 2019). Especially, our results highlight the importance and role of self-thinning process in regulating AGB variations in early successional forests. According to self-thinning theory, trees undergo density-dependent competition and mortality in the early succession stages (Weiner, 1990; West et al., 2009; Lin et al., 2016). Intriguingly, density-dependent competition can proceed in two different modes, namely asymmetric and symmetric competition (Weiner, 1990; Lin et al., 2016). Asymmetric competition may lead the emergence of a few large trees that can disproportionately exploit more resources and space for growth and survival, and suppress other smaller trees, increasing size inequality in tree populations (Weiner, 1990). On the other hand, under symmetric competition, competing trees trend to share resources and space equally and thus lead similar size structures in tree populations (West et al., 2009; Lin et al., 2016). Our results suggest that asymmetric competition is the main competitive process shaping the build-up of AGB in early successional temperate forests via the dominant effect of large-diameter trees. Moreover, our study suggests the possibility that the dominant large trees that emerge in the early stage of forest succession may persist into late stages of succession in the absence of sever disturbances such as fires, disease and typhoon.

In more detail with multiple pathways from pSEMs, large-diameter trees directly and positively regulated both AGBs in the overstory and whole community, and indirectly affected the AGBs mainly via the stem density of remaining trees. Although large-diameter trees affected the CD and FD components of remaining trees, the indirect effects on the AGBs via the both components were very low. These results suggest that AGB of either overstory or whole community is controlled in a complementary way that decreases remaining tree density as large-diameter tree DBH increases and vice versa. That is, large-diameter trees with overwhelming competitive ability exclude remaining trees and overrule the attributes of remaining trees in AGBs for the overstory and whole community levels (Ali et al., 2019a; Ali et al., 2020). These results indicate that large-diameter trees are acquisitive and limit available resources to remaining trees in the overstory and whole community in our early successional temperate forests (e.g., Lutz et al., 2014). Therefore, the growth and fitness of remaining trees in the overstory and whole community may be largely determined by a small number of large-diameter trees (Lindenmayer and Laurance, 2017). Under the metabolic scaling theory, we found that a small number of large-diameter trees regulated forest AGBs in the overstory and whole community, regulating a direct relationship between tree size, density, and stand-level AGB (Enquist and Niklas, 2001; West et al., 2009). Moreover, large-diameter trees can moderate the effects of CEC on overstory and whole AGBs. Interestingly, for the direct and indirect effects of CEC, the indirect effect via large-diameter trees was the larger than the direct effect (approximately three times the direct effect). Recent studies on the role of large-diameter trees in mediating abiotic drivers on AGB in tropical (Ali et al., 2019a) and moist temperate, semi-humid, and semiarid forests (Ali et

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

al., 2020) have shown that the indirect effects of abiotic drivers (e.g., edaphic, topographic, and climatic factors) are substantially larger than the direct effects. In particular, our results for the effect of soil fertility on large-diameter tree DBH represent that the magnitude of the effect of these large-diameter trees on forest structure and function depends on the stand conditions (i.e., soil fertility). The effect of large-diameter trees on stand structure and function is larger in stands with fertile soils than in stands with non-fertile soils. In stands with non-fertile soils, the large-diameter trees effect is replaced by the density effect of remaining trees, resulting in a different stand structure and AGB pattern. These results are consistent with previous studies on the predominance of size-asymmetric competition with larger individuals in fertile soils (Weiner, 1990; Pretzsch and Biber, 2010) and the dominance of size-symmetric competition under a limitation of belowground resources (van Kuijk et al., 2008; Pretzsch and Biber, 2010). After all, the structure and biomass pattern in early successional forests may proceed as large-diameter trees-centric process or remaining trees-centric process depending on site conditions such as soil fertility. Therefore, our results indicate that interactions between self-thinning and resource availability affect the structure and function across forest stands during early succession.

The effect of large-diameter trees on AGB was attenuated in the understory, where the effect of stem density on AGB overwhelmed other predictors. Higher stem density, defined by species and functional trait diversity, can increase space packing and lead to higher wood production (Morin, 2015). Recent studies also reported that stem density strongly affects AGB (Fotis et al., 2018; Ali et al., 2020). The pSEM results showed that stem density had the strongest direct effect on understory AGB via a negative interaction with understory SE. These results suggest that vegetation quantity (i.e., stem density) and quality (i.e., SE) complement each other to regulate understory AGB. Recent studies showed that stem density increases with species diversity (i.e., more species are generally recorded in denser forest stands), which has a stronger direct effect on AGB than high SR (Fotis et al., 2018). Moreover, recent studies also documented that understory AGB was primarily controlled by understory attributes rather than overstory attributes (Yuan et al., 2019; Chun et al., 2020).

The explanatory powers of models incorporating the large-diameter tree term as a predictor for overstory and whole community AGBs increased approximately 2–3 times for both full and combined models, respectively, compared with models not incorporating large-diameter trees term (Figures 2 and 3) consistent with the results of Ali et al. (2019a). Our results suggest that AGB across forest strata is controlled by different processes within early successional temperate forests; i.e., overstory and whole community AGBs are primarily regulated by the direct contribution of large-diameter trees, with an especially strong effect at higher soil fertility, and understory AGB was primarily determined by stem density. In addition, the development of understory in terms of structure and function may depend on other abiotic factors such as water, other soil nutrients (e.g., nitrogen, phosphorus), and light conditions associated with stand-specific canopy conditions (Alvarez-Clare et al., 2013; Matsuo et al., 2021), although not analyzed in our study.

We found that CEC was the primary abiotic driver explaining the size (i.e., DBH) of large-diameter trees and AGB variation. CEC is a useful indicator of soil fertility because CEC represents the capacity of the soil to provide nutrients for plants (Doughty et al., 2018). In general, the soil fertility hypothesis predicts that AGB and productivity increases with higher soil nutrient availability and that plants grow faster with high resource availability (Prado-Junior et al., 2016). Indeed, increased

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

CEC was correlated with the DBHs of large-diameter trees in this study across forest strata. Moreover, higher CEC contributed to higher understory AGB via increases in understory stem density, although the importance was lower than the overstory. Slik et al. (2013) reported that soil fertility is an important positive correlate for large-diameter tree density and forest AGB at global and continental scales, especially in Asia and South America. Here, our results also re-emphasize that soil fertility is an important driver of large-diameter trees and forest AGB, although this result differed from our initial expectation that climatic factors would be the best predictors. However, the Global Aridity Index Database (cgiarcsi.community) classified all our study plots as humid sites (aridity index > 0.65; Table S1) indicating that drought may not be a principal limiting factor at any of them. Moreover, we found that CEC indirectly affected understory AGB, suggesting that biotic interactions (i.e., intraspecific and interspecific interactions) in the understory are more important than abiotic factors in driving understory AGB (Halpern and Lutz, 2013; Ali et al., 2019b). Although the effects of climatic and topographic factors varied among forest strata (i.e., overstory, understory and whole community) and models (i.e., models with and without a large-diameter trees term, and combined and full models), the two factors still have significant effects on AGBs. Especially, PC_{clim} as a climatic factor have significant positive effects on overstory and whole AGBs but not understory AGB. From PCA results (Table S4), PC_{clim} had strong positive correlations with moisture-related variables such as MAP and aridity, and negative correlation with MAT. These results indicate that moisture-related variables are involved in driving high AGBs and the large-diameter threshold (Slik et al., 2013) in overstory and whole community. However, PC_{topo} as a topographic factor had negative effects on overstory and understory AGBs with the term of large-diameter trees in full modes, but the factor has positive effects on AGBs in overstory and whole community. These results indicate that different topographic components are involved in controlling AGBs depending on the presence or absence of large-diameter trees.

5 Conclusions

Here, we show that that large-diameter trees have an overwhelming effect on AGB in early-successional temperate forests, likely reflecting strong competitiveness and exploitative resource use of them. Moreover, large-diameter trees mediate the effects of abiotic drivers on AGBs in overstory and whole community and play an important role in both controlling the diversity and structure of remaining trees (e.g., CD and SS drivers in this study). The only exception is that understory AGB primarily depends on the stem density in the understory itself, indicating that large trees do not necessarily limit understory development. In addition, our study highlights the mechanisms of biomass dominance of large-diameter trees associated with self-thinning process and resource availability in early successional forests. Our study advocates the need to carefully consider large-diameter trees in conservation and management of even early-successional forests, as they given their influence on total AGB have strong importance for forest ecosystem functions and services (e.g., Lutz et al., 2018), sustainable forest management (e.g., Yuan et al., 2021), and biodiversity (e.g., Harris et al., 2021). Therefore, we suggest that further studies need to include the roles and functions of large-diameter trees on the multifunctionality and stability of forest ecosystems (Ali

© Author(s) 2022. CC BY 4.0 License.

and Wang, 2021), and the sensitivity and importance of large-diameter trees and their dominant forests to climate change in the global carbon sequestration (Phillips et al., 2010; Stephenson et al., 2014; Bennett et al., 2015; Bordin et al., 2021).

Data availability. All data sources are publicly available. National Forest Inventory (NFI) of South Korea are available from Korea Forest Service (www.forest.go.kr). Climactic variables are available from WorldClim (www.worldclim.org) or the Global Aridity Index and Potential Evapotranspiration Climate Database (cgiarcsi.community). Soil variables are available from the SoilGrids database (https://soilgrids.org). All data analyzed in this paper are available through the corresponding author upon request.

Author contributions. CBL designed and initiated the study. CBL and MKL contributed to the integration, visualization, and interpretation of the results. AA, JAL, ZY and JCS contributed to the discussion of scientific questions and the revision of the manuscript. AA and CBL contributed to the integration and interpretation of the data. CBL led the writing of the paper with the support of AA, JAL ZY, and JCS

Competing interests. The contact author has declared that neither they nor their co-authors have any competing interests

Acknowledgements. We would like to thank Miss Eun-Sol Park and Mr. Hyun-Seok Park for their invaluable help with data analysis in this study.

Financial support. This study was conducted with the support of the R&D Program for Forest Science Technology (project no. 2019150C10-2123-0301) of the Korea Forest Service (Korea Forestry Promotion Institute) and the National Research Foundation of Korea (NRF) grant funded by the government of Korea (MSIT) (no. 2020R1A2C2011226). AA is currently supported by the Faculty Startup Research Funding for establishing Forest Ecology Research Group at Hebei University (Special Project No. 521100221033). JCS considers this work a contribution to his VILLUM Investigator project "Biodiversity Dynamics in a Changing World" funded by VILLUM FONDEN (grant 16549).

References

Ali, A., and Yan, E.R.: The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest, For. Ecol. Manag., 401, 125–134, https://doi.org/10.1016/j.foreco.2017.06.056, 2017.

Ali, A., Lin, S. L., He, J. K., Kong, F. M., Yu, J. H., et al.: Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests, Glob. Chang. Biol., 25, 2810–2824, https://doi.org/10.1111/gcb.14707, 2019a.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Ali, A., Chen, H. Y. H., You, W. H., and Yan, E. R.: Multiple abiotic and biotic drivers of aboveground biomass shift with forest stratum, For. Ecol. Manag., 436, 1–10, https://doi.org/10.1016/j.foreco.2019.01.007, 2019b.

Ali, A., Sanaei, A., Li, M., Nalivan, O. A., Pour, M. J., et al.: Big-tree–energy mechanism underlies forest diversity and aboveground biomass, For. Ecol. Manag., 462, 117968, https://doi.org/10.1016/j.foreco.2020.117968, 2020.

Ali, A., and Wang, L. Q.: Big-sized trees and forest functioning: current knowledge and future perspectives, Ecol. Indic., 127, 107760, https://doi.org/10.1016/j.ecolind.2021.107760, 2021.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., et al.: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, For. Ecol. Manag., 259, 660–684, https://doi.org/10.1016/j.foreco.2009.09.001, 2010.

Alvarez-Clare, S., Mack, M. C., and Brooks, M.: A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest, Ecology, 94, 1540–1551, https://doi.org/10.1890/12-2128.1, 2013.

Baltzer, J. L, Veness, T., Chasmer, L. E., Sniderhan, A. E., and Quinton, W. L.: Forests on thawing permafrost: fragmentation, edge effects, and net forest loss, Glob. Chang. Biol., 20, 824–834, https://doi.org/10.1111/gcb.12349, 2014.

Bastin, J. F., Rutishauser, E., Kellner, J. R., Saatchi, S., Pélissier, R., et al.: Pan-tropical prediction of forest structure from the largest trees, Glob. Ecol. Biogeogr., 27, 1366–1383, https://doi.org/10.1111/geb.12803, 2018.

Bennett, A. C., Mcdowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J.: Larger trees suffer most during drought in forests worldwide, Nat. Plants, 1, 15139, https://doi.org/10.1038/nplants.2015.139, 2015.

Bordin, K. M., Esquivel-Muelbert, A., Bergamin, R. S., Klipel, J., Picolotto, R. C., Frangipani, M. A., et al.: Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests, For. Ecol. Manag., 490, 119126, https://doi.org/10.1016/j.foreco.2021.119126, 2021.

Chu, C., Lutz, J. A., Král, K., Vrška, T., Yin, X., et al.: Direct and indirect effects of climate on richness drive the latitudinal diversity gradient in forest trees, Ecol. Lett., 22, 245–255, https://doi.org/10.1111/ele.13175, 2019.

Chun, J. H., Ali, A., and Lee, C. B.: Topography and forest diversity facets regulate overstory and understory aboveground biomass in a temperate forest of South Korea, Sci. Total Environ., 744, 140783, https://doi.org/10.1016/j.scitotenv.2020.140783, 2020.

Conti, G., and Díaz, S.: Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems, J. Ecol., 101, 18–28, https://doi.org/10.1111/1365-2745.12012, 2013.

Cook-Patton, S. C., Leavitt, S. M., Gibbs, D., Harris, N. L., Lister, K., et al.: Mapping carbon accumulation potential from global natural forest regrowth, Nature, 585, 545–550, https://doi.org/10.1038/s41586-020-2686-x, 2020.

Doughty, C. E., Goldsmith, G. R., Raab, N., Girardin, C. A. J., Farfan-Amezquita, F., et al.: What controls variation in carbon use efficiency among Amazonian tropical forests?, Biotropica, 50, 16–25, https://doi.org/10.1111/btp.12504, 2018.

Enquist, B. J., and Niklas, K. J.: Invariant scaling relations across tree-dominated communities, Nature, 410, 655–660, https://doi.org/10.1038/35070500, 2001.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Enquist, B. J., West, G. B., Charnov, E. L., and Brown, J. H.: Allometric scaling of production and life-history variation in vascular plants, Nature, 401, 907–911, https://doi.org/10.1038/44819, 1999.

Estrada-Villegas, S., Bailón, M., Hall, J. S., Schnitzer, S. A., Turner, B. L., et al.: Edaphic factors and initial conditions influence successional trajectories of early regenerating tropical dry forests, J. Ecol., 108, 160–174, https://doi.org/10.1111/1365-2745.13263, 2020.

Fotis, A. T., Murphy, S. J., Ricart, R. D., Krishnadas, M., Whitacre, J., et al.: Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest, J. Ecol., 106, 561–570, https://doi.org/10.1111/1365-2745.12847, 2018.

Franklin, J. F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh D.A., et al.: Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir as an example, For. Ecol. Manag., 155, 399–423, https://doi.org/10.1016/S0378-1127(01)00575-8, 2002.

Graham, M. H.: Confronting multicollinearity in ecological multiple regression, Ecology, 84, 2809–2815, https://doi.org/10.1890/02-3114, 2003.

Grime, J. P.: Benefits of plant diversity to ecosystems: immediate, filter and founder effects, J. Ecol., 86, 902–910, https://doi.org/10.1046/j.1365-2745.1998.00306.x, 1998.

Halpern, C. B., and Lutz, J. A.: Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions, Ecol. Monogr, 83, 221–237, https://doi.org/10.1890/12-1696.1, 2013.

Harris, D. J., Ebika, S. T. N., Sanz, C. M., Madingou, M. P. N., Morgan, D. B.: Large trees in tropical rain forests require big plots, New Phytol., 3, 282–294, https://doi.org/10.1002/ppp3.10194, 2021.

Heinrich, V. H. A., Dalagnol, R., Cassol, L. G., Rosan T. M., de Almeida, C. T., et al.: Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climae change, Nat. Comm., 12, 1785, https://doi.org/10.1038/s41467-021-22050-1, 2021.

Jucker, T., Bouriaud, O., Avacaritei, D., and Coomes, D. A.: Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes, Ecol. Lett., 17, 1560–1569, https://doi.org/10.1111/ele.12382, 2014.

Korea Forest Service: Statistical yearbook of forest, Korea Forest Service, Deajeon, 2019. (in Korean). Available from https://www.forest.go.kr

Korea Forest Research Institute: The 5th national forest inventory report, Korea Forest Service, Daejeon, 2011. (in Korean). Available from https://www.forest.go.kr

Laliberté, E., and Legendre, P.: A distance-based framework for measuring functional diversity from multiple traits, Ecology, 91, 299–305, https://doi.org/10.1890/08-2244.1, 2010.

Lefcheck, J. S.: piecewiseSEM: piecewise structural equation modelling, 2020. Available from https://github.com/jslefche

Legendre, P., and Legendre, L.: Numerical ecology, Elsevier, Amsterdam, 1998.

Lin, Y., Berger, U., Yue, M., and Grimm, V.: Asymmetric facilitation can reduce size inequality in plant populations resulting in delayed density-dependent mortality, Oikos, 125, 1153–1161, https://doi.org/10.1111/oik.02593, 2016.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F: Global decline in large old trees, Science, 338, 1305–1306, https://doi.org/10.1126/science.1231070, 2012.

Lindenmayer, D. B., and Laurance, W. F.: The ecology, distribution, conservation and management of large old trees, Biol. Rev., 92, 1434–1458, https://doi.org/10.1111/brv.12290, 2017.

Lohbeck, M., Poorter, L., Martínez-Ramos, M., and Bongers, F.: 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, 2015.

Lutz, J. A., Larson, A. J., Furniss, T. J., Freund, J. A., Swanson, M. E., et al.: Spatially non-random tree mortality and ingrowth maintain equilibrium pattern in an old-growth Pseudotsuga-Tsuga forest, Ecology, 95, 2047–2054, https://doi.org/10.1890/14-0157.1, 2014.

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., et al.: Global importance of large-diameter trees, Glob. Ecol. Biogeogr., 27, 849–864, https://doi.org/10.1111/geb.12747, 2018.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., et al.: Old-growth forests as global carbon sinks, Nature, 455, 213–215, https://doi.org/10.1038/nature07276, 2008.

Matsuo, T., Martínez-Ramos, M., Bongers, F., van der Sande, M. T., and Poorter, L.: Forest structure drives changes in light heterogeneity during tropical secondary forest succession, J. Ecol., 109, 2871–2884, https://doi.org/10.1111/1365-2745.13680, 2021.

Meakem, V., Tepley, A. J., Gonzalez-Akre, E. B., Herrmann, V., Muller-Landau, H. C., et al.: Role of tree size in moist tropical forest carbon cycling and water deficit responses, New Phytol, 219, 947–958, https://doi.org/10.1111/nph.14633, 2018.

Morin, X.: Species richness promotes canopy packing: a promising stem towards a better understanding of the mechanisms driving the diversity effects on forest functioning, Funct. Ecol., 29, 993–994, https://doi.org/10.1111/1365-2435.12473, 2015.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., et al.: A large and persistent carbon sink in the world's forests, Science, 333, 988–993, https://doi.org/10.1126/science.1201609, 2011.

Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C., et al.: Drought-mortality relationships for tropical forests, New Phytol, 187, 631–646, https://doi.org/10.1111/j.1469-8137.2010.03359.x, 2010.

Poorter, L., Bongers, F., Aide, T. M., Zambrano, A. M. A., Balvanera, P., et al.: Biomass resilience of Neotropical secondary forests, Nature, 530, 211–214, https://doi.org/10.1038/nature16512, 2016.

Poorter, L., van der Sande, M. T., Arets, E. J. M. M., Ascarrunz, N., Enquist, B. J., et al.: Biodiversity and climate determine the functioning of Neotropical forests, Glob. Ecol. Biogeogr., 26, 1423–1434, https://doi.org/10.1111/geb.12668, 2017.

Prado-Junior, J. A., Schiavini, I., Vale, V. S., Arantes, C. S., van der Sande, M. T., et al.: Conservative species drive biomass productivity in tropical dry forests, J. Ecol., 104, 817–827, https://doi.org/10.1111/1365-2745.12543, 2016.

Pretzsch, H., and P. Biber.: Size-symmetric and size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe, Can. J. Forest Res., 40, 370–384, https://doi.org/10.1139/X09-195, 2010.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., et al.: Role of forest regrowth in global carbon sink dynamics, Proc. Natl. Acad. Sci. USA, 116, 4382–4387, https://doi.org/10.1073/pnas.1810512116, 2019.

R Development Core Team.: R: a language and environment for statistical computing, The R Foundation for Statistical Computing, Vienna, 2021.

Sheil, D., Eastaugh, C. S., Vlam, M., Zuidema, P. A., Groenendijk, P., et al.: Does biomass growth increase in the largest trees? Flaws, fallacies and alternative analyses, Funct. Ecol., 31, 568–581, https://doi.org/10.1111/1365-2435.12775, 2017.

Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., et al.: Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics, Glob. Ecol. Biogeogr., 22, 1261–1271, https://doi.org/10.1111/geb.12092, 2013.

Son, Y. M., Kim, R. H., Lee, K. H., Pyo, J. K., Kim, S. W., et al.: Carbon emission factors and biomass allometric equations by species in Korea, National Institute of Forest Science, Seoul, 2014.

Stephenson, N. L., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., et al.: Rate of tree carbon accumulation increase continuously with tree size, Nature, 507, 90–93, https://doi.org/10.1038/nature12914, 2014.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., et al. The influence of functional diversity and composition on ecosystem processes, Science, 277, 1300–1302, https://doi.org/10.1126/science.277.5330.1300, 1997.

van der Plas, F.: Biodiversity and ecosystem functioning in naturally assembled communities, Biol. Rev., 94, 1220–1245, https://doi.org/10.1111/brv.12499, 2019.

van Kuijk, M., N.P.R. Anten, R.J. Oomen, D.W. van Bentum, and M.J.A. Werger.: The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest sucesssion in Vietnam, Oecologia, 157, 1–12, https://doi.org/10.1007/s0042-008-1048-4, 2008.

West, G. B., Enquist, B. J., and Brown, J. H.: A general quantitative theory of forest structure and dynamics, Proc. Natl. Acad. Sci. USA, 106, 7040–7045, https://doi.org/10.1073/pnas.0812294106, 2009.

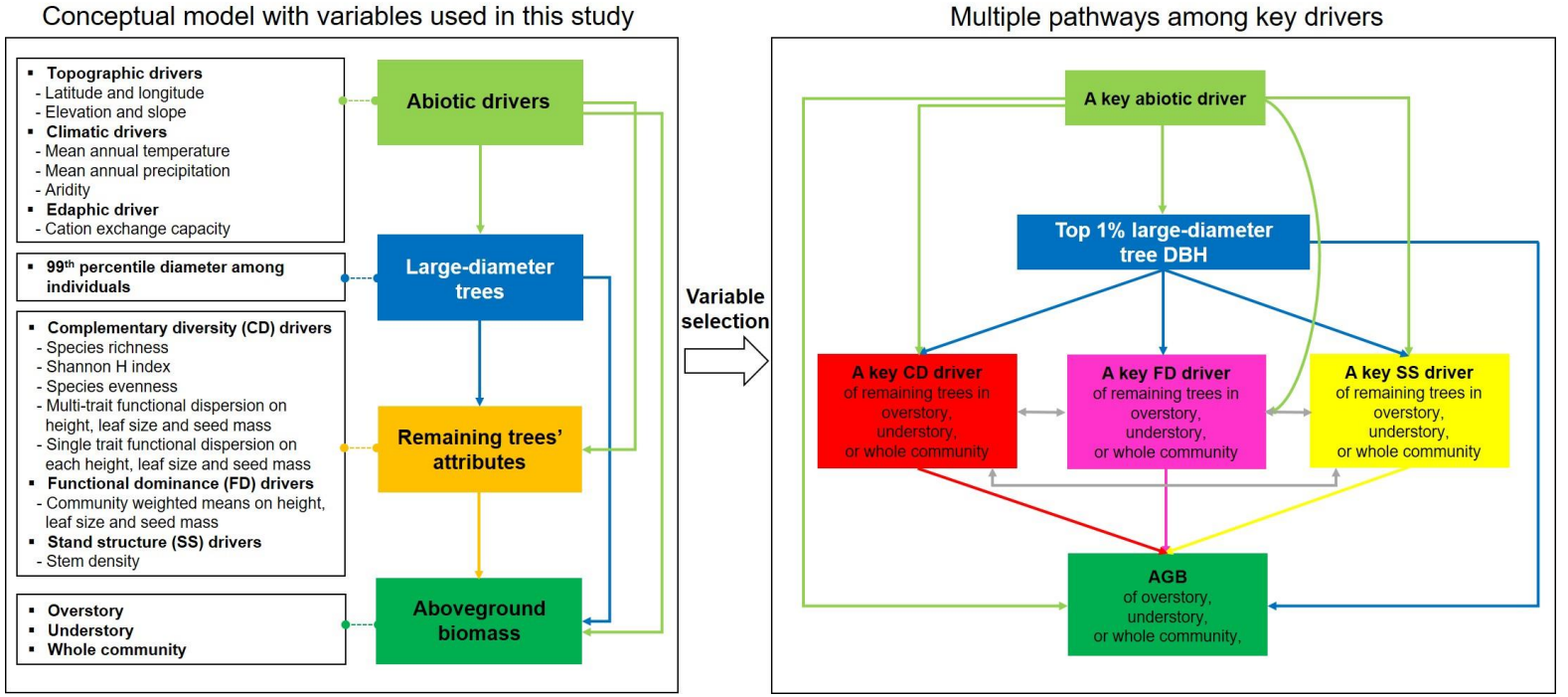
Weiner, J.: Asymmetric competition in plant populations, Trends Ecol. Evol., 5, 360–364, https://doi.org/10.1016/0169-5347(90)90095-U, 1990.

Yuan, Z., Ali, A., Jucker, T., Ruiz-Benito, P., Wang, S., et al.: Multiple abiotic and biotic pathways shape biomass demographic processes in temperate forests, Ecology, 100, e02650, https://doi.org/10.1002/ecy.2650, 2019.

Yuan, Z., Ali, A., Sanaei, A., Ruiz-Benito, P., Jucker, T., et al.: Few large trees, rather than plant diversity and composition, drive the above-ground biomass stock and dynamics of temperate forests in northeast China, For. Ecol. Manag., 481, 118698, https://doi.org/10.1016/j.foreco.2020.118698, 2021.

Zhang, Y., Chen, H. Y. H., and Reich, P. B.: Forest productivity increase with evenness, species richness and trait variation: a global meta-analysis, J. Ecol., 100, 742–749, https://doi.org/10.1111/j.1365-2745.2011.01944.x, 2012.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.



490 **Figure 1: Conceptual model indicating how the attributes of large-diameter trees (the largest 1% by DBH) and remaining trees combined with abiotic drivers affect the aboveground biomass (AGB) of the overstory, understory, and whole community. Abbreviations: CD, complementary diversity; FD, functional dominance; SS, stand structure.**

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

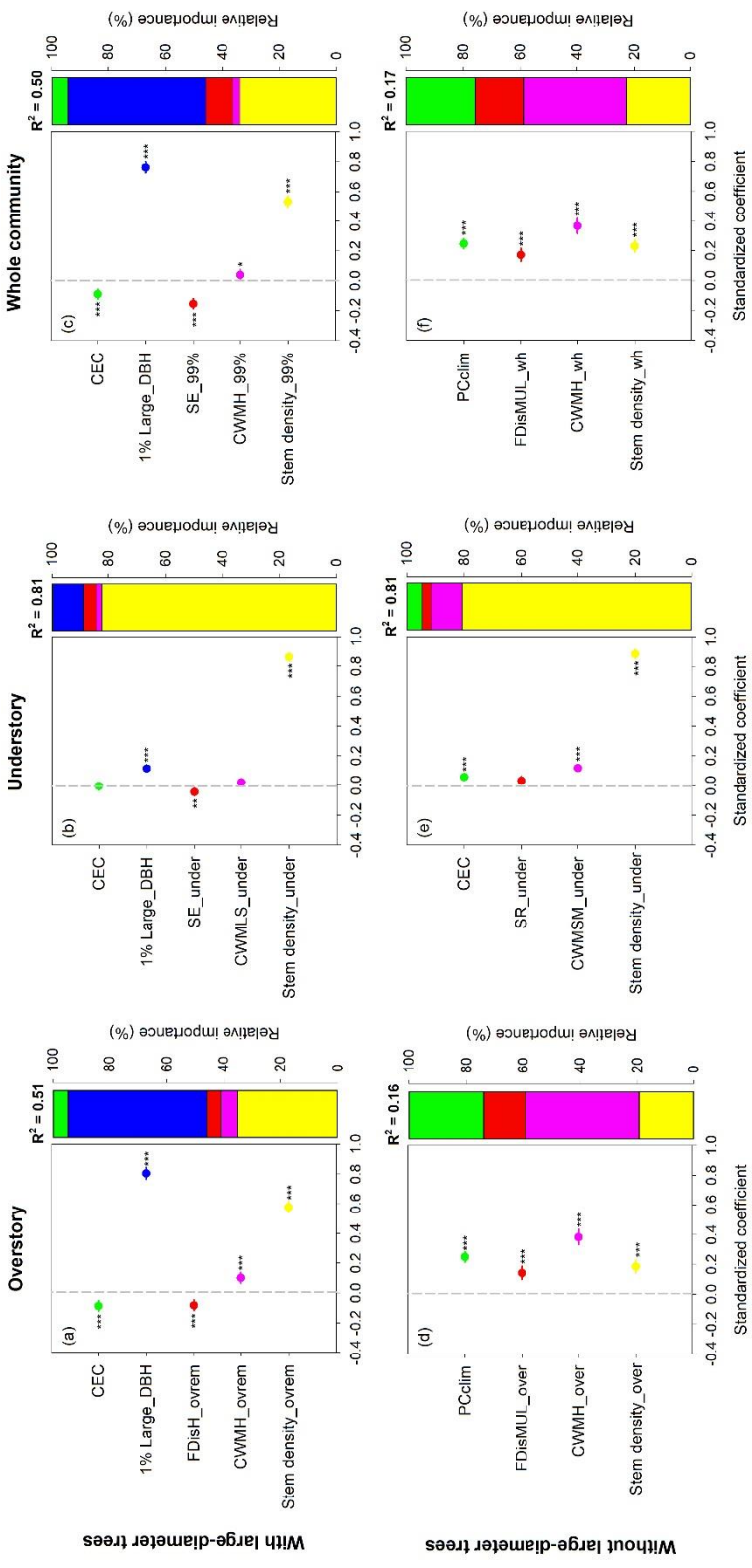


Figure 2: Relative effects of multiple predictors on the aboveground biomass (AGB) of (a) overstory, (b) understory, and (c) whole community from combined models. The average parameter estimates (standardized regression coefficients) of model predictors are shown with 95% confidence intervals together with relative importance expressed as the percentage of explained variance. The relative importance of each predictor was calculated as the ratio between the parameter estimates of the predictor and the sum of all parameter estimates described as a percentage. Abbreviations: PCclim, the first axis of principal component analysis for climatic variables; CEC, cation exchange capacity; 1% Large_DBH, 1% large-diameter tree DBH; SE, species evenness; SR, species richness; FDis, functional dispersion; CWM, community-weighted mean; H, maximum height; LS, leaf size; SM, seed mass; MUL, multi-trait including maximum height, leaf size, and seed mass; 99%, 99% remaining trees excluding the 1% large-diameter trees; wh, whole community; over, overstory; ovrem, overstory remaining trees excluding the 1% large diameter trees in overstory; under, understory. Significance levels are * $P <$ 0.05, ** $P < 0.01$, and *** $P < 0.001$.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

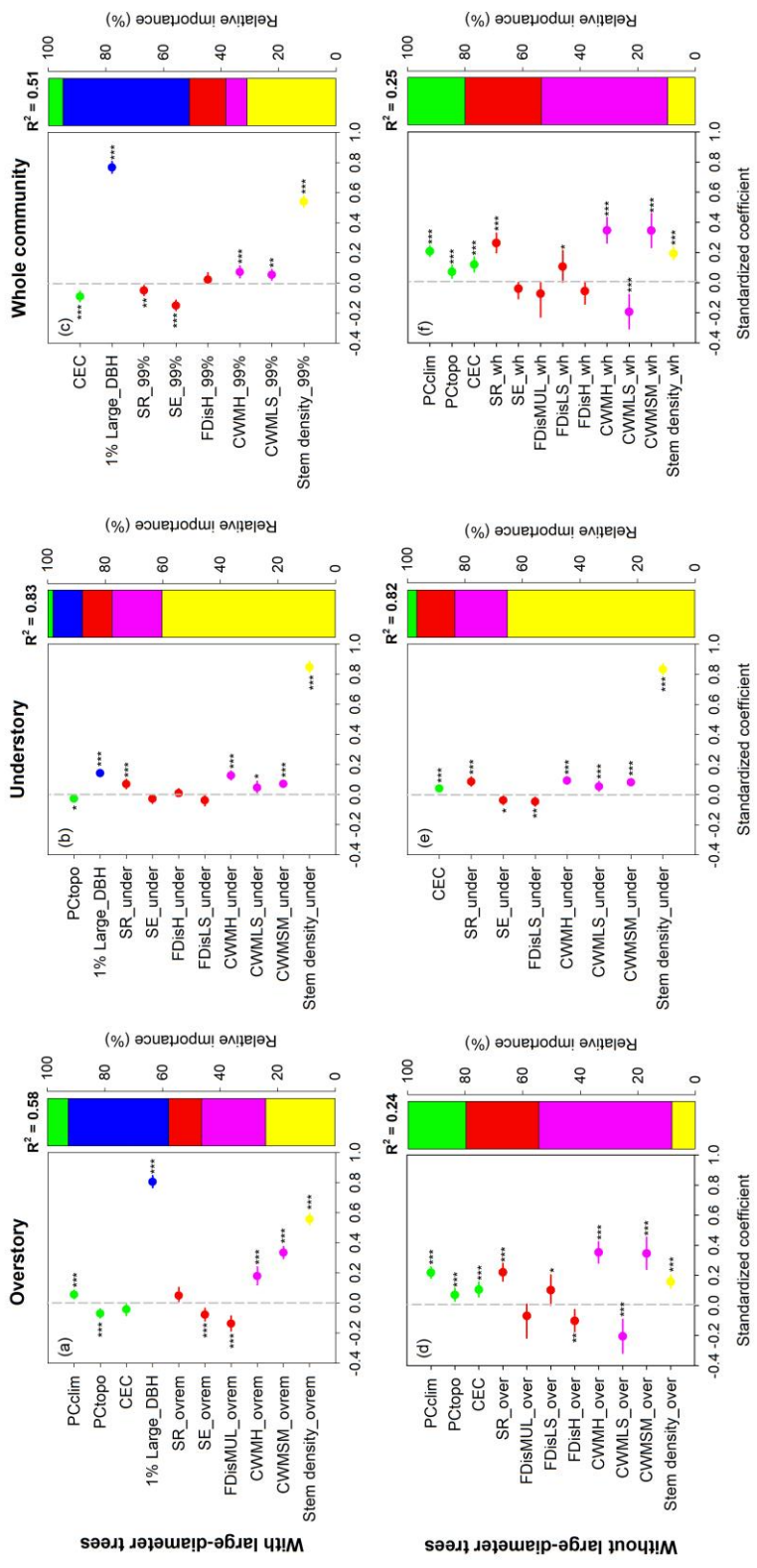


Figure 3: Relative effects of multiple predictors on the aboveground biomass (AGB) of (a) overstory, (b) understory, and (c) whole community from full models. The average parameter estimates (standardized regression coefficients) of model predictors are shown with 95% confidence intervals along with relative importance expressed as the percentage of explained variance. The relative importance of each predictor was calculated as the ratio between the parameter estimate of the predictor and the sum of all parameter estimates described as a percentage. Abbreviations: PCclim, the first axis of PCA for climatic variables; PCtopo, the first axis of PCA for topographic variables; CEC, cation exchange capacity; 1% Large_DBH, 1% large-diameter tree DBH; SE, species evenness; SR, species richness; FDis, functional dispersion; CWM, community-weighted mean; H, maximum height; LS, leaf size; SM, seed mass; MUL, multi-trait including maximum height, leaf size, and seed mass; 99%, 99% remaining trees excluding the 1% large-diameter trees; wh, whole community; over, overstory; ovrem, overstory remaining trees excluding the 1% large diameter trees in overstory; under, understory. Significance levels are * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

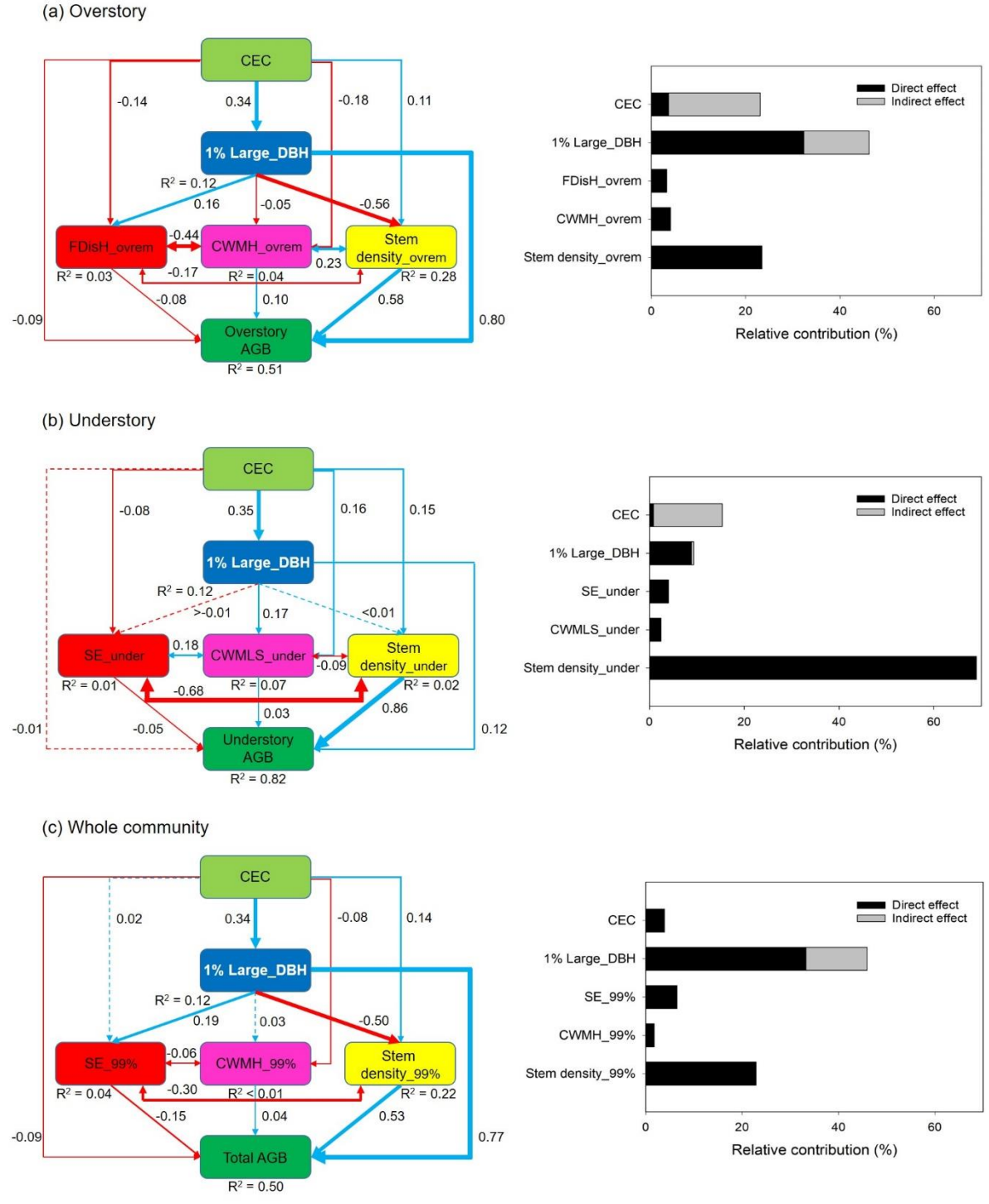


Figure 4: Piecewise structural equation models (left) and relative contributions (right) for testing relationships between abiotic drivers, large-diameter tree DBH, 99% remaining trees' attributes, and the aboveground biomass (AGB) of (a) overstory, (b)

https://doi.org/10.5194/bg-2022-60
Preprint. Discussion started: 10 March 2022
© Author(s) 2022. CC BY 4.0 License.

understory, and (c) whole community in the temperate forests of South Korea. In piecewise structural equation models, blue and red arrows indicate positive and negative pathways, respectively. Solid and dashed arrows represent significant and nonsignificant pathways, respectively. Standardized coefficients are shown for each pathway and covariance. The relative contribution was calculated as the ratio between the parameter estimate of the predictor and the sum of all parameter estimates expressed as a percentage. Abbreviations for the variables are shown in Figure 3.