**Differential responses of forest strata species richness to paleoclimate and forest structure**

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**Abstract**

Regional factors, such as historical and contemporary climate conditions, and local factors, such as vegetation structural attributes, can influence current patterns of plant species richness but their relative roles remain unknown, particularly across forest strata. Here, we used a multi-scale survey of temperate forest plots across a large region of Northeast China to explore the relative importance of environmental factors (paleoclimate, contemporary climate, topography and anthropogenic disturbance) and forest structural attributes (stem abundance, stand basal area and tree size variation) on tree, shrub, and herb species richness. Although environmental and forest structural factors all played a role in explaining plant species richness patterns, their relative roles varied in direction and magnitude depending on forest stratum. Tree species richness increased with the magnitude of change in temperature since the Last Glacial Maximum (Anomaly$_{MAT}$) but declined with increasing magnitude of change in precipitation (Anomaly$_{MAP}$). By contrast, herb species richness declined with increasing Anomaly$_{MAT}$ but increased with Anomaly$_{MAP}$, highlighting contrasting processes for tree and herb species richness driven by paleoclimate. Contemporary climate played a lesser role in explaining species richness, but tree species richness increased with diurnal temperature range, shrub species richness increased with the climatic moisture index, and herb species richness increased with both climatic variables. Herb species richness also increased with disturbance intensity, whereas tree and shrub richness declined. Overall, plant species richness increased significantly with all forest structural attributes, except for stem abundance, which had a negative effect on herb species richness, and forest structure mediated the linkages between plant species richness and disturbance or climate. The pronounced influence of paleoclimate on forest plant species richness highlights the potential threat of current climate change for forest diversity. Together, simultaneous consideration of past and current climate as well as forest structural attributes could improve our understanding of the complex mechanisms shaping patterns of plant species richness across forest strata.

## 1. Introduction

Understanding current patterns of plant species richness and their underlying mechanisms and drivers are increasingly important due to the loss of biodiversity driven by anthropogenic activities (Hawkins et al., 2003; Hooper et al., 2012; Svenning et al., 2015). Although many potential factors can influence plant diversity patterns, climate is considered to be the primary driver determining the patterns of plant species richness (O'Brien, 1993; Francis and Currie, 2003). Many studies have examined the influences of climatic factors (past and contemporary conditions) on geographic patterns of species richness across a wide range of spatial scales (Kreft and Jetz, 2007; Feng et al., 2014; Irl et al., 2015; Keil and Chase, 2019; Zuloaga et al., 2019), but the results are highly variable. Discrepancies among studies could arise because current patterns of plant richness can be in part the result of a network of locally interacting individuals (Michalet et al., 2015), which are also influenced by forest stand structure (the size and number of individuals; Chu et al., 2019), and forest structural attributes are also closely related to climatic factors (Hakkenberg et al., 2016; Chu et al., 2019). However, the effects of regional (climate) and local (stand structure attributes) factors on plant species richness are generally studied separately. Hence, we do not know how and whether climate factors and stand structural attributes interact to drive plant species richness patterns, particularly across forest strata.

The influential role of past and current climatic factors as key determinants of plant species richness has been widely recognized (Wang et al., 2009; Svenning et al., 2015). Specifically, contemporary climate variables such as temperature and precipitation are generally recognized as the main drivers of geographic patterns of forest diversity (Ammer, 2019), but the effects of these factors vary even within the same regions (Eiserhardt et al., 2011). For example, growing season temperature is the most important factor shaping plant species distributions in northeast Asia (Wang et al., 2009), whereas precipitation plays a major role in Inner Asia (Liu et al., 2018) and North America (Harrison et al., 2006; Zhang et al., 2014). Besides current climate, paleoclimate can also have long-lasting influences on the patterns of species diversity (Bruelheide et al., 2018) by determining refugia, colonization, migration, and extinction (Svenning and Skov, 2007b; Jimenez-Alfaro et al., 2018; Guo et al., 2020). For instance, in temperate forests, the Last Glacial Maximum (LGM) had a measurable imprint for understanding current tree species richness (Svenning and Skov, 2007b), whereas both the LGM and current climate influenced understory herb species richness (Jiménez-Alfaro et al. 2018). The divergent responses of different plant forms to climatic factors are attributable to their distinct ecological niches, climate tolerances and dispersal abilities (Ordonez and Svenning, 2017). Thus, understanding the response of plant species to climatic factors is of vital importance both for conserving

and predicting the changes of forest diversity to future climate changes (Sommer et al., 2010; Harrison et al., 2020). However, very few studies have examined the relative contribution of paleoclimate and contemporary climate across different forest strata (e.g. trees, shrubs, and herbs), even though the strata may be formed by species with different biogeographical histories within a single forest ecosystem (Xu et al., 2019b).

In addition to past and current climate, topography (e.g., elevation, slope, and aspect) and anthropogenic disturbance play important roles in shaping patterns of forest species diversity. Topographic factors are important and easily measured abiotic variables influencing species diversity (Liu et al., 2014; Irl et al., 2015). Topography not only directly influences the distribution of plant species but also drives variation in microclimate, which in turn affects forest species diversity (Jucker et al., 2018). There is increasing evidence that elevation, as a key topographic variable, has a substantial effect on species diversity across different forest strata, but the associated mechanisms are still under debate (Costa et al., 2005). For example, some studies have found a hump-shaped pattern of plant species richness across elevational gradients (Colwell and Hurtt, 1994), but negative (Bachman et al., 2004) or positive patterns (Bruun et al., 2006) were also reported. In addition, other topographic variables such as slope and aspect may have stronger effects on understory richness (e.g., shrub and herb) than on overstory tree species (Murphy et al., 2015). Anthropogenic disturbance (e.g., logging) plays an important role in shaping plant species diversity by creating gaps that alter light availability and soil fertility, and increase the heterogeneity of forest structure (Thom and Seidl, 2016; Danneyrolles et al., 2019). According to the intermediate disturbance hypothesis (IDH), higher species diversity is found at intermediate disturbance intensity (Connell, 1978) but this is still debated. For example, there is some support for the IDH in forest ecosystems (Biswas and Mallik, 2010), but other studies show that species diversity does not always follow the expected patterns of the IDH and instead shows increasing or decreasing trends (Thom and Seidl, 2016) depending on disturbance type, frequency and severity, or differences across forest strata.

Forest ecosystems are often structurally developed and multilayered, therefore, stand structure mirrors environmental conditions (topography and soil condition) as well as local plant interactions (Cook, 2015). Stand structural attributes (tree size variation, stem abundance and stand basal area) have been proposed to explain the variation of plant species richness (Chu et al., 2019) by altering resource availability and utilization (Hakkenberg et al., 2016). However the influence of different structural attributes on species diversity may vary depending on forest stratum (Cook, 2015; Chu et al., 2019). Specifically, a greater number

of individual trees (i.e., higher stem abundance) is expected to result in greater species diversity (Srivastava and Lawton, 1998; Kaspari et al., 2000; Evans et al., 2006), but a higher proportion of large individuals may suppress species richness due to competition for resources (e.g., light, water and nutrients; Craine et al., 2013; Hakkenberg et al., 2016). Similarly, greater stand basal area, which is inseparable from stem abundance, may be a result of either many smaller stems or fewer larger individuals, and either case could lead to declining species richness through competition for resources. In addition, tree size variation could enhance species richness by creating more ecological niches (Terborgh, 1985) but also reduce species richness due to size-asymmetric competition for resources (Hakkenberg et al., 2016).

Here, we investigate the direct and indirect effects of environmental variables (paleoclimate, contemporary climate, topography, and disturbance) and forest structural attributes (stem abundance, stand basal area and tree size variation) on plant species richness across forest strata (Figure 1). Using a unique dataset compiled from 801 temperate forest plots sampled in Northeast China, we aimed to explore the influences of environmental factors and forest structural attributes in explaining patterns of plant species richness across forest strata. Specifically, we addressed the following two main questions: 1) What are the direct and indirect pathways by which environmental factors influence variation in plant species richness across forest strata? Here, we hypothesized that environmental factors influence plant richness both directly and indirectly by shaping forest structural attributes, but the strength of the effects would vary depending on forest stratum. 2) How do forest structural attributes explain plant species richness across forest strata? Here, we hypothesized that greater forest structural diversity would create more niches, thus enhancing resource use complementarity and promoting plant species richness.

## 2. Materials and methods

### 2.1 Study area

This study was conducted in the greater Changbai Mountain area (39.9º - 48.1º N, 122.6º - 133.9º E) in northeast China, spanning Heilongjiang, Jilin and Liaoning provinces (Figure 1). The study area encompasses c. 40,0000 km$^2$ and has a temperate continental climate. The annual mean temperature is approximately 7 °C and annual precipitation is 600-1000 mm, which mainly falls between June and September. The most important forest type in northeast China is Broadleaved-Korean pine (*Pinus koraiensis*) mixed forest. The main tree species at our study sites were *Pinus koraiensis*, *Tilia amurensis*, *Quercus mongolica* and *Fraxinus mandshurica;* the main shrub species were *Rhododendron aureum, Lonicera japonica, Philadelphus*

*schrenkii, Ribes andshuricum* and *Corylus mandshurica;* and the main herb species were *Arisaema heterophyllum, Brachybotrys paridiformis* and *Cardamine leucantha.*

## 2.2 Vegetation sampling

We compiled data from 801 standardized plots of 900 $m^2$ each (30 m $\times$ 30 m; Figure 1), which were established and surveyed in July-August from 2008 to 2012. In each plot, trees with a diameter at breast height (DBH) ≥ 1 cm were identified, tagged and measured for DBH. We divided each 900 $m^2$ plot into 36 subplots (5 m $\times$ 5 m), and randomly selected 10 subplots to record shrub species abundances. To survey herbaceous species, we set up one micro-plot (1 m $\times$ 1 m) within each of the ten subplots. In total, 1162 species were recorded across the 801 plots, including 109 tree species, 123 shrub species and 930 herb species. Additionally, we recorded topographical data using the longitude and latitude obtained by GPS in the center of each 30 m $\times$ 30 m plot. Plant nomenclature followed the plant list (www.theplantlist.org/) in the *plantlist* package (Zhang, 2018).

## 2.3 Quantification of environmental factors

The contemporary climate data for each plot was extracted from the CRU TS4.03 database with 0.5º spatial resolution (Harris et al., 2020). The mean annual values of seven climate variables in each plot were calculated based on monthly data from 1901 to 2012: potential evapotranspiration (PET, mm day$^{-1}$), mean annual precipitation (MAP, mm), diurnal temperature range (DTR, °C), monthly average daily minimum temperature (Tmin, °C), monthly average daily maximum temperature (Tmax, °C), daily mean temperature (Tmean, °C) and wet day frequency (WET, days). We then calculated the climatic moisture index (CMI) as the difference between mean annual precipitation and potential evapotranspiration (Table S1).

For paleoclimate, we first extracted Last Glacial Maximum (LGM) annual temperature and precipitation from WorldClim (www.worldclim.org). The LGM data was obtained for two scenarios: the Community Climate System Model version 3 (CCSM3) and the Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2). Then, we calculated two variables representing temperature anomaly (Anomaly$_{MAT}$) and precipitation anomaly (Anomaly$_{MAP}$) based on contemporary annual means minus LGM annual means. We also calculated the annual velocity of change in temperature and precipitation (Velocity$_{MAT}$ and Velocity$_{MAP}$) from the LGM to present (Loarie et al., 2009; Sandel et al., 2011). Contemporary climate variables were processed in R (R Development Core Team, 2019), while paleoclimate and topography variables were

processed in ArcMap 10.2. (Environmental Systems Research Institute, West Redlands, CA). A digital elevation model of 30 m $\times$ 30 m grid size was used to extract topographical variables, namely elevation, slope, and aspect. The aspect data were split into two components: northness = cos(aspect) and eastness = sin(aspect) (Hirzel et al., 2002). Disturbance severity was recorded at each plot as three disturbance intensity levels, 1) low, comprising primary forests with no or slight signs of human activity; 2) medium, comprising secondary forests with obvious traces of anthropogenic disturbance; and 3) high, comprising secondary damaged forests with strong and continuous anthropogenic disturbance. We then treated disturbance levels as numerical variables (coded as 1, 2 and 3) for further analyses (see classification details in supporting information Table S2).

## 2.4 Quantification of forest structural attributes

In each plot, we calculated three forest structural attributes: stem abundance (SA, total number of stems), tree size variation (TSV, coefficient of variation of tree DBH, calculated as the standard deviation/mean) and stand basal area (SBA, the sum of stem basal area). The summary information for all variables is given in Table S1.

## 2.5 Statistical analyses

Prior to statistical analysis, we limited collinearity issues among environmental variables by removing variables with a variance inflation factor > 5 (Supporting Information Table S3). Thirteen variables were retained for analysis, including two contemporary climate variables (CMI and DTR), four paleoclimate variables (Anomaly$_{MAT}$, Anomaly$_{MAP}$, Velocity$_{MAT}$ and Velocity$_{MAP}$), three topographical variables (altitude, slope and aspect), disturbance level, and three forest structural variables (SBA, TSV and SA). Subsequently, we explored the relative influence of the 13 variables as potential predictors of plant species richness using separate multiple linear regression models for tree, shrub and herb richness, we then calculated the relative importance of predictors, which is expressed as the ratio between the standardized regression coefficient of a given predictor and the sum of all standardized regression coefficients of all predictors. To complement the multiple linear regression models, in which the most important variables were identified, we also used subset regression analysis and selected the optimal model using the lowest Akaike Information Criterion (AICc) value (Burnham and Anderson, 2004). We used $\Delta$AICc = 2 as the cutoff point to determine whether a subset was a better fit to the data, and then selected the most parsimonious subset (lowest number of the

explanatory variables) in the full model (Table S4; Burnham and Anderson, 2004; Bartoń, 2016) via the *dredge* function in the *MuMIn* package (Bartoń, 2016).

We used the significant explanatory variables selected by multiple linear regression and subset regression analysis to construct structural equation models (SEMs) to quantify the direct and indirect effects of environmental factors and forest structural attributes on plant species richness across forest strata (Figure 2). Specifically, we calculated the direct, indirect, and total effects of predictors on response variables through mediators. Before conducting the SEM analysis, we used generalized least squares (GLS) models to check residual spatial autocorrelation, and found no strong spatial autocorrelation amongst tested variables (Supporting Information Table S5). We then constructed individual SEMs for tree, shrub and herb species richness, and evaluated each model fit using multiple statistical indices: traditional Chi-square ($\chi^2$) test (with $P > 0.05$), the comparative fit index (CFI) and the standardized root mean square residual (SRMR) index (Malaeb et al., 2000; Rosseel, 2012). To better interpret the SEM results, we performed Pearson's correlations and assessed bivariate relationships (simple linear regression) between variables according to our hypothesized paths in the conceptual model (Supporting Information Figures S1-S4). Prior to all analysis, all numerical variables were standardized (Z-transformation) and the SEM analyses were done using the *lavaan* package in R (Rosseel, 2012; R Development Core Team, 2019).

## 3. Results

### 3.1. Drivers of plant species richness

Multiple linear regression revealed that two forest structural attributes were important explanatory factors for plant species richness: tree, shrub and herb species richness increased with tree size variation (Figure 3; Table S4) and whereas both tree and shrub species richness increased with stem abundance (Figure 3a,b), herb species richness declined with increasing stem abundance (Figure 3c). For paleoclimate variables, Anomaly$_{MAP}$ and Anomaly$_{MAT}$ were significant predictors of forest plant species richness, but the relationships varied among strata. Tree species richness declined with Anomaly$_{MAP}$ whereas herb species richness increased (Figure 3a,c). Conversely, herb species richness declined with Anomaly$_{MAT}$ (Figure 3c), but tree and shrub richness increased (Figure 3a,b). Plant species richness was not related to either Velocity$_{MAT}$ or Velocity$_{MAP}$ (Figure 3). For current climate, both DTR and CMI were important predictors of plant species richness. Tree and herb species richness both increased with DTR (Figure 3a,c) but there was no relationship for shrub richness. However, shrub and herb species richness increased with CMI (Figure 3b,c) but tree

species richness was not related to CMI. Among the topographical variables, only altitude had any explanatory power, whereby shrub species richness declined with altitude (Figure 3b). The relationships between plant species richness and disturbance intensity also varied among strata, whereby tree and shrub species richness declined with increasing disturbance (Figure 3a,b), but herb species richness increased (Figure 3c). Finally, there was a positive association between herb species richness and shrub species richness (Figure 3c), but neither were related to tree species richness. Forest structural attributes explained 16% on average (range: 14-20%) of the variation in plant species richness, and the percentage of variance explained was highest for herb species richness (Figure 3c). Paleoclimate factors explained on average 16% (range: 13%–21%) of the variation in plant species richness, and the percentage of explained variance was higher for shrub species richness (Figure 3b). Finally, disturbance explained 23%, 18% and 14% of the variation in tree, shrub and herb species richness, respectively (Figure 3).

*3.2. Interactive effects of main drivers on plant species richness*

As multiple linear regression only reveals the direct relationships between plant species richness and potential explanatory variables, we used structural equation models (SEMs) to explore interactions between explanatory variables and their relationships with plant species richness (Figures 4 and 5). The best-fit SEMs explained 26%, 11% and 14% of the total variation in tree, shrub and herb species richness, respectively. Overall, plant species richness increased with tree size variation (Figure 4; Tables S6-S8) and the relationship was strongest in herbs (Figure 4c). Tree and shrub species richness also increased with increasing stem abundance (Figure 4a,b), whereas herb species richness declined (Figure 4c). The relationships between plant species richness and paleoclimate variables differed among strata, whereby tree species richness increased with Anomaly$_{MAT}$ but declined with Anomaly$_{MAP}$, whereas herb species richness declined with Anomaly$_{MAT}$ but increased with Anomaly$_{MAP}$. Shrub species richness increased with Anomaly$_{MAT}$ but there was no relationship with Anomaly$_{MAP}$. Plant species richness was also related to contemporary climate: tree and herb species richness increased with DTR (Figure 4a), shrub species richness increased with CMI (Figure 4b), and herb species richness increased with both DTR and CMI (Figure 4c). The relationship between disturbance intensity and plant species richness differed among forest strata: tree and shrub species richness decreased with disturbance intensity (Figure 4a,b), whereas herb species richness increased (Figure 4c).

Tree size variation was positively associated with both stem abundance and stand basal area (Figure 4)

and all three attributes showed opposing relationships with paleoclimate and current climate: tree size variation, stem abundance and stand basal area all increased with Anomaly$_{MAT}$ and Anomaly$_{MAP}$, but declined with increasing CMI and DTR. However, forest structural attributes only mediated the indirect positive association between Anomaly$_{MAT}$ and tree, shrub or herb species richness (Figure 5; Tables S6-S8). Forest structure was also related to disturbance, whereby stem abundance and tree size variation increased with disturbance intensity, whereas stand basal area declined (Figure 4). Hence, forest structural attributes mediated positive indirect relationships between tree or shrub richness and disturbance intensity (Figure 5; Tables S6-S8), as well as a negative indirect relationship between herb species richness and disturbance (Figure 5; Tables S6-S8). Finally, the positive indirect associations between tree, shrub or herb species richness and stem abundance or stand basal area were mediated by tree size variation (Figure 5; Tables S6-S8).

## 4. Discussion

Here, for the first time, we explored how interacting environmental factors and forest structural attributes explain plant species richness patterns across forest strata in a large temperate region of northeast China. Although we found that environmental factors and forest structural attributes all played a role in shaping plant species richness, the key factors explaining plant species richness patterns differed among forest strata. Overall, forest structural attributes enhanced plant species richness, indicating that greater heterogeneity likely increases the variety and availability of niche space. However, tree and herb species richness showed divergent relationships with paleoclimate variables and disturbance. Nonetheless, the prominent influence of paleoclimate factors on the patterns of plant species richness highlights the potential threat of future climate change for forest diversity.

*4.1 Relationships between plant species richness and past and current climate*

Our study points to a dominant role of paleoclimate in shaping geographic patterns of plant species in temperate forests. Since the LGM, climate change oscillation has promoted environmental heterogeneity, potentially influencing species diversity (Svenning and Skov, 2007b; Stewart et al., 2016; Guo et al., 2020). Biogeographic history may thus complement the effect of contemporary climate along continental and regional gradients (Svenning and Skov, 2007b; Xu et al., 2019a). In our study, the strong relationships between Anomaly$_{MAT}$ or Anomaly$_{MAP}$ and plant species richness suggests that forest plants were unequally

distributed during postglacial shifts, reflecting regional environmental variation (Svenning and Skov, 2007a). Nevertheless, although the LGM had a more dramatic effect in Europe, contemporary climate plays a greater role in shaping plant species richness (Svenning and Skov, 2007b), whereas in northeast China, paleoclimate since the last LGM appears to have had a substantial effect on forest plant diversity. In this context, our study provides new evidence for an important legacy effect of paleoclimate for forest diversity across large scales (Jimenez-Alfaro et al., 2018; Saladin et al., 2020).

Previous studies have pointed out the major and controlling role of contemporary climate in shaping plant species richness (Shen et al., 2012; Chu et al., 2019; Guo et al., 2020) because high temperatures enhance plant growth, reproduction, and reduce winter death, which increases species diversity (the ambient energy hypothesis; Hawkins et al., 2003). We used diurnal temperate range (DTR) to represent current temperature regimes, as it is strongly related to both maximum and minimum temperature, and its general effect can be also associated with regional temperature variations (Braganza et al., 2004). Our finding that tree and herb species richness increased significantly with DTR therefore confirms the important role of contemporary variation in temperature in temperate forests, and the similar response of trees and shrubs to DTR supports the ambient energy hypothesis, possibly due to the greater energy requirement of woody species. In addition, the stronger relationships between contemporary climate variables and herb species richness likely reflects differences in generation times across life-forms that create the forest strata (Leathwick et al., 1998). Herbs generally have shorter generation times than woody plants, and are thus more likely to respond rapidly to changes in the contemporary climate. The relationship between herb species richness and CMI further indicates that the herbaceous layer is competing with the forest canopy strata for moisture. Indeed, a sizeable proportion of rainfall does not reach the forest floor (Anderson et al., 1969) and herbs have relatively shallow roots compared to trees and shrubs, which makes herb species more sensitive to precipitation change (Anderson et al., 1969; Craine et al., 2013; Westerband et al., 2017; Jimenez-Alfaro et al., 2018).

Disturbance, particularly logging and land use change, has been recognized as one of the key determinants shaping forest plant species richness by creating mixed-aged forest structures (Frelich, 2008; Aponte et al., 2020). We found that the relative strength and magnitude of disturbance on forest structural attributes are not general but rely on specific forest attributes and strata. Increasing stem abundance and tree size variation but declining stand basal area with increasing disturbance intensity indicate that the primary impact of disturbance is the loss of large trees, followed by rapid growth of pioneer species, which

increases the number of stems and the overall size heterogeneity of the stand. Changes in forest structure with both climate and disturbance intensity resulted in indirect associations between disturbance and plant species richness, indicating that anthropogenic disturbance thus also potentially affects the response of forest plants to climate via changes in forest structure (Brice et al., 2019; Danneyrolles et al., 2019). Indeed, the indirect relationships between disturbance and plant species richness, mediated by forest structure, contrasted with the direct relationships, indicating that forest structural attributes can mitigate the effect of disturbance on plant species richness.

We found little evidence for the intermediate disturbance hypothesis in our study, as tree and shrub species richness tended to decline with increasing disturbance, whereas herb species abundance increased. Strong disturbance will create large canopy gaps which provides the herbaceous layer with more solar radiation and precipitation, thus promoting herb species richness (Zhang et al., 2014). In addition, the rapid regeneration ability of many herbaceous species likely confers greater resilience to disturbance than shrubs or trees. Moreover, differences in reproduction rates and dispersal ability among plant functional groups will also determine community assembly patterns and processes (Sandel et al., 2011).

The relative importance of topography likely depends upon the spatial scale under study, with strong regional effects interacting with climate (Keil and Chase, 2019). Our study focused on a single region with relatively similar evolutionary history, but with a large geographic extent that reflects strong biogeographical gradients. Thus, it is likely that, by combining current and past climate, we captured much of the variation in abiotic effects, including some of the influence of differences in topography (Qiu et al., 2014). Nevertheless, the decline in shrub species richness with elevation reflects regional altitudinal gradients, whereas the absence of a relationship between elevation and herb species richness suggests that herbaceous species are more strongly influenced by the microclimate created by woody vegetation (Bai et al., 2011).

### 4.2 The influence of forest structural attributes

We found a clear association between forest structural attributes and species richness, although the relationships varied in direction and magnitude depending on forest stratum (Figures 3 and 4). Among the three forest structural variables, tree size variation was most strongly related to tree and shrub species richness, whereas herb species richness declined with stem abundance. These two variables are correlated with stand basal area, but capture distinct aspects of structural heterogeneity, indicating that structurally

complex forests could be beneficial for plant species richness (Clark, 2010). More specifically, a complex forest structure increases the diversification of space configurations and create more niches, thus improving resource complementarity (Yachi and Loreau, 2007) and resulting in a higher species richness. The positive relationship between tree or shrub species richness and tree size variation is likely related to various mechanisms including tree crown complementarity, niche differentiation, and resource heterogeneity (Williams et al., 2017), which improves light utilization efficiency by forming a heterogeneous light environment (Yachi and Loreau, 2007; Hardiman et al., 2013; Wang et al., 2018), and promotes understory vegetation and shade-tolerant species richness (Valladares and Niinemets, 2008). The links between tree size variation, tree species richness and shrub species richness also supports previous work describing mutualistic interactions between trees and shrubs (Wang et al. 2019).

Besides the direct relationships between forest structural attributes and plant species richness, forest structure also plays an indirect mediating role through abiotic factors. The indirect positive associations between tree, shrub or herb species richness and Anomaly$_{MAT}$, which were mediated via forest structural attributes, might be attributed to the beneficial effect of warming temperatures on forest primary productivity and hence the abundance of large trees, thus increasing tree size variation. The strong overall influence of paleoclimate (both direct and indirect) suggests an important role for climatic refugia in the study region during the LGM, with legacy effects on forest structure and species richness.

Inconsistent with our results, a recent study found a strong association between stem abundance and tree species richness along a latitudinal gradient (Chu et al., 2019). Across such a large scale, the presence of tropical and subtropical forests contribute to large differences among regions, with higher abundance and number of species in the tropics, where stem abundance and plant species richness are more connected (LaManna et al., 2017). By contrast, our regional study only included temperate forests, where species richness and the number of individuals are lower, and both intraspecific and interspecific competition are less intense, resulting in weaker links between diversity and stem abundance.

## 5. Conclusions

Our study demonstrates the complementary roles of environmental factors and forest structural attributes in shaping plant species richness patterns. However, the predictive power of climate and forest structure varied in direction and magnitude depending on forest stratum. In particular, tree and herb species richness patterns displayed distinct and often opposing relationships with paleoclimate variables, highlighting that

tree and herb species richness are shaped by divergent processes over different time-frames. Greater plant species richness was generally associated with a heterogenous forest structure, although herb species richness declined with increasing tree stem abundance. Importantly, differences in forest structural attributes partly explained the decline in tree and shrub species richness but the increase in herb species richness with disturbance. The pronounced effects of paleoclimate and recent disturbance on the patterns of plant species richness across forest strata highlights the potential threat of on-going global changes for forest diversity. Together, simultaneous consideration of past and current climate conditions and forest structural attributes could greatly improve our understanding of the complex mechanisms shaping plant species richness patterns across forest strata.

## AUTHORS' CONTRIBUTIONS

X.W. and S.W. conceived the study. S.W., J.Y., J.Ye., Z.H., S.F., F.L., Z.Y. and X.W helped in the collection of forest censuses data. S.W., A.S. and X.W conducted statistical analyses. S.W., A.S. and X.W. wrote the first draft supported by B.J.-A., S.P. and E.J.S. All authors contributed to the revisions of the manuscript.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Accessibility

The datasets analyzed during the current study are available from the corresponding authors upon request. Climate data were obtained from publicly available resources, and can be found at worldclim.org and catalogue.ceda.ac.uk/uuid.

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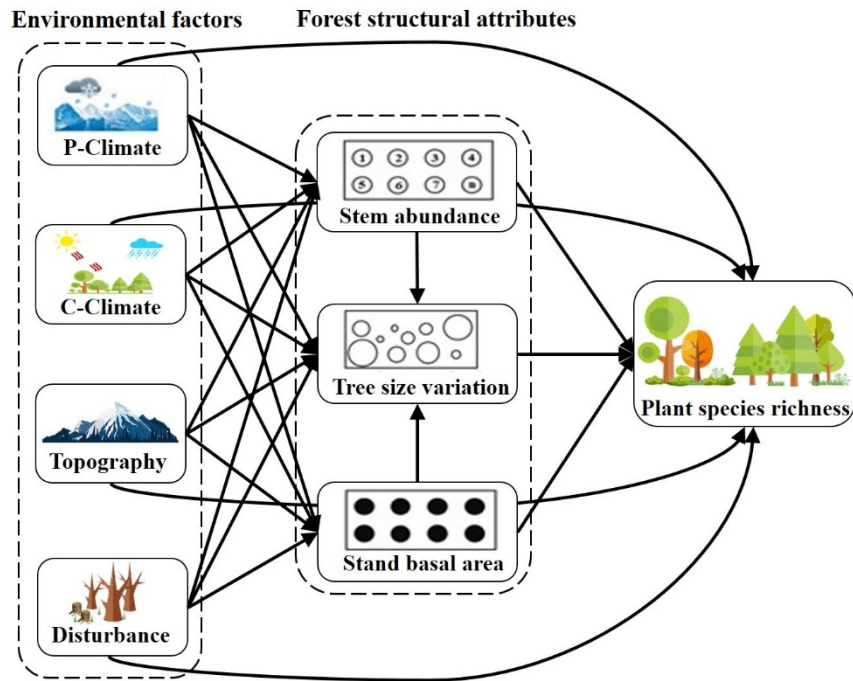
**Figure 1.** Location of the study region (a) and sampling plots (b) in the greater Changbai Mountains, northeast China. The location of the study region is indicated in gray and sample plots (30 m × 30 m) are indicated with black dots. Within each tree plot, 10 squares were randomly selected for shrub surveys (5 m × 5 m) with 10 nested micro-plots to survey herbaceous plants (1 m × 1 m).

**Figure 2.** A conceptual model of hypothesized linkages among environmental variables (paleoclimate, contemporary climate, topography and disturbance), forest structural attributes (stem abundance, tree size variation and stand basal area) and plant species richness (tree, shrub and herbs), where P-Climate is paleoclimate and C-Climate is contemporary climate.
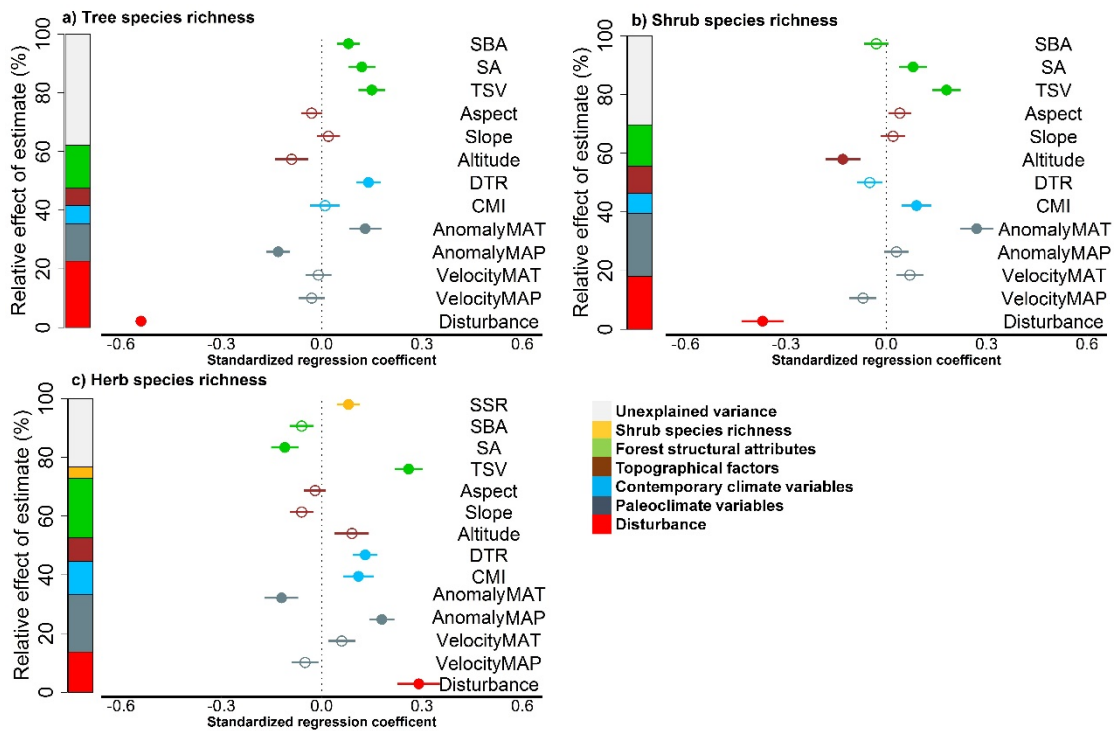
**Figure 3.** Explanatory power of predictor variables for (a) tree, (b) shrub and (c) herb species richness, from multiple regression models. Each variable was standardized, and their effect sizes (circles) were compared to determine differences in the strength of predictor variables. Filled circles indicate significant effects ($P \leq 0.05$), and means ±1 *SE* are shown. The relative importance of each factor (expressed as the percentage of variance explained) is shown. Velocity$_{MAP}$ and Velocity$_{MAT}$ indicate the speed of change in mean annual precipitation or temperature, respectively, between the last glacial maximum (LGM) and present-day; Anomaly$_{MAP}$ and Anomaly$_{MAT}$ indicate the magnitude of change in mean annual precipitation or temperature, respectively, between the last glacial maximum (LGM) and present-day; CMI is the climatic moisture index; DTR is the diurnal temperature range, TSV is tree size variation; SA is stem abundance; SBA is stand basal area and SSR is shrub species richness.
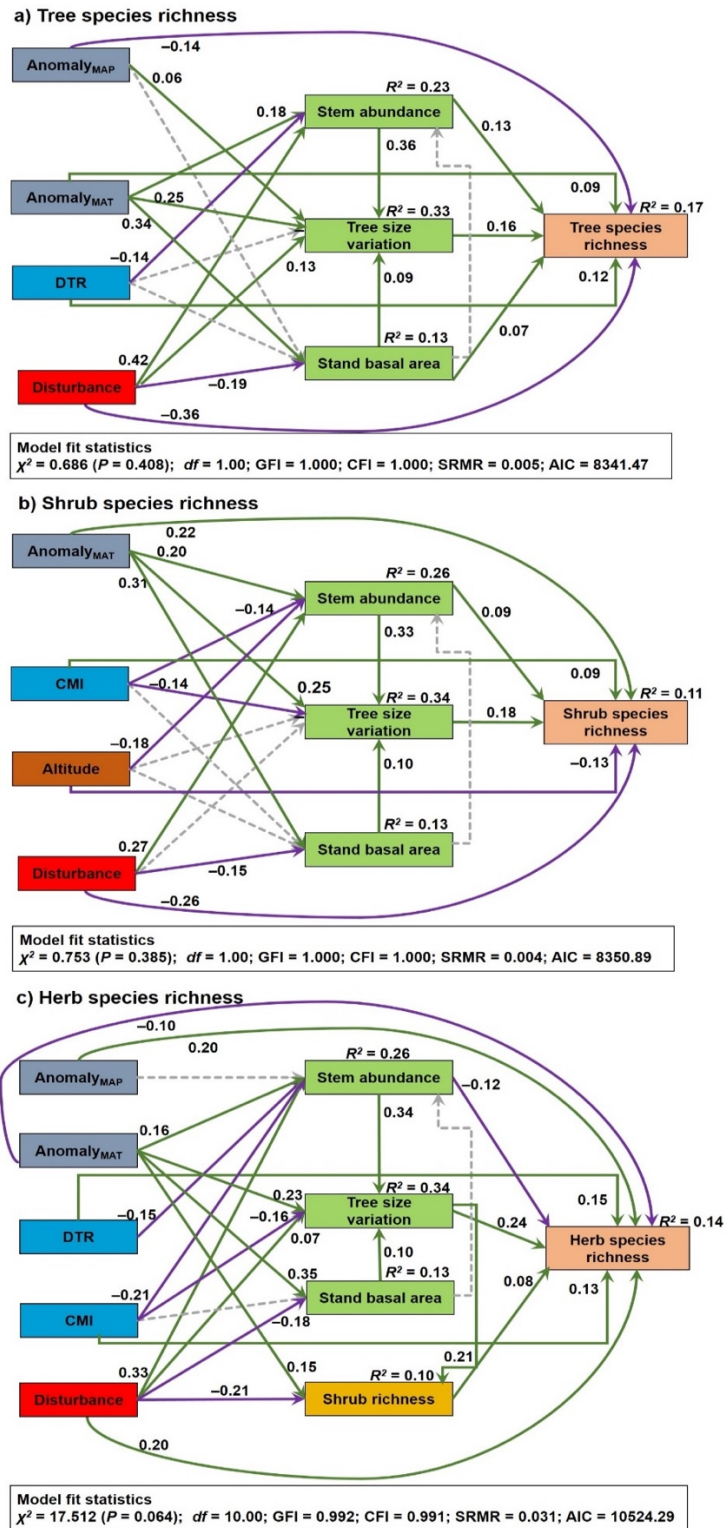
**Figure 4.** Structural equation models (SEMs) linking plant species richness to environmental factors (paleoclimate, contemporary climate, topography and disturbance) and forest structural attributes (stem abundance, tree size variation and stand basal area) for (a) tree, (b) shrub and (c) herb species. Solid green and purple arrows represent significant ($P \leq 0.05$) positive and negative relationships, respectively, and dashed grey arrows represent non-significant relationships that were retainined in the best-fit model. Model fit statistics are given below each panel, where CFI is the comparative fit index, SRMR is the standardized root mean square residual index and AIC is the Akaike Information Criterion. All other abbreviations follow the legend to Figure 3.
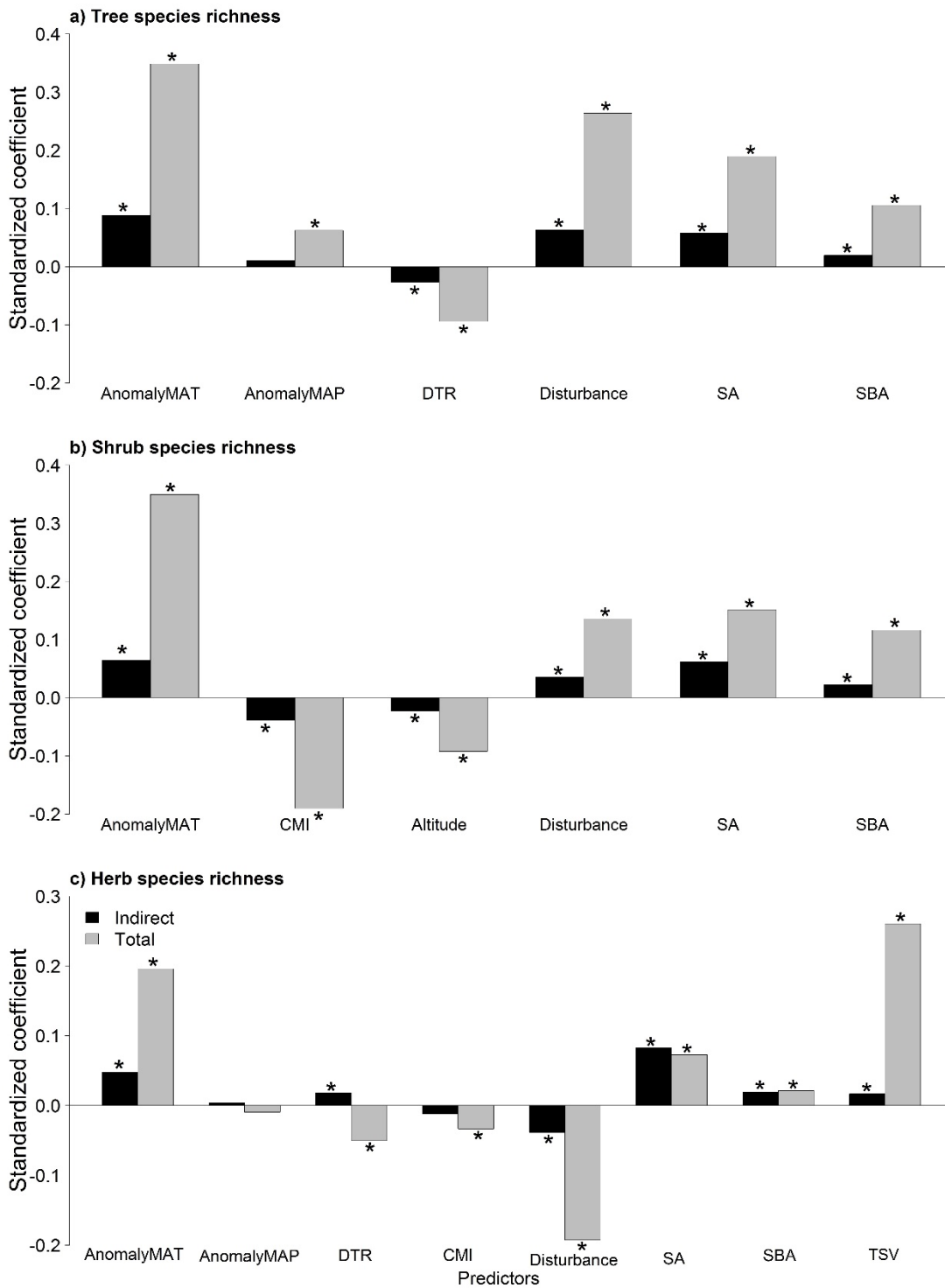
**Figure 5.** Standardized coefficients representing the magnitude of indirect and total linkages between a) tree, b) shrub and c) herb species richness and environmental factors or forest structural attributes in north-east China. Asterisks indicate significance at $P \leq 0.05$ and bars without asterisks show non-significant linkages. Note that only those variables with indirect associations to plant species richness are shown. Abbreviations follow the legend to Figure 3.