Master's Thesis of Landscape Architecture

Niche complementarity and selection effect explain the difference of aboveground biomass density patterns inside and outside of protected areas

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Abstract

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Forests play a crucial role in providing essential ecosystem services and mitigating climate change through carbon sequestration. Understanding the patterns of aboveground biomass in forests is essential for assessing their carbon storage potential. Remote sensing techniques, such as the Global Ecosystem Dynamics Investigation (GEDI) mission of the National Aeronautics and Space Administration, provide valuable data for estimating aboveground biomass density at large spatial scales. This study examined the correlation of aboveground biomass density with the functional diversity and composition of the forests in South Korea, both within and outside of protected areas. Two ecological hypotheses, namely the niche complementarity and selection effect hypotheses, were evaluated using linear mixed models, with average age class as a random variable. Niche complementarity was evaluated using 5 different functional diversity values, and selection effect was evaluated using 3 community weighted mean (CWM) for each functional traits. We found that the niche complementarity hypothesis showed inconsistent results when the data of areas within and outside of the protected forests were analyzed, whereas the selection effect hypothesis demonstrated consistent results. Notably, niche complementarity is predominantly significant within the protected areas, indicating that functional diversity can elucidate patterns of biomass density in these areas. The research provides insights into the factors that promote biomass density and the relationship between biomass and biodiversity that can contribute to the development of effective forest management strategies and conservation efforts.

Keywords : GEDI, Forest type map, Functional diversity, Ecological niche, Age class, National scale, Linear mixed models
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Chapter 1. Introduction

1.1. Study background

Forests are widely recognized as important ecosystems that provide critical services such as carbon sequestration, soil conservation, water regulation, and biodiversity conservation that are essential for sustaining ecological processes and supporting human well-being (Bonan, 2008; Jactel et al., 2017; Díaz et al., 2015). Aboveground biomass is a critical parameter in the global carbon cycle as it provides an estimate of the amount of carbon stored in forests (Houghton et al., 2009). The measurement of aboveground biomass is important because it can be used for the assessment of carbon sequestration potential of forests, which is crucial in mitigating climate change (Asner et al., 2010).

However, measuring aboveground biomass can be a costly and time-consuming task, particularly when dealing with large areas and diverse forest types (Mitchard et al., 2013). Remote sensing techniques have emerged as valuable tools for estimating biomass at large scales, providing an efficient and cost-effective alternative to field-based measurements (Asner et al., 2009). Remote sensing can utilize various types of data, such as satellite imagery, light detection and ranging (LiDAR), and radio detection and ranging, to estimate biomass with high accuracy and precision (Shen et al., 2018; Xiao et al., 2019).

The National Aeronautics and Space Administration’ s (NASA) Global Ecosystem Dynamics Investigation (GEDI) mission is a spaceborne LiDAR system designed to measure the vertical structure and biomass of forests (Dubayah et al., 2022). GEDI data have the potential to improve our understanding of ecological mechanisms by providing detailed measurements of forest structure and biomass at a global scale, which can be used to assess forest carbon stocks and dynamics, biodiversity, and forest health. One of the most significant datasets produced by the GEDI is the aboveground biomass density (AGBD) data that provides estimates of biomass stored in forest canopies (Hancock et al., 2019).

Ecological research on the relationship between biomass and diversity is currently being conducted, utilizing hypotheses related to the coexistence of species within ecosystems. Niche complementarity and selection effects have emerged as key concepts in understanding species coexistence and its effect on ecosystem dynamics, process, and ecosystem functioning (Poorter et al., 2015; Mensah et al., 2016, Mensah et al., 2018), and in explaining the diversity-carbon relationship. The concept of function in functional diversity encompasses the unique roles and contributions of organisms in maintaining ecosystem functioning and services (Hector et al., 1999). Function can include a range of ecological processes, such as nutrient cycling, pollination, seed dispersal, and pest regulation, among others. Niche complementarity refers to the idea that species can coexist by utilizing different resources or performing different functions within an ecosystem (Tilman, 1997). In contrast, the selection effect highlights the role of dominance of species traits in determining their competitive ability and subsequent survival (Chesson, 2000, Mensah et al., 2016). Both niche complementarity and selection effects have been shown to be important mechanisms underlying species coexistence and community dynamics (Levine & HilleRisLambers, 2009, HilleRisLambers et al., 2012).

The study of niche complementarity and selection effects is critical to our understanding of species coexistence and community dynamics, both within and outside of protected areas, since protected areas are important for conserving biodiversity and providing habitat for a wide range of species (Joppa et al., 2016; Watson et al., 2014). However, protected areas are also subject to a range of threats, including habitat fragmentation, invasive species, and climate change (Brooks et al., 2002; Parmesan, 2006). The biomass density patterns, which are closely linked to carbon sequestration and climate change mitigation, have been found to differ within and outside of protected areas (Cianciaruso et al., 2010; Pradhan et al., 2019). In the Republic of Korea (South Korea), habitat loss, fragmentation, degradation, and climate change are major threats to biodiversity, posing significant challenges to conservation and management of ecosystem (Ministry of Environment et al., 2018; Adhikari et al., 2018). Niche complementarity and selection effects can provide insights into the ecological mechanisms that promote coexistence and species diversity in the face of these threats, and help guide conservation and management efforts, both inside and outside protected areas (Levine & HilleRisLambers, 2009).

1.2. Purpose of research

This study investigated the relationship between forest aboveground biomass density and functional diversity and composition within both protected and non-protected areas of South Korea by utilizing the latest data and approaches in biomass quantification and diversity in forests. The evaluation was conducted by utilizing the AGBD measured by the GEDI mission to statistically quantify the effect of both niche complementarity and selection effect. This study aimed to provide a comprehensive understanding of the functional factors that promote aboveground biomass density and the relationship between biomass and biodiversity within and outside of protected areas, at a country scale, taking into account the differences in forest characteristics. By investigating the functional diversity and its relationship with AGBD, this research seeks to shed light on the role of species' functions in shaping the patterns of biomass distribution and dynamics in forest ecosystems.

In contrast to previous studies that focused on identifying similar relationships (Wondimu et al., 2021; Wallis et al., 2023), this research was conducted at a national scale. This comprehensive approach will provide valuable insights for informing governmental management plans and future conservation efforts. By investigating the functional diversity and its relationship with AGBD, this research seeks to shed light on the role of species' functions in shaping the patterns of biomass distribution and dynamics in temperate forest ecosystems. This study will contribute to the development of more effective forest management strategies and policies by providing valuable insights into the relationship between biodiversity and ecosystem functioning in South Korea’s forests.

Chapter 2. Literature Review

2.1. Functional diversity and composition

Functional diversity is a crucial component of biodiversity that encompasses the variety of functional roles that different species play within an ecosystem. It is defined as the range of functional traits, including morphological, physiological, and behavioral characteristics, that determine how an organism interacts with its environment and contributes to ecosystem processes (Mouillot et al., 2013a; Díaz et al., 2013). Functional diversity has been shown to have important implications for ecosystem functioning and services. For example, studies have demonstrated that higher levels of plant functional diversity are associated with increased primary productivity, nutrient cycling, and carbon storage in terrestrial ecosystems (Gross et al., 2017).

Functional diversity indices are essential for quantifying the variation in functional roles and traits among species within an ecosystem. Functional richness, functional evenness, functional divergence, and functional dispersion are five widely used indices that provide different aspects of functional diversity (Villéger et al., 2008; Mouillot et al., 2013b) (Table 1, Figure 1).

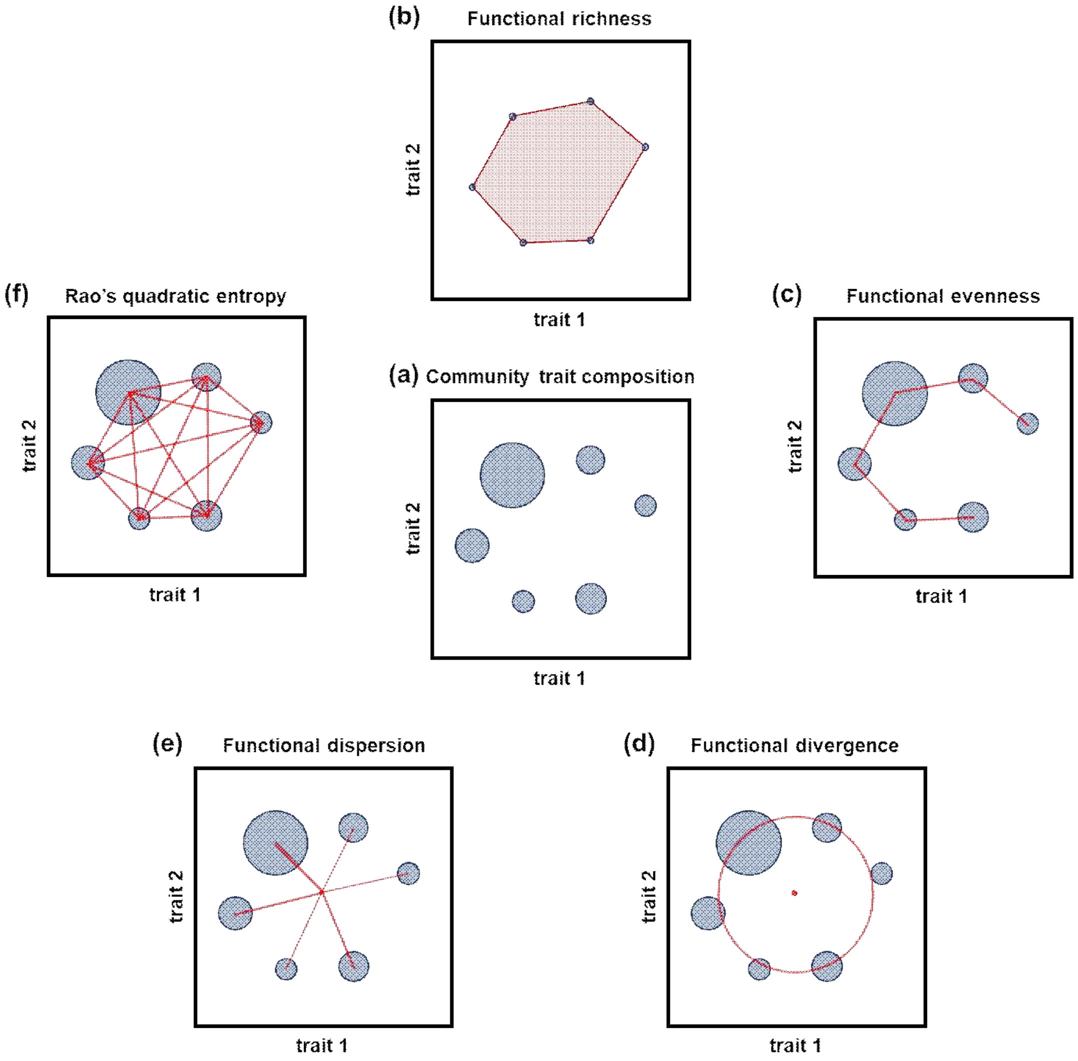

Figure 1. Graphical representation of different functional diversity indices from a community. Each circle represents a species position in trait matrix and the size of the circle shows the abundance of each species. (a) Community trait composition, (b) functional richness, (c) functional evenness, (d) functional divergence, (e) functional dispersion, (f) Rao's quadratic entropy

Functional Richness (FRic) refers to the amount of space occupied by traits of all species in the trait space of a community, and when multiple traits are utilized, it is derived by calculating the convex hull in the trait space. Functional

Evenness (FEve) represents the evenness of trait distribution in the trait space (Mason et al., 2005), and it can be defined as the functional regularity index (FRO) for a single trait. To evaluate the evenness in a T-dimensional space using T-number of traits, the minimum spanning tree (MST) is employed. MST evaluates the connectivity of all points in the T-dimensional space through the shortest paths and is computed using the R package "ape".

To assess abundance-based evenness, the weighted evenness (EW_l) is calculated by dividing the sum of the lengths of S-1 branches connecting S points representing S number of species by the sum of the relative abundances of the two species (Equation 1). $dist(i,j)$ represents the Euclidean distance between species i and species j, and w_i represents the relative abundance of species i. Furthermore, by dividing the sum of for each branch, the partial weighted evenness (PEW) can be derived (Equation 2). When all species are evenly distributed, the value of EW_l is expected to be 1/(S-1). As PEW_l changes, the evenness decreases, and thus functional evenness can be calculated using Equation 3.

$$EW_l = \frac{dist(i,j)}{w_i + w_j} \quad (1)$$

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l} \quad (2)$$

$$FEve = \frac{\sum_{l=1}^{S-1} \min(PEW_l, \frac{1}{S-1}) - \frac{1}{S-1}}{1 - \frac{1}{S-1}} \quad (3)$$

Functional Divergence (FDiv) can be defined as the extent to which a cluster occupies space in the trait space based on abundance (Mason et al., 2005). The center of gravity (G_V) of each species is determined in the trait space, and the average distance from G_V to S points representing S number of species to is used to derive functional divergence. However, functional divergence is an index that does not account for the relative abundance of each species and is solely based on the presence or absence of species in the trait space.

To address the limitation of functional divergence that does not account for the relative abundance of each species, Laliberté and Legendre (2010) proposed Functional Dispersion (FDis) as a complementary measure. Functional Dispersion is derived by calculating the average distance from each species to the centroid (c) of all species in the trait space (Equations 4 and 5). c represents the centroid with weighted contributions from abundance in an i-dimensional trait space, a_j represents the relative abundance of species j, and Z_j represents the distance from species j to the centroid. Therefore, clusters with the same FRic but different positions in the trait matrix can exhibit different FDis (Su et al., 2022).

$$c = [c_i] = \frac{\Sigma a_j x_{ij}}{\Sigma a_j} \quad (4)$$

$$FDis = \frac{\Sigma a_j Z_j}{\Sigma a_j} \quad (5)$$

Rao's quadratic entropy (RaoQ) is a diversity index that can be derived by calculating the average distance between species (Ricotta & Moretti, 2011). Both FDis and RaoQ are indices derived through distance calculations in the trait space. However, FDis has the potential advantage over RaoQ in cases where there are no weights, such as presence and absence data, as it does not require weighting factors (Laliberté & Legendre, 2010).

Table 1. Functional diversity indices evaluated

Name of Indice	Attribute	Reference
Functional Richness (FRic)	The quantity of space occupied by traits in the trait space, represented by the convex hull	Mason et al., 2005
Functional Evenness (FEve)	The evenness of trait distribution in the trait space	Mason et al., 2005
Functional Divergence (FDiv)	The average distance from each species to the center of gravity of traits (G_V) in the trait space.	Mason et al., 2005
Functional Dispersion (FDis)	The average distance from each species to the centroid (c) in the trait space	Laliberté & Legendre, 2010
Rao’s Quadratic Entropy (RaoQ)	The average distance between two species in the trait space	Rao, 1982 Botta-Dukát, 2005

These five indices provide complementary information about the functional diversity of communities, and their application can help to identify the mechanisms driving ecosystem functioning and the response of ecosystems to environmental change. Functional dominance (single functional trait index) was calculated by the community weight mean (CWM) of each unit cell for each functional trait. CWM is the mean of each species trait value weighted by the relative abundance of that species (Cavanaugh et al., 2014).

The coherence of the relationship between biodiversity components and ecosystem function is variable across studies, with some showing positive correlations between species diversity and aboveground biomass, while others showing negative or no correlation at all. For instance, positive relationships were found between species richness and aboveground biomass in a primary *Pinus kesiya* forest in Yunnan of southwest China (Li et al., 2018) and in tropical forests (Poorter et al., 2015), as well as between diversity and aboveground biomass in a natural temperate spruce and pine forest (Zhang and Chen, 2015). Conversely, a negative relationship was reported between species diversity and biomass storage in a European pine forest (Szwagrzyk and Gazda, 2007), and some studies have found no significant correlation between aboveground biomass and tree species diversity in forest ecosystems (Whittaker and Heegaard, 2003).

Wallis et al.(2023) examined the relationship between hyperspectral reflectance and aboveground carbon content in forests, testing the relative importance of tree composition and diversity in mediating this relationship. The findings suggest that tree composition, but not diversity, plays a crucial role in mediating the link between hyperspectral data and forest carbon content, highlighting the potential of hyperspectral remote sensing. Wondimu et al.(2021) investigated the relationship between species diversity, functional diversity, and aboveground biomass carbon in a dry evergreen Afromontane forest using structural equation modeling and linear mixed model. Results showed that both selection effects (functional dominance) and niche complementarity (functional diversity) were important for aboveground carbon storage prediction, but the effects of functional diversity were greater than functional dominance effects.

2.2. GEDI aboveground biomass

The Global Ecosystem Dynamics Investigation (GEDI) is a NASA mission designed to provide global observations of forest canopy height, structure, and biomass (Dubayah et al., 2020). One of the most significant datasets produced by GEDI is the AGBD data, which provides estimates of biomass stored in forest canopies (Hancock et al., 2019).

Dubaya et al.(2022) provides detailed explanation for this dataset. The GEDI is the first mission prupose-built for creating the kind of mapped estimes of AGBD. The mission, which uses lidar instruments attached to the International Space Station (ISS), consists of 3 lasers producing a total of 8 beam ground transects. It utilizes a hybrid estimation to create exhaustive coverage of mean biomass estimates from an incomplete sample of modeled biomass values of L4A product and provides GEDI L4B AGBD data with non-overlapping 1km × 1km spatial grids. The data is based on observations from mission week 19 to mission week 138, corresponding to April 2019 through August 2021.

As GEDI is a relatively new data product, there has been limited research conducted on its capabilities and applications. This data has significant implications for understanding the environment, including carbon cycle dynamics, climate change, and biodiversity conservation. Recent studies have demonstrated the usefulness of GEDI AGBD data in characterizing forest structure (Lefsky et al., 2021), monitoring forest degradation, and assessing forest carbon stocks (Lefsky et al., 2021; Neigh et al., 2021). Liang et al.(2023) assessed the effectiveness of protected areas in storing carbon stocks utilizing forest structural information and AGBD. The findings suggest that protected areas in Tanzania have higher biomass densities than unprotected forests and that community-governed protected areas are the most effective category for preserving forest structure and AGBD. It is anticipated that future research efforts will provide a more comprehensive understanding of GEDI's utility.

Chapter 3. Materials and Methods

To evaluate and understand the relationship between forest biomass density and functional diversity and composition effect inside and outside of protected areas in South Korea, a three step research flow was designed: Data acquisition, data processing, statistical analysis (Figure 2).

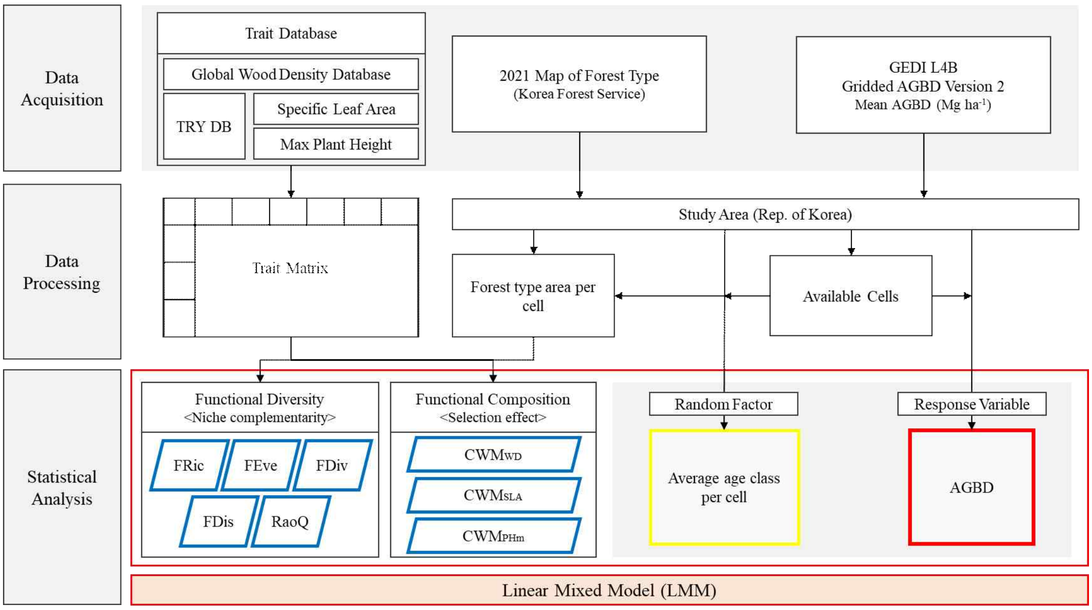

Figure 2. Study Flow

3.1. Study area

The study area included the forested areas of South Korea that are predominantly coniferous, followed by broadleaved, mixed forests (Korea Forest Service, 2020). *Pinus densiflora* and *Quercus acutissima* are the most dominant species, and approximately 87% of these trees belong age classes III—V (30

—50 years old), owing to the National Greening Program established from 1950 to 1980 (Korea Forest Service, 2020; Bae et al., 2022).

South Korea has a temperate climate characterized by hot summers and cold winters, with raining seasons during the summer, influenced by the East Asian monsoon system. The soils are generally acidic, with low nutrient availability and organic matter content, and a high proportion of clay and silt particles. The dominant soil types in South Korea are ultisols, andisols, and inceptisols, which have developed from a range of parent materials including granite, basalt, and volcanic ash.

3.2. Data

A forest map that includes vector-based information on forest types and age classes, as of the year 2021, was obtained from the Korea Forest Service. The map provides species composition classified into 42 forests types, excluding unstocked forest land and bamboo forest and other non-forest types (Table 2). Protected forest areas in South Korea were obtained from the World Database on Protected Areas (WDPA). The WDPA is a database developed and managed by the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) and the International Union for Conservation of Nature (IUCN) (UNEP-WCMC & IUCN, 2023). This database is considered to be the most comprehensive global source of information on terrestrial and marine protected areas, containing information on over 250,000 protected areas worldwide. Therefore, it serves as a valuable tool for understanding the status, trends, and effectiveness of protected areas in conserving biodiversity and supporting sustainable development (UNEP-WCMC et al., 2018; UNEP-WCMC & IUCN, 2023). The WDPA is utilized by researchers, policymakers, and practitioners around the world to support evidence-based decision-making for biodiversity conservation and management (Dudley et al., 2018; UNEP-WCMC & IUCN, 2023). To exclude non-natural forests such as natural monuments, marine protected areas, disaster prevention reserves, etc., protected areas designated by the Ministry of the Environment of Republic of Korea were selected (Table 3, Figure 3).

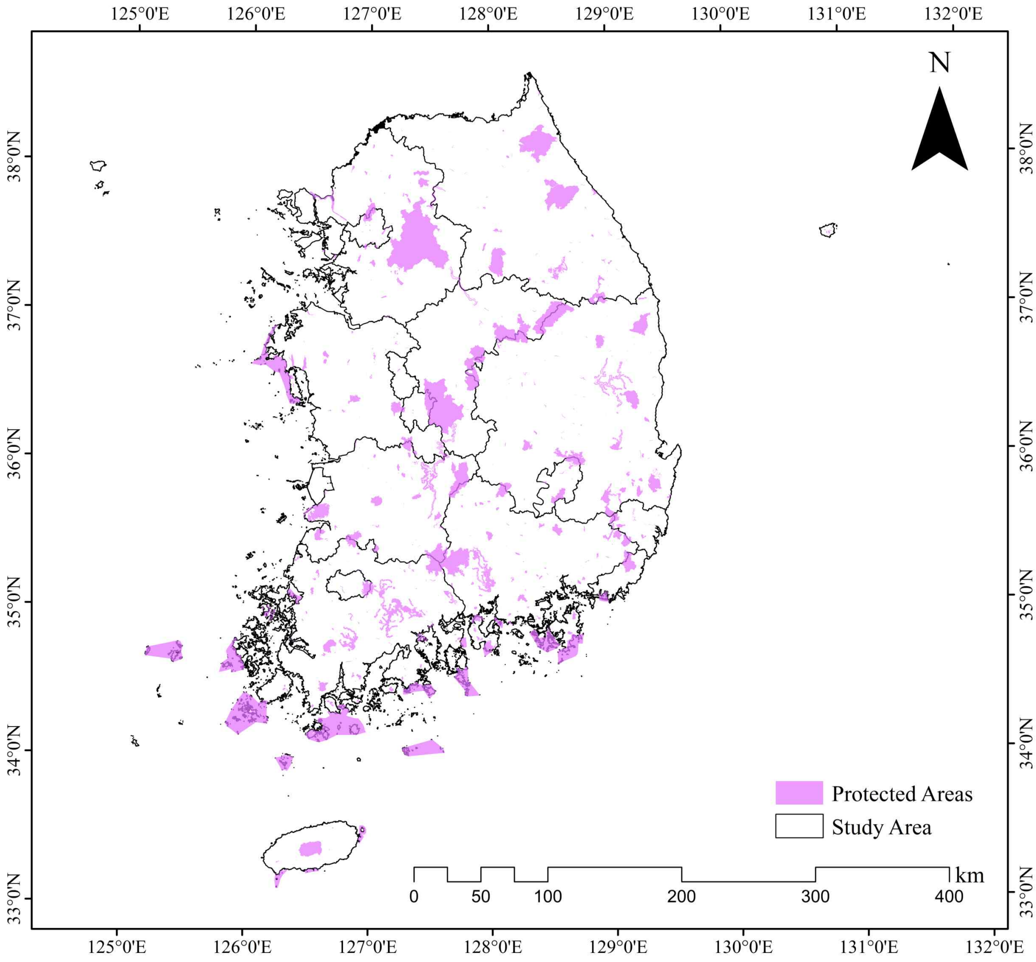

Figure 3. Protected areas designated by the Ministry of Environment in the Republic of Korea

The aboveground biomass density was evaluated using the Global Ecosystem Dynamics Investigation's (GEDI) GEDI L4B Gridded Aboveground Biomass Density, Version 2 data. The GEDI is a mission designed by NASA to provide global data of forest canopy height, structure, and biomass (Dubayah et al., 2022). One of the most significant datasets produced by the GEDI is the mean AGBD data, which provides estimates of biomass stored in forest canopies (Hancock et al., 2019). This product provided 1km × 1km estimates of aboveground biomass density for the period April 2019 to August 2021 between 51.6° and −51.6° latitude, published in March 2022 (Dubayah et al., 2022). The observed data that were in the boundary of South Korea were included in the research. Figure 4 represents the available GEDI's mean AGBD data within South Korea. The observed data points were classified into distinct categories, based on their inclusion or exclusion within designated protected areas (Appendix A). Subsequently, cells characterized by forest cover of 90% or greater were specifically chosen for subsequent statistical investigation.

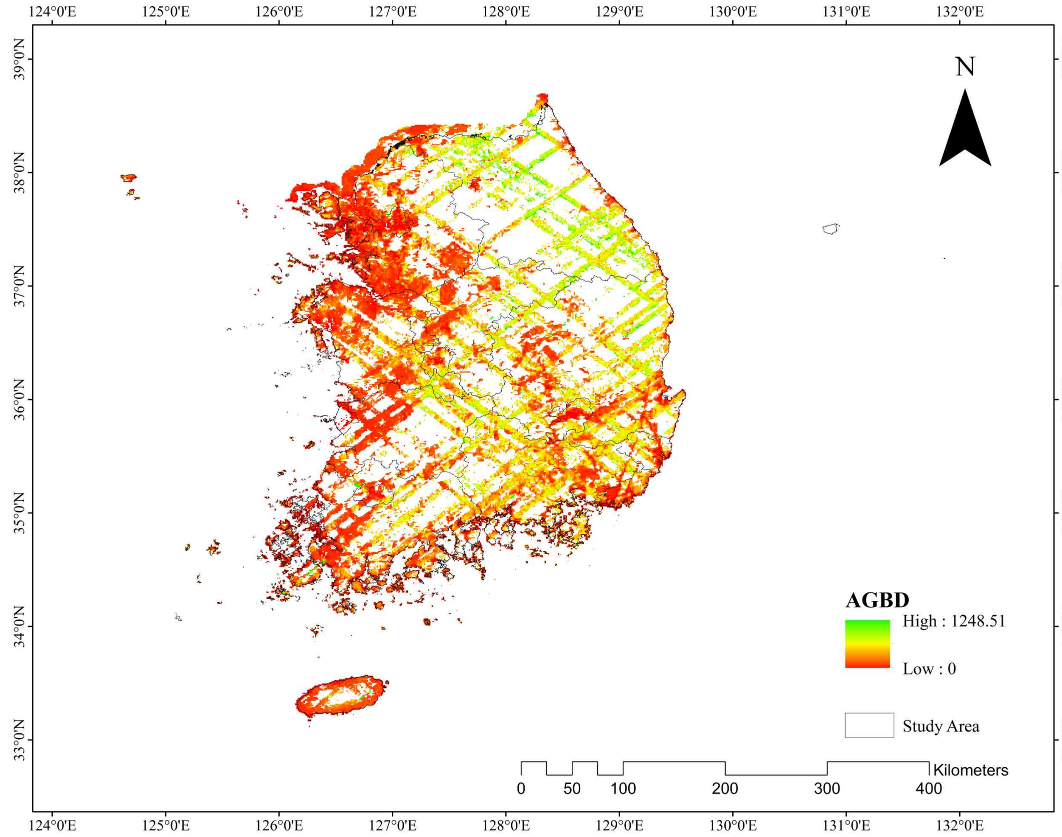

Figure 4. Available GEDI aboveground biomass density data (AGBD) in Republic of Korea (unit: Mg ha^{-1})

Table 2. Classification of map of forest type by Korea Forest Service

Code	Species Composition
11	*Pinus densiflora*
12	*Pinus koraiensis, Pinus parviflora, Pinus pumila, Pinus strobus*
13	*Larix gmelini, Larix kaempferi*
14	*Pinus rigida, Pinus taeda, Pinus banksiana*
15	*Pinus thunbergii*
16	*Abies holophylla, Abies koreana, Abies nephrolepis*
17	*Chamaecyparis obtuse, Chamaecyparis pisifera*
18	*Cryptomeria japonica, Taxodium distichum, Metasequoia glyptostroboides*
19	*Picea abies, Picea koraiensis*
20	*Torreya nucifera, Cephalotaxus harringtonii*
21	*Ginko biloba*
10	Coniferous
31	*Quercus acutissima*
32	*Quercus mongolica*
33	*Quercus variabilis*
34	*Quercus aliena, Quercus dentata, Quercus serrata*
35	*Alnus japonica, Alnus incana, Alnus firma*
36	*Acer pictum*
37	*Betula pendula, Betula costata*
38	*Betula schmidtii, Betula chinensis, Betula dahurica*
39	*Castanea crenata*
40	*Fraxinus rhynchophylla, Fraxinus mandshurica*
41	*Carpinus laxiflora, Carpinus tschonoskii*
42	*Styrax japonicus, Styrax obassis*
43	*Juglans regia, Juglans mandshurica*
44	*Liriodendron tulipifera*
45	*Populus deltoides, Populus tomentiglandulosa, Populus canadensis_x, Populus tremula*
46	*Prunus serrulate, Prunus avium, Prunus sargentii, Prunus serrulate, Prunus yedoensis_x*
47	*Zelkova serrata*
48	*Crornus controversa, Cornus macrophylla, Cornus walteri*
49	*Robinia pseudoacacia*
30	Deciduous broad-leaved
61	*Quercus myrsinifolia, Quercus acuta, Quercus glauca, Quercus salicina, Quercus gilva*
62	*Castanopsis sieboldii*
63	*Cinnamomum camphora*
64	*Daphniphyllum macropodum*
65	*Dendropanax trifidus*
66	*Betula ermanii*
67	*Machilus thunbergii*
68	*Neolitsea aciulata, Neolitsea sericea, Cinnamomum yabunikkei*
60	evergreen broad-leaved
77	mixed forest

Table 3. List of protected areas designated by Ministry of Environment

	Protected Area Type
1	National Park
2	County Park
3	Provincial Park
4	Wildlife Protection Area
5	Special Island
6	Ecosystem and landscape Conservation Area
7	Wetland Protected Area
8	Riparian Buffer Zone
9	Water Source Protection Area
10	Special Measure Areas

3.3. Calculating diversity and composition

Three functional trait, that are related to wood and foliage structures, were applied to quantify functional diversity and compositions; wood density (WD), specific leaf area (SLA), and maximum plant height (PHm). Wood density was retrieved from Global Wood Density Database (Zanne et al., 2009). The other two traits were extracted from the TRY database (Kattge et al., 2020). For WD and SLA, the average of multiple values was used when multiple values were provided for a single species. When the species' value was missing, the average value of the same genus was used. For coniferous, deciduous broad-leaved, and evergreen broad-leaved, the average of the corresponding species among the species included in Table 2 was used. For mixed-forest, the average of all species included in Table 2 was used.

For functional diversity indices, functional richness (FRic), fuctional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao' s quadratic entropy (RaoQ) was calculated with "FD" package in R. The community weighted mean (CWM) for wood density (CWM_{WD}), specific leaf area (CWM_{SLA}), and maximum plant height (CWM_{PHm}) was estimated at each plot, again using the "FD" package. All calculation was processed in R version 4.2.3 (R Core Team, 2023)

3.4. Statistical analysis

Linear mixed-effects model (LMM) is statistical models that can be used to analyze correlation between data (Galecki and Burzykowski, 2013). Compared to traditional methods like ANOVA or regression, LMMs offer increased accuracy and efficiency by appropriately modeling the dependence structure among multiple observations. (Gibbons et al., 2010; Gelman & Hill, 2009; West et al., 2022).

In this study, each measure of functional diversity, namely FRic, FEve, FDiv, FDis, and RaoQ, along with three functional composition measures (CWM_{WD}, CWM_{SLA}, CWM_{PHm}), were included as fixed factors. The average age class of the unit area was considered as a random factor. The first analysis utilized a reduced dataset consisting of 861 units, while the second analysis for outside the protected areas utilized a larger dataset comprising 8140 units. The LMMs were performed using the "lmer" function, and the p-values were calculated from the F test based on Satterthwaite approximations to the degree of freedom with the "lmerTest" pacakge in R (Bates et al., 2015; Kuznetsova et al., 2016). Marginal R^2 (R^2m), which represents the proportion of variance explained by the fixed effect alone, and conditional R^2 (R^2c), which quantifies the proportion of variance explained by both fixed and random effects were calculated (Nakagawa & Schielzeth, 2013). All statistical analysis was performed using R version 4.2.3 (R core Team, 2023).

Chapter 4. Results and Discussion

4.1. Results

The results of LMM analyses of the data of areas inside and outside of the protected areas are presented in Tables 4 and 5, respectively. By comparing the results of the two LMMs, we can determine whether AGBD is explained differently inside the protected areas than outside the protected areas. In both models, the AGBDs were modeled using functional diversity variables (FRic, FEve, FDiv, FDis and RaoQ) and variables for selection effect (CWM_{WD}, CWM_{SLA}, and CWM_{PHm}), with random intercepts for average age class.

For the LMMs for the areas inside the protected areas (Table 4), a number of diversity indices demonstrated significant associations with AGBD. Specifically, the complementarity effect factors, FRic ($\beta = 299.66$, $p < 0.001$) and RaoQ ($\beta = 2144.93$, $p < 0.001$) exerted significant effects on AGBD, indicating that these indices were positively correlated with increased AGBD. FDis ($\beta = -821.82$, $p < 0.001$), however, exerted a significantly negative effect on AGBD. Similarly, the selection effect factors CWM_{WD} ($\beta = 181.62$, $p < 0.001$) and CWM_{PHm} ($\beta = 3.38$, $p < 0.001$) exerted a positive effect on AGBD. FEve ($p = 0.628$), FDiv ($p = 0.627$) and CWM_{SLA} ($p = 0.233$) did not demonstrate significant associations with AGBD in the initial model.

Conversely, the LMM for the outside of protected areas yielded distinct results compared to the initial model (Table 5). Only one diversity index, FDiv ($\beta = -27.85$, $p < 0.001$), exhibited significantly negative associations with AGBD. Every CWM factor exerted significant effects on AGBD, suggesting that the higher values of these CWM indices were positively related to increased AGBD outside of protected areas. FDis ($\beta = 14.76$, $p = 0.796$) did not exert a significant effect on AGBD in the second model.

Within the confines of protected areas, fixed factors accounted for 6.4% of the observed variation in AGBD, whereas outside these areas, the fixed factors explained 7.0% of the variation. Notably, both the fixed and random factors collectively accounted for a substantial proportion of the variation in AGBD, with the respective models explaining 16.4% of the variation for inside the protected areas and 22.7% of the variation for outside the protected areas.

Table 4. Result of the linear mixed model that evaluates the effect of functional diversity and composition on aboveground biomass density inside the protected areas (n=861). Abbreviations: Est, coefficient estimates; SE, standard errors; df, degree of freedom; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; CWM_{WD}, community weighted mean of wood density; CWM_{SLA}, community weighted mean of specific leaf area; CWM_{PHm}, community weighted mean of plant maximum height; AGC_{aver}, average age class of forest; R^2m, marginal R^2; R^2c, conditional R^2

		Est	**SE**	**df**	**Pr (>|t|)**
Fixed effects	(Intercept)	-19.22	44.41	578.89	0.665
	FRic	299.66	76.00	851.62	<0.001
	FEve	4.58	9.44	849.87	0.628
	FDiv	-7.14	14.66	849.38	0.627
	FDis	-821.82	182.48	851.65	<0.001
	RaoQ	2144.93	523.94	851.97	<0.001
	CWM_{WD}	181.62	50.70	851.41	<0.001
	CWM_{SLA}	0.66	0.55	851.75	0.233
	CWM_{PHm}	3.38	0.86	849.81	<0.001
Random effects	AGC_{aver}	266.7			
	Residual	2243.2			
	R^2m	0.064			
	R^2c	0.164			

Table 5. Result of the linear mixed model that evaluates the effect of functional diversity and composition on aboveground biomass density outside the protected areas (n=8140). Abbreviations: Est, coefficient estimates; SE, standard errors; df, degree of freedom; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao’s quadratic entropy; CWM$_{WD}$, community weighted mean of wood density; CWM$_{SLA}$, community weighted mean of specific leaf area; CWM$_{PHm}$, community weighted mean of plant maximum height; AGC$_{aver}$, average age class of forest; R^{2}m, marginal R^2; R^{2}c, conditional R^2

		Est	**SE**	**df**	**Pr (>|t|)**
Fixed effects	(Intercept)	-248.21	18.75	97.28	<0.001
	FRic	-58.09	22.44	8130.73	0.010
	FEve	-7.89	3.52	8127.38	0.025
	FDiv	-27.85	5.42	8129.26	<0.001
	FDis	14.76	57.20	8130.38	0.796
	RaoQ	176.42	172.89	8131.00	0.308
	CWM$_{WD}$	414.95	17.79	8130.27	<0.001
	CWM$_{SLA}$	1.38	0.13	8129.21	<0.001
	CWM$_{PHm}$	4.65	0.25	8130.31	<0.001
Random effects	AGC$_{aver}$	523.7			
	Residual	2582.7			
	R^{2}m	0.070			
	R^{2}c	0.227			

Overall, the functional diversity indices displayed inconsistent significance in their ability to explain the forest AGBD within and outside the protected areas. However, consistent patterns were observed for functional dominance indices. Notably, the variable FEve did not demonstrate any significant association with the AGBD in both models. In areas outside the protected areas, a significant negative association was observed between the FDiv and forest AGBD. This finding suggests that the relationship between functional diversity and AGBD may vary in regions that lack protective measures.

Specifically, CWM_{WD} and CWM_{PHm}, which represent selection effect, demonstrated a positive association with AGBD inside and outside the protected areas. While CWM_{SLA} showed a positive association with AGBD only outside the boundaries of protected areas. Notably, the estimated coefficients for CWM_{WD} were more than twice as high outside the boundaries of the protected areas compared to those within. Similarly, the coefficient for CWM_{PHm} was also higher outside the protected areas than inside.

4.2. Discussion

Comparison of the functional diversity indices between the two models revealed notable disparities in the associations between diversity indices and AGBD, contingent upon the presence of the protected areas. Notably, FRic, FDis, and RaoQ displayed significant associations with the AGBD exclusively in the protected areas, indicating that the presence of protected areas may augment the positive effects of diversity indices on the AGBD. Conversely, FDiv demonstrated significantly negative associations with the AGBD solely in the model applied outside the protected areas, suggesting that the complementarity effect is exhibited primarily inside the protected areas. In contrast to the findings of previous studies on unmanaged forests, functional dispersion exhibited a significantly negative effect on aboveground biomass (Ziter et al., 2013). In forests within the protected areas of South Korea, RaoQ displayed the strongest effect on AGBD. Our findings underscore the importance of considering species' functional strategies in the context of sustainable forest management, with the aim of simultaneously achieving biodiversity conservation and carbon sequestration.

This aligns with the conclusions of a previous study that investigated the role of functional strategies, specifically the mass ratio effect, across forest strata and stand age (Lee et al., 2022).

In relation to our results, the previous study's findings provide a theoretical framework to interpret the observed effects of diversity indices on the AGBD inside and outside protected areas. The positive effect of FRic and RaoQ on the AGBD in the first model aligns with the notion that functional strategies related to species' co-existence can contribute to increased carbon sequestration and biodiversity conservation in protected areas (Le Bagousse-Pinguet et al., 2019). Conversely, the significant associations of FDiv and CWM of all traits with the AGBD in the second model suggest the importance of functional strategies, specifically the selection effect, in promoting carbon sequestration outside of protected areas.

With respect to the selection effect, a greater degree of consistency was observed in results obtained with the CWM_{WD} and CWM_{PHm}. Although, few studies oppose this argument (Stegen et al., 2009), this phenomenon can be attributed to the pivotal role that wood density plays in biomass stocks, representing a salient and unsurprising outcome (Phillips et al., 2019). The low marginal R^2 and conditional R^2 values can be attributed to the complexity of the model evaluating multiple fixed factors simultaneously. Nevertheless, the evident differentiation between protected areas and non-protected areas presents an opportunity for potential utilization in the formulation of future forest management policies at a national level.

In South Korea, the standing forest area experienced a notable decline until the 1950s; however, by 1980, the standing area had increased from 35% to 64%, owing to the National Greening Program's rapid forestation efforts (Bae et al., 2022). Presently, the standing forest areas established between the 1950s and 1970s account for approximately 50% of the nation's forest area. Despite intensive plantation efforts in forests with trees belonging predominantly to age classes III–V, the present study revealed selection effect to be more consistent than the niche complementarity effect. However, the forest inside the protected areas exhibited different patterns compared to the forests outside them, in this study. This study revealed that within protected areas in South Korea, forests exhibit more active niche differentiation and utilization compared to outside areas, indicating stronger ecological relationships within protected areas. Further research is being conducted to explore variations that may arise based on the edge effect and on the proximity to the boundaries of protected areas and the surrounding landscape (Nasimento & Laurance, 2004; Morreale et al., 2021). Understanding the changes in aboveground biomass in forests along these gradients is essential, and therefore, continuous research within and outside of protected areas is needed to enhance our understanding of forests during the transition to old climax forests. In non-protected areas, the high explanatory power of the $\mathrm{CWM}_{\mathrm{WD}}$ can be utilized to guide future plantation and species management for mitigating the effects of climate change.

As the GEDI is a relatively new data product, very few studies have been conducted delineating its capabilities and applications. The GEDI dataset has marked implications for understanding the environment, including carbon cycle dynamics, climate change, and biodiversity conservation. Recent studies have demonstrated the usefulness of the GEDI AGBD data in characterizing forest structure (Lefsky et al., 2021), monitoring forest degradation, assessing forest carbon stocks (Neigh et al., 2021), and assessing the effectiveness of protected areas in storing carbon (Liang et al., 2023). Future research efforts are expected to provide a comprehensive understanding of the utility of GEDI.

Nonetheless, this study has several limitations. Firstly, this national-scale analysis did not consider the variations and differences between individual forests. Incorporating these factors into the analysis would reveal more accurate and insightful results. However, one must note that the computational and temporal resources required for calculating the national-scale analysis are substantial, which restricted the feasibility of incorporating additional factors at the individual forest level. Secondly, the utilization of forest map data classified according to functionally similar species may result in inaccurate outcomes. Employing the data at the species level is preferable for achieving precise results, despite the time-consuming and costly process involved in the production of such data. This approach would enable the calculation and assessment of functional diversity and composition for each individual species. Thirdly, the evaluation in this study was notably limited by the spatial extent of the GEDI product. Future investigations that extend the limited spatial boundaries will contribute to a comprehensive assessment of the results by encompassing all forested areas at finer scales. Despite these limitations, we believe the findings of this study have notable implications that would help understand the forest dynamics and can be applied to future forest management plans.

Chapter 5. Conclusion

This study aimed to evaluate the temperate forests of South Korea regarding two common hypotheses explaining the ecological processes related to biomass pattern: niche complementarity hypothesis and selection effect hypothesis. Previous studies have reported inconsistent findings of impact analyses of forests (Ruiz−Jaen and Potvin, 2010; Finegan et al., 2015; Mensah et al., 2016). The results of this study imply that the relationship between functional diversity and AGBD is not consistent in both protected and non−protected areas. However, functionally diverse forests exhibited a significantly positive association with AGBD specifically within protected areas of South Korea. This finding highlights the importance of considering niche complementarity as a relevant factor in understanding the dynamics of aboveground biomass within protected forest areas.

The selection effect, as represented by the CWM_{WD} and CWM_{PHm}, exhibited a positive association with AGBD both inside and outside of the protected areas. The analysis revealed that the niche complementarity effect was a significant factor contributing to the explanation of AGBD exclusively within protected areas. However, one must acknowledge the presence of unexplained spatial variations that have the potential to influence the relationship between the variables under consideration. These spatial variations introduce complexities and highlight the need for further investigations to comprehensively understand the underlying mechanisms that shape the relationship between functional diversity and AGBD.

These findings have crucial implications for forest management and conservation in South Korea, where most of the forested areas are managed under government plans, and in other regions with similar forest ecosystems and management plans. The high explanatory power of CWM_{WD}, especially in non-protected areas, suggests that monitoring and utilizing the selection effect can guide plantation and species management to mitigate the effects of climate change. Nevertheless, further research is necessary to comprehensively understand the drivers of AGBD and the role of functional diversity in forest ecosystems.

The results of this study are consistent with previous research that has emphasized the importance of wood density in biomass storage (Lutz et al., 2018) and the variability in the effects of functional diversity indices on ecosystem functioning (Stegen et al., 2009). Additionally, this study highlights the need for continued research and monitoring of protected areas and forest ecosystems, particularly in the context of the changing climate and land use patterns, as emphasized in other studies (Lindenmayer et al., 2012; Chazdon et al., 2016). Overall, this study provides valuable insights into the significant drivers of aboveground biomass density in forest ecosystems at a country scale, emphasizing the importance of considering both selection and niche complementarity effects in understanding the role of functional diversity in ecosystem functioning.

Further research examining the distribution of forests that are susceptible to climate change will enable a comprehensive understanding of the dynamics of forests in countries with similar forest types that undergone abrupt changes such as those in South Korea.

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Abstract in Korean

산림은 필수적인 생태계 서비스를 제공하고 탄소 흡수와 저장을 통해 기후 변화 완화에 중요한 역할을 한다. 산림의 지상부 바이오매스 양상을 이해하는 것은 탄소 저장 잠재력을 평가하는 데 필수적이다. NASA의 Global Ecosystem Dynamics Investigation (GEDI) 미션과 같은 원격탐사 기술은 대규모 공간 범위에서 지상부 바이오매스 밀도를 추정한 유용한 데이터를 제공한다. 본 연구는 대한민국의 산림에서 지상부 바이오매스 밀도와 기능적 다양성 및 기능적 구성과의 상관관계를 분석하였으며, 보호지역 내외의 지역을 비교 분석하였다. 평균 영급을 랜덤 변수로 하는 선형 혼합 모델 (linear mixed model; LMM)을 사용하여 '생태적 지위 상보성 가설'과 '선택효과 가설'이라는 두 가지 생태학적 가설을 평가하였다. 생태적 지위 상보성을 평가하기 위해 총 5가지의 기능적 다양성 지수 값이 이용되었고, 선택효과를 평가하기 위해 3가지 형질에 대한 community weighted mean (CWM) 값이 이용되었다. 결과적으로, 생태적 지위 상보성 가설의 변수들은 보호지역 내외의 데이터를 분석할 때 일관된 결과를 보여주지 않았으며, 선택효과 가설의 변수들은 보호지역 내부와 외부에서 일관된 결과를 보였다. 특히, 보호지역 내에서만 생태적 지위 상보성의 변수가 일부 유의한 것으로 나타났으며, 이는 기능적 다양성이 이러한 지역의 생물량 밀도 패턴을 설명할 수 있음을 의미한다. 본 연구는 산림의 지상부 바이오매스 축적과 생물다양성 간의 관계를 이해하여 효과적인 산림 경영 전략과 보전 계획 수립에 기여할 수 있는 중요한 통찰을 제공한다.

주요어 : GEDI, 임상도, 기능적 다양성, 생태적 지위, 영급, 국가 수준 공간적 범위, 선형혼합모델
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Appendix

Appendix A GEDI aboveground biomass density values inside and outside the protected areas