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Interactions between biotic and abiotic factors shape phylogenetic community assembly in southern range-margin *Picea jezoensis* forests

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Identifying factors that control community formation is crucial for understanding biodiversity patterns. Although numerous studies utilize either within- or among-community indicators to explain community formation processes, few have assessed the additional insights gained by integrating the two. Accordingly, we examined *Picea jezoensis* forests in South Korea and northeastern China using complementary within- and among-community approaches and discuss the implications of interpreting these metrics together: (1) we identified the abiotic (e.g., topography and climate) and biotic (e.g., stand structural diversity and community-weighted proportion values of dormancy and dispersal forms) controls of phylogenetic community structure (net relatedness index [NRI] and nearest taxon index [NTI]) across forest strata (whole strata, upperstory, and understory) using piecewise structural equation modeling (pSEM); and (2) we quantified among-community phylogenetic differentiation by decomposing phylogenetic beta diversity (PBD) into turnover and nestedness and testing their relationships with climatic distance, geographic distance, and pairwise elevational difference. (3) We explored how within-community phylogenetic structure (NRI/NTI) relates to among-community phylogenetic differentiation (PBD components). Our results showed that the primary drivers of phylogenetic structure varied by forest strata and metric. Specifically, elevation, mean annual temperature (MAT), and community-weighted proportion (CWP)-based dormancy forms were the dominant predictors for NRI in both the whole strata and understory. In contrast, NTI were primarily shaped by abiotic factors (elevation and MAT) in the upperstory, while biotic constraints—specifically dormancy forms—showed a greater contribution in the understory. Furthermore, among PBD components, turnover was the primary contributor and was strongly associated with climatic distance. This climatic influence remained dominant even after controlling for geographic distance. In contrast, nestedness was best explained by pairwise elevational differences. By bridging within- and among-community metrics, this study helps contextualize how local-level assembly signals may scale up into regional phylogenetic patterns, offering a more unified understanding of forest community formation across spatial scales.

KEYWORDS

beta diversity, biodiversity, climate change, environmental filtering, phylogenetic community structure, subalpine

1 Introduction

Identifying the effects of gradients in both biotic and abiotic factors on community formation, as well as clarifying their underlying mechanisms, has long been a core research topic in community ecology (Gaston, 2000; Swenson, 2011). These gradient effects can be explained as the result of complex interactions involving environmental filtering (Ricklefs, 2004; Kraft et al., 2015) caused by abiotic factors (e.g., climate, topography, and soil), biotic interactions such as interspecific competition and facilitation (Tokeshi, 1990; Schlägel et al., 2020), and spatial processes such as dispersal limitation (Qian et al., 2020) or historicity (Fukami, 2015). However, the relative importance of these mechanisms can significantly differ depending on the observed spatial scale or local context (Ricklefs, 2004; Schlägel et al., 2020). Therefore, separating and quantifying the contributions of each mechanism remains crucial for understanding community assembly mechanisms and provides a sound basis for interpreting the dynamics of community characteristics in response to environmental changes and disturbances (e.g., wildfires, droughts, and disease and pest outbreaks).

As an approach toward understanding these recent complex community assembly processes, research utilizing the functional traits and phylogenetic information of species has been actively conducted (Lasky et al., 2015; Gianuca et al., 2017; Tatsumi et al., 2019). Functional traits (e.g., specific leaf area, seed mass) are indicators of the response to and interaction of species with their environment, and phylogenetic information reflects the evolutionary history shared by species. These two types of information serve complementary roles in understanding community assembly. Phylogenetic information enables the inference of community assembly patterns by leveraging the evolutionary relationships among species (Cadotte et al., 2008; Flynn et al., 2011). Specifically, because evolutionary history often reflects signals in functional traits, phylogeny serves as a robust proxy for unmeasured functional data, thereby enhancing the consistency (Blomberg et al., 2003). Furthermore, this phylogenetic approach provides a mechanistic basis for cross-validating trait-based inferences, as analyzing the phylogenetic structure of coexisting species is widely used to infer community assembly (Webb et al., 2002). This method enables the identification of how phylogenetic relatedness among species within a community deviates from a null model and is structured, as well as the inference derived from quantification using indicators such as the net relatedness index (NRI) and nearest taxon index (NTI) (Webb et al., 2002). However, analyzing within-community patterns alone is insufficient to fully explain how multiple communities change spatially and link to larger-scale evolutionary and biogeographic processes (Swenson et al., 2006). In other words, a key challenge remains: linking local community assembly processes to macro-level processes such as regional speciation or habitat specialization.

In this context, phylogenetic beta diversity (PBD) is an indicator that explicitly reflects phylogenetic information by measuring the total branch length of each community relative to the branch lengths shared by species across multiple communities (Graham and Fine, 2008; Cavender-Bares et al., 2009). The indicator enables identification of

how the current spatial variation in community composition relates to evolutionary mechanisms such as speciation or trait evolution (Graham and Fine, 2008). Baselga (2010) suggested a framework that decomposes beta diversity into two components: turnover, which reflects replacement of lineages (or species) among sites, and nestedness, which reflects differences arising when one community represents a subset of another due to lineage loss or limited colonization. Applied to elevational gradients, this partitioning allows us to evaluate whether phylogenetic compositional differences are driven primarily by lineage replacement along environmental gradients (turnover) or by progressive lineage loss toward harsher, higher-elevation environments (nestedness). For instance, on the one hand, Hamid et al. (2020) targeted the Kashmir Himalaya and found that communities on top surfaces at higher elevations contributed more strongly to nestedness. This finding showed that species extinction and slow immigration in extreme environments, such as high mountains (e.g., glacier-covered areas), indicate that differences between communities primarily arise from species subset formation. As such, PBD offers a robust way to quantify shifts in phylogenetic composition along geographic and environmental gradients, and to infer whether such differences are driven primarily by dispersal limitation (spatial constraints) or environmental filtering (habitat constraints) (Harrison et al., 1992; Freestone and Inouye, 2006). Furthermore, an approach that combines PBD, which shows differences between communities, with phylogenetic community structure, which reflects phylogenetic structure within communities, provides an integrated framework for understanding community assembly mechanisms operating across multiple spatial scales (Qian et al., 2014; Lee et al., 2025b). Qian et al. (2014) examined Changbaishan in China, analyzing phylogenetic structures within communities and phylogenetic differences between communities to explain how local-level assembly processes diverge from or interact with broader regional-scale assembly mechanisms. Lee et al. (2025b) examined subalpine *Abies* forests in South Korea and clarified, in an integrated manner, how environmental filtering and disturbance factors determined species arrangement, and how these internal patterns scaled up to PBD differences between areas. Although integrating within- and among-community phylogenetic metrics involves challenges—particularly due to their divergent sensitivities to spatial scale and grain—their combined application serves as a critical bridge for reconciling local-scale assembly rules with regional phylogenetic patterns (Swenson et al., 2006; Fine and Kembel, 2011). Here, we use NRI/NTI to describe how lineages are arranged within communities and PBD to summarize how community phylogenetic composition differs among communities, thereby linking within-community phylogenetic structure to among-community phylogenetic differentiation within a single interpretive framework. By interpreting these metrics together, we explore how within-community phylogenetic structure relates to broader patterns of phylogenetic differentiation among communities.

Recent studies have examined community assembly mechanisms in various regions. However, existing studies on Northeast Asian subalpine coniferous forest ecosystems have primarily focused on predicting changes in potential habitat distribution in response to environmental changes (Koo et al., 2016; Lee et al.,

2025a) or on describing the structure and dynamics of stands (Takahashi et al., 2003; Qian and Liu, 2025). Notwithstanding, research elucidating the ecological principles underlying the rapid forest restructuring process, i.e., the community assembly mechanism, is lacking. Therefore, the current study examined subalpine *Picea jezoensis* (Siebold & Zucc.) Carrière forests in South Korea and the Baekdu (Changbai) Mountain and its surrounding area in Northeast China. The target research area lies at the phytogeographic southern limit of *P. jezoensis*, making it easier to observe early responses to climate change than in *P. jezoensis* forests in other regions. As these southern-limit populations harbor a unique regional species pool and exist at the ecological threshold of the species' climatic envelope, they are characterized by pronounced demographic declines and accelerated stand restructuring (Kim et al., 2019; Lee et al., 2024). However, it remains unclear which of the complex controlling factors influencing community formation play a pivotal role in these dynamic environments. This study targeted high-altitude coniferous forests vulnerable to environmental change, used phylogenetic information, and aimed to clarify the relationships between within- and between-community structures and various environmental and geographical factors to identify the drivers of community formation mechanisms. In this regard, this study attempted to answer the following key questions: (1) What are the main drivers of within-community phylogenetic structure (NRI/NTI), and how do these factors differ among forest layers? (2) What factors (e.g., climatic, geographic, and elevational difference) drive the turnover and nestedness components of between-community phylogenetic beta diversity (PBD), and how are these components related to within-community phylogenetic structure (NRI/NTI)?

Based on these research questions, this study aimed to fill knowledge gaps regarding community assembly mechanisms at the local level and suggest implications from an integrated approach to phylogenetic community structure and PBD.

2 Materials and methods

2.1 Study area and vegetation survey

We conducted field surveys in the southern (Jiri Mountain), central (Gyebang Mountain), and northern (Baekdu Mountain and its surrounding area) regions of the Korean Peninsula. Jiri Mountain in the south of the Korean Peninsula is designated as a national park, with a highest elevation of 1,915 m (33°23'N, 127°52'E). Gyebang Mountain in the central region is located within Odaesan National Park, with a highest elevation of 1,577 m (37°47'N, 128°23'E). These two study sites are located in South Korea. Baekdu Mountain in the northern region of the Peninsula has a highest elevation of 2,749 m (42°00'N and 128°10'E) and is located on the border between China and North Korea. The field surveys were conducted from 2021 to 2022; data were collected during the active tree-growth period, and from *P. jezoensis* and *P. jezoensis*–*Abies nephrolepis* (Trautv. ex Maxim.) Maxim forests (Figure 1; Supplementary Figure S1). The vegetation survey entailed dividing circular plots with a radius of 11.3 m (400 m² per plot). Dominance was calculated by combining species coverage and abundance within each plot, which were categorized by strata (i.e., tree, sub-tree, shrub, and herb layers) using the phytosociological method of Braun-Blanquet (1964). The dominance of each

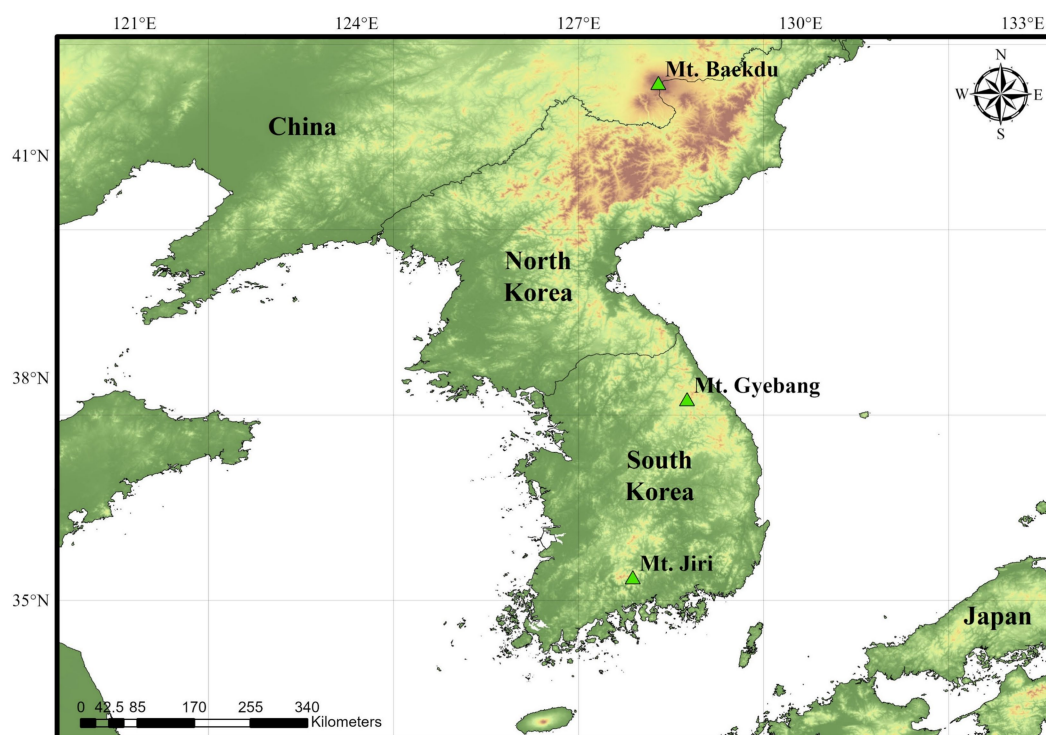


FIGURE 1

Distribution of field survey sites: Mt. Jiri (southern part), Mt. Gyebang (central part), and Mt. Baekdu and its surrounding area (northern part) of the Korean Peninsula.

species according to the Braun–Blanquet scale is as follows: r, rare species; +, coverage <1%; 1, coverage 1–5%; 2, coverage >5 to 25%; 3, coverage >25 to 50%; 4, coverage >50 to 75%; 5, coverage >75 to 100% (Canullo et al., 2012). Diameter measurements were conducted on all individual trees with a diameter at breast height (DBH) of 6 cm or greater within the survey plots. These data were used to statistically analyze stand structural diversity. As for environmental factors, elevation, degree of slope, and latitude/longitude coordinates were recorded at the center of each quadrat using a Garmin GPSMAP 64 s handheld GPS (Garmin, Olathe, KS, USA) and a Suunto Clinometer (Suunto Oy, Vantaa, Finland). Furthermore, we directly measured rock exposure within survey sites in the field and evaluated it using a 4-grade scale ($\leq 10\%$: 0, 11–30%: 1, 31–50%: 2, $\geq 51\%$: 3). Consequently, we conducted field surveys in a total of 51 plots: 15 plots on Jiri Mountain, 18 plots on Gyeong Mountain, and 18 plots on Baekdu Mountain and its surrounding area. Most plots were spaced more than 200 m apart, although some were positioned closer to accommodate the narrow distribution of the species in specific areas. Across mountain regions, the plots captured an elevational and associated climatic gradient (e.g., temperature and moisture conditions), whereas within-region environmental variability was comparatively limited, as indicated by coefficients of variation that were not pronounced (Supplementary Table S1). This sampling design captures microsite-driven shifts in species composition on steep Northeast Asian mountain slopes by targeting the elevational belt of *P. jezoensis* forests, while accounting for their patchy distribution and practical constraints (e.g., permitting requirements and access limitations) on plot placement. Supplementary Table S1 describes the environmental characteristics of the survey plots per mountain in more detail.

2.2 Measurement of abiotic and biotic factors

This study comprised two main sections: (1) identification of the controlling factors influencing phylogenetic community structure, and (2) exploration of the drivers of PBD patterns. This chapter integrates and describes the process of obtaining the variables used in these two research sections.

Climate variables encompassed mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET), mean temperature of growing season days (gst), temperature seasonality, and precipitation seasonality. Data for these variables for 1990–2020 were extracted from the CHELSA v2.1 dataset (<https://www.chelsa-climate.org/>) and quantified for each plot (Karger et al., 2017). Topographic environmental variables included elevation, rock exposure, and slope, which were directly measured in the field. Additionally, the Digital Elevation Model data of SRTM v3 (resolution: 30 m) was used to determine the topographic position index. All topographic environmental variables were employed as abiotic drivers in the analysis.

Biotic drivers included taxonomic diversity, stand structural diversity, and the community-weighted proportion (CWP) values of traits. Taxonomic diversity was estimated for three strata, i.e., whole strata, upperstory (tree and sub-tree layers), and understory (shrub and herb layers), to calculate species richness (SR), species diversity (SD; Shannon's H'), and species evenness (Pielou's). Taxonomic diversity was estimated using PC-ORD ver 7. To quantify stand structural diversity, we calculated the mean DBH, the standard deviation of DBH (DBH STD), and the coefficient of variation of DBH (DBH CV) for woody plants with a DBH

of 6 cm or greater within each plot. We examined the functional characteristics of plants that exerted a main impact on community assembly mechanisms using the CWP values of traits as functional features of biological communities. Functional traits serve as measurable proxies for plant life history processes that are difficult to measure directly (Reich, 2014), contributing to the identification of community formation mechanisms in line with environmental gradients (Lavorel and Garnier, 2002).

Furthermore, quantifying how environmental selection for a specific functional trait changes the average trait value within a community allows us to reflect the process by which dominant or subdominant species with that trait are replaced by species with different traits (Garnier et al., 2004; Louault et al., 2005). We calculated CWP separately for species classified by dormancy and disseminule form, based on species coverage across strata (whole strata, upperstory, understory). We calculated CWP separately for species classified by dormancy and disseminule form, based on species coverage across strata (whole strata, upperstory, understory). Dormancy and disseminule forms were selected because they capture two trait axes that are relevant to subalpine community assembly: seasonal persistence under climatic filtering and colonization under dispersal–establishment constraints (Körner, 1998; Weiher and Keddy, 1995). In subalpine environments, cold stress, frost, and a shortened growing season can favor life forms with protected perennating organs, making dormancy form a useful proxy for persistence strategies (Raunkiaer, 1934; Körner, 1998). In contrast, post-disturbance regeneration is often concentrated in spatially patchy microsites suitable for establishment (e.g., canopy gaps), where recruitment may depend on propagule availability and establishment ability; thus disseminule form can summarize community-level variation in dispersal/colonization potential (Harper, 1977; Nathan and Muller-Landau, 2000). By using these traits, we evaluated how such assembly mechanisms—filtering of hardy species and spatial constraints on migration—drive community dynamics during vegetation restructuring in subalpine forests. The dormancy and disseminule-form characteristics for each species followed the system proposed by Lee (1996), which supplemented the life-form classifications suggested by Raunkiaer (1934) and Numata and Kotaki (1975); detailed information is provided in Table 1. The calculation of CWP for each trait category is as follows. First, a species-by-site matrix was constructed, including the coverage values of species found in each plot. Next, relative coverage (p_i) was obtained by dividing the coverage of each species by the total coverage within the plot. Since dormancy and disseminule forms are categorical traits, we calculated CWP to represent the relative dominance of each functional category within the community (Vaessen et al., 2023). The CWP for a specific trait category (k) was calculated as follows (Equation 1):

$$CWP_k = \sum_{i=1}^S p_i \times I_{ik}, \quad (1)$$

where S is the total number of species at the site, p_i is the relative coverage of species i , and I_{ik} is an indicator variable equal to 1 if species i belongs to trait category k , and 0 otherwise. In the final analysis, to prevent bias from rare traits, we excluded the dormancy and disseminule form categories found in fewer than 10 plots.

2.3 Phylogenetic community structure metric calculations

The phylogenetic community structure of *P. jezoensis* forests was calculated based on the classification of three forest strata

TABLE 1 Abbreviations and descriptions for dormancy and disseminule forms.

Abbreviation	Description
Dormancy form	
H	Hemicryptophytes
MM	Megaphanerophytes
N	Nanophanerophytes
Th(w)	Therophyte (winter annual)
M	Microphanerophytes
G	Geophyte
Th, Th(w)	Therophyte (summer annual) and Therophyte (winter annual)
Th	Therophytes
Ch	Chamaephytes
Disseminule form	
D4	No special modification for dissemination
D1	Disseminated widely by wind or water
D2	Disseminated by attaching to or being consumed by animals and humans
D4,2	Plants with disseminule forms of both D4 and D2
D3	Disseminated by mechanical propulsion of dehiscence of fruits
D2,4	Plants with disseminule forms of both D2 and D4
D4,1	Plants with disseminule forms of both D4 and D1

For disseminule forms involving two dispersal modes (e.g., D4,2), the order of the codes indicates both the primary (first) and secondary (second) dissemination modes.

(whole strata, upperstory, understory). The whole strata had 68 families, 137 genera, and 232 species; the upperstory had 17 families, 24 genera, and 39 species; and the understory had 65 families, 131 genera, and 222 species. Species information and traits (dormancy and disseminule forms) by forest strata are described in [Supplementary Table S2](#). Phylogenetic trees of the surveyed tree species were constructed based on the GBOTB.extended. TPL backbone tree within the R package “V. PhyloMaker2” ([Jin and Qian, 2022](#)), considering forest strata. NRI and NTI were also estimated to evaluate phylogenetic community structure. NRI was calculated based on the mean pairwise phylogenetic distance, and NTI was based on the mean nearest taxon distance ([Equations 2 and 3](#)). To test the statistical significance of these indices, we employed the taxa.labels null model ([Webb et al., 2002](#)) with 999 randomizations. This model was selected because it keeps the observed community composition fixed while randomizing phylogenetic relatedness by shuffling tip labels, thereby testing whether the observed mean pairwise phylogenetic distance (MPD)/mean nearest taxon distance (MNTD) and thus (NRI/NTI) deviates from random expectations given the observed community membership ([Kembel, 2009](#)). In contrast, swap-based null models (e.g., independent swap) randomize the community matrix while constraining species frequencies and/or sample richness, thereby testing a different null hypothesis about compositional constraints, rather than the phylogeny-randomization (tip-shuffling) approach used here; accordingly, we adopted taxa.labels as our primary null model. All four indexes were calculated using the “ses.mpd” and “ses.mntd” functions from the “picante” package in R ([Kembel et al., 2010](#)).

$$NRI = -1 \times (MPD_{\text{observed}} - \text{MeanMPD}_{\text{randomized}}) / SD(MPD_{\text{randomized}}) \quad (2)$$

$$NTI = -1 \times (MNTD_{\text{randomized}} - \text{MeanMNTD}_{\text{randomized}}) / SD(MNTD_{\text{randomized}}) \quad (3)$$

If the NRI or NTI value is greater than 0, it indicates phylogenetic clustering, meaning that species within communities are phylogenetically more closely related than with the null expectation. Conversely, if the value is less than 0, it indicates phylogenetic overdispersion, implying that allied species are separated far away, or that the communities consist of phylogenetically distant species ([Webb et al., 2002](#)). This study evaluated whether within-community phylogenetic structure differed from the null expectation across three forest strata (whole strata, upperstory, and understory) by testing whether NRI and NTI values within each stratum deviated from zero using a one-sample Wilcoxon signed-rank test (two-sided). Plot-level departures from the null expectation were additionally classified using the conventional standardized threshold ($|NRI|$ or $|NTI| > 1.96$). Furthermore, quantitatively compared NRI and NTI across forest strata and identified the main abiotic and biotic factors controlling these indices.

2.4 Conceptual model construction

We utilized piecewise structural equation modeling (pSEM) ([Lefcheck, 2016](#)) to determine the impacts of abiotic and biotic factors on phylogenetic community structure (NRI, NTI) and to identify causal pathways among these factors. The conceptual model ([Figure 2](#)) was specified *a priori* based on community assembly theory, in which climatic and topographic gradients shape habitat conditions and stand context, and these changes can interact with biotic processes (e.g., competition and facilitation) to generate non-random phylogenetic structure within communities. Accordingly, we specified hierarchical paths linking environment, stand structure, trait/diversity attributes, and NRI/NTI, while allowing direct environmental effects to capture unmeasured influences. Direct paths from environment to NRI/NTI were retained to accommodate additional influences not fully represented by intermediate variables. This study conducted analyses across three forest strata (whole strata, upperstory, and understory) to better understand the mechanisms of formation in each stratum. CWP dormancy in the upperstory is almost homogeneously composed of two types: megaphanerophytes (MM) and microphanerophytes (M). The data used in this study also showed little variability in CWP dormancy in the upperstory (Only two types—megaphanerophytes and microphanerophytes—are present). Therefore, the CWP dormancy variable was excluded from the conceptual model for the upperstory analysis. Next, the variables used in the analysis were log-transformed to satisfy the assumptions of normality and linearity. Thereafter, all variables were standardized to the same scale. We also performed Pearson correlation analysis to address multicollinearity issues and removed one variable ($|r| \geq 0.70$; [Supplementary Figure S2](#)) among two variables with high correlation coefficients. After checking the variance inflation factor (VIF) values for the final set of variables, we confirmed that all variables had VIF values below 5, indicating no multicollinearity problems. Next, we performed multi-model inference to identify the main variables with the greatest influence on NRI and NTI within each variable category ([Figure 2](#)). This method evaluates all possible combinations of explanatory variables to identify the most robust predictors among the candidate models.

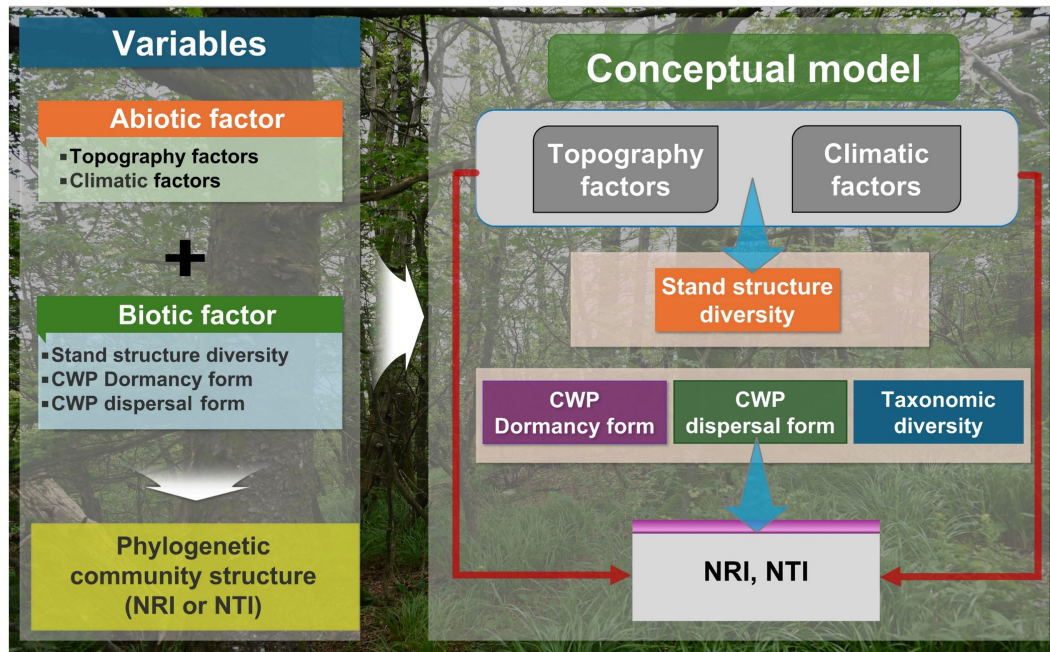


FIGURE 2

Conceptual models for verifying the hypothesized relationships among biotic and abiotic factors affecting the phylogenetic community structure in the whole strata, upperstory, and understory of *Picea jezoensis* forests.

Specifically, we used a model-averaging approach to calculate the average standardized coefficients and relative importance of each variable across all candidate models, ensuring the selection of the most influential factors. Based on the conceptual model, we finally selected the variable with the highest standardized regression coefficients (β) as the representative variable of each category (Supplementary Figures S3,S4). We also used the generalized least squares model to assess whether these selected variables were influenced by spatial autocorrelation. To this end, we constructed a model including geographic coordinates (latitude and longitude) as a spatial effect and a non-spatial model without this effect and compared the Akaike information criterion values to evaluate the fit of these two models (Legendre and Legendre, 2012). The analysis revealed that the influence of spatial autocorrelation differed depending on forest strata and indicators (NRI or NTI) (Supplementary Table S3). As spatial structure was detected in some models, we incorporated geographic coordinates (latitude and longitude) as exogenous covariates to account for spatial dependence. This adjustment helps account for spatial structure in the data and reduces the likelihood that path estimates are influenced by spatial proximity, thereby supporting more reliable inference on the direct and indirect effects of environmental and biotic predictors (Legendre and Legendre, 2012). Subsequently, we performed pSEM analysis according to the conceptual model (Figure 2). We initially started with a full pathway model including all possible pathways, then gradually improved the model by identifying and removing statistically insignificant pathways through a d-separation test (Shipley, 2013).

2.5 Quantification of PBD

We integrated all communities without classifying the strata into upperstory and understory and analyzed PBD to comprehensively understand the overall phylogenetic variation within the community. PBD is a branch-length-based dissimilarity index, calculated as the ratio of shared to unique branch lengths between two communities (Leprieur et al., 2012). Following Baselga (2010), the analysis

separated total dissimilarity into two components: turnover, representing species replacement/turnover between sites, and nestedness, representing species overlap. We employed the vegetation survey data collected from *P. jezoensis* forests and calculated the Sørensen pairwise dissimilarity index (via the `phylo.beta.pair` function) to estimate the total dissimilarity of the communities. All analyses were performed using the “betapart” package in R (Baselga and Orme, 2012).

2.6 PBD analysis

We performed simple and multiple regression analyses on the distance matrix to assess the relationship between beta diversity components (turnover and nestedness) and three factors: (i) geographic distance (calculated using Haversine distance between sites in km), (ii) climatic distance (calculated as Euclidean distance based on Z-score standardized variables; MAT, MAP, temperature seasonality, and precipitation seasonality), and (iii) pairwise elevational difference (calculated as the absolute difference in elevation between sites). Statistical significance was determined based on permutation (Legendre et al., 1994; Legendre and Legendre, 2012). After extracting standardized regression coefficients and the coefficient of determination (R^2) through simple regression analysis, we quantified the directionality and relative strength of the effect of each independent variable on the dependent variable, as well as the overall explanatory power of the model (Qian et al., 2020). Meanwhile, it has been noted that changes in geographic distance frequently show high covariance with those in environmental conditions in natural ecosystems, making it difficult to clearly separate the relative contributions of environmental filtering and dispersal limitation to beta diversity variation (Gilbert and Lechowicz, 2004; Qian et al., 2020). Therefore, we performed multiple regression on distance matrixes (MRM), using geographical distance, climatic distance, and pairwise elevational difference as explanatory variables. We estimated standardized partial regression coefficients to compare the unit effects of each

explanatory variable on pairwise beta diversity while controlling for the influence of other variables (Baselga and Leprieur, 2015; Qian et al., 2020, 2021). For this model, the multiple coefficient of determination (R^2) was reported. To address the independence issue between paired survey sites, we used a permutation test ($n = 999$) to assess the statistical significance of regression coefficients and coefficients of determination. We also followed the MRM-based variance partitioning method recommended in previous studies (Gilbert and Lechowicz, 2004; Qian et al., 2020, 2021) to explicitly distinguish the effects of variables explaining dispersal limitation (geographical distance) from the effects of climatic conditions (climatic distance). Specifically, in line with Qian et al. (2013) and Mazel et al. (2017), we attributed both the unique climatic variance and geographically structured climatic variation to climatic distance. This is based on the rationale that climatic variables are strongly structured geographically at large spatial scales; therefore, joint effects should be interpreted as indirect climatic influences rather than purely geographic ones (Mazel et al., 2017). We separated the total explained variance (R^2) through MRM-based variance partitioning as follows: (i) the variance independently explained by geographic distance (dispersal limitation), (ii) the variance independently explained by climatic distance (environmental gradient), and (iii) the variance explained by geographically structured climatic variation (i.e., variance jointly explained by both variables, such as geographic and climatic distances).

3 Results

3.1 Phylogenetic structure of *P. jezoensis* forests

The phylogenetic structure of *P. jezoensis* forests exhibited contrasting features between NRI and NTI (Figure 3). As for NRI, the mean values were less than 0 across all forest strata (i.e., whole strata, upperstory, and understory), indicating an overall structure of phylogenetic overdispersion among species; Wilcoxon signed-rank tests confirmed that this deviation from zero was statistically significant across all strata ($p < 0.001$). In contrast, NTI showed mean values greater than 0 across all strata, indicating a subtle tendency for phylogenetic clustering among species within the community. However, this clustering was statistically significant only for the whole strata and upperstory ($p < 0.05$), while the understory did not significantly differ from the null expectation ($p = 0.187$). Considering stratum-specific patterns, the upperstory showed the most negative NRI (median around -1), indicating a stronger tendency toward phylogenetic overdispersion than the other strata. Notably, although many plots fell within the neutral range ($|NRI| < 1.96$ or $|NTI| < 1.96$), some plots in each stratum showed significant deviations ($|NRI| > 1.96$ or $|NTI| > 1.96$). Meanwhile, although the mean NTI values for all forest strata did not exceed 1, they were positive compared with NRI.

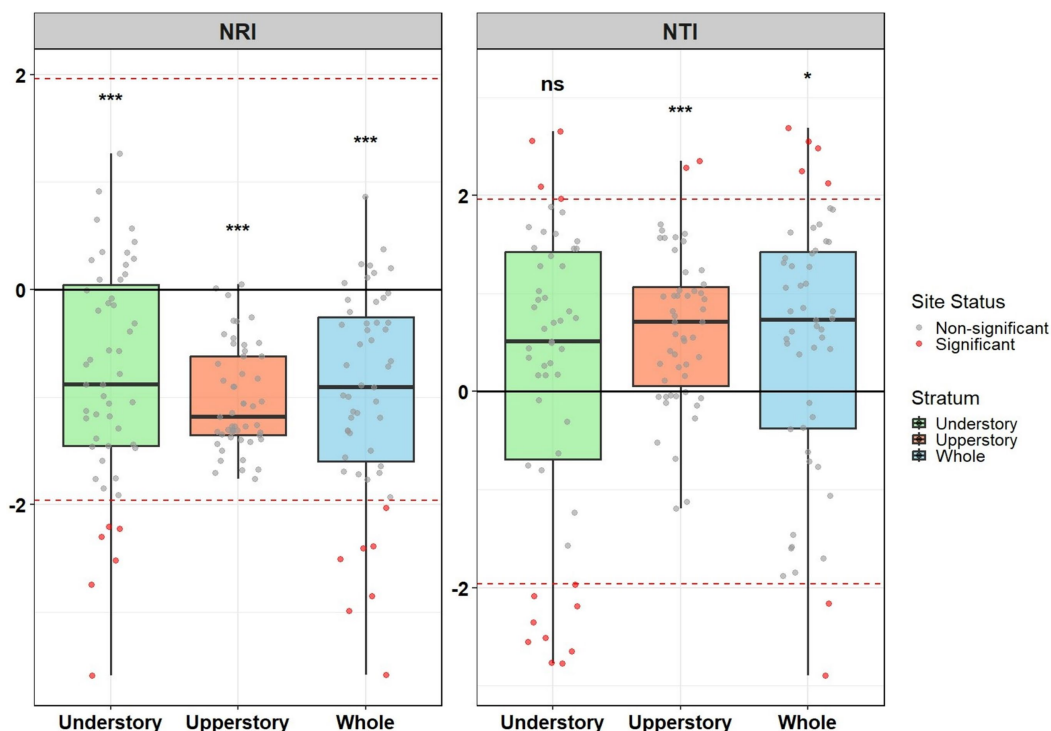


FIGURE 3

Phylogenetic community structure (Net Relatedness Index [NRI] and Nearest Taxon Index [NTI]) across different forest strata in *Picea jezoensis* forests. Boxplots illustrate the distribution of standardized effect size values for the NRI and NTI. Individual survey sites are represented by jittered points, with red points indicating statistically significant departures from the null expectation ($|NRI|$ or $|NTI| > 1.96$, $p < 0.05$) and gray points indicating non-significant values. The solid horizontal line at zero represents the null expectation (random assembly). Dashed red lines indicate the significance thresholds of $+1.96$ (phylogenetic clustering) and -1.96 (phylogenetic overdispersion). Asterisks above the boxplots denote the significance of the median deviation from zero based on the Wilcoxon signed-rank test (*** $p < 0.001$; * $p < 0.05$; ns: not significant).

3.2 Drivers of community assembly mechanisms in *P. Jezoensis* forests

Each forest stratum in the *P. jezoensis* forests was influenced by different factors controlling NRI; whole strata and understory exhibited overall similarity, but differences were observed in some variables (Figure 4). Regarding NRI in the whole strata, SR ($\beta = 0.22$), the CWP dormancy form (G) ($\beta = 0.46$), and MAT ($\beta = 0.50$) had significant positive direct effects, whereas elevation ($\beta = -0.48$) exerted a significant negative direct effect. Furthermore, elevation ($\beta = 0.37$) exerted a significant positive direct effect on the CWP dormancy form (G) (Figure 4a). As for NRI in the upperstory, only slope ($\beta = -0.34$) exerted a significant negative direct effect; slope ($\beta = 0.31$) and MAT ($\beta = 0.44$) had significant positive effects on SR. Additionally, MAT ($\beta = 0.31$) exerted a significant positive direct effect on the CWP disseminule form (D4) (Figure 4b). Regarding NRI in the understory, MAT ($\beta = 0.51$), SR ($\beta = 0.26$), and the CWP dormancy form (G) ($\beta = 0.44$) exerted significant positive direct effects, whereas elevation ($\beta = -0.42$) exerted a significant negative direct effect (Figure 4c). While elevation had a significant positive impact on the CWP dormancy form (G) ($\beta = 0.34$), it exerted a significant negative effect on the CWP disseminule form (D1) ($\beta = -0.29$). Comparison of the relative importance of abiotic and biotic factors based on standardized regression coefficients (β) revealed that abiotic factors tended to make a relatively greater contribution.

In *P. jezoensis* forests, the factors controlling NTI varied across forest strata. In the whole strata, no variable exerted a significant impact on NTI (Figure 5), while rock exposure ($\beta = -0.27$) exerted a significant negative direct impact on the CWP disseminule form (Figure 5a). In the upperstory, elevation ($\beta = 0.34$) and SR ($\beta = 0.45$) had a significant positive direct impact on NTI, whereas the CWP disseminule form (D2) ($\beta = 0.33$) and MAT ($\beta = 0.44$) exerted a significant negative impact on NTI. Additionally, DBH CV ($\beta = 0.34$) exerted a significant positive direct impact on the CWP disseminule form (D2) (Figure 5b). MAT ($\beta = 0.45$) and DBH CV ($\beta = 0.27$) had a significant positive direct effect on SR. As for NTI in the understory, CWP dormancy (Ch) ($\beta = -0.31$) had a significant negative direct effect, and no variables with positive impacts were observed (Figure 5c). MAT exerted a significant negative effect on the CWP disseminule (D2, 4) ($\beta = -0.36$) and dormancy (Ch) ($\beta = -0.58$) form. Similar to the NRI results, comparison of the relative importance of abiotic and biotic factors based on standardized regression coefficients (β) revealed a greater contribution from abiotic factors. Meanwhile, in the understory, only biotic factors exerted significant effects on NTI.

3.3 PBD in *P. Jezoensis* forests

Analysis of the total dissimilarity of *P. jezoensis* forests based on turnover and nestedness revealed that turnover explained most of the total dissimilarity, whereas the contribution of nestedness was relatively lower (Figure 6). These findings confirm

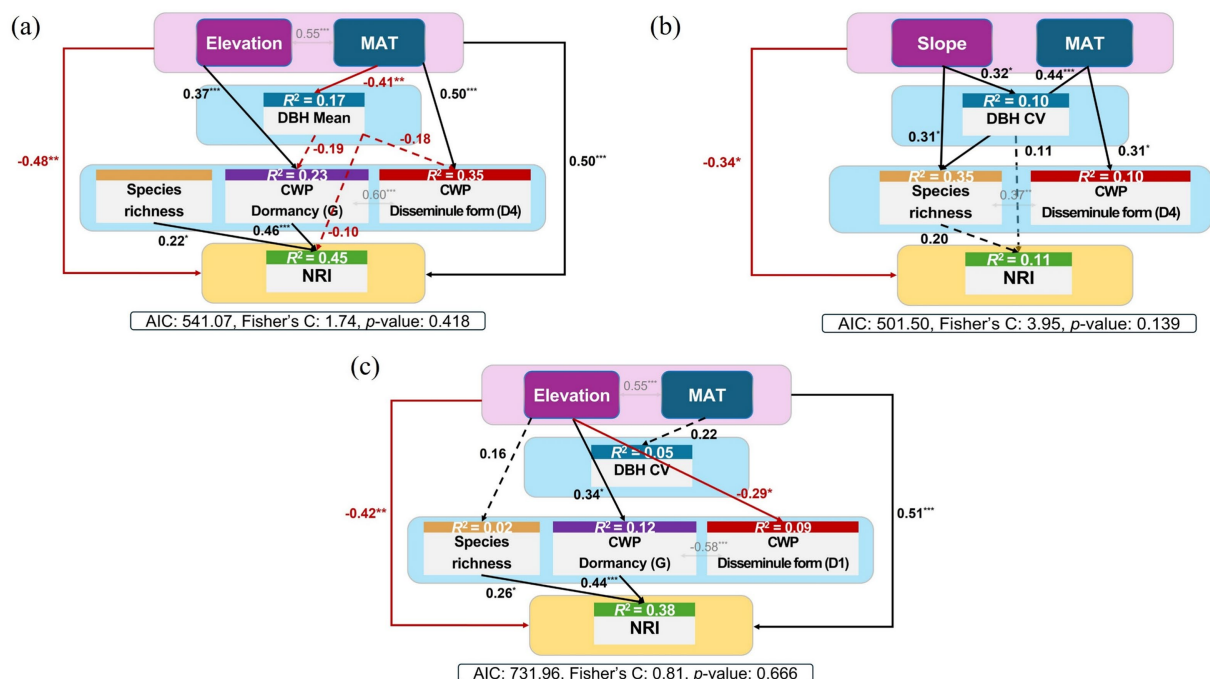


FIGURE 4

Piecewise structural equation models (pSEMs) were employed to test the relationships between biotic and abiotic drivers and the phylogenetic structure (net relatedness index; NRI) within *Picea jezoensis* forests. The models were analyzed separately for three strata: (a) Whole strata, (b) Upperstory, and (c) Understory. For the path diagrams: Black and red arrows represent positive and negative paths, respectively. Gray arrows indicate estimated covariances. Solid arrows denote significant relationships ($p < 0.05$). Dashed arrows denote non-significant relationships ($p > 0.05$). All paths and covariances were reported using standardized coefficients. MAT, Mean annual temperature; DBH CV, Coefficient of variation of diameter at breast height; DBH Mean, Mean diameter at breast height; Dormancy (G), Geophyte; Disseminule form (D1), Disseminated widely by wind or water; Disseminule form (D4), No special modification for dissemination.

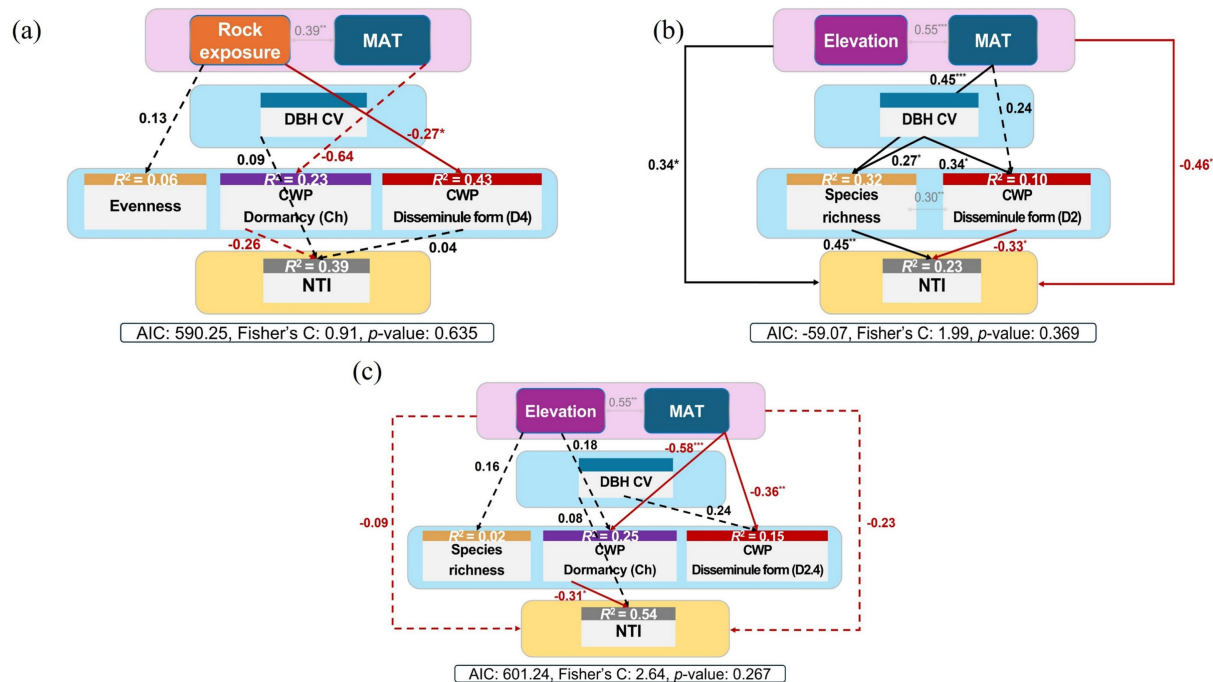


FIGURE 5

Piecewise structural equation models (pSEMs) were employed to test the relationships between biotic and abiotic drivers and the phylogenetic structure (nearest taxon index; NTI) within *Picea jezoensis* forests. The models were analyzed separately for three strata: (a) Whole strata, (b) upperstory, and (c) understory. For the path diagrams: Black and red arrows represent positive and negative paths, respectively. Gray arrows indicate estimated covariances. Solid arrows denote significant relationships ($p < 0.05$). Dashed arrows denote non-significant relationships ($p > 0.05$). All paths and covariances were reported using standardized coefficients. MAT, Mean annual temperature; DBH CV, Coefficient of variation of diameter at breast height. Evenness was quantified using Pielou's index, Dormancy (Ch), Chamaephytes, Dissemimule form (D2,4), Plant with dissemimule forms of both D2 and D4, Dissemimule form (D2), Dissemimule form (D4), Having no special modification for dissemination.

that species composition differences between communities in *P. jezoensis* forests across the Korean Peninsula are chiefly controlled by turnover.

3.4 Relationship between beta diversity components and geographic distance, climatic distance, and elevational differences

Total dissimilarity exhibited significant relationships with all variables used in the analysis (Table 2). Among the variables, climatic distance explained total dissimilarity most effectively, followed by geographic distance and pairwise elevational difference, in that order. As for the turnover factor, climatic distance exhibited the strongest explanatory power, followed by geographic distance; however, no significant relationship with pairwise elevational difference was observed. Nestedness did not exhibit a significant relationship with climatic and geographic distances, but was significantly related to pairwise elevational difference. In the multiple regression model assessing the complex effects of variables such as geographic and climatic distances, as well as pairwise elevational difference, turnover showed relatively greater explanatory power for variation in the dependent variable compared with nestedness (Table 2). Specifically, climatic distance was confirmed to be the strongest variable explaining turnover after controlling for the effects of geographic distance and pairwise elevational difference. Conversely, when controlling for geographic and climatic distances, pairwise elevational difference was the only variable that significantly affected nestedness.

3.5 Partitioning of variance in beta diversity driven by geographic and climatic distances

Geographic and climatic distances explained 41.9% of the variance in PBD (Table 3). These variables explained significantly more variance in the turnover factor than in the nestedness factor of PBD, with the explanatory power for the turnover factor ($R^2 = 31.8\%$) being remarkably higher than that for the nestedness factor. Regarding the unique effects of each variable on the significant models (PBD, turnover), the unique contribution of geographic distance explained 1.9% of PBD variance and 1.4% of turnover variance. Conversely, the unique contribution of climatic distance explained 9.7% of PBD variance and 7.5% of turnover variance, with relatively greater explanatory power than geographic distance. In addition to these unique components, the total effect of climatic distance—encompassing both its unique contribution and spatially structured climatic variation—accounted for a substantial fraction of the explained variance in turnover and PBD patterns. Nestedness did not show a statistically significant relationship with any of the variables.

4 Discussion

This study examined phylogenetic community structure and PBD patterns in *P. jezoensis* forests across the Korean Peninsula and assessed the abiotic and biotic controls underlying these patterns. Our results revealed that the primary drivers of community assembly

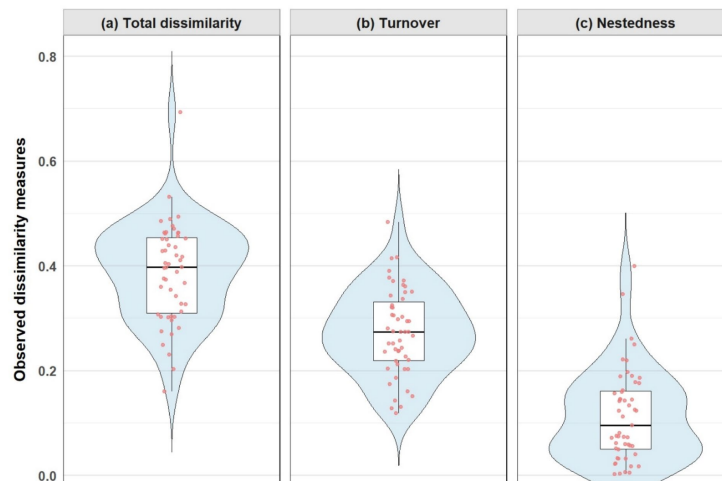


FIGURE 6
(a) Total dissimilarity (b) turnover, and (c) nestedness in *Picea jezoensis* forests.

TABLE 2 Results of simple and multiple regression based on distance matrices, showing the association between beta diversity metrics (total dissimilarity, turnover, and nestedness) and geographic, climatic, and pairwise elevational difference (Elev.diff).

Simple regression based on distance matrices						
Index	Geographical distance		Climatic distance		Elev.diff	
	Coefficients	R^2	Coefficients	R^2	Coefficients	R^2
Total dissimilarity	0.564**	0.318**	0.629**	0.396**	0.336**	0.113**
Turnover	0.493**	0.243**	0.552**	0.304**	−0.050 ^{ns}	0.002 ^{ns}
Nestedness	0.031 ^{ns}	0.001 ^{ns}	0.033 ^{ns}	0.001 ^{ns}	0.406**	0.165**

Multiple regression based on distance matrices				
Index	Geographical distance	Climatic distance	Elev.diff	R^2
Total dissimilarity	0.193**	0.441**	0.141*	0.434**
Turnover	0.216**	0.472**	−0.261**	0.379**
Nestedness	−0.042 ^{ns}	−0.074 ^{ns}	0.441**	0.175**

Standardized regression coefficients and coefficients of determination (R^2) are presented. Statistical significance was tested using a permutation test. ** $p < 0.001$, * $p < 0.05$, ns $p > 0.05$.

TABLE 3 The variance in the beta diversity index and its components explained by the total effect of climatic and geographic distances Model (Total R^2); the total effect of climatic distance, including its unique and spatially structured effects (Climatic); the unique effect of geographic distance (Geographical.unique); and the unique effect of climatic distance (Climatic.unique).

Index	Model (Total R^2)	Climatic	Geographical.unique	Climatic.unique
Total dissimilarity	0.419	0.396	0.019	0.097
Turnover	0.318	0.304	0.014	0.075
Nestedness	−0.001 ^{ns}	0.001 ^{ns}	−0.001 ^{ns}	−0.001 ^{ns}

The coefficient of determination (R^2) was derived from Multiple Regression on distance Matrices (MRM); the models for Total Dissimilarity and Turnover were significant ($p < 0.05$), whereas the model for nestedness was not significant ($p > 0.05$). ns, not significant.

differed depending on the phylogenetic scale (NRI vs. NTI) and across forest strata. Specifically, elevation and MAT were the dominant predictors for NRI across the whole strata and understory. In contrast, NTI-based patterns were more strongly influenced by abiotic (elevation and MAT) factors in the upperstory, while biotic factors (CWP Dormancy Ch) showed a greater contribution in the understory. The beta diversity in *P. jezoensis* communities was dominated by turnover

and was significantly influenced by climatic and geographic distances. In particular, climatic distance exerted a much stronger impact on PBD and turnover than did geographic distance. Conversely, nestedness showed a close relationship with pairwise elevational difference. Variance partitioning corroborated these patterns by showing that climatic distance contributed more uniquely than geographic distance to PBD and turnover, whereas nestedness was not explained by

geographic or climatic distance. Here, we discuss the implications of these main findings and the integrated analysis of PBD and phylogenetic community structure.

4.1 Abiotic and biotic controls of within-community structure in *P. jezoensis* forests

In *P. jezoensis* forests, among abiotic factors, elevation had a negative direct impact on NRI in both the whole strata and understory, whereas MAT exerted a positive direct effect. Their standardized regression coefficients (β) exhibited a higher contribution than most biotic factors. Generally, in resource-abundant and temperate low-elevation environments, competitive exclusion functions as the main mechanism driving community assembly, leading to overdispersion tendencies (Machac et al., 2011; Liang et al., 2023). Furthermore, in environments such as tropical highlands, species from different but ancient lineages in tropical lowlands are expected to adapt independently (niche convergence), resulting in the discovery of species with distant phylogenetic relationships (Qian and Ricklefs, 2016). Research in high-elevation mountains in Northeast Asia reported a tendency for species belonging to a small number of lineages that have successfully adapted to high-elevation environments to cluster together (Liang et al., 2023). Moreover, the mortality of high-altitude dominant species can create open forest gaps and improve light conditions within stands, intensifying interspecific competition and potentially causing overdispersion (Burns and Strauss, 2012; Lee et al., 2024b). Meanwhile, overdispersion should not be interpreted solely as a consequence of competition; it may also arise from historical biogeographic processes and unmeasured niche axes (e.g., microclimate or soils). These factors can define the composition and breadth of the regional species pool and, in turn, shape community composition, generating phylogenetic patterns that extend beyond the explanatory scope of contemporary competition (Ricklefs, 2004; Kraft et al., 2015). Therefore, phylogenetic overdispersion at high elevations should be carefully interpreted. Our results revealed a clear divergence between phylogenetic scales: while NTI remained consistently positive (clustering at the terminal level) across all strata, NRI tended toward negative values (overdispersion at the basal level). This scale-dependent contrast suggests that different assembly processes operate at different evolutionary depths in *P. jezoensis* forests. The findings of the current study regarding NRI do not support the simple competition-based hypothesis often associated with overdispersion. If competition were the main driver of the observed negative NRI, the generally expected increase in SR could be interpreted as a process intensifying competition by adding phylogenetically heterogeneous species. In this case, it can be expected to negatively affect NRI (or NTI). However, in this study, SR exhibited a positive direct effect on both NRI and NTI. This suggests that the negative NRI values are not a result of active competition, but rather reflect a wide phylogenetic species pool composed of distantly related ancient lineages that have coexisted through historical biogeographic assembly. In this sense, basal-scale overdispersion (negative NRI) can be viewed as a signature of the broad evolutionary breadth of the regional flora—i.e., communities drawing species from multiple deep lineages shaped by long-term biogeographic assembly—rather than a signal attributable to a single contemporary interaction mechanism. In contrast, the consistently positive NTI across all forest strata reflects that strong environmental filtering acts more intensely on terminal clades, selecting closely related species that share

conserved physiological traits—such as cold tolerance—required for subalpine environments.

It can be assumed that the process of increasing species numbers within a specific community strengthens local clustering through the influx of phylogenetically closely related species adapted to that environment, rather than through the influx of heterogeneous species (i.e., inducing competition). This implies that an increase in species occurred through the addition of species within a specific clade adapted to *P. jezoensis* forests, not through random immigration. In other words, a strong environmental filter already shaped a phylogenetically biased species pool at the terminal scale, and this effect appears to intensify as SR increases. This pattern is consistent with the assembly theory, which explains the phylogenetic structure of communities based on environmental filtering and niche conservatism (Webb et al., 2002; Wiens and Graham, 2005; Cavender-Bares et al., 2009; Mayfield and Levine, 2010). Additionally, considering the dynamic characteristics of the target area, where recent withering of coniferous trees and structural changes are ongoing, such environmental variability may also be related to the selective survival and establishment of a specific clade.

The biotic factor, CWP dormancy form (G; geophytes), exerted a positive impact on the NRI in the whole strata and understory through elevation. Previous studies have reported that geophytes are mainly distributed in environments characterized by lower average temperatures and precipitation and greater seasonal temperature variability (Raunkiaer, 1934; Evans et al., 2014; Howard et al., 2019). Furthermore, by eliminating their aboveground parts under unfavorable conditions and persisting through dormancy and resource storage in their subterranean perennial organs, geophytes can continue surviving even in highly variable cold and dry environments (Howard et al., 2019). Especially, by protecting perennating buds and stored reserves belowground, geophytes can avoid freezing damage and rapidly regrow after snowmelt under short growing seasons, linking their dominance to cold/seasonality-driven constraints (Howard et al., 2019). On this basis, the interplay between altitude (as a top-level environmental filter) and trait-level responses (geophyte dominance) potentially strengthens the phylogenetic clustering of understory communities, indicating that abiotic constraints and functional traits jointly shape community assembly. This finding is similar to the results of a global-scale analysis, which show that geophyte dominance is pronounced in cold and dry climates with high temperature variability (Howard et al., 2019). Furthermore, the fact that the same trait also positively influenced NRI in the whole strata supports a hierarchical assembly process, in which enhanced geophyte dominance and phylogenetic structure in the understory contribute to phylogenetic clustering patterns in the whole strata. Thus, the reinforcement of local clustering by elevation gradients, alongside phylogenetically conserved functional traits, supports the hypothesis that high-elevation communities assemble based on ecological niches (Wiens and Graham, 2005) and extends our understanding by suggesting that species-specific growth features control community assembly mechanisms.

Meanwhile, the average NTI value, reflecting the phylogenetic structure at the fine-scale within communities, consistently showed positive values across all forest strata, indicating that clustering patterns composed of phylogenetically similar species predominate throughout *P. jezoensis* forests. Regarding environmental factors influencing NTI, the controlling factors differed distinctly between the upperstory and understory. In the upperstory, elevation positively

influenced NTI but negatively influenced MAT, indicating that phylogenetic clustering tendencies within the woody community are strengthened at higher elevations and lower temperatures. In other words, *P. jezoensis* forests in the study area can be interpreted as exhibiting phylogenetic clustering overall, with environmental filtering enhancing phylogenetic clustering in the upperstory community under high-elevation and low-temperature conditions. This pattern was similar to the findings of previous studies reporting phylogenetic clustering of woody plants under strong environmental filtering (e.g., climate and elevation) in the high-elevation forests of Northeast Asia (Luo et al., 2023; Li et al., 2025; Lee et al., 2025b). Among biotic factors, the CWP disseminule form (D2; dispersion by animals and humans) negatively influenced NTI in the upperstory. This suggests that animal- and human-dispersed species weaken clustering among allied species. However, judging the impact on species undergoing establishment and regeneration, such as those in the upperstory, is challenging. Thus, further research is required to clarify the relevant specific mechanisms. Unlike in the upperstory, only biotic factors significantly influenced NTI in the understory. The CWP dormancy form (Ch; chamaephytes) had a negative indirect effect on NTI via MAT. Chamaephytes are low-growing plants with perennating buds near the ground surface. They are known to adapt to cold, dry conditions with high climate variability by utilizing the buffering effects of soil and snow cover (Ellenberg and Mueller-Dombois, 1974; Körner, 2003). Considering these ecological features, as MAT decreases, the relative dominance of species with this life form may increase (CWP Ch increases). Given these adaptive advantages, this life form may have arisen repeatedly across different lineages; consequently, species sharing it may co-occur without being each other's closest relatives. This negative effect on NTI may partially offset the prevalent tip-level clustering (NTI) observed across the study plots. This finding is consistent with existing knowledge that chamaephytes are a life form well adapted to dominate in cold highland conditions (Körner, 2003); it also suggests that the harsher the environment, the more particular functional features are favored. Meanwhile, since these features are not limited to a single lineage but are shared across diverse clades, the dominance of functional types can instead cause phylogenetic overdispersion. As such, when discussing community formation processes, consideration of plant functional traits such as dormancy and disseminule forms, along with phylogenetic indicators, provides important clues for understanding which species with particular traits are selected to dominate within communities along altitude and climate gradients, and how this process reorganizes phylogenetic structure (NRI and NTI) within the community.

Our results show that the dominance of specific functional traits (CWP) acts as a primary biotic driver, generating divergent phylogenetic signals between basal (NRI) and terminal (NTI) scales. Specifically, when trait dominance reflects phylogenetically conserved features, it can strengthen similarity among deep lineages, yielding a positive influence on the phylogenetic structure at deeper levels (Kraft et al., 2007; Cavender-Bares et al., 2009). In contrast, when the same functional features are acquired convergently across multiple clades, functionally similar but phylogenetically distant species can co-occur, producing a negative impact and promoting overdispersion at the terminal scale (Wiens and Graham, 2005; Kraft et al., 2007). These trait-phylogeny linkages suggest that, in the southern-range-margin *P. jezoensis* stands, community reorganization under climate change may not follow a single directional trajectory, underscoring the

importance of tracking CWP-based functional dominance together with phylogenetic structure within an adaptive conservation and management framework. In particular, the intensification of CWP dominance alongside phylogenetic reorganization at higher elevations suggests that community assembly is a multi-process outcome resulting from the convergence of environmental filtering and functional trait selection in cold, highly variable environments. However, these patterns alone provide limited basis for forecasting whether warming will strengthen filtering (e.g., by favoring drought/heat-tolerant lineages) or relax it via reduced cold stress; further tests are needed to determine how shifts in climatic drivers reshape the coupling between CWP dominance and phylogenetic structure.

4.2 Drivers of *P. jezoensis* PBD across climatic and geographic distance, and elevational difference

Among the two factors constituting the PBD of *P. jezoensis* forests across the South Korea and northeastern China, turnover was the primary contributor and was closely related to climatic distance. Notably, after controlling for climatic effects, the unique explanatory power of geographic distance was significantly diminished. Furthermore, the influence of climatic distance remained high even after controlling for pairwise elevational differences and geographic distance. Specifically, the strong effect of climatic distance, even after accounting for geographic distance, is more consistent with climate-associated lineage replacement (i.e., niche-based species sorting along climatic gradients) than with dispersal limitation. This interpretation points to a climate-driven sorting process, whereby community differentiation tracks species-specific responses to climatic regimes rather than spatial proximity alone (Cavender-Bares et al., 2009). This pattern is similar to findings from research on coniferous forests in China's Baima Snow Mountain, where species turnover along an altitude gradient was better explained by environmental factors (e.g., temperature and moisture) than by spatial distance (Yang et al., 2016), supporting the interpretation that beta diversity is primarily driven by environmental filtering. Furthermore, studies on Chinese angiosperms reported that taxonomic beta diversity and PBD were primarily explained by climatic gradients (Qian et al., 2020), suggesting that the patterns observed in the current study are similar to these findings at a broader spatial scale.

Nestedness did not correlate with geographic and climatic distances, but was significantly related to pairwise elevational differences. These results suggest that while the broad-scale latitudinal gradient in *P. jezoensis* forests across the South Korea and northeastern China mainly influences PBD patterns through species turnover, the elevation gradient within mountains is more closely involved in creating subset structures through the selective loss or persistence of specific clades and functional types. Meanwhile, at the continental scale, nestedness is reportedly closely related to extinction and subsequent resettlement processes driven by past climate history, such as glacial cover during the last glacial period. In particular, higher-latitude regions covered by glaciers until recently tend to show a greater relative contribution of the nestedness component to beta diversity (Dobrovolski et al., 2012). In this context, the observed nestedness-elevational-difference relationship in *P. jezoensis* forests across South Korea and northeastern China can be inferred to reflect a process in which intensified environmental constraints (e.g., cold temperatures

and prolonged snowfall) associated with larger between-site differences in elevational range induce selective loss of certain clades, resulting in high-elevation communities being organized as subsets of low-elevation communities. Notably, this nestedness–elevational-difference relationship exhibited different patterns across tree species, even within the same subalpine coniferous forests on the South Korea. Lee et al. (2025b) studied *Abies koreana* and found that the main component of beta diversity was turnover, consistent with the findings of the current study. However, they found that nestedness showed a significant positive correlation with geographic distance. Considering that the study sites were distributed within a limited latitudinal range in the southern part of South Korea and northeastern China, the authors interpreted nestedness–geographic distance as the result of cumulative local environmental differences and disturbance factors (e.g., competition due to habitat structure differences between mountains and invasive plants) that increase with distance, thereby reinforcing the subset structure rather than reflecting a simple distance effect. Comparing these results with those from *P. jezoensis* forests suggests species-specific spatial controls of nestedness within subalpine conifer forests, with geographic distance being more relevant for *A. koreana* and elevational differences for *P. jezoensis*. Specifically, this contrast suggests that the spatial gradient most closely linked to nestedness may differ between the two species within subalpine conifer forests. Since *P. jezoensis*—a relatively tall upperstory conifer—tends to occupy relatively isolated high-elevation habitats, its nestedness may be more responsive to elevational differences that intensify climatic and physiological constraints than to geographic distance. In contrast, for *A. koreana*, between-mountain separation may better reflect constraints on dispersal and establishment, together with the accumulation of site-specific disturbance pressures, thereby reinforcing subset structures independently of the vertical gradient (Lee et al., 2025b). Overall, this comparison underscores that the two species may follow distinct assembly pathways, reflecting differences in habitat range, disturbance exposure, and regional species-pool structure.

4.3 Integrating within- and among-community metrics to elucidate community assembly mechanisms

This section, we integrate phylogenetic community structure (NRI/NTI) with PBD (turnover and nestedness) to clarify how site-level assembly signals propagate to broader-scale phylogenetic differentiation among communities. This combined perspective provides a more nuanced view of community assembly than any single metric alone, because it connects within-community phylogenetic organization to between-community compositional divergence across environmental space (Fine and Kembel, 2011; Lee et al., 2025b).

First, nestedness can be interpreted as a spatial consequence of elevation-linked environmental filtering. Nestedness was unrelated to geographic and climatic distances but covaried with pairwise elevational differences, suggesting that within-mountain elevational contrasts are particularly important for generating subset patterns. Importantly, our within-community results provide a mechanistic bridge for this pattern. In the pSEM, elevation altered functional composition by increasing the dominance of stress-tolerant dormancy types (e.g., geophytes), and this trait shift was associated with stronger phylogenetic structure at the basal scale (NRI). This linkage implies that as elevational

contrasts among sites increase, high-elevation communities are more likely to retain a restricted set of clades and life-form strategies that can persist under colder and more seasonal conditions, thereby forming phylogenetically filtered subsets relative to lower elevations. In other words, the same elevational driver that reorganizes functional dominance and within-community phylogenetic structure locally can manifest spatially as nestedness when communities are compared across increasingly different elevational settings. Second, turnover was most closely associated with climatic distance, suggesting deterministic niche-based sorting across climatic gradients. In contrast to nestedness, turnover tracked climatic distance, consistent with deterministic differences in assembly conditions among sites along climate gradients. When interpreted alongside the within-community results, this suggests that local community structure is not arranged randomly: temperature-related constraints (e.g., MAT) and associated shifts in functional composition (including cold-adapted life forms such as chamaephytes and other CWP components) restructure phylogenetic relatedness at different evolutionary depths (NRI vs. NTI). As climatic divergence among sites increases, these site-specific assembly outcomes become increasingly distinct, and the among-community consequence is greater lineage replacement—i.e., phylogenetic turnover—rather than simple subset formation. Thus, turnover can be interpreted as the spatial outcome of repeated, climate-contingent local assembly that produces different phylogenetic compositions across regions.

Taken together, our results support a hierarchical linkage across scales, in which local within-community assembly signatures (CWP-based life-form dominance and NRI/NTI) extend to regional among-community phylogenetic differentiation (PBD): abiotic gradients (elevation and temperature) reshape CWP-based life-form dominance and within-community phylogenetic structure (NRI/NTI), and as these locally structured communities are distributed across environmental space, they generate distinct PBD components—nestedness where elevational contrasts favor subset formation, and turnover where climatic divergence favors lineage replacement. This integrated interpretation clarifies how local assembly signatures propagate to regional phylogenetic differentiation in *P. jezoensis* forests.

5 Conclusion

This study assessed subalpine *P. jezoensis* forests across the South Korea and northeastern China, utilized abiotic and biotic factors to identify the controlling factors driving compositional differences within and between communities. Furthermore, it sought to clarify the insights that an integrated analysis of these two indicators provides for understanding community formation mechanisms. The results confirmed that the influence of abiotic and biotic factors on community internal structure (NRI and NTI) varied depending on forest strata and internal indicators. These findings emphasize the importance of analyzing each forest stratum separately when clarifying community assembly mechanisms, as the formation mechanisms of plant species constituting communities differ across forest strata. Additionally, this study quantified the biotic factors—dormancy and disseminule forms—through the CWP index. By elucidating the direct and indirect effects of CWP-based life-form composition

(dormancy and dispersal forms) on within-community phylogenetic structure in relation to abiotic factors, this study deepens our understanding of community formation mechanisms. Future research on functional trait analyses will enhance the understanding of the factors driving dynamic community responses to environmental change. Meanwhile, separating PBD into turnover and nestedness and analyzing the relationships with climatic and geographic distances, as well as pairwise elevational difference, revealed that turnover was predominantly influenced by climatic distance, further supporting the fact that *P. jezoensis* forests across the South Korea and northeastern China were controlled by environmental filtering. Additionally, we expanded our understanding of community formation mechanisms by analyzing both within- and between-community indicators together. Such an integrated approach illustrates how local-scale assembly processes scale up to drive regional-scale differentiation, providing refined insights into community assembly mechanisms.

Although our study was not designed as an applied management assessment, the assembly signatures identified here provide a transferable framework for conserving climate-sensitive subalpine forests—especially at range margins—using southern-range *P. jezoensis* forests as a case study. Because turnover dominated PBD and was most strongly associated with climatic distance, ongoing climate change may promote continued lineage and species replacement among regions. This pattern suggests that conservation planning may benefit from securing a network of sites that represents climatic heterogeneity across the landscape, rather than concentrating protection within a narrow climate band. In contrast, the elevational sensitivity of nestedness implies that communities at higher elevations may increasingly function as filtered subsets under intensifying environmental constraints, highlighting the value of protecting elevational microrefugia and maintaining within-mountain habitat continuity. Moreover, stratum-specific controls of phylogenetic structure indicate that upperstory and understorey may require stratified monitoring approaches, emphasizing the need for stratum-resolved tracking of community restructuring. Taken together, our results suggest that management discussions in climate-sensitive subalpine forests should consider both regional-scale climate-driven compositional turnover and within-landscape community restructuring along key environmental gradients, with attention to habitat continuity and microrefugia.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

S-JL: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. A-RJ: Investigation,

Writing – review & editing. S-RL: Investigation, Writing – review & editing. D-BS: Data curation, Investigation, Resources, Writing – review & editing. Y-EK: Investigation, Writing – review & editing. J-GB: Data curation, Funding acquisition, Investigation, Project administration, Resources, Writing – review & editing, Supervision. S-HO: Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that Generative AI was not used in the creation of this manuscript.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1795519/full#supplementary-material>

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