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ORIGINAL PAPER

Topographic and environmental characteristics drive phylogenetic diversity and vegetation traits in *Larix kaempferi* plantations in South Korea

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Abstract Global diversification of the structure and composition of artificial forests and partial or complete conversion to natural forests is an important task for improving long-term biodiversity and counteracting climate change. *Larix kaempferi* is a tree species used widely in forests throughout northeast Asia that plays an important role in converting artificial forests to mixed forests. However, the phylogenetic diversity (PD) of the species remains unclear. We investigated *L. kaempferi* forests formed in Gayasan National Park, South Korea, categorized the community types, and quantified species composition, PD, and phylogenetic community structure depending on the vegetation type. Furthermore, we explored the factors regulating biodiversity in *L. kaempferi* forests to provide insights for promoting forests with high structural diversity. We observed unique vegetation characteristics and community formation mechanisms depending on the local environment, with vegetation types located in valleys and at the bottom of slopes having the highest PD. We revealed how the structural properties and local conditions of forests affect phylogenetic community structure for each vegetation type, leading to competitive interactions and competitive exclusion. For all vegetation types, PD showed a gradually increasing trend with older stand age, but piecewise structural equation modeling analysis showed that topographic environmental factors are the main factors regulating PD. Our findings highlight the need to introduce customized management approaches suited to the characteristics of each community rather than using the same method for all communities. This approach is crucial because species composition, ecological properties, rate of succession, and surrounding environmental conditions differ between vegetation types. In addition, by presenting management strategies to improve biodiversity depending on vegetation type, we expanded existing knowledge on the conversion of artificial forests to mixed forests. Our study provides important insights into establishing strategies for managing artificial coniferous forests and the mechanisms of community formation with changes in species composition after forest creation.

Keywords *Larix kaempferi* · Phylogenetic diversity · Vegetation traits · Topographic characteristics · Artificial forests

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Introduction

Understanding community formation mechanisms is essential for interpreting species interactions and evolutionary

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histories, as well as for informing biodiversity conservation and management strategies (Webb et al. 2002; Cavender-Bares et al. 2009; Lawley et al. 2013; Socolar et al. 2016). Recent ecological studies emphasize that phylogenetic diversity (PD), which reflects evolutionary relationships among species, complements traditional species diversity (SD) and functional diversity (FD) by providing deeper insights into community assembly processes and ecosystem functioning (Cadotte et al. 2008; Tucker et al. 2018). Particularly, PD has been proposed as a reliable proxy for FD under the assumption that evolutionary diversification leads to functional trait differentiation, enhancing niche complementarity and thereby influencing ecological processes like biomass production and species interactions (Cadotte et al. 2008; Cavender-Bares et al. 2009). Phylogenetic diversity (PD), defined as the sum of evolutionary history within a community, provides critical insights into how evolutionary relationships influence community assembly. PD is particularly valuable for revealing whether community structures are shaped predominantly by deterministic processes (e.g., environmental filtering, competition among closely related species), such as environmental filtering or competition among closely related species, or by stochastic processes (e.g., random dispersal), such as random dispersal events (Cavender-Bares et al. 2009; Cadotte and Tucker 2017). The fundamental mechanism underlying PD involves the assumption that closely related species share similar ecological traits due to their common evolutionary history, known as phylogenetic niche conservatism. However, this assumption can vary depending on the trait and ecological context, highlighting the necessity for empirical validation of the phylogenetic signal in functional traits relevant to specific ecological processes (Maherali and Klironomos 2007; Cahill et al. 2008). Recent studies emphasize PD's importance in predicting community responses to ecological disturbances, such as biological invasions or climate change, reinforcing its relevance to conservation goals (Srivastava et al. 2012; Winter et al. 2013; Tucker et al. 2018). In the last several years, PD research on plant communities has been conducted in various regions worldwide. However, despite growing global interest, most studies have predominantly focused on natural forests (Mastrogianni et al. 2019; Liu et al. 2019; Xiao et al. 2020; Cao et al. 2021), indicating the need to expand PD research into a broader range of ecosystems.

Plantation forests (e.g., simple forests formed for commercial purposes) account for approximately 3% of forests worldwide, with an area of around 131 million ha, and planted forests (e.g., all types of planted forests, including artificial and various other planted forests, such as restored and urban forests) account for 45% of the total area (FAO 2020). Plantation forests not only produce timber products but also increase the terrestrial carbon storage capacity, effectively mitigating the effects of climate change (Nagaike 2000; Hartley 2002; Lu et al. 2015). Recently, in the US and Europe, efforts have been made to diversify the structure and composition of artificial coniferous forests. This initiative aims to gain various benefits from forest ecosystems and achieve partial or total conversion to natural forests (Ammer et al. 2008; Spracklen et al. 2013; Barsoum and Henderson 2016). This approach is favored because, unlike monocultures, mixed forests are reportedly more resistant to abiotic damage due to climate change (e.g., drought and weather extremes) and biotic disturbances (e.g., pest outbreaks and plant diseases), resulting in enhanced biodiversity, adaptability, and resilience (Bolte et al. 2009; Chavardès et al. 2021; Jactel et al. 2021). To effectively implement this approach, it is imperative to investigate how vegetation community structures change following plantation establishment, as well as to identify the key factors that drive biodiversity enhancement In this regard, Germany has conducted pioneering research addressing biodiversity changes associated with plantation forest management. For instance, a recent study conducted in central Germany compared plant species diversity and composition immediately after afforestation and 30 years later to document the transition from even-aged pure coniferous forests to mixed-species forests (Seliger et al. 2023a; b). These studies highlight critical issues such as biodiversity decline and structural homogenization in monoculture plantations, providing important baseline information for sustainable forest management strategies in Central Europe. On the other hand, a study in Northeast China conducted an analysis of plantation forests using functional and phylogenetic diversity over time following thinning (Xie et al. 2023). Through this analysis, it was revealed that environmental filtering plays a pivotal role in the assembly of tree communities, providing new insights into farm management and sustainable development. Nevertheless, studies focusing specifically on phylogenetic diversity within plantation forests after afforestation remain limited. Therefore, quantifying the factors that determine PD in artificial forest ecosystems and the changes in forests with succession forms an important basis not only for sustainable forest management but also for improving the biodiversity of post-afforestation artificial forests and establishing conservation strategies.

Larix kaempferi (Lamb.) Carrière is endemic to the central Honshu region in Japan (Nakamura and Krestov 2005) and has been planted widely in South Korea from valleys to mountain ridges, usually at altitudes of 1000 m or below. It has also been introduced to regions in China, such as the northeast, north, southwest, and the Inner Mongolia Autonomous Region, for forestry production, becoming established as a major coniferous species from lowlands to the sub-alpine zone (Shao 1985; Park and Fowler 1983; Wu et al. 2021). Thus, *L. kaempferi* has been introduced to various regions in several countries for planting, and a range of studies have been conducted. For example, studies have

been performed to investigate changes in soil microbe communities after *L. kaempferi* introduction (Chen et al. 2015), changes in distribution with climate change (Wu et al. 2021), fertilization effects (Li et al. 2018), and species diversity with stand age (traditional studies on species diversity; Nagaike et al. 2003). However, studies on the PD and phylogenetic structure of *L. kaempferi* communities are limited, and little research on changes in species composition and forest structure depending on the community characteristics has been conducted. Here, we conducted a study in Gayasan National Park, South Korea, with the aim of exploring management strategies for converting artificial coniferous forest ecosystems to forests with diverse structures and functions. This study also aimed to reduce the knowledge gap concerning the PD of *L. kaempferi* forests.

Our objectives were (1) to analyze the characteristics of communities in *L. kaempferi* forests and elucidate succession trends depending on stand age. Specifically, we aimed to analyze differences in species diversity, PD, and community structure in different community types and evaluate the effects of various environmental factors on community patterns. We also analyzed changes in PD and phylogenetic community structure with stand age and topographic position. (2) We assessed the differences in factors regulating PD depending on the forest stratum in *L. kaempferi* forests and deduced the mechanisms underlying *L. kaempferi* community formation based on the results. Diversity patterns are evaluated by forest stratum due to the differing formation mechanisms between upper and lower vegetation (Ali and Yan 2018; Chun et al. 2019; Chun and Lee 2019). While upper vegetation settles into a sustainable state after achieving dominance in a competitive process, the survival of lower vegetation can be affected by environmental conditions and the species in the overstory (Chun et al. 2019; Chun and Lee 2019). Therefore, when upper and lower vegetation are analyzed as a single community, it can be difficult to clearly distinguish differences in the formation mechanisms for species in each stratum or the factors mediating these mechanisms (Ali et al. 2018; Ali and Yan 2018; Chun et al. 2019; Chun and Lee 2019). In our analysis, we distinguished between the whole strata, upperstory (tree and sub-tree layers), and understory (shrub and herb layers). (3) Based on the results of the above analyses, we aimed to understand the factors regulating biodiversity in *L. kaempferi* forests and the vegetation characteristics in different community types. This understanding would help identify the communities that need to be prioritized for management to improve biodiversity and to suggest effective management strategies.

We anticipate that our findings will provide important insights into management strategies for artificial coniferous forests and community formation mechanisms with changes in species composition after planting. These insights will provide key guidelines for managing artificial forests planted broadly worldwide.

Materials and methods

Study area and field survey

Gayasan National Park, located in the temperate southern region of South Korea, was designated as a national park in 1972. It has a peak altitude of 1430 m and a total area of 76.256 km^2. According to the Korea Forest Service (KFS) map of forest types (1:5000), the ratio of natural forest in this region is 80.21% while that of artificial forest is 12.58%, with the majority being *L. kaempferi*, at 3.13 km^2 (61.16%; Table S1). The mean annual temperature is 13.2 °C, and the mean annual precipitation is 1295.84 mm based on records from 1990 to 2020 provided by the Korea Meteorological Administration in Hapcheon (located approximately 20 km from Gayasan National Park) (Fig. 1).

We conducted a field survey during the active tree-growth period from June to September 2024 in unmanaged *L. kaempferi* plantation forests. This study specifically focused on unmanaged plantations of *L. kaempferi* to investigate ecological characteristics, succession processes, and factors regulating PD within plantation ecosystems. No silvicultural treatments or management activities have been implemented since the initial plantation establishment. Before the survey, we referred to the KFS map of forest types (1:5000) to determine the age classes of the *L. kaempferi* forests in Gayasan National Park (Fig. S1). Based on this, we aimed to acquire an even range of standard sites in *L. kaempferi* forests corresponding to various age classes. The age classes are described in more detail in Sect. "Abiotic and biotic driver data collection" of the Materials and Methods. For the vegetation survey, circular plots with a 5.65-m radius (approximately 100m^2) were established. The dominance of species within plots, combining coverage and abundance, was assessed by stratum (tree, sub-tree, shrub, and herb layers) following the phytosociological survey method of Braun-Blanquet (1964). The dominance of each species was allocated as follows based on the Braun-Blanquet scale: r, rare species; +, coverage < 1%; 1, coverage 1%–5%; 2, coverage > 5–25%; 3, coverage > 25–50%; 4, coverage > 50–75%; 5, coverage > 75–100% (Canullo et al. 2012). For the tree diameter survey, we measured all trees in the plots with a diameter at breast height (DBH) of at least 4 cm. For environmental factors, a handheld GPS (64S; Garmin, Olathe, KS, USA) and a clinometer (Suunto, Vantaa, Finland) were used to record the altitude, slope, and geographic coordinates. The distance between the trees and the plot center was measured using a hypsometer (Vertex; Haglöf, Järfälla, Sweden), ensuring that the survey could

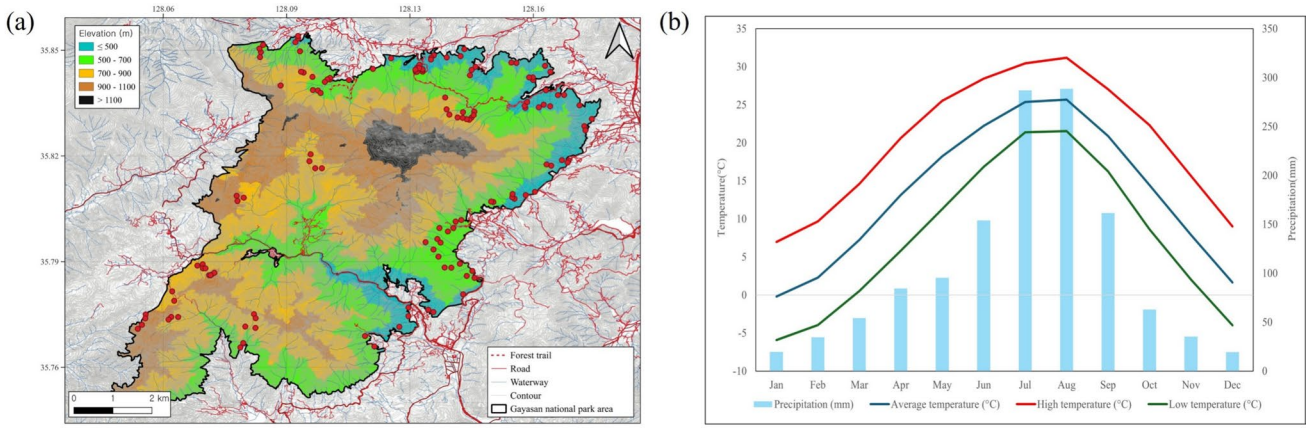


Fig. 1 The geographic location and climatic conditions of Gayasan National Park in South Korea are presented; **a** shows the geographic locations and topographic maps of 129 plots surveyed within the *L. kaempferi* forests in Gayasan National Park; **b** illustrates temperature and precipitation data for the period from 1992 to 2020, using meteorological data from the Hapcheon region, located approximately 20 km from Gayasan National Park

be conducted systematically within the plots. A total of 129 plots were included in the survey.

Classification and data processing

Based on the data collected from the 129 plots in the vegetation survey, we used the two-way indicator species analysis (TWINSPAN) method to categorize community types in the *L. kaempferi* forests. TWINSPAN is useful for deriving character species per vegetation unit (VU) and simultaneously classifying plant species and stands (Hill 1979). In particular, it is viewed as an effective method in complex terrains where steep slopes and diverse environmental conditions significantly affect vegetation patterns, such as in northeast Asia, and is widely used in such regions (Yang et al. 2022; Lee et al. 2024; Zhang et al. 2024). Therefore, we determined that TWINSPAN would be suitable for accurately identifying the types of communities in *L. kaempferi* forests and comparing the characteristics of different species compositions. After categorizing community types using TWINSPAN, we used the method of Curtis and McIntosh (1951) to calculate the importance values (IVs) of species in the communities. To calculate the IVs for woody trees (DBH $\geq$ 4 cm), the relative coverage, frequency, and density were summed and averaged; for relative coverage, we used the ratio of the basal area of the corresponding species relative to the total basal area. To calculate the IVs for lower vegetation, the relative coverage and frequency were summed and averaged; for relative coverage, we used the ratio of the coverage of the corresponding species relative to the total coverage. Based on the VUs determined using TWINSPAN, we used data from the tree diameter survey to analyze the distribution of DBHs by age class in order to ascertain vegetation succession trends. The size classes in the distribution of DBHs provide important information for determining the state of forest vegetation succession (Harcombe and Marks 1978; Barbour et al. 1987). Next, to compare relative quantitative indices for the vegetation, we used PC-ORD ver 7 (MjM Software Design, Gleneden Beach, OR, USA) to calculate species richness (SR), species diversity (SD, Shannon H′) (Shannon 1948), and species evenness (SE, Pielou's) (Pielou 1969). In addition, after calculating the PD and phylogenetic community structure (net relatedness index (NRI) or nearest taxon index (NTI)), we analyzed the changes depending on stand age and topographic position. Taxonomy diversity and PD were calculated separately for the whole strata, upperstory, and understory. The calculation of PD is described in detail in Section "Phylogenetic tree construction".

Statistical analyses

We performed redundancy analysis (RDA) to investigate the environmental factors related to plant species growing in *L. kaempferi* forests. We included topographic, climatic, and age class factors in the analysis and differentiated between plant species in the upperstory (tree and sub-tree layers) and the understory (shrub and herb layers). All species with a frequency of <10 and *L. kaempferi* were excluded from the analysis. The variables included in the analysis all showed a variance inflation factor (VIF) <5, and we applied a log transformation to the variables to increase linearity and normality. R studio and the "vegan" package (R Foundation for Statistical Computing, Vienna, Austria) were used for statistical analysis.

Abiotic and biotic driver data collection

This study was divided into two sections: (1) We investigated community types in *L. kaempferi* forests, examined vegetation characteristics by age class, and statistically analyzed the relationships between species and environmental factors. (2) We investigated the factors regulating PD in different forest strata. Here, we explain the process of acquiring the variables used in these two sections. For climate variables, the mean annual temperature, mean annual precipitation, potential evapotranspiration (PET), and near-surface wind speed (sfcWind) were used in the analysis. These variables were obtained from the CHELSA v2.1 dataset (https://www.chelsa-climate.org/) and quantified in each plot; data from 1990 to 2020 were included (Karger et al. 2017). For topographic variables, we used altitude, slope, and topographic position (TP) data that had been measured on-site. Here, TP was divided into four levels: 1 (ridge, upper slope), 2 (middle slope), 3 (lower slope), and 4 (valley) (Zhang et al. 2009). Digital topographic maps (1:5000) from the South Korean National Geographic Information Institute were used to generate a digital elevation model, and the equation of Beven and Kirkby (1979) was used to calculate the topographic wetness index (TWI) based on this model.

As biotic drivers, we selected taxonomic diversity, stand structural characteristics, and age class. For taxonomic diversity, SR, SD, and SE were calculated separately for the whole strata, upperstory (tree and sub-tree layers), and understory and then used in the analysis. To quantify the stand structural characteristics, we calculated the mean DBH, standard deviation of DBH (DBH STD), and coefficient of variation of DBH (DBH CV) based on woody plants in each plot with a DBH ≥ 4 cm. We quantified age class in each plot using data from the KFS forest types map (1:5000). The forest types map was composed as part of the National Forest Inventory, using field surveys and aerial photography in parallel. Age class was determined using an increment borer to collect samples from the dominant or co-dominant trees. These trees were defined as trees with crowns occupying 50% or more of the canopy. Age class was classified in 10-year bins. For example, tree age class "3" refers to trees with an age of 21–30 years that are dominant in the canopy of some plots (Lee et al. 2022).

Phylogenetic tree construction

In 129 *L. kaempferi* forests, the number of species recorded across different forest strata was as follows: the whole strata comprised 232 species (68 families and 137 genera); the overstory included 39 species (17 families and 24 genera); and the understory contained 222 species (65 families and 131 genera). We determined PD to investigate the factors regulating biodiversity in *L. kaempferi* forests. We calculated PD by forest stratum, differentiating between the whole strata, upperstory (tree and sub-tree layers), and understory (shrub and herb layers). To this end, we used the 'phylo.maker' function in the "V.PhyloMaker2" package in R (Jin and Qian 2022) and generated phylogenetic trees for species with standardized scientific names in each stratum. Next, we quantified PD in each stratum using the 'pd' function in the "picante" package in R (Kembel et al. 2010). We used biotic and abiotic drivers to determine whether the PD showed any patterns depending on the stratum.

Subsequently, we calculated the NRI and NTI to show changes in the PD and phylogenetic community structure in each stratum depending on the TP and stand age of *L. kaempferi* forests. In this process, we excluded the upperstory and only calculated the NRI and NTI for the whole strata and understory. This is because it was not possible to calculate phylogenetic structure indices for the upperstory in some plots because we only observed the single species *L. kaempferi*, meaning that branch length and relatedness could not be calculated. These indices (NRI or NTI) were selected because they are useful for measuring phylogenetic structure properties in each community at various spatial scales (Yang et al. 2014; Hu et al. 2022; Wang et al. 2024). The NRI is calculated based on the mean pairwise phylogenetic distance (MPD), as shown in Eq. 1.

$$\mathrm{NRI} = -1 \times (\mathrm{MPD}_{\mathrm{observed}} - \mathrm{meanMPD}_{\mathrm{randomized}})/\mathrm{SD}(\mathrm{MPD}_{\mathrm{randomized}}) \quad (1)$$

The NTI is calculated based on the mean nearest taxon distance (MNTD), as shown in Eq. 2.

$$\mathrm{NTI} = -1 \times (\mathrm{MNTD}_{\mathrm{randomized}} - \mathrm{meanMNTD}_{\mathrm{randomized}}) / \mathrm{SD}(\mathrm{MNTD}_{\mathrm{randomized}}) \quad (2)$$

To evaluate the mean state of the phylogenetic structure based on the variance in the mean phylogenetic distance between all species in the community, we selected a "taxa labels" null model and repeated the calculations 999 times to satisfy statistical requirements (Webb et al. 2002; Jarzyna et al. 2021). These indices were all calculated in R, using the "picante" package and the "ses.mpd" and "ses.mntd" functions (Kembel et al. 2010). The patterns of change in PD and phylogenetic community structure (NRI or NTI) were expressed based on the TP for each VU differentiated by TWINSPAN.

Model construction

To comprehensively explore the relationships between abiotic and biotic drivers affecting PD and ascertain the causal relationships between these factors, we used piecewise structural equation modeling (pSEM), which is considered the most suitable approach for this purpose (Lefcheck 2016).

As mentioned above, we calculated PD separately for each forest stratum (whole strata, upperstory, and understory), and to analyze the factors regulating PD in each stratum, we constructed a model according to the following procedure. We applied a log transformation to improve the normality and linearity of the variables used in the analysis. Additionally, we performed normalization to ensure uniformity of the variables. In addition, when two variables showed a strong correlation in Pearson correlation analysis ($|r| \geq 0.75$), one of the variables was excluded from the analysis (Fig. S2). Multicollinearity was assessed using VIFs, and all variables showed a VIF < 5, suggesting that the model results were not significantly affected by multicollinearity. Next, we used multi-model inference tests to identify the variables in each category with the largest effects on PD depending on the forest stratum (Fig. S3). Specifically, among the variables in each category suggested by the conceptual model (Fig. 2), we selected the variables with the highest standardized regression coefficients (β). Furthermore, based on the methodology recommended by Legendre and Legendre (2012), we used a generalized least squares model and compared two types of models: a spatial model that included geographic coordinates as spatial effects and a non-spatial model without these effects (Table S2). The model fit was assessed using Akaike's information criterion (AIC). We found that the effects of spatial autocorrelation differed depending on the stratum for each species (Table S2). While we detected spatial autocorrelation effects on PD for each variable in the upperstory, no clear effect of spatial autocorrelation on PD was observed in the whole strata or understory (Table S2). As such, when we analyzed the factors regulating PD in the upperstory, we included the geographic coordinates in the statistical analysis, but we omitted them for analysis of the whole strata and understory. We then performed analysis using pSEM according to the conceptual model (Fig. 2). Initially, we started with the saturated model, including all possible paths. Next, we used a d-separation test to gradually improve the initial model by identifying and removing unimportant paths (Shipley 2013). Model fit was assessed using Fisher's C statistic and the *p*- and AIC values.

Results

Species composition and structure characteristics of the *L. kaempferi* forests

Using TWINSPAN analysis, we divided the *L. kaempferi* forests into four VUs (Fig. 3). Each of the four VUs showed distinct vegetation characteristics depending on their different locational conditions, including topographic environment characteristics and altitude (Tables 1 and 2). Thus, we determined that these four VUs were sufficient to effectively capture the species composition and environmental gradients of *L. kaempferi* forests in the study area. The environmental characteristics (e.g., TP, age class, etc.) of the TWINSPAN-identified communities are detailed in Supplementary Table S3. VU I was located at the lowest altitude, mostly on lower slopes. Along with *L. kaempferi*, other dominant species included *Styrax japonicus* and *Quercus serrata* in the upperstory and *Oplismenus undulatifolius* and *Lindera erythrocarpa* in the understory. VU II was characterized by the highest TWI and was mostly located on lower slopes or in valleys. In this VU, *Cornus controversa*, *L. erythrocarpa*,

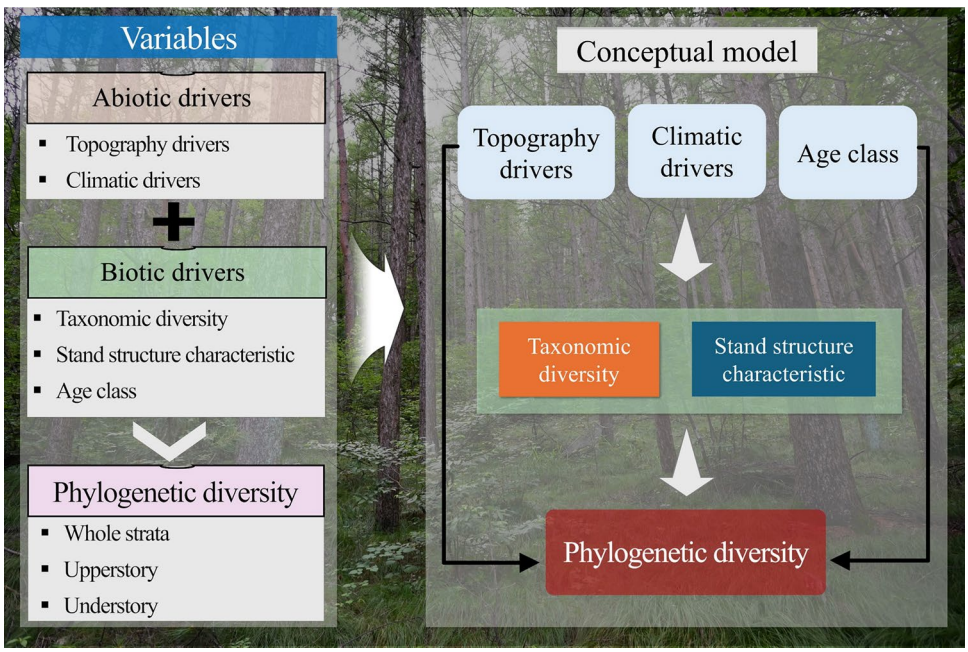


Fig. 2 A conceptual model to test the hypothetical relationships between biotic and abiotic factors and phylogenetic diversity across whole strata, upperstory, and understory levels in *Larix kaempferi* forests, a coniferous plantation within Gayasan National Park, South Korea

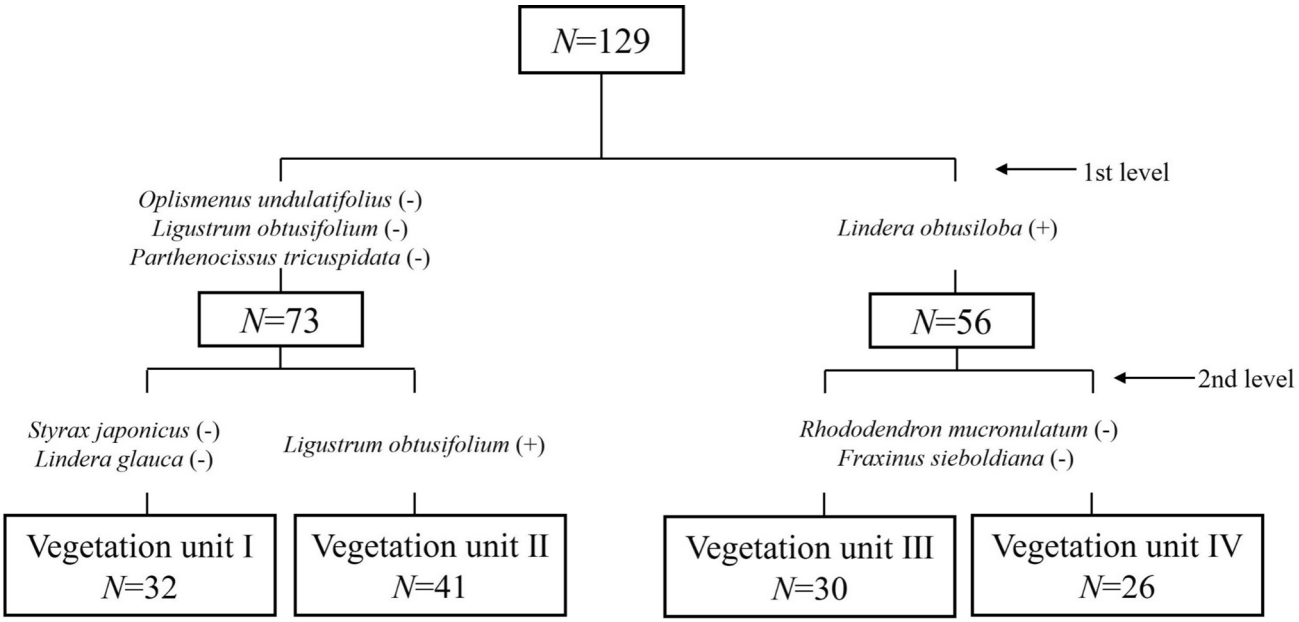


Fig. 3 Results of the TWINSPAN analysis based on 129 *L. kaempferi* plots in Gayasan National Park

Table 1 The basic environmental characteristics and metrics of phylogenetic diversity for the four vegetation units classified by TWINSPAN

VU	Slope position	Elevation (m)	Slope (°)	TWI	SR	PD	NRI	NTI
Ⅰ	Lower–middle slope	470	19	4.9	23	2751	−0.69	0.93
Ⅱ	Lower slope–valley	508	12	5.4	28	3257	−0.08	0.15
Ⅲ	Lowe slope–ridge	661	18	4.2	17	2294	−0.85	0.86
Ⅳ	Lower–middle slope	831	20	4.8	17	2304	−0.48	0.18

All values represent the mean, with NRI and NTI presented to two decimal places. Elevation, slope, SR, and PD are presented as integers, while TWI is shown to one decimal place. Both taxonomy diversity and phylogenetic metrics (NRI, NTI, and PD) were calculated for the whole strata

Fraxinus lanuginosa, *O. undulatifolius*, *Lindera obtusiloba*, and *Hydrangea serrata* showed high IVs. VU III was characterized by the lowest TWI of the four VUs and had a higher altitude than the previous two types, showing a higher ratio of survey sites between the middle slopes and ridge compared with that of the other VUs. When we analyzed the IVs, *Quercus mongolica* and *Q. serrata* showed high IVs in the upperstory, while *Rhododendron mucronulatum*, *L. obtusiloba*, and *Carex fusanensis* showed high IVs in the understory. In particular, the species showing high IVs in the understory were those adapted to dry conditions on upper slopes or ridges, where winds are strong and sunlight is abundant. VU IV had the highest altitude of all the VUs and was mostly found on lower or middle slopes. The main vegetation in this VU included *Styrax obassia*, *Q. serrata*, *Q. mongolica*, *L. obtusiloba*, and *L. erythrocarpa.* When we analyzed the IVs across all VUs, *Quercus* spp. were found in the upperstory throughout, while *L. obtusiloba*, *L. erythrocarpa*, and *O. undulatifolius* showed high IVs in the understory in most VUs. VU II showed the highest SR and PD compared with those of the other community types. Overall, all four community types showed overdispersed community structures based on the NRI value, while the NTI value was positive, indicating phylogenetic clustering between closely related species.

RDA analysis

We used RDA analysis to investigate the factors related to plant species growing in the upper- and understories. For the upperstory, we found that the age of *L. kaempferi* stands was closely related to *Q. serrata* and *T. trichocarpum*, while *Q. mongolica* showed a strong correlation with sfcWind (Fig. 4). In addition, most species thrived in environments that contrasted with the stand age variables. In the understory, the TP and slope were the main factors affecting the presence of understory vegetation. *H. serrata* was closely correlated with TP and DBH Mean, and this appears to be related to the high density of *L. kaempferi* in valleys. Meanwhile, the slope variable was closely related to *L.*

Table 2 The IVs results for each VU were divided into upperstory and understory, and the top 15 species with the highest IVs were presented for each VU

Stratum	Species	VU Ⅰ	VU Ⅱ	VU Ⅲ	VU Ⅳ
Upperstory	*Larix kaempferi* (Lamb.) Carrière	52.93	61.93	51.70	54.49
	Quercus serrata Thunb	6.12	4.68	5.70	5.20
	Quercus mongolica Fisch. ex Ledeb	0.84	1.02	8.53	4.18
	Lindera erythrocarpa Makino	1.20	4.98	1.05	4.25
	Styrax japonicus Siebold & Zucc	8.65	0.33	–	1.48
	Cornus controversa Hemsl	0.98	5.77	0.80	2.86
	Pinus densiflora Siebold & Zucc	5.88	0.38	3.35	0.73
	Fraxinus rhynchophylla Hance	–	3.85	4.54	1.56
	Castanea crenata Siebold & Zucc	5.52	2.74	–	–
	Toxicodendron trichocarpum (Miq.) Kuntze	1.96	1.86	3.13	0.41
	Lindera obtusiloba Blume	–	1.21	0.57	4.39
	Styrax obassia Siebold & Zucc	–	–	0.93	4.75
	Fraxinus sieboldiana Blume	0.36	0.32	3.46	1.32
	Acer pseudosieboldianum (Pax) Kom	0.77	0.35	1.15	2.91
	Carpinus laxiflora (Siebold & Zucc.) Blume	3.82	0.35	0.76	–
Understory	*Lindera obtusiloba* Blume	2.91	8.43	8.13	27.11
	Oplismenus undulatifolius (Ard.) Roemer & Schuit	13.96	12.05	1.24	1.85
	Lindera erythrocarpa Makino	9.26	6.08	3.98	7.59
	Rhododendron mucronulatum Turcz	1.20	2.41	14.04	0.94
	Carex fusanensis Ohwi	–	1.01	7.00	4.59
	Toxicodendron trichocarpum (Miq.) Kuntze	2.91	2.12	4.57	1.11
	Parthenocissus tricuspidata (Siebold & Zucc.) Planch	2.03	7.00	0.58	0.44
	Rhododendron schlippenbachii Maxim	0.64	0.36	7.53	1.49
	Hydrangea serrata var. *acuminata* (Siebold & Zucc.) Nakai	0.27	6.22	0.61	2.29
	Carex lanceolata Boott	5.88	0.90	1.35	0.77
	Symplocos sawafutagi Nagam	0.35	1.68	2.54	4.06
	Quercus serrata Thunb	2.18	1.70	2.67	1.13
	Styrax japonicus Siebold & Zucc	5.52	0.46	0.97	0.59
	Styrax obassia Siebold & Zucc	–	0.26	2.47	4.53
	Fraxinus sieboldiana Blume	1.00	0.40	4.25	0.32
	Schisandra chinensis (Turcz.) Baill	0.09	1.41	0.46	3.94
	Callicarpa japonica Thunb	1.66	1.40	0.68	1.23
	Tripterygium regelii Sprague & Takeda	–	0.25	2.56	1.46
	Dryopteris chinensis (Baker) Koidz	1.70	0.90	1.12	0.27
	Sasa borealis (Hack.) Makino & Shibata	0.17	–	3.53	0.14

erythrocarpa, *R. schlippenbachii*, *R. mucronulatum,* and *C. fusanensis*. Climatic variables contributed greatly to explaining the variation in the RDA axis but did not show clear relationships with specific species. In addition, we observed that vegetation thrived in topographic locations such as valleys with high TWI, as well as steep upper slopes and ridges.

Variations in phylogenetic metrics according to stand age and topographic position

PD showed an increasing trend in the whole strata and understory with increasing stand age, whereas, in the upperstory, it showed irregular variations depending on the TP (Fig. 5). Overall, PD decreased as the age class increased from 3 to 4, and then showed an increasing trend as the age class progressed toward 6. In age class 6 stands, we observed relatively high PD on the middle and lower slopes. NRI showed irregular patterns in most VUs and tended to become lower than or closer to 0 as the age class increased. Of the VUs, only VU Ⅱ showed an increase in NRI with increasing stand age and was characterized by high NRI in valley conditions. NTI showed similar properties depending on the VU. First, for the VU I and II of the whole strata, NTI showed an increasing trend with older stand age in the lower

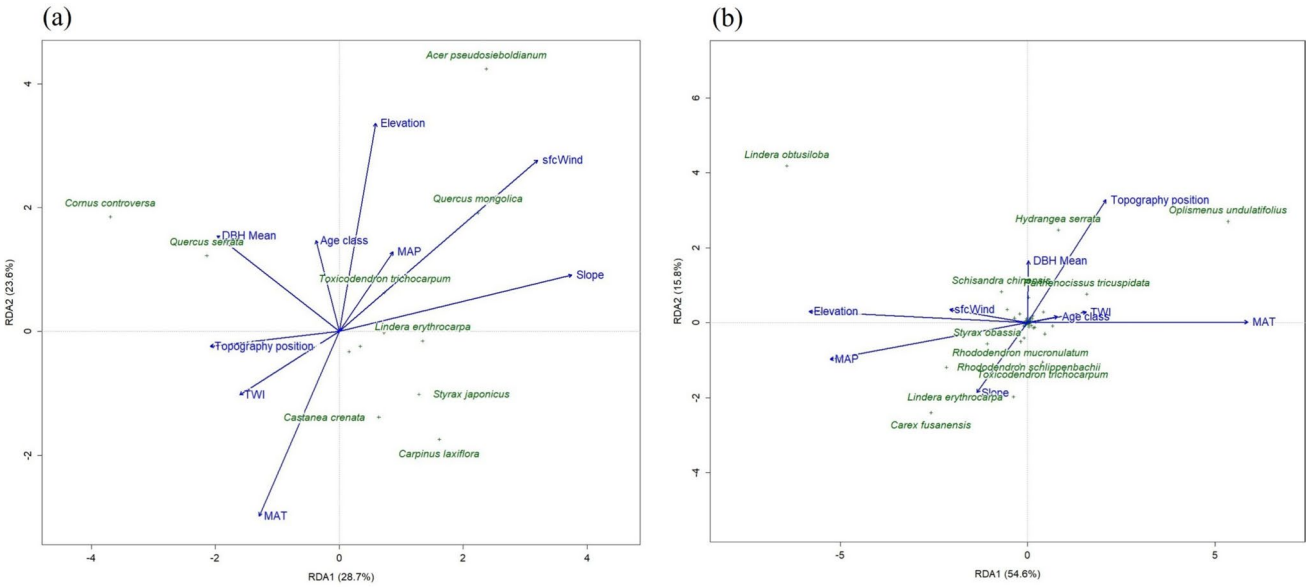


Fig. 4 Analysis of RDA between plant species coverage data and topography, climate, and stand characteristics; **a** RDA analysis was performed between upperstory plant species and topography, climate, and stand characteristics; **b** RDA analysis was performed between understory plant species and topography, climate, and stand characteristics. For the analysis, plant species with a frequency of occurrence of at least 10 times were used. The topographic position was categorized into 5 levels: 1 (Ridge, Upper slope), 2 (Middle slope), 3 (Lower slope), and 4 (Valley). The '+' symbol indicates the positions of species. To enhance the readability of the plot, species that were centrally clustered regardless of environmental variables were omitted from the display

slope. Meanwhile, the change was minimal in the understory, indirectly demonstrating that the upperstory affected the NTI in the whole strata. In addition, while VU Ⅰ showed an increasing trend of NTI in valleys when the age class changed from 5 to 6, VU Ⅱ showed an overall decreasing trend, demonstrating differences depending on the VU. In particular, VU Ⅲ and Ⅳ showed high NTI at age class 3, which gradually decreased with older stand age or tended to return to similar levels as those of age class 3.

DBH distribution by age class of *L. kaempferi* forests

Based on the tree diameter survey data from the 129 plots, we analyzed the distribution of DBH classes in *L. kaempferi* forests with an age class of 3–6 (Fig. 6). Over time, *L. kaempferi* showed an overall increase in density from 10–19.9 to 20–39.9 cm classes, and then rapidly decreased in age class 6 stands. Likewise, various woody plants became increasingly prominent as the age class increased from 3 to 5 and achieved peak density at age class 5. In age class 6 stands, the density of *L. kaempferi* was relatively low compared with that in other age classes, and the density of ≥ 20 cm woody plants, excluding *L. kaempferi,* was also lower than that at age class 5. Of these, *Q. serrata* and *C. controversa* showed sustained growth, and young trees also persistently entered the stands. Overall, the trees that entered the stand and had a DBH ≥ 15 cm mostly consisted of *Quercus* spp., as well as *C. laxiflora*, *C. controversa,* and *F. rhynchophylla*, which do not need much sunlight.

Drivers of phylogenetic diversity across forest strata

We conducted a pSEM analysis using the data from the 129 plots. In *L. kaempferi* forests, we observed differences in the main factors regulating PD between the upper- and understories (Fig. 7). The age class variables had a direct positive effect on PD in the whole strata but did not show significant effects in the upper- and understories. Climatic drivers only showed a direct positive effect in the whole strata, whereas SD had direct positive effects in all forest strata. The upper- and understories differed in topographic drivers. In the upperstory, the TP had a direct positive effect on PD, whereas, in the understory, elevation had a direct negative effect on PD, demonstrating clear differences in regulating factors between forest strata. Moreover, stand structure characteristic drivers did not significantly affect PD in any forest strata. In the understory, elevation and sfcWind had indirect negative effects on PD, mediated by SD.

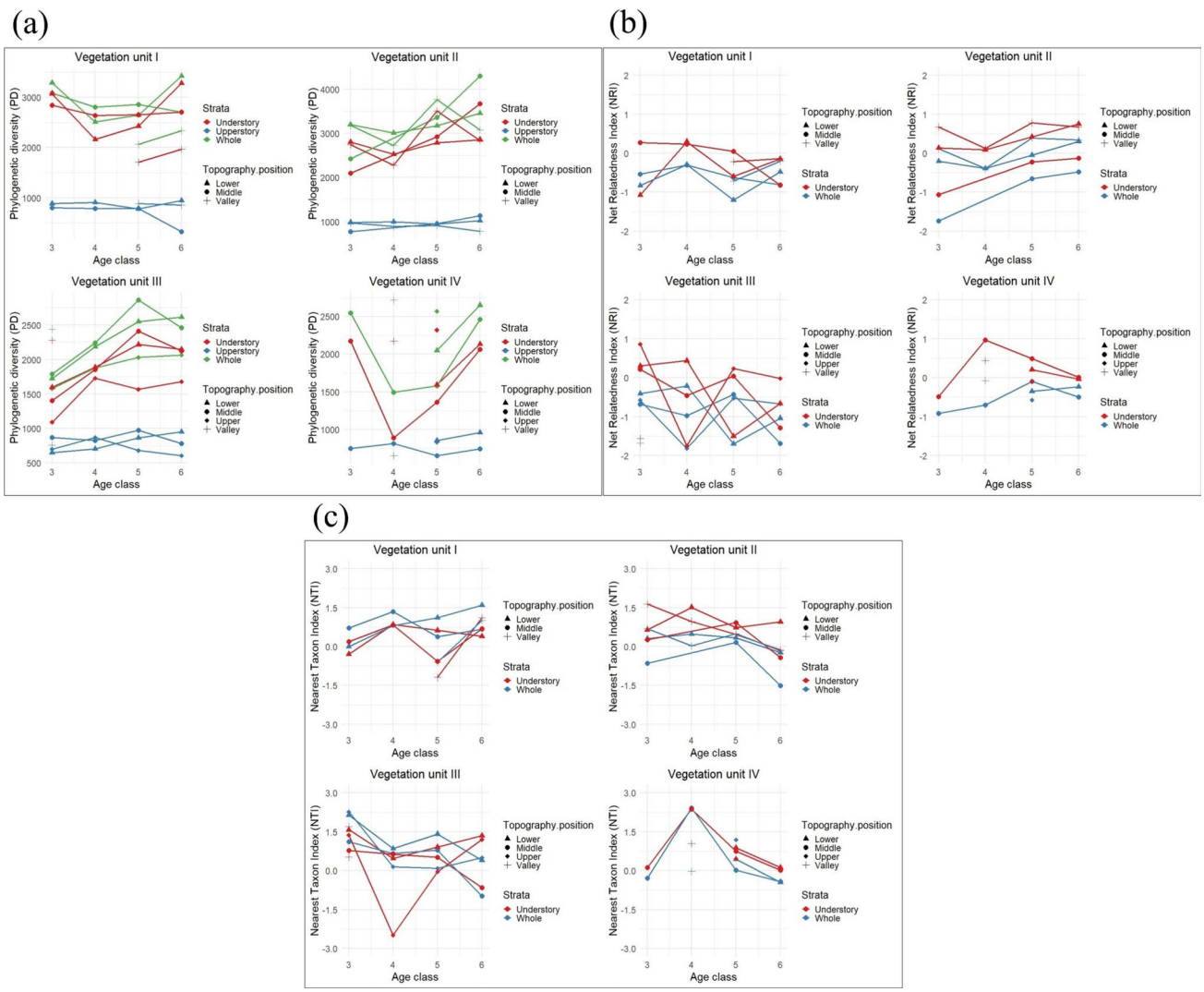


Fig. 5 Changes in phylogenetic metrics (PD, NRI, and NTI) according to stand age and topographic position across forest strata of vegetation units identified by TWINSPAN analysis; **a** shows changes in PD by vegetation unit; **b** illustrates changes in NRI by vegetation unit; **c** represents changes in NTI by vegetation unit

Discussion

Characteristics of *L. kaempferi* forest structure

Our results demonstrated that, depending on locational conditions, the entry of species with distinct ecological characteristics is causing a shift in *L. kaempferi* communities from monospecific to unique mixed communities. This change could be more clearly understood by investigating species composition in VUs defined using TWINSPAN, calculating IVs, measuring DBH class distribution, and performing RDA analysis. Although various upperstory vegetation species entered the communities depending on the local environment, *Quercus* spp. showed high IVs in all VUs. This was similar to a previous study in the Hoosier National Forest in South Indiana in the US, where *Quercus* spp. were a dominant constituent of plantations where *Pinus echinata* and *Pinus strobus* were dominant (Duffy et al. 2024). Woody plants in the Pinaceae family, such as *L. kaempferi*, release tannins and various other allelochemicals, promoting soil acidification and reducing soil fertility in the stand (Lee and Monsi 1963; Rice 1984; Landeweert et al. 2001). In this context, *Quercus rubra* has a better affinity for acidic soil compared with that of other species (Finzi et al. 1998; Bigelow and Canham 2002). In our study, *Quercus* spp. was dominant irrespective of altitude or local environment, suggesting that this species has a better affinity for acidic soil than other species, and it could play an important role in the transition for Pinaceae stands to mixed forests. Moreover, RDA analysis supported the finding that the local environment and TP are closely related to the species entering *L. kaempferi*

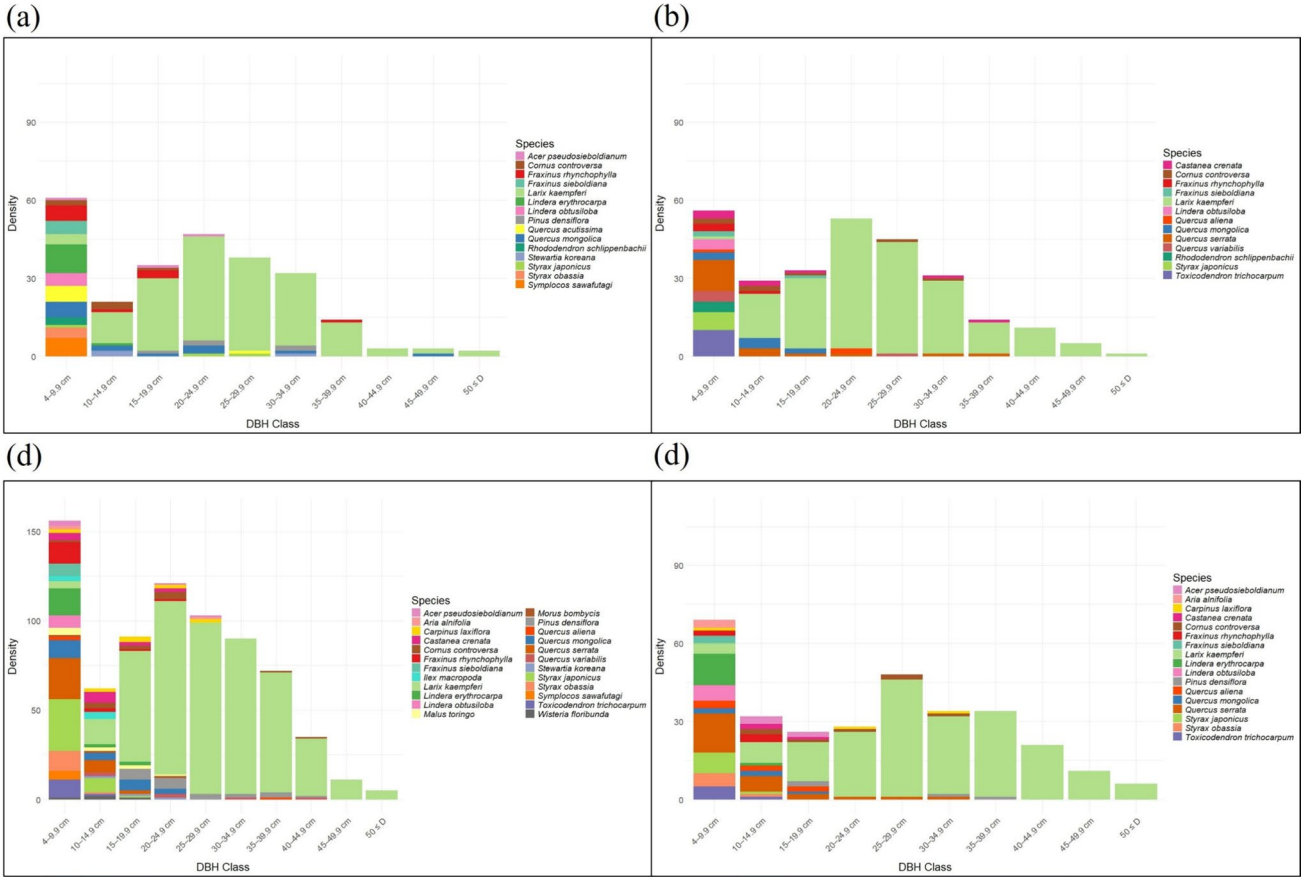


Fig. 6 Diameter class distribution of *L. kaempferi* forests by age class, based on data from 129 plot surveys; **a** age class 3; **b** age class 4; **c** age class 5; **d** age class 6. Species with a density of less than 3 in each age class were not included

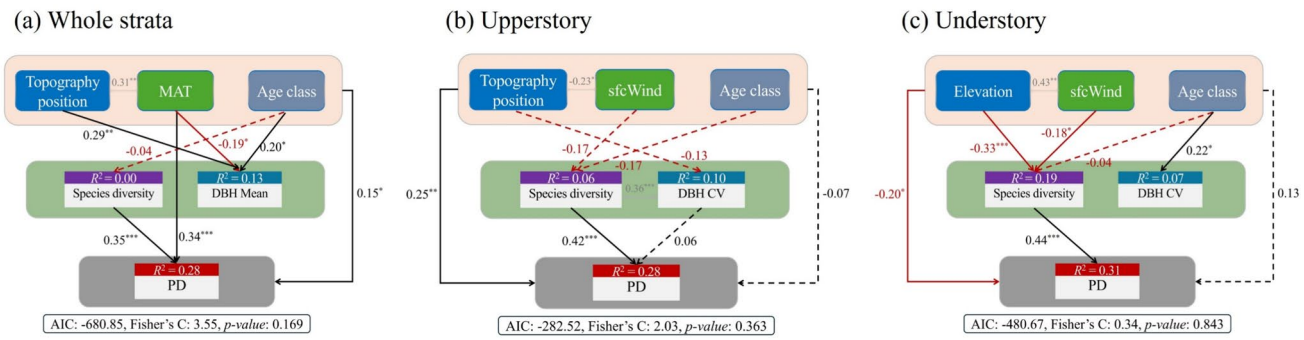


Fig. 7 Piecewise structural equation models (pSEMs) were used to test the relationships between biotic and abiotic drivers and the phylogenetic diversity at three levels in *L. kaempferi* forests; **a** Whole strata; **b** Upperstory; **c** Understory. Black and red arrows represent positive and negative paths, respectively, while gray arrows indicate estimated covariances. Solid and dashed arrows denote significant ($p < 0.05$) and non–significant ($p > 0.05$) relationships, respectively. Standardized coefficients were used for all paths and covariances. MAP: Mean annual temperature; sfcWind: near-surface wind speed; DBH CV: Coefficient of variation of diameter at breast height; DBH Mean: Mean diameter at breast height

forests. Compared with upperstory vegetation, which has already established dominance through competition with other species, these trends are even more prominent among understory vegetation. Although these results could be interpreted to result from differences due to the elevation gradient, we observed species that appeared persistently and showed high IVs irrespective of elevation (e.g., *L. obtusiloba*, *L. erythrocarpa*, *O. undulatifolius*, and others).

Generally, in dark coniferous forests such as *L. kaempferi* forests, light penetration is restricted by high trees, making highly shade-tolerant species more competitive (Oh et al. 2021). Hence, it can be interpreted that in *L. kaempferi* forests, local environmental factors and stand structural characteristics have a larger impact on the species composition of understory vegetation than does the elevation gradient. Phylogenetic community structure is used as an index to infer community formation mechanisms (Webb et al. 2002; Pastore and Scherer 2016), and we were able to confirm that the different VUs showed distinct properties for NTI and NRI, indicating the involvement of different mechanisms. Among the VUs, the topographic environmental characteristics of VU 1 included the lowest altitude and a lower rate of other disturbances (e.g., entry of various plant species due to increased elevation, soil erosion due to rain, trees falling in valleys or other steep slopes, etc.). The *L. kaempferi* forests formed under these conditions had dense canopies that restricted light penetration into the stand, causing phylogenetic clustering of species with strong shade tolerance and leading to a higher NTI. This supports the idea that phylogenetic clustering was observed specifically in this VU because, rather than evolutionary differentiation over time due to the entry of diverse species through competitive interactions with existing species (Losos et al. 2003), in the absence of major disturbance, species with similar ecological needs coexisted from the beginning. Thus, we can infer that stand structure characteristics and abiotic factors (e.g., local environment, etc.) interact to affect VU I, and canopy cover management can be highlighted as an important management strategy to induce the entry of more species (Doyon et al. 2008; Coote et al. 2013; Puettmann et al. 2016). Canopy cover management can help stimulate the development of understory vegetation by promoting light penetration into the stand and improve structural diversity by enabling shade-tolerant and light-requiring species to coexist (Wagner et al. 2011; Doyon et al. 2008; Coote et al. 2013; Puettmann et al. 2016; Ujházy et al. 2017). VU II had the highest NRI value of all the VUs, even though it was still negative. This VU was mostly found in valleys and lower slopes, where TWI was high. These environments promote the entry of diverse plant species. Specifically, a moist environment provides favorable conditions for species of a certain phylogeny (e.g., species preferring moist environments), suggesting that, even if various species enter the community, they are likely to form a phylogenetically close community. This implies that environmental filtering due to topographic characteristics has important effects on community formation. Our results show that *L. kaempferi* communities demonstrate unique vegetation characteristics and community formation mechanisms for each local environment. Furthermore, because each community shows distinct characteristics, rather than adopting a single management approach for all *L. kaempferi* forests, our findings highlight the need to introduce management strategies suited to each community's characteristics.

Changes in phylogenetic characteristics and DBH distribution according to stand age

Previous studies on SD in *L. kaempferi* forests have mostly focused on a traditional approach, where all species are treated equally (Nagaike et al. 2003). Therefore, research on PD is relatively scarce. In this context, we aimed to interpret the spatial distribution and phylogenetic relationships of species by quantifying the changes in PD and phylogenetic community structure (NRI or NTI) in distinct VUs with stand age, forest stratum, and TP. Overall, PD in the whole strata and understory slightly decreased when shifting from age class 3–4 and then showed a gradually increasing trend, whereas PD in the upperstory showed irregular patterns. *L. kaempferi* grows rapidly (Mamet et al. 2019; Wu et al. 2021) and, due to its height, forms forests with restricted light penetration. After initial planting, before the canopy closes entirely, ample light penetration enables the entry of various early successional species. However, once the canopy becomes closed, pioneer species reportedly gradually recede due to late successional species (Poorter et al. 2024; Lee et al. 2024). We also observed this process in our study, and the magnitude of changes differed depending on TP characteristics. This suggests that the conditions formed by the local characteristics affect the rate of species entry. Meanwhile, the somewhat irregular results in the upperstory suggest that, as observed in the distribution of DBH with increasing stand age, the survival and recession of plant species in the community is intertwined with complex interactions such as strong shade formation by *L. kaempferi* and the resulting microclimate. In summary, even among species that become established in the stand, while some are likely to persist with increasing stand age (e.g., *Quercus* spp. and *Carpinus laxiflora* in our study), some species will gradually recede as canopy cover increases. This is consistent with previous studies in forests that form dense canopies, where highly shade-tolerant species were the major constituent species (Oh et al. 2021; Seliger et al. 2023a). In VU III, the PD in the whole strata and understory showed a gradually increasing trend with older stand age. In addition, NRI and NTI showed an overdispersed pattern at age class 4, but a trend toward gradual clustering with increasing stand age was observed. Compared with other VUs, these communities were relatively frequent in plots from middle to upper slopes (including ridges). In this environment, strong winds shake the canopy, naturally enabling light penetration, and this can be expected to facilitate the initial entry of diverse

species into the understory vegetation. However, over time, the high sunlight and strong winds create an edaphic climax, and only species that have adapted to these conditions are likely to survive. In other words, species that have adapted to a dry environment are established as the major constituents of the community (Zhao et al. 2020). Continual monitoring and further research are required to investigate the possibility of competitive exclusion leading to a higher PD in stands of age class 6 or higher. Overall, the phylogenetic community structure (NRI and NTI) of all VUs showed irregular patterns with increasing stand age, but a trend toward overdispersion was observed over time compared with that of the initial state at age class 3. This supports the competitive interactions that arise when multiple species enter and recede in communities.

Identification of factors regulating the PD of *L. kaempferi* forests

We discovered that the factors regulating PD in *L. kaempferi* forests differ depending on the forest stratum. In particular, while age class had a direct positive effect on PD in the whole strata, it did not significantly affect the upper- and understories individually. Different topographic environmental factors were found to have important effects in different strata. In the upperstory, TP had a direct positive effect on PD. As TP increases, more wet conditions, such as those in lower slopes and valleys, are represented, suggesting that these environments are suitable for habitation by phylogenetically diverse trees. This suggests that the PD of upperstory species in *L. kaempferi* forests could be affected more by environmental filtering (i.e., differences in local conditions) than by stand age. This is consistent with a previous study in *Robinia pseudoacacia* forests planted broadly throughout China (Zhao et al. 2020). Several previous studies have focused on stand age as the most important factor affecting SD (Kirby 1988; Sykes et al. 1989; Gilliam et al. 1995). However, in our results, the relationship between PD and stand age was not statistically significant for all strata, and we only observed a significant effect in the whole strata. This is similar to a previous Japanese study of *L. kaempferi* forests using stand age and traditional indices of SD (e.g., SR and SD), in which a linear relationship was not observed (Nagaike et al. 2003). Generally, species diversity (SD) gradually increases as stand age, due to the development of a larger, more complex vegetation structure characterized by enhanced vertical stratification and spatial heterogeneity. This structural complexity is often associated with changes in canopy structure and light conditions, providing microhabitats that support diverse species coexistence. However, in the case of *L. kaempferi* plantation forests, increased stand age typically results in taller trees with closed canopies, thus limiting light availability. Consequently, the anticipated increase in structural heterogeneity and canopy gaps that usually accompanies stand aging may not occur. Indeed, our results indicated that while stand structural characteristics were directly influenced by stand age, these structural changes did not significantly mediate indirect effects of age class on PD. Therefore, in *L. kaempferi* plantation forests, changes in tree age itself result in only sluggish variations in stand structural heterogeneity, suggesting that niche differentiation driven by topographic environmental differences is the more important factor affecting PD. This suggests that differences in light availability and the microclimates formed due to local conditions can have important effects on SD and PD. In particular, our findings support previous studies in which different mechanisms were reported for different strata (Ali and Yan 2018; Chun et al. 2019; Chun and Lee 2019; Lee et al. 2022). Post-planting, evolutionary differences may emerge between upper- and understory vegetation due to distinct mechanisms, highlighting the need to analyze strata separately. In addition, in the understory, sfcWind and elevation had indirect negative effects on PD, and an effect due to the interaction between these two factors is likely. For example, wind strength tends to increase with higher altitude, leading to an increase in the formation of exposed environments compared with those protected from the wind. Thus, these two factors can interact to create a harsher microenvironment, but this will need to be confirmed through further research into microenvironment characteristics and the mechanisms of species composition (Qin et al. 2017). In addition, soil nutrient factors such as phosphorus content may influence PD through environmental filtering processes, as demonstrated in recent studies (Xie et al. 2023). Although our model did not explicitly include variables such as phosphorus or nitrogen availability, incorporating these factors in future analyses may help clarify the complex mechanisms regulating phylogenetic diversity more comprehensively.

Management strategies for enhancing biodiversity in *L. kaempferi* forests

According to our findings, all VUs showed a gradually increasing trend in PD with increasing stand age. However, pSEM analysis revealed that stand age did not have a statistically significant effect on PD in the individual strata (e.g., under- and upperstories). Moreover, IV analysis showed that, for most dominant species, shade-tolerant species showed higher IVs. In particular, for upperstory vegetation, because the number of individuals reaching the canopy was limited compared with that for *L. kaempferi*, active forest management is needed to achieve a qualitative long-term increase in biodiversity (Seliger et al. 2023a). Thus, promoting the structural diversity of communities and activating various ecological functions using thinning to adjust the density

of certain dominant species is essential (Yamamoto 2000; Heinrichs and Schmidt 2009; Piwczyński et al. 2016; Zhao et al. 2020; Seliger et al. 2021). We propose management strategies based on the vegetation type in order to improve the biodiversity of artificial forests. The reason we propose management strategies based on the vegetation type is that communities are strongly affected by environmental filtering and show different responses depending on natural and artificial changes and local environmental characteristics (Dinnage 2009; Turley and Brudvig 2016; Zhao et al. 2020). As such, if a single management strategy is applied without considering vegetation type, the effects could be limited if the unique properties of the forest ecosystem are overlooked. By differentiating types based on our findings and suggesting a management strategy that accounts for vegetation characteristics and various environmental and surrounding conditions (e.g., accessibility), we aimed to enhance our knowledge of the conversion of artificial coniferous forests to mixed forests. VU I is located on lower slopes, with low wind exposure and restricted light penetration; therefore, intervention is limited by local topographic environmental characteristics (Fig. 8b). For this reason, disturbance is less likely compared with that in other stands, and species that thrive in shaded environments are dominant. In these conditions, we propose that community diversity be increased using artificial methods to facilitate light penetration, encouraging the entry of early successional plants with a high need for light. Furthermore, given that thinning method selection is important, we propose introducing row thinning/line thinning (i.e., removing tree rows along the original planting lines) (Hamilton 1980) to minimize physical damage to the remaining trees and understory vegetation. This approach will improve biodiversity (Hamilton 1980). For stands in valleys with high TWI, similar to VU II, as well as improving biodiversity through thinning, prevention of disasters also needs to be considered. Coniferous trees such as *L. kaempferi* are shallow-rooted, lacking initial root development compared with that in broadleaf trees, and the weaker tensile strength of their roots makes them vulnerable to strong winds (Karizumi 1979; Oh et al. 2011). Given these characteristics, locations with high soil moisture content and high planting density can suffer from a domino-like collapse due to soil erosion and strong winds, increasing the risk of disasters (Fig. 8c). For this reason, selectively felling some trees or saplings at rotation age is important if they are at greater risk of falling due to strong winds, resulting from rapid vertical growth combined with slow horizontal growth. In conditions such as VU II, introducing forest management to promote light penetration and form a suitable environment for plant growth can not only help to maximize biodiversity but also help to prevent disasters. Compared with the other VUs, VU III and IV showed higher IVs for woody trees in the understory. Meanwhile, these VUs showed unfavorable characteristics for an artificial approach and are located at relatively

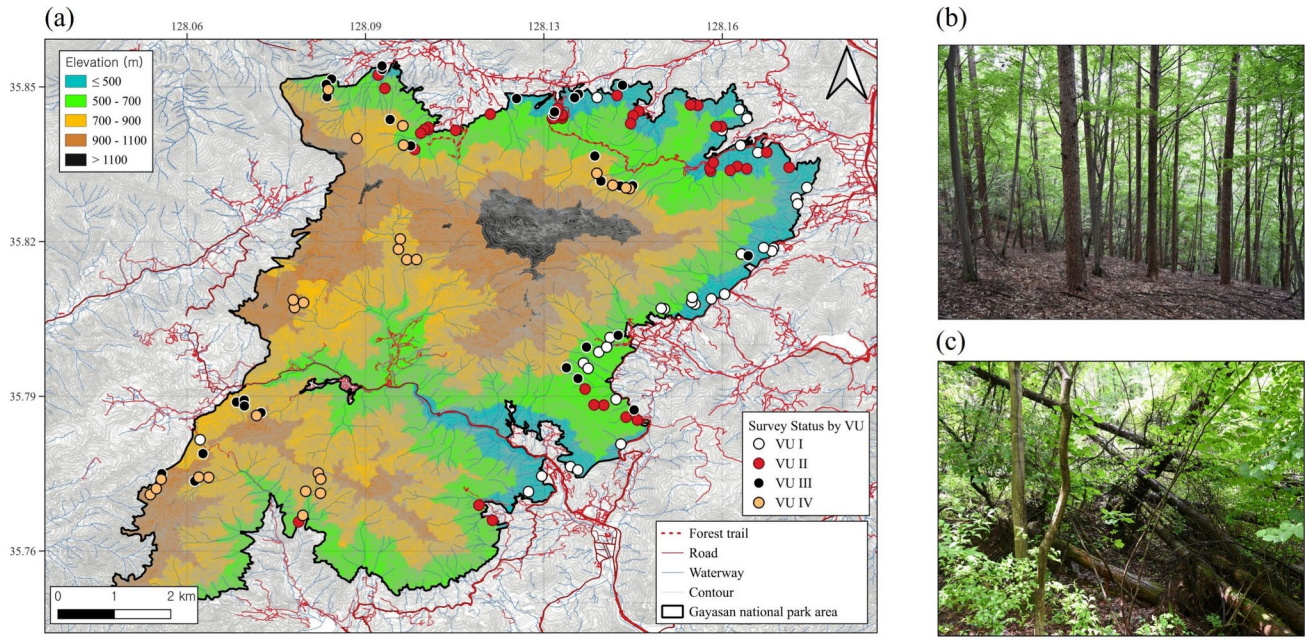


Fig. 8 Distribution of Survey Sites by VU and Site Overview; **a** Distribution of survey sites by VU, classified through TWINSPAN. Compared to VU I and II, VU III and IV show restricted accessibility due to forest trails and roads; **b** An overview of a survey site representative of the vegetation characteristics of VU I. The dense canopy of *L. kaempferi* delays the recruitment of species in the understory; **c** A survey site belonging to VU II, where trees have fallen like dominoes due to strong winds in a shallow-rooted and moist soil environment near the valley

high altitudes (Fig. 8a). Attempting artificial intervention in these locations not only incurs high costs due to the construction of work roads but is also likely to cause damage to the forest ecosystem. In particular, because woody tree species gradually enter the community, compared with other VUs, we can surmise that light penetration into the stand will increase. Therefore, in locations with these topographic environmental properties, rather than attempting excessive work, it may be more suitable to select regions where projects can be performed first, run pilot trials, and then monitor the effectiveness before gradually expanding these projects. The strategies we have suggested can be applied according to the tree characteristics, topographic environment, and on-site working conditions. By ascertaining the vegetation and environmental characteristics of different vegetation types, the VUs requiring artificial intervention can be more effectively identified. Identifying priorities for biodiversity improvement (e.g., VU Ⅰ and Ⅱ) can be useful for ecological conservation planners establishing working methods and plans (Forest et al. 2007). Conducting vegetation and tree diameter surveys alongside artificial forest management is not only useful for understanding the vegetation characteristics of stands but also provides important reference material for verifying tree species that can be revised within the artificial forest (e.g., analysis of DBH distribution). Furthermore, introducing adaptive management based on follow-up monitoring and identifying and preparing for potential problems is essential in the construction of an efficient monitoring system for converting artificial forests to mixed forests. Since our survey was limited to forests in a temperate southern region, it will be important to conduct further studies comparing results between various regions to bridge the knowledge gap necessary for conversion to mixed forests.

Conclusion

We studied *L. kaempferi* forests in Gayasan National Park, South Korea, to distinguish vegetation types and compare differences in species composition, thereby verifying the unique vegetation characteristics associated with different stand ages and topography. We found that these differences were affected by the local habitat conditions, and PD was regulated by different abiotic factors depending on the forest stratum. Furthermore, we observed how forest structural properties and local conditions affect phylogenetic community structure for each vegetation type, leading to competitive interactions and exclusion. Overall, PD showed an increasing trend with older stand age, but to improve the economic and public function of artificial coniferous forests and promote structural diversity, partial forest management interventions will be necessary. In particular, considering the rotation age of *L. kaempferi*, rather than allowing the forests to remain unmanaged, active management will be important to qualitatively improve biodiversity. In the long term, this could lead to stands with higher biodiversity and uniform forest characteristics by promoting natural entry and regrowth of broadleaf trees. In this context, by differentiating between vegetation types and ascertaining the ecological and environmental characteristics of stands, we highlighted the need to introduce customized management strategies suited to the characteristics of each community rather than applying the same methods in all cases. This approach will not only help with setting priorities for projects but will also help with establishing adaptive management policies through the partial implementation of forest management and monitoring of its effectiveness. Furthermore, our study provides important basic data for the conversion of artificial forests to mixed forests worldwide. Our findings highlight the need for forest management to improve long-term biodiversity, and we propose that quantifying phylogenetic structural properties and diversity can form an important basis for biodiversity conservation (Zhao et al. 2020).

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Data availability The data of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

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References

Ali A, Yan ER (2018) Consequences of phylogenetic conservativeness and functional trait similarity on aboveground biomass vary across subtropical forest strata. For Ecol Manag 429:28–35. https://doi.org/10.1016/j.foreco.2018.06.042

Ali A, Lohbeck M, Yan ER (2018) Forest strata-dependent functional evenness explains whole-community aboveground biomass

through opposing mechanisms. For Ecol Manag 424:439–447. https://doi.org/10.1016/j.foreco.2018.05.015
Ammer C, Bickel E, Kölling C (2008) Converting Norway spruce stands with beech: a review of arguments and techniques. Austrian J Forest Sci 125(1):3–26
Barbour MG, Burk J, Pitts WD (1987) Terrestrial Plant Ecology, 2nd edn. The Benjamin/Cummings Publishing Company Inc, Menlo Park, California
Barsoum N, Henderson L (2016) Converting planted non-native conifer to native woodlands: a review of the benefits, drawbacks and experience in Britain. For Commiss Res Note 024:1–10
Beven KJ, Kirkby MJ (1979) A physically based, variable contributing area model of basin hydrology/Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. Hydrol Sci Bull 24(1):43–69. https://doi.org/10.1080/02626667909491834
Bigelow SW, Canham CD (2002) Community organization of tree species along soil gradients in a north-eastern USA forest. J Ecol 90(1):188–200. https://doi.org/10.1046/j.0022-0477.2001.00655.x
Bolte A, Ammer C, Löf M, Madsen P, Nabuurs GJ, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in Central Europe: climate change impacts, strategies and integrative concept. Scand J for Res 24(6):473–482. https://doi.org/10.1080/02827580903418224
Braun-Blanquet J (1964) Pflanzensoziologie: Grünzüge der Vegetationsgrunde, 3rd edn. Springer Vienna, Wien
Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? Trends Ecol Evol 32(6):429–437. https://doi.org/10.1016/j.tree.2017.03.004
Cadotte MW, Cardinale BJ, Oakley TH (2008) Evolutionary history and the effect of biodiversity on plant productivity. Proc Natl Acad Sci U S A 105(44):17012–17017
Cahill JF, Kembel SW, Lamb EG, Keddy PA (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? Perspect Plant Ecol Evol Syst 10(1):41–50. https://doi.org/10.1016/j.ppees.2007.10.001
Canullo R, Allegrini MC, Campetella G (2012) Reference field manual for vegetation surveys on the CONECOFOR LII network, Italy (National Programme of Forest Ecosystems Control—UNECE, ICP Forests). Braun-Blanquetia 48:5–65
Cao JH, Qi R, Liu T, Li B, Gao BQ, Chen XL, Zhao Y, Zhao ZG (2021) Patterns of species and phylogenetic diversity in *Picea purpurea* forests under different levels of disturbance on the northeastern Qinghai-Tibetan Plateau. Glob Ecol Conserv 30:e01779. https://doi.org/10.1016/j.gecco.2021.e01779
Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. Ecol Lett 12(7):693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x
Chavardès RD, Gennaretti F, Grondin P, Cavard X, Morin H, Bergeron Y (2021) Role of mixed-species stands in attenuating the vulnerability of boreal forests to climate change and insect epidemics. Front Plant Sci 12:658880. https://doi.org/10.3389/fpls.2021.658880
Chen FQ, Song NN, Chen GH, Wang JZ (2015) Effects of exotic species *Larix kaempferi* on diversity and activity of soil microorganisms in Dalaoling National Forest Park. Ecol Process 4:10. https://doi.org/10.1186/s13717-015-0037-x
Chun JH, Lee CB (2019) Temporal changes in species, phylogenetic, and functional diversity of temperate tree communities: insights from assembly patterns. Front Plant Sci 10:294. https://doi.org/10.3389/fpls.2019.00294
Chun JH, Kim HH, Lim JH, Lee CB (2019) Plant diversity patterns and the drivers on a long-term riparian forest research site in Mt. Gyebang, south Korea. J Agric Life Sci 53(5):13–23. https://doi.org/10.14397/jals.2019.53.5.13
Coote L, Dietzsch AC, Wilson MW, Graham CT, Fuller L, Walsh AT, Irwin S, Kelly DL, Mitchell FJG, Kelly TC, O'Halloran J (2013) Testing indicators of biodiversity for plantation forests. Ecol Indic 32:107–115. https://doi.org/10.1016/j.ecolind.2013.03.020
Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32(3):476–496. https://doi.org/10.2307/1931725
Dinnage R (2009) Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. PLoS ONE 4(9):e7071. https://doi.org/10.1371/journal.pone.0007071
Doyon F, Yamasaki S, Duchesneau R (2008) The use of the natural range of variability for identifying biodiversity values at risk when implementing a forest management strategy. For Chron 84(3):316–329. https://doi.org/10.5558/tfc84316-3
Duffy PJ, Jacobs DF, Kabrick JM, Thornton CD, Swaim JT, Jenkins MA (2024) Response of understory vegetation to long-term occupancy by introduced *Pinus* species in temperate deciduous hardwood forests. For Ecol Manage 572:122310. https://doi.org/10.1016/j.foreco.2024.122310
FAO (2020) Global Forest Resources Assessment 2020: key findings. https://www.fao.org/interactive/forest-resources-assessment/2020/en/. Accessed 30 Jan 2025
Finzi AC, Canham CD, Van Breemen N (1998) Canopy tree–soil interactions within temperate forests: species effects on pH and cations. Ecol Appl 8(2):447–454. https://doi.org/10.1890/1051-0761(1998)008[0447:CTSIWT]2.0.CO;2
Forest F, Grenyer R, Rouget M, Davies TJ, Cowling RM, Faith DP, Balmford A, Manning JC, Procheş S, van der Bank M, Reeves G, Hedderson TAJ, Savolainen V (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445(7129):757–760. https://doi.org/10.1038/nature05587
Gilliam FS, Turrill NL, Adams MB (1995) Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecol Appl 5(4):947–955. https://doi.org/10.2307/2269345
Hamilton GJ (1980) Line thinning. Forestry Commission Archive: Leaflet 77.
Harcombe PA, Marks PL (1978) Tree diameter distributions and replacement processes in southeast Texas forests. For Sci 24(2):153–166. https://doi.org/10.1093/forestscience/24.2.153
Hartley MJ (2002) Rationale and methods for conserving biodiversity in plantation forests. For Ecol Manag 155(1–3):81–95. https://doi.org/10.1016/S0378-1127(01)00549-7
Heinrichs S, Schmidt W (2009) Short-term effects of selection and clear cutting on the shrub and herb layer vegetation during the conversion of even-aged Norway spruce stands into mixed stands. For Ecol Manage 258(5):667–678. https://doi.org/10.1016/j.foreco.2009.04.037
Hill MO (1979) TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York
Hu Y, Li XY, Guo AX, Yue P, Guo XX, Lv P, Zhao SL, Zuo XA (2022) Species diversity is a strong predictor of ecosystem multifunctionality under altered precipitation in desert steppes. Ecol Indic 137:108762. https://doi.org/10.1016/j.ecolind.2022.108762
Jactel H, Moreira X, Castagneyrol B (2021) Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. Annu Rev Entomol 66:277–296. https://doi.org/10.1146/annurev-ento-041720-075234
Jarzyna MA, Quintero I, Jetz W (2021) Global functional and phylogenetic structure of avian assemblages across elevation and latitude. Ecol Lett 24(2):196–207. https://doi.org/10.1111/ele.13631
Jin Y, Qian H (2022) V.PhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants.

Plant Divers 44(4):335–339. https://doi.org/10.1016/j.pld.2022.05.005
Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the Earth's land surface areas. Sci Data 4:170122. https://doi.org/10.1038/sdata.2017.122
Karizumi N (1979) Illustrations of tree roots. Seibundo Shinkosha Publishing, Tokyo
Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26(11):1463–1464. https://doi.org/10.1093/bioinformatics/btq166
Kirby KJ (1988) Changes in the ground flora under plantations on ancient woodland sites. Forestry 61(4):317–338. https://doi.org/10.1093/forestry/61.4.317
Landeweert R, Hoffland E, Finlay RD, Kuyper TW, van Breemen N (2001) Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. Trends Ecol Evol 16(5):248–254. https://doi.org/10.1016/S0169-5347(01)02122-X
Lawley V, Parrott L, Lewis M, Sinclair R, Ostendorf B (2013) Self-organization and complex dynamics of regenerating vegetation in an arid ecosystem: 82 years of recovery after grazing. J Arid Environ 88:156–164. https://doi.org/10.1016/j.jaridenv.2012.08.014
Lee IK, Monsi M (1963) Ecological studies on *Pinus densiflora* forest. 1. Effect of plant substances on the floristic composition of the undergrowth. Bot Mag Tokyo 76:400
Lee HI, Seo YO, Kim H, Ali A, Lee CB, Chung Y (2022) Species evenness declines but specific functional strategy enhances aboveground biomass across strata in subtropical–warm-temperate forests of South Korea. For Ecol Manag 512:120179. https://doi.org/10.1016/j.foreco.2022.120179
Lee SJ, Lee AR, Byeon JG, Oh SH (2024) Pre-drought effects on northern temperate trees and vine invasion in forest gaps hindering regeneration. Sci Total Environ 951:175707. https://doi.org/10.1016/j.scitotenv.2024.175707
Lefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Meth Ecol Evol 7(5):573–579. https://doi.org/10.1111/2041-210X.12512
Legendre P, Legendre L (2012) Numerical ecology, 3rd edn. Elsevier, Amsterdam
Li JY, Wu GX, Guo QX, Korpelainen H, Li CY (2018) Fast-growing *Larix kaempferi* suffers under nutrient imbalance caused by phosphorus fertilization in larch plantation soil. For Ecol Manag 417:49–62. https://doi.org/10.1016/j.foreco.2018.02.046
Liu MX, Che YD, Jiao J, Li LR, Jiang XX (2019) Exploring the community phylogenetic structure along the slope aspect of subalpine meadows in the eastern Qinghai–Tibetan Plateau, China. Ecol Evol 9(9):5270–5280. https://doi.org/10.1002/ece3.5117
Losos JB, Leal M, Glor RE, De Queiroz K, Hertz PE, Rodríguez Schettino L, Lara AC, Jackman TR, Larson A (2003) Niche lability in the evolution of a Caribbean lizard community. Nature 424(6948):542–545. https://doi.org/10.1038/nature01814
Lu YH, Coops NC, Wang TL, Wang GY, Lu YH, Coops NC, Wang TL, Wang GY (2015) A process-based approach to estimate Chinese fir (*Cunninghamia lanceolata*) distribution and productivity in Southern China under climate change. Forests 6(2):360–379. https://doi.org/10.3390/f6020360
Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316(5832):1746–1748. https://doi.org/10.1126/science.1143082
Mamet SD, Brown CD, Trant AJ, Laroque CP (2019) Shifting global *Larix* distributions: northern expansion and southern retraction as species respond to changing climate. J Biogeogr 46(1):30–44. https://doi.org/10.1111/jbi.13465
Mastrogianni A, Kallimanis AS, Chytrý M, Tsiripidis I (2019) Phylogenetic diversity patterns in forests of a putative refugial area in Greece: a community level analysis. For Ecol Manag 446:226–237. https://doi.org/10.1016/j.foreco.2019.05.044
Nagaike T (2000) A review of ecological studies on plant species diversity in plantation ecosystems. J Jpn for Soc 82(4):407–416
Nagaike T, Hayashi A, Abe M, Arai N (2003) Differences in plant species diversity in *Larix kaempferi* plantations of different ages in central Japan. For Ecol Manag 183(1–3):177–193. https://doi.org/10.1016/S0378-1127(03)00105-1
Nakamura Y, Krestov PV (2005) Coniferous forests of the temperate zone of Asia. In: Anderson F (ed) Ecosystems of the world. 6: Coniferous forests. Elsevier, Amsterdam, pp 163–220
Oh JH, Hwang JS, Cha DS (2011) Analysis of slope stability effect of arbors' roots-on tensile strength of the roots. Korean J Environ Ecol 25(1):31–36
Oh SH, Kim JS, Cho JH, Cho HJ (2021) Vegetation types and ecological characteristics of *Larix kaempferi* plantations in baekdudaegan protected area, South Korea. J Korean Soc for Sci 110(4):530–542
Park YS, Fowler DP (1983) A provenance test of Japanese larch in eastern Canada, including comparative data on European larch and tamarack. Silvae Genet 32:96–101
Pastore AI, Scherer BP (2016) Changes in community phylogenetic structure in a North American forest chronosequence. Ecosphere 7(12):e01592. https://doi.org/10.1002/ecs2.1592
Pielou EC (1969) An introduction to mathematical ecology. Wiley, Hoboken
Piwczyński M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. For Ecol Manag 376:231–237. https://doi.org/10.1016/j.foreco.2016.06.011
Poorter L, van Der Sande MT, Amissah L, Bongers F, Hordijk I, Kok J, Lohbeck M (2024) A comprehensive framework for vegetation succession. Ecosphere 15(4):e4794
Puettmann KJ, Ares A, Burton JI, Dodson EK (2016) Forest restoration using variable density thinning: lessons from Douglas-fir stands in western Oregon. Forests 7(12):310. https://doi.org/10.3390/f7120310
Qin H, Dong G, Zhang YB, Zhang F, Wang MB (2017) Patterns of species and phylogenetic diversity of *Pinus tabuliformis* forests in the eastern Loess Plateau, China. For Ecol Manag 394:42–51. https://doi.org/10.1016/j.foreco.2017.03.030
Rice EL (1984) Alleopathy. Academic Press, London
Seliger A, Puffpaff S, Manthey M, Kreyling J (2021) Management options for the conversion of allochthonous coniferous forest patches towards more natural species composition in the Vorpommersche Boddenlandschaft National Park, NE Germany. Balt for. https://doi.org/10.46490/bf533
Seliger A, Ammer C, Kreft H, Zerbe S (2023a) Diversification of coniferous monocultures in the last 30 years and implications for forest restoration: a case study from temperate lower montane forests in Central Europe. Eur J for Res 142(6):1353–1368. https://doi.org/10.1007/s10342-023-01595-4
Seliger A, Ammer C, Kreft H, Zerbe S (2023b) Changes of vegetation in coniferous monocultures in the context of conversion to mixed forests in 30 years: implications for biodiversity restoration. J Environ Manag 343:118199. https://doi.org/10.1016/j.jenvman.2023.118199
Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27(3):379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x
Shao XZ (1985) Study on the ecological survey of *Larix kaempferi*. Shandong for Sci Technol 1:9–18 (**(in Chinese)**)
Shipley B (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94(3):560–564. https://doi.org/10.1890/12-0976.1

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends Ecol Evol 31(1):67–80. https://doi.org/10.1016/j.tree.2015.11.005

Spracklen BD, Lane JV, Spracklen DV, Williams N, Kunin WE (2013) Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain. For Ecol Manag 310:204–212. https://doi.org/10.1016/j.foreco.2013.08.001

Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N (2012) Phylogenetic diversity and the functioning of ecosystems. Ecol Lett 15(7):637–648. https://doi.org/10.1111/j.1461-0248.2012.01795.x

Sykes JM, Lowe VPW, Briggs DR (1989) Some effects of afforestation on the flora and fauna of an upland sheepwalk during 12 years after planting. J Appl Ecol 26(1):299–320

Tucker CM, Davies TJ, Cadotte MW, Pearse WD (2018) On the relationship between phylogenetic diversity and trait diversity. Ecology 99(6):1473–1479. https://doi.org/10.1002/ecy.2349

Turley NE, Brudvig LA (2016) Agricultural land-use history causes persistent loss of plant phylogenetic diversity. Ecology 97(9):2240–2247. https://doi.org/10.1002/ecy.1443

Ujházy K, Hederová L, Máliš F, Ujházyová M, Bosela M, Čiliak M (2017) Overstorey dynamics controls plant diversity in age-class temperate forests. For Ecol Manag 391:96–105. https://doi.org/10.1016/j.foreco.2017.02.010

Wagner S, Fischer H, Huth F (2011) Canopy effects on vegetation caused by harvesting and regeneration treatments. Eur J Forest Res 130(1):17–40. https://doi.org/10.1007/s10342-010-0378-z

Wang BZ, Yang XH, Zhu YJ, Tu Y, Wang DY, Indree T (2024) Plant diversity mediates the response of ecosystem multifunctionality to climate factor in Eastern Eurasian Steppe. Glob Ecol Conserv 50:e02827. https://doi.org/10.1016/j.gecco.2024.e02827

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Evol Syst 33:475–505

Winter M, Devictor V, Schweiger O (2013) Phylogenetic diversity and nature conservation: where are we? Trends Ecol Evol 28(4):199–204. https://doi.org/10.1016/j.tree.2012.10.015

Wu CY, Chen DS, Shen JP, Sun XM, Zhang SG (2021) Estimating the distribution and productivity characters of *Larix kaempferi* in response to climate change. J Environ Manag 280:111633. https://doi.org/10.1016/j.jenvman.2020.111633

Xiao YM, Yang LC, Nie XQ, Li CB, Xiong F, Wang LL, Zhou GY (2020) Examining differences in phylogenetic composition enhances understanding of the phylogenetic structure of the shrub community in the northeastern Qinghai-Tibetan Plateau. Ecol Evol 10(13):6723–6731. https://doi.org/10.1002/ece3.6402

Xie J, Fang S, Yan QL (2023) Effects of thinning on functional and phylogenetic diversity of regenerated woody plants in plantations over time. Appl Veg Sci 26(3):e12737. https://doi.org/10.1111/avsc.12737

Yamamoto SI (2000) Forest gap dynamics and tree regeneration. J for Res 5(4):223–229. https://doi.org/10.1007/BF02767114

Yang J, Zhang GC, Ci XQ, Swenson NG, Cao M, Sha LQ, Li J, Baskin CC, Ferry Slik JW, Lin LX (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. Funct Ecol 28(2):520–529. https://doi.org/10.1111/1365-2435.12176

Yang J, Li EH, Yang C, Xia Y, Zhou R (2022) Effects of south-to-north water diversion project cascade dams on riparian vegetation along the middle and lower reaches of the Hanjiang River, China. Front Plant Sci 13:849010. https://doi.org/10.3389/fpls.2022.849010

Zhang XP, Wang MB, Liang XM (2009) Quantitative classification and carbon density of the forest vegetation in Lüliang Mountains of China. Plant Ecol 201(1):1–9. https://doi.org/10.1007/s11258-008-9507-x

Zhang M, Peng PH, Shi SL, Wang GY (2024) The environmental interpretation of *Pinus yunnanensis* community differentiation after the invasion of *Ageratina adenophora* in Panxi region, China. Community Ecol 25(1):45–64. https://doi.org/10.1007/s42974-023-00170-6

Zhao Y, Li M, Wang XH, Deng JY, Zhang ZZ, Wang BT (2020) Influence of habitat on the phylogenetic structure of *Robinia pseudoacacia* forests in the eastern Loess Plateau, China. Glob Ecol Conserv 24:e01199. https://doi.org/10.1016/j.gecco.2020.e01199

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