

Tree growth and regeneration dynamics at a mountain ecotone on Changbai Mountain, northeastern China: Which factors control species distributions? ¹

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Abstract: To improve our understanding of climate-driven long-term dynamics of eastern Asian mountain forests, we used field surveys and dendrochronological techniques to examine regeneration density, growth rate of mature trees, and growth sensitivity to climate of 3 common coniferous tree species at their respective altitudinal distribution limits on Changbai Mountain, northeastern China. The studied species were Manchurian fir (*Abies nephrolepis*, distributed between 780 and 1750 m asl), Korean pine (*Pinus koraiensis*, 780 and 1300 m asl), and Jezo spruce (*Picea jezoensis* var. *komarovii*, 1000 and 1750 m asl). Regeneration densities did not differ significantly among the elevations except for Jezo spruce, which showed a significantly lower regeneration density at 1000 m asl as compared to 1300 and 1750 m asl. All 3 species showed a significantly higher basal area increment (BAI) at the middle part of their distribution ranges than at their limits. The growth of Manchurian fir and Jezo spruce exhibited higher sensitivity to precipitation than to temperature at their lower distribution limits, and the inverse pattern was observed at the upper limit. In all cases the correlations between growth and the respective climate variable were positive, except for the correlation between Jezo spruce growth and precipitation. Growth of Korean pine was positively correlated with spring temperature and summer moisture at its lower distribution limit and with summer temperature at its upper limit. Our study suggests that elevational limits of forest vegetation were likely constrained by climate factors affecting growth of dominant species rather than those controlling regeneration density.

Keywords: Asian temperate forests, climate change, dendrochronology, ecotone, mountain forests.

Résumé: Afin d'améliorer notre compréhension de la dynamique à long terme de l'influence des facteurs climatiques sur les forêts de montagne de l'est de l'Asie, nous avons réalisé des relevés sur le terrain et utilisé des méthodes dendrochronologiques pour examiner la densité de régénération, le taux de croissance d'arbres matures et la sensibilité au climat de la croissance de trois espèces communes de conifères à leurs limites respectives de répartition altitudinale dans le massif Changbai, au nord-est de la Chine. Les espèces étudiées étaient le sapin de Mandchourie (*Abies nephrolepis*, retrouvé entre 780 et 1750 m asl), le pin de Corée (*Pinus koraiensis*, 780 à 1300 m asl) et l'épinette Jezo (*Picea jezoensis*, 1000 à 1750 m asl). La densité de régénération ne variait pas significativement entre les élévations, sauf pour l'épinette Jezo qui avait une densité de régénération significativement plus faible à 1000 m qu'à 1300 m et 1750 m asl. L'accroissement de la surface terrière pour les trois espèces était significativement plus élevée dans la partie centrale de leur aire de répartition qu'aux limites. La croissance du sapin de Mandchourie et de l'épinette Jezo montrait une plus grande sensibilité aux précipitations qu'aux températures à leurs limites inférieures de répartition alors que le patron inverse était observé à leurs limites supérieures. Dans tous les cas, les corrélations entre la croissance et une variable climatique en particulier étaient positives, sauf pour la corrélation entre la croissance de l'épinette Jezo et les précipitations. La croissance du pin de Corée était corrélée de façon positive avec les températures printanières et l'humidité estivale à sa limite inférieure de répartition et avec les températures estivales à sa limite supérieure. Notre étude suggère que les limites altitudinales de la forêt sont probablement contraintes par des facteurs climatiques affectant la croissance des espèces dominantes plutôt que par des facteurs régissant la densité de la régénération.

Mots-clés: changements climatiques, dendrochronologie, écotone, forêts de montagne, forêts tempérées asiatiques.

Nomenclature: Xu *et al.*, 2004.

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Introduction

Climate warming may have a major impact on forest ecosystems (Boisvenue & Running, 2006) by affecting physiological processes (Way & Oren, 2010), tree sensitivity to environmental variability (Allen *et al.*, 2010), and natural disturbance regimes (Bergeron *et al.*, 2010). In the Northern Hemisphere, the average annual temperature in the mid- and high latitudes increased by 0.74 °C from 1906 to 2005, and climate models predict an additional increase of 1.6–6.4 °C by 2100 (Solomon, Qin & Manning, 2007). Changes in climate may be affecting growth, establishment, and distribution of species in many boreal and temperate forests (Peñuelas & Boada, 2003; Gamache & Payette, 2005; Jump, Hunt & Peñuelas, 2006). In mountain ecosystems, trees respond to climate change by shifting the position of their elevational ranges (Grace, Berninger & Nagy, 2002; Kullman, 2002; Peñuelas & Boada, 2003). However, there are factors that limit the possibilities for such migration. These include seed dispersal limitations, competition pressure from resident species in new habitats, and local soil conditions (Brubaker, 1986; Stephenson, 1990; Peterson & Peterson, 1994; Korner & Paulsen, 2004).

The climate of northeastern China has become warmer and drier over the last century (Qian & Zhu, 2001; Qian & Qin, 2006). Climate records show an increase in the annual mean temperature by 2 °C between the 1900s and the 1990s (Qian & Zhu, 2001) and a decrease in summer precipitation by $-0.81 \text{ mm} \cdot \text{y}^{-1}$ between the 1960s and the 2000s (Liang, Li & Liu, 2011). Climate models predict a further increase in annual mean temperature of 4.6 °C towards the end of the 21st century (He *et al.*, 2005), which may result in a northward or an elevational extension of distribution limits for dominant coniferous species (Xu & Yan, 2001; He *et al.*, 2005).

Recruitment and tree growth are particularly sensitive to climate change at species' distribution limits due to an increased frequency of sub-optimal environmental conditions causing seedling and sapling mortality, growth declines, and tree mortality (Brubaker, 1986; Lescop-Sinclair & Payette, 1995; Wang, Zhang & Ma, 2006). Responses of recruitment and growth to climate vary along the elevational gradient (Gworek, Wall & Bruss, 2007; Yu *et al.*, 2011). Temperature regime tends to be critically important for seedling establishment and tree growth at species' upper elevational limits (Tranquillini, 1979). Trees at upper limits often respond to climate warming with an increase in regeneration density (Szeicz & MacDonald, 1995) and radial growth (Frank & Esper, 2005). Water availability and biotic interactions tend to control recruitment and growth at middle to lower limits (Stephenson, 1990). Drought stress and increase in competition at lower limits may therefore lead to low regeneration density and decline in radial growth (Gworek, Wall & Bruss, 2007; Peng *et al.*, 2008; Rigling *et al.*, 2013). Elevational zones separating different bioclimatic domains (termed ecotones; Odum, 1983) provide numerous examples of strong climate control of regeneration and tree growth (Peñuelas & Boada, 2003; Peng *et al.*, 2008; Takahashi *et al.*, 2011).

The northern slope of Changbai Mountain hosts major forest types of northeastern China, including broadleaved–Korean pine (*Pinus koraiensis*) forests and spruce–fir (*Picea jezoensis* var. *komarovii* – *Abies nephrolepis*) forests. These communities have remained largely undisturbed by human activities (Wang *et al.*, 1980; Barnes, Xu & Zhao, 1992). As in other mountain ecosystems, numerous distribution limits are observed along the elevational gradient of the mountain (Yu *et al.*, 2011), providing suitable sites for the study of climate–growth relationships.

Most dendrochronological studies in this region have been conducted on a single tree species (Yu *et al.*, 2006; 2013) or at a single elevation (Gao *et al.*, 2010; Gao, Wang & Zhao, 2011); only 1 has focused on the growth response of multiple species to climate change along the entire elevational gradient (Yu *et al.*, 2011). All of these studies have suggested that temperature, precipitation, and soil moisture limit tree growth on Changbai Mountain, and that climate change may affect forest structure in this mountain region. However, growth data alone are inadequate to identify factors behind changes in a species distribution or forest composition (Brubaker, 1986; Wang, Zhang & Ma, 2006), since such dynamics may also be related to the recruitment patterns (Silva *et al.*, 2012; Fisichelli, Frelich & Reich, 2013) and natural disturbance regimes (Flannigan & Bergeron, 1998; Vila-Cabrera *et al.*, 2012).

The aim of this study was to advance our understanding of the factors controlling the vegetation of the broadleaved–Korean pine/spruce–fir forest ecotone (BKSFE) on Changbai Mountain and to discuss its dynamics under the future climate. We evaluated recruitment and growth of the Korean pine, Jezo spruce, and Manchurian fir at their elevational distribution limits and upscaled these results to discuss forest composition at the upper and lower edges of BKSFE. Although the selected species were the main canopy dominants along the BKSFE, they possess different life strategies. Korean pine is a shade-intolerant canopy species (as trees older than 40–50 y), Jezo spruce is a shade-tolerant canopy species, and Manchurian fir is a shade-tolerant species typically dominating sub-canopy. We hypothesized that

- 1) regeneration density would decline at the tree distribution limits, as compared to the central part of tree distribution;
- 2) the growth rate of mature trees would decline at their distribution limits, as compared to the central part of their distributions; and
- 3) tree species would be more temperature-sensitive at higher elevations and more precipitation-sensitive at lower elevations.

To test these hypotheses, we studied the regeneration density (hypothesis 1) and basal area increment of the canopy trees (BAI, hypothesis 2) and used dendroclimatic analyses to study the trees' growth sensitivity to climate (hypothesis 3) across their distributions. Finally, we combined our knowledge of climate effects on regeneration and growth with data on forest composition to discuss potential effects of climate change on the dynamics of the BKSFE.

Methods

STUDY AREA

The study was conducted in northeastern China, on the northern slope of Changbai Mountain within the territory of the Changbaishan Natural Reserve (41°31'–42°28'N, 127°9'–128°55'E, Figure 1). The area has a temperate continental climate, with long, cold winters and wet summers. Mean annual temperature varies from 2.8 °C in the lower reaches (700 m asl) to –7.3 °C at the top of the mountain (2691 m asl). Mean annual precipitation varies from 750 to 1340 mm along this gradient (Zhao, 1981). About 70% of the annual precipitation falls between June and September (Appendix I, Figure 1). Below 1700 m asl, the topography of the area is gentle, with slope inclinations below 5°. Above 1700 m asl, the slopes are relatively steep, with an average angle exceeding 20°. Volcanic soils overlying a deep layer of volcanic ash are common across the study area (Shao, 1996). Soil type varies from moderately deep mountain brown forest soil (about 50 cm) at 750–1100 m asl to more shallow (about 20 cm deep) mountain brown coniferous forest soil at 1100–1700 m asl (ECJF, 1988).

Forest vegetation is composed of broadleaved–Korean pine forests at 750–1100 m asl, spruce–fir forests at 1100–1700 m asl, and Erman's birch (*Betula ermanii*) forests from 1700 to 2000 m asl (Wang *et al.*, 1980).

Each forest type possesses a unique assemblage of sub-canopy trees and shrubs (Table I). The distributions of Manchurian fir, Korean pine, and Jezo spruce are limited to 700–1800 m asl, 700–1300 m asl, and 900–1800 m asl, respectively (Figure 1). Two forest ecotones are formed along this elevational gradient. The BKSFE ranges from 1000 to 1300 m asl, with the canopy dominated by Korean pine and Jezo spruce and the sub-canopy by Manchurian fir. The spruce–fir/alpine dwarf birch forest ecotone is located between 1700 and 1800 m asl, with Jezo spruce and Erman's birch dominating the canopy layer and Manchurian fir dominating the sub-canopy layer.

CLIMATE DATA

The closest meteorological stations to the sampling sites are the Open Research Station of Changbai Mountain Forest Ecosystems (ORS, 740 m asl), the Tianchi meteorological station (TC, 2623 m asl), and Songjiang town (SJ, 601 m asl) meteorological station (Figure 1). Comparison of climate records (mean and maximum monthly temperatures and total monthly precipitation) among the 3 stations showed significant correlations ($P < 0.05$). A check for homogeneity in the climate data from the 3 stations, using Mann–Kendall and Double-Mass tests, found no indications of abrupt changes in climate records, indicating that data from any of these stations could represent the climate

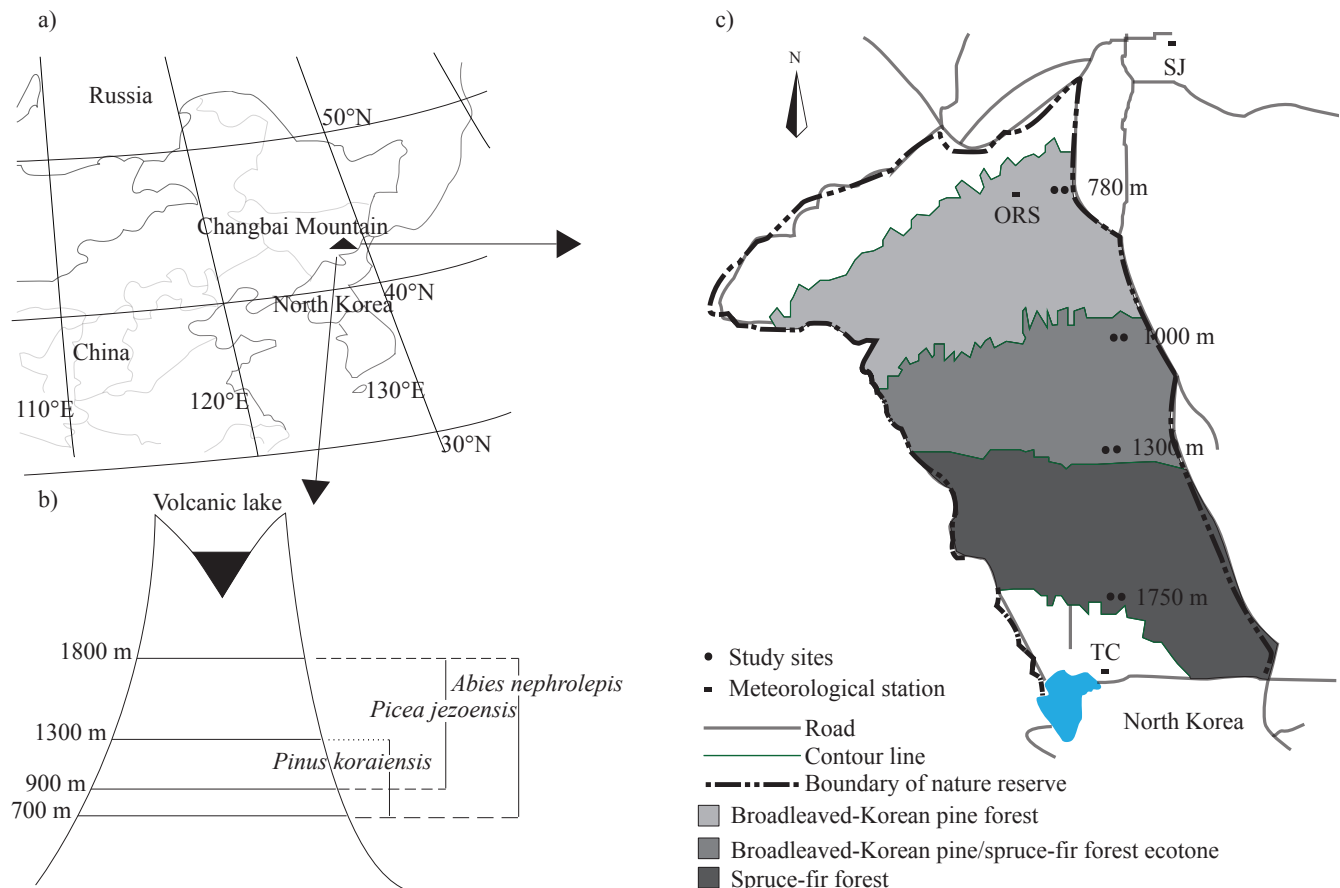


FIGURE 1. Location of the Changbai Mountain Natural Reserve in the Northeastern China (a), distribution of species by elevation (b), and location of the meteorological stations (SJ: Songjiang town, ORS: Open Research Station, TC: Tianchi) and study sites (c).

TABLE I. Community structure of major forest types along the elevational gradient on the northern slope of Changbai Mountain, based on data from Xu et al., 2004.

Forest zone	Elevation (m)	Canopy species	Understory species	Shrub species
Erman's birch forest	1700–2000	<i>Betula ermanii</i> <i>Larix olgensis</i>	<i>Sorbus pohuashanensis</i> <i>Alnus mandshurica</i>	<i>Rhododendron chrysanthum</i>
Spruce-fir/alpine dwarf birch forest ecotone	1700–1800	<i>Picea jezoensis</i> <i>Betula ermanii</i> <i>Larix olgensis</i>	<i>Sorbus pohuashanensis</i> <i>Abies nephrolepis</i> <i>Acer ukurunduense</i>	<i>Rhododendron chrysanthum</i> <i>Vaccinium uliginosum</i> <i>Lonicera caerulea</i>
Spruce-fir forest	1100–1700	<i>Picea jezoensis</i> <i>Abies nephrolepis</i>	<i>Betulla costata</i> <i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i> <i>Sorbus pohuashanensis</i>	<i>Rosa acicularis</i> <i>Ribes maximowiczianum</i> <i>maximowiczianum</i> <i>Lonicera maximowiczii</i>
Broadleaved-Korean pine/spruce-fir forest ecotone	1000–1300	<i>Pinus koraiensis</i> <i>Picea jezoensis</i> <i>Larix olgensis</i>	<i>Abies nephrolepis</i> <i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i>	<i>Lonicera chrysantha</i> <i>Lonicera maximowiczii</i>
Broadleaved-Korean pine forest	750–1100	<i>Pinus koraiensis</i> <i>Tilia amurensis</i> <i>Fraxinus mandshurica</i> <i>Quercus mongolica</i> <i>Phellodendron amurense</i> <i>Ulmus japonica</i> <i>Betulla costata</i> <i>Betula platyphylla</i> <i>Populus ussuriensis</i> <i>Populus davidiana</i>	<i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i> <i>Acer pseudosieboldianum</i> <i>Acer mono</i> <i>Prunus padus</i> <i>Tilia mandshurica</i> <i>Syringa amurensis</i> <i>Malus baccata</i> <i>Maackia amurensis</i>	<i>Philadelphus schrenkii</i> <i>Corylus mandshurica</i> <i>Ribes mandshuricum</i> <i>Drutzis parviflora</i> <i>Evonymus pauciflora</i> <i>Berberis amurensis</i> <i>Viburnum burejaeticum</i> <i>Viburnum opulus</i> <i>Lonicera praeflorens</i> <i>Lonicera chrysantha</i>

of the study area. In the analyses, we used data produced by the SJ station since it had the longest record (1958–2007) as compared to the other stations (ORS, 1982–2007; TC 1959–1988) and showed a generally higher correlation with growth than data from the ORS and TC stations.

Analysis of climate dynamics from 1958 to 2007 revealed that annual minimum and mean temperatures had increased since 1970, but annual total precipitation did not show any sustained changes during the 50-y period (Appendix I; Figure 2).

FIELD SAMPLING AND INITIAL DATA TREATMENT

We selected sampling plots at 4 elevations (780, 1000, 1300, and 1750 m asl), corresponding to the middle and marginal parts of the species distributions (Figure 1). At each elevation we established two 20 × 80-m plots, with the longer side perpendicular to the slope. Each plot was divided into 4 subplots (20 × 20 m). In each plot, we recorded the species identity and diameter at breast height (DBH, 1.3 m) of all trees with DBH greater than 1 cm. In the 4 corners of each subplot, we established one 5 × 5-m and one 2 × 2-m plot to record the presence of shrub and herb species, respectively. To assess the contribution of tree species to the canopy, we calculated importance values (IV; Cottam & Curtis, 1956) based on the average of relative density and relative dominance of a species in each plot. Relative density is the proportion of individuals of a species in the total number of individuals of all species, while relative dominance is the proportion of the total basal area of a species in the total basal area for all species within a plot. To demonstrate the variation of forest structure along the altitudinal gradient, we combined our own inventory

data with the data from a published study (Xu et al., 2004; Table I).

One 20 × 20-m subplot was selected randomly within each plot to count the amount of regeneration (seedlings >1 cm in diameter at the stem base and <1.3 m in height). Regeneration density of each species in the selected subplot was expressed as number of stems per hectare, and was then converted into a species- and elevation-specific average. Since destructive collection of samples is not allowed within the Natural Reserve, we used age data from our earlier study (Zhang et al., 2014) to add in discussion of recruitment patterns.

In each plot, we cored 12 to 17 dominant trees of each studied species at DBH. One core was taken per tree at elevations 1000 and 1300 m, while 2 cores were extracted at elevations 780 and 1750 m (Appendix II & III). Tree-ring samples were dried, mounted, and sanded until ring boundaries were clearly visible. Cores were visually cross-dated using the pointer year technique (Stokes & Smiley, 1968). Ring widths were measured to the nearest 0.01 mm by LinTab measuring stage, and the data quality was verified using the COFECHA program (Holmes, 1983). In total, 92 cores of Manchurian fir, 103 cores of Korean pine, and 115 cores of Jezo spruce were dated and used for dendro-chronological analyses. Since the pairs of plots located at the same elevation were ecologically similar and within 200–500 m of each other, we combined data for each altitude to produce 9 altitude- and species-specific chronologies (Appendix III).

Field sampling was carried out in 2012 (for elevation 780 m), 2008 (1000 and 1300 m), and 2009 (1750 m). Although we could find trees of all 3 studied species at elevations above their present upper

distribution limits, we established plots only below those limits, since the higher trees were sparsely distributed, making it impossible to obtain sufficient replication for the dendrochronological analyses.

We collected soil samples from the mineral layer (20–30 cm) to characterize the soil texture and pH in each plot. One pit was dug in the central part of each subplot, and 4 soil samples were collected from each plot. The soil samples from the same plot were mixed together, air dried at 20 °C for 1 week, and sieved through a 2-mm grid. Soil texture was quantified using the hydrometer method (Sheldrick & Wang, 1993), and pH was measured in 0.01 M CaCl₂ at a 1:5 soil solution ratio.

STATISTICAL ANALYSES

To test hypothesis 1, we evaluated differences between regeneration density among the elevations for each species by using one-tailed ANOVA with type III sum of squares and LSD *post hoc* tests, using elevation as independent factor. The analysis was conducted in SPSS 13.0 (Park, 2009) at 0.05 significance level.

To test hypothesis 2, we analyzed variability of species growth rate along the elevational gradient. We averaged all single-tree chronologies into a mean chronology for each species and elevation and converted tree-ring width increment into basal area increment (BAI) to obtain average BAI over 1996–2005, since the value of BAI was a better representation of the tree growth rate than diameter increment (Pedersen, 1998). As in the regeneration density analyses, we used ANOVA with LSD *post hoc* tests to test the effect of elevation on growth. We used the most recent 10-y frame in this analysis because this period covered the mature phase in the trees' lifespan for all species, enabling us to minimize age-related effects on growth. Furthermore, selecting the most recent decade helped minimize the potential impact of past stand-specific disturbances on the growth dynamics. To further evaluate variability in growth rates along the elevation gradient, we calculated mean diameter growth rate of the 3 species at 3 elevations by dividing DBH by tree ages. As with the analyses of BAI dynamics, we used ANOVA to assess the effect of elevation on average growth.

To test hypothesis 3, we used response function analysis of monthly and seasonal climate variables and annual tree-ring increments. We removed the age- and size-related trends in tree growth by detrending chronologies with a cubic spline with a 50% frequency response at 60 y, using the ARSTAN program (Cook & Peters, 1981). Ring width values were transformed into index values by dividing the observed chronology values by the predicted values. This detrending procedure retained high-frequency variation and filtered out low-frequency age- and disturbance-related trends. Autoregressive modeling was performed on each detrended series to remove temporal autocorrelation and amplify common signals (Cook *et al.*, 1990). The resulting residual chronologies were used in the analyses of climate–growth relationships at annual scale (Cook *et al.*, 1990).

We used response function correlations to assess association between annual growth and climate variables. A response function is a principal component regression to solve the problem of collinearity among climatic predictors (Briffa & Cook, 1990; Morzuch & Ruark, 1991)

and is often used to evaluate climate–growth relationships. Correlation coefficients of response functions were calculated using the DendroClim2002 program (Biondi & Waikul, 2004) over the common interval 1958–2007. Climate data included mean monthly temperature and total monthly precipitation from July of the previous year to September of the current year, as climate conditions of the previous year might have an effect on tree growth in the current year (Fritts, 1976). We also considered known seasonal weather patterns in the study area (Yu *et al.*, 2013) and used the mean maximum temperature and the total sum of precipitation of the previous autumn (September–October), the current spring (April–May), and the current summer (June–August). We preferred maximum temperature over mean temperature since the former produced more statistically significant results and might have a stronger influence on growth processes than mean temperature (Oberhuber, 2004).

Results

SOIL CHARACTERISTICS AND TREE-RING CHRONOLOGIES

Soil texture and pH were similar among sites and did not show a clear elevational pattern (Appendix IV). A majority of sites had a high sand content (>70%) and acid soil conditions.

The 9 tree-ring chronologies ranged from 122 to 354 y in length. Jezo spruce had the longest chronology, extending back to 1654 (Appendices III and V). Mean sensitivity (MS) of the chronologies increased with decreasing elevation. The contribution of the first principal component (PC1) in the data sets of the Korean pine chronologies increased with elevation, while the PCs obtained on the Manchurian fir and Jezo spruce data sets did not show any trend (Appendix III). We observed high signal-to-noise ratios (SNR), expressed population signals (EPS), and amount of variability accounted for by the first PCs in all site residual chronologies, indicating a strong population-wide signal.

FOREST COMPOSITION

The forest composition and importance values of canopy dominants varied across the elevation gradient. The diversity in canopy and understory strata decreased with increase in elevation (Table II). Species diversity in all 3 strata was higher at the lowest (46 species at 780 m) than at the highest elevation (16 at 1750 m). In the BKSFE (1000–1300 m), the differences in species numbers were higher for the canopy and understory strata (15 *versus* 9 species) than for either the shrub or the herb strata (9 *versus* 7 species and 11 *versus* 10 species, respectively). The studied coniferous trees showed the lowest importance values (IV) at their respective lower distribution limits (Table II). Manchurian fir and Korean pine showed the highest IV at the centre of their distributions, whereas Jezo spruce had the highest IV at its upper limit. For Manchurian fir, high IV was largely attributable to its high density, while for Korean pine and Jezo spruce high IVs were due to their high basal area. This was particularly true for Korean pine, which exhibited a high relative dominance (22.7%) and a low relative density (6.7%) at its upper limit (at 1300 m). IV of broadleaved trees was negatively correlated with elevation.

TABLE II. Diversity and importance values (IV) of canopy trees by elevation (E) on the northern slope of Changbai Mountain. Broadleaved trees (BT) include canopy dominants *Tilia amurensis*, *Quercus mongolica*, *Fraxinus mandshurica*, *Acer mono*, *Betula platyphylla*, and *Populus davidiana*. Standard deviation (SD) of the respective mean values is indicated in parentheses. Values of Relative Density (RDe) and Relative Dominance (RDo) are in percents.

Elevation (m)	Numbers of species				Broadleaved species				<i>A. nephrolepis</i>				<i>P. koratensis</i>				<i>P. jezoensis</i>			
	All trees		Herbs		RDe	RDo		IV	RDe	RDo		IV	RDe	RDo		IV	RDe	RDo		IV
	BT		Shrubs																	
780	18 / 15		13	15	25.6 (2.4)	37.8 (3.1)	31.7 (2.9)		3.8 (0.6)	8.0 (1.8)	5.9 (0.9)		4.3 (1.5)	6.2 (2.8)	5.3 (1.9)		—	—	—	—
1000	15 / 11		9	11	18.2 (3.1)	24.5 (5.3)	21.4 (4.3)		35.8 (6.2)	17.2 (2.7)	26.5 (5.1)		5.1 (2.3)	26.5 (5.7)	15.8 (4.1)		5.8 (1.2)	5.0 (3.7)	5.4 (2.7)	
1300	9 / 4		7	10	0.4 (0.1)	0.6 (0.2)	0.5 (0.2)		71.9 (2.9)	15.5 (4.2)	43.7 (3.3)		6.7 (1.7)	22.7 (3.1)	14.7 (2.3)		10.3 (4.7)	16.5 (5.8)	13.4 (5.1)	
1750	5 / 2		3	8	—	—	—		23.0 (4.6)	14.5 (3.9)	18.8 (4.0)		—	—	—		27.9 (2.7)	36.0 (3.5)	31.9 (3.8)	

REGENERATION DENSITY

There was no significant difference in the regeneration densities of Manchurian fir and Korean pine among the elevations (Figures 2a and b; Appendix VI). Regeneration of Manchurian fir and Korean pine was abundant at all elevations, with the density exceeding 565 seedlings·ha⁻¹ (Figure 2a). Neither species showed a significant tendency towards a higher regeneration density at the midpoint of their distribution range (Figure 2b). Jezo spruce was the only species that showed significant differences in regeneration densities between its lower distribution limit (222 ± 46 seedlings·ha⁻¹) and the central part of its distribution (1441 \pm 449) (Figure 2b; Appendix VI). The recruitment data from BKSFE showed multimodal patterns of age structure in all 3 species (Appendix II). Despite the occurrence of significant warming during the 1970s and 1980s (Appendix I; Figure 2), we did not observe an increase in recruitment of the 3 species (Appendix II), which suggests a temporally stable pattern of recruitment.

DYNAMICS OF BAI AND CLIMATE–GROWTH RELATIONSHIPS

Korean pine had the largest 10-y mean BAI among the 3 species, while the BAI of Manchurian fir was the lowest (Figure 2c). BAI was significantly different in

pair-wise comparisons between species at each elevation (Appendix VI). All 3 species showed a significantly higher BAI at the central part of their distribution range (Figure 2d). Korean pine had the lowest BAI at its lower limit, while Manchurian fir and Jezo spruce showed the lowest BAI at their upper limits (Figure 2d). Analysis of average growth rates over whole tree lifespans showed patterns similar to those seen in the analysis of BAI dynamics: all 3 species showed the highest growth rate at the middle rather than the limits of their distributions (Appendix VI).

All 3 species revealed higher sensitivity to temperature than to precipitation at their upper limits, and the inverse pattern was observed at their lower limits (Table III; Figures 3 and 4). At their respective upper limits, positive responses to temperature occurred during the current year summer (for Korean pine and Jezo spruce) and the current year spring (for Manchurian fir) (Table III; Figure 3). At their respective lower limits, a positive effect of precipitation during the previous year autumn was observed (Table III; Figure 4). Jezo spruce differed from the 2 other species in terms of its response to monthly climate variability. Growth at spruce's lower and middle distribution ranges responded negatively to precipitation of the current April (Figure 4).

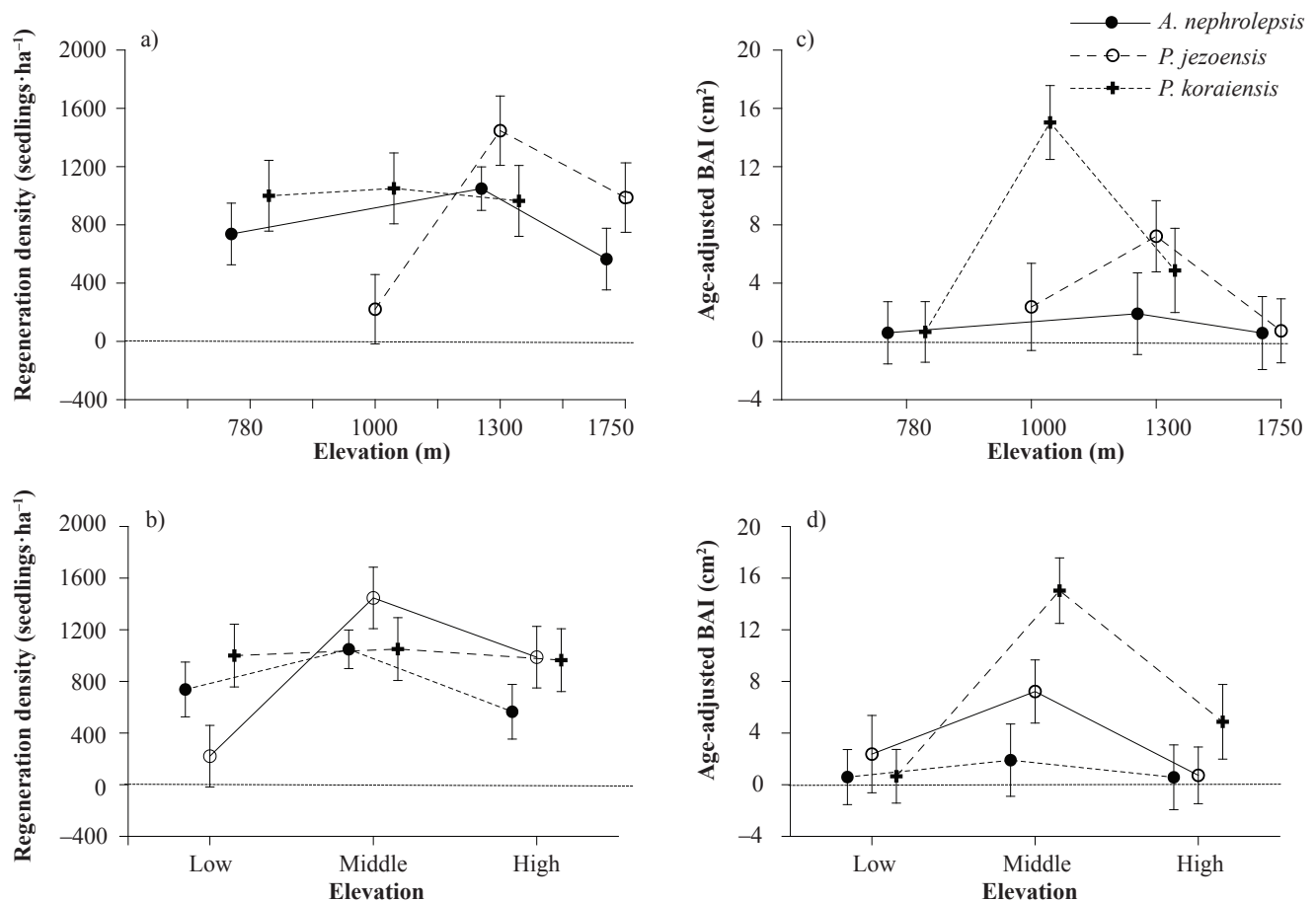
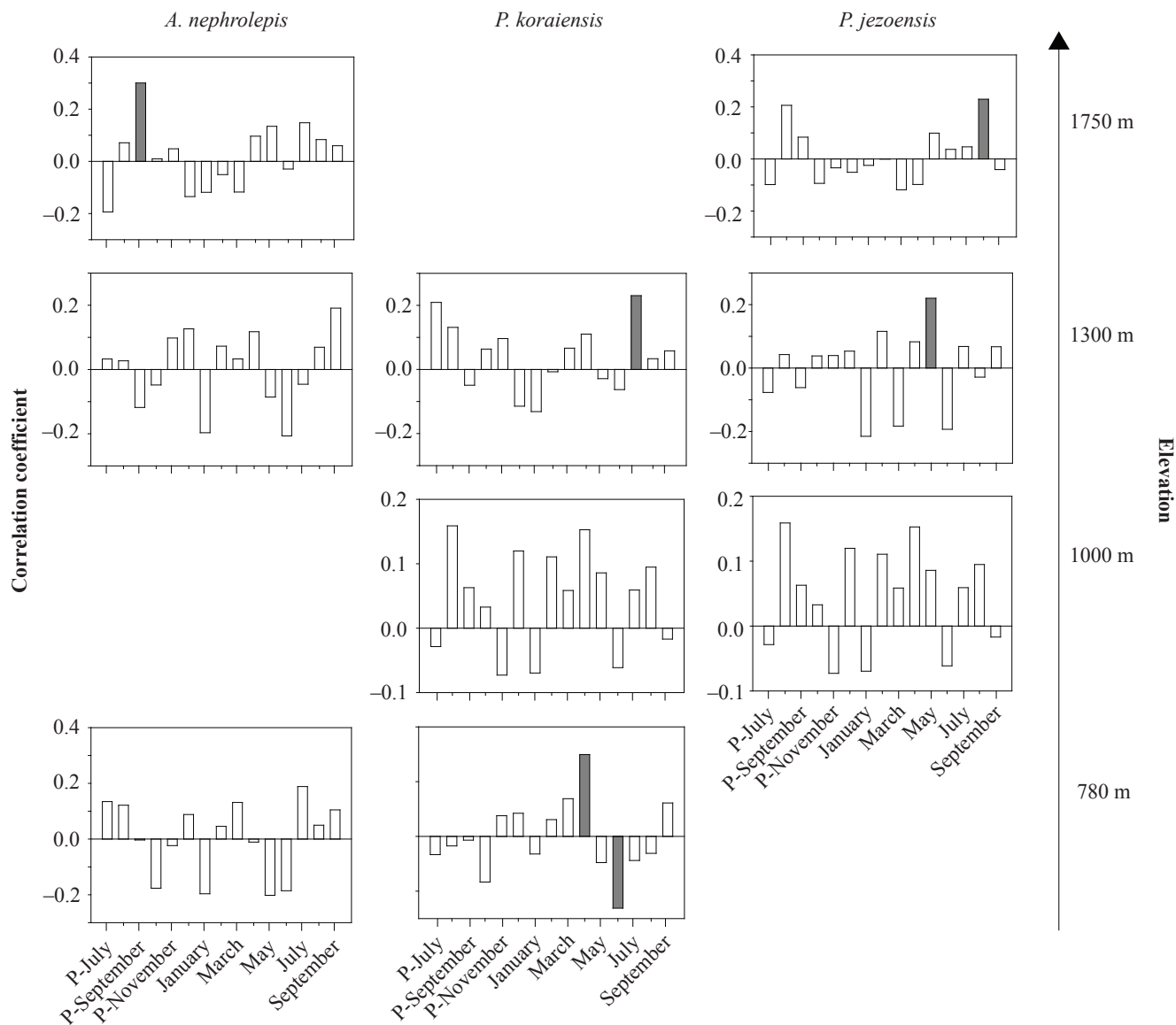


FIGURE 2. Regeneration density and basal area increment (BAI) over 1995–2006 for 3 dominant species along the elevational gradient in the Changbai Mountain. In a) and c), x-axis represents the real elevation of the species distribution, while x-axis of b) and d) shows the relative position along the elevational gradient

TABLE III. Response function coefficients between tree growth and seasonal climate variables. Asterisk indicates significant correlations (0.05 level). Maximum temperature refers to the mean maximum temperature of respective season.

Climate variable	Season	<i>A. nephrolepis</i>			<i>P. koraiensis</i>			<i>P. jezoensis</i>		
		780 m	1300 m	1750 m	780 m	1000 m	1300 m	1000 m	1300 m	1750 m
Precipitation	Previous autumn (Sept–Oct)	0.38 *	0.24	0.12	0.37 *	0.15	0.15	0.30*	–0.17	0.07
	Current spring (April–May)	–0.11	–0.04	–0.25	–0.01	0.04	–0.04	–0.32*	–0.06	–0.18
	Current summer (June–Aug)	0.1	0.12	0.1	0.36 *	0.1	0.21	–0.01	0.16	0.17
Maximum temperature	Previous autumn (Sept–Oct)	–0.06	–0.04	0.2	0.09	–0.05	0.23	–0.06	0.03	0.08
	Current spring (April–May)	–0.06	0.03	0.25*	0.09	0.05	0.17	0.13	0.12	0.13

FIGURE 3. Response function analyses between the residual chronologies of *A. nephrolepis*, *P. koraiensis* and *P. jezoensis* and mean temperatures from the previous year July (P-July) to the current year September on the northern slope of the Changbai Mountain for the period 1958–2007. Grey bars indicate significant response coefficients at $p < 0.05$.

Discussion

Our study detected no clear pattern in regeneration densities along the elevational gradient in 2 out of the 3 studied species (rejecting hypothesis 1) and a decline

in the growth rate of mature trees towards their distribution limits (supporting hypothesis 2). We also observed similar climate–growth relationships in the 3 studied species along the elevational gradient, the growth being precipitation-sensitive at the respective lower distribution

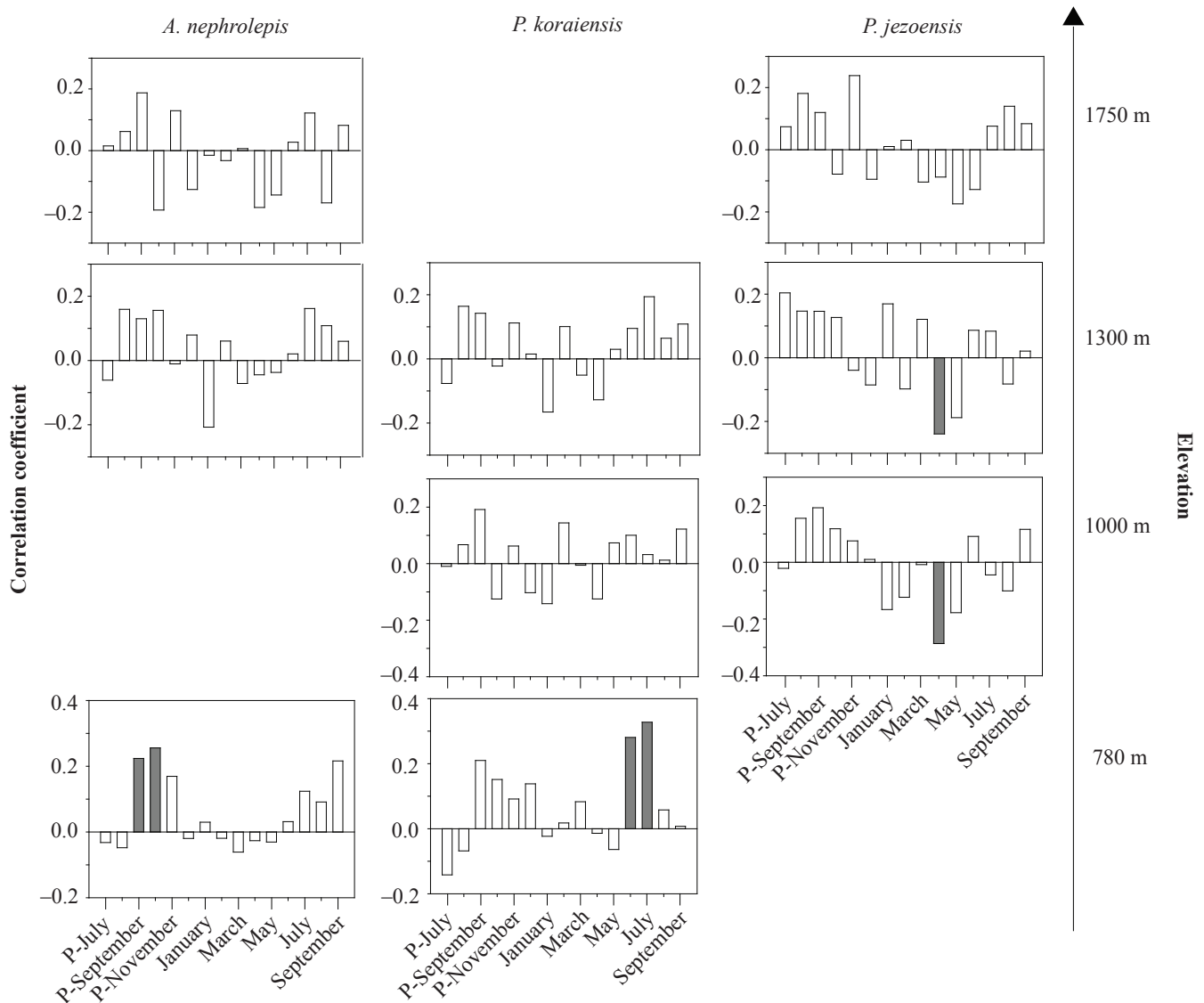


FIGURE 4. Response function analyses between residual chronologies of *A. nephrolepis*, *P. koraiensis* and *P. jezoensis* and precipitation from the previous year July (P-July) to the current year September on the northern slope of the Changbai Mountain for the period 1958–2007. Grey bars indicate significant response coefficients at $p < 0.05$.

limits and temperature-sensitive at the upper limits, which supported hypothesis 3. Based on these findings, we conclude that climate influence on the position of BKSFE on Changbai Mountain is likely realized through the control of tree growth rather than of regeneration. The future drier and warmer climate will likely change relative growth rates of the canopy dominants, which in turn may lead to changes in their relative abundances and eventually affect the structure, diversity, and position of the BKSFE.

PATTERN OF REGENERATION DENSITY ALONG THE ELEVATIONAL GRADIENT

Climate effects on regeneration density differed among the 3 species. Observed regeneration patterns failed to support our hypothesis suggesting regeneration-level control of the distribution limits for Korean pine and Manchurian fir. Both species have been shown to be abundant seed producers (Wang *et al.*, 1959; Okitsu, Ito & Li, 1995) that

successfully regenerate along the studied gradient. In addition, seedlings of pine and fir can tolerate lower light levels than seedlings of co-occurring broadleaved species, which likely made them competitive under conditions of high canopy closure (0.7–0.9), typically observed in these forests (Xu *et al.*, 2001). In contrast, regeneration of Jezo spruce appeared to be negatively affected by the climate conditions at its lower limit, supporting our 1st hypothesis. Although Jezo spruce is also capable of producing large seed crops and has shade-tolerant seedlings, soils with low water-holding capacity may limit seedling survival and growth (Iijima *et al.*, 2006). The sites at the lower limit of this species were generally drier than those at its upper limit (Chi, Zhang & Li, 1981; Jiang *et al.*, 2003), which might disfavour spruce regeneration due to reduced water availability. Negative effects of drought on seedlings are often caused by poor root development and associated decline in nutrient assimilation, effects that have been reported in

Jezo (Iijima *et al.*, 2006) and in other spruces (Chhin & Wang, 2008; Slugeňová *et al.*, 2011).

GROWTH RATES AND IMPORTANCE VALUES ALONG THE ELEVATIONAL GRADIENT AND DIVERSITY OF THE BKSFE

All 3 species showed the highest BAI and mean diameter growth rate at the middle of their respective distribution ranges, which supports our second hypothesis and suggests that current species distributions are centred in the area with climatic optima for the growth rates. Two of the 3 studied species (Manchurian fir and Korean pine) also showed the highest importance values (IV) here, likely indicative of their competitive advantage in the middle of their distribution ranges.

Importance values of studied canopy dominants varied between their respective lower and upper limits, suggesting that forest composition might be controlled by different factors. At their lower limits, both competition with broadleaved species (Table I) and the climate (see next subsection) might be limiting canopy abundance of the coniferous species and their range expansion towards lower elevations. In contrast, the high IV of the 3 studied species at their upper limits may be caused by the lack of broadleaved trees at high elevation (above 1100 m). This suggests a direct climate effect on forest structure through limiting distribution of broadleaved species towards higher elevations. Indeed, the annual average temperature for the upper limits of all 3 species was below -0.75°C (Jiang *et al.*, 2003), supporting the idea that low temperature is a limiting factor for upward expansion of broadleaved trees.

Variation in forest composition of the BKSFE pointed to the important role of climate controlling the structure of the studied ecotone. An increase in elevation was associated with a decline in diversity across all forest strata (Table II). Canopy dominants and undercanopy trees appeared to be moderately sensitive to changes in environmental conditions along the BKSFE. In both groups the commonness of tree species was high (55% and 57%, respectively) across the whole BKSFE. Importantly, no new species (*i.e.*, species absent at the lower limit of the ecotone) were recorded in either canopy or undercanopy strata at the upper limit of the BKSFE (Table I). This pattern was likely related to the gradient in trees' tolerance of low temperatures, which saw broadleaved species gradually disappearing from the canopy with increasing elevation (Table II). In contrast, shrubs and herbs were more sensitive to environmental variations, as indicated by the small proportion of species that reached the upper limit of the BKSFE, 36% of shrubs and only 22% of herbs. Considering the more open conditions (with deciduous trees) at the forest floor, it is not surprising to find that ground vegetation at the lower limit of the BKSFE contains more shade-intolerant species than ground vegetation at the upper limit (Xu *et al.*, 2004). Variation in the species composition of these strata might, therefore, be partly due to changes in the degree of canopy openness along the BKSFE.

GROWTH SENSITIVITY TO CLIMATE

Tree growth was more sensitive to climate at the lower than at the upper limits, as indicated by the pattern of mean sensitivity of tree-ring chronologies (Appendix III) and the

more frequently observed significant correlations between climate data and chronologies at low elevations as compared to other parts of the distribution ranges (Table III; Figures 3 and 4). Adequate soil water reserves at the end of the previous growing season might be important for tree growth at the respective lower limits. An increase in precipitation during the previous autumn was positively correlated with growth (Table III; Figure 4), and likely facilitated accumulation and storage of carbohydrates used for the next year's growth (Ettl & Peterson, 1995; Liang *et al.*, 2001). The soils on Changbai Mountain are rich in volcanic float stone with low water-holding capacity (Yu *et al.*, 2011), which might lead to a limiting effect of soil moisture on growth. Earlier dendrochronological studies have pointed to the summer water deficit as an important factor limiting the growth of Korean pine at its lower distribution limit (Yu *et al.*, 2011; 2013). In our study, we demonstrated that moisture conditions of both the current summer and the previous autumn affected Korean pine growth at its lower limit. In contrast, Manchurian fir at the same elevation did not show response to water stress, probably due to the species' lower evapotranspiration demand as a shade-tolerant sub-canopy tree. Positive effects of precipitation in the previous autumn have previously been shown for growth of subalpine conifers at the species' lower distribution limits in northern China (Gao *et al.*, 2013), including specifically for Korean pine on Changbai Mountain (Yu *et al.*, 2011).

At the species' upper limits, summer (June through August) temperature positively affected the growth of the Korean pine and Jezo spruce and had a similar though non-significant effect on Manchurian fir (Figure 4). Higher temperatures during the growing period probably increase activity of the cambial tissue, promoting the radial growth (Kozłowski, 1962). In addition, an increase in temperature might imply a longer growing season. As compared to the middle parts of their respective distributions, the growing season at the upper limits was 27 d shorter for both Manchurian fir and Jezo spruce and 28 d shorter for Korean pine (Chi, Zhang & Li, 1981). For Manchurian fir and Jezo spruce at their upper elevations (1750 and 1300 m, respectively), a positive effect of spring temperatures on growth (Table III; Figure 3) was apparently related to the thawing rate of the snowpack and the onset of the physiologically active period (Tranquillini, 1979; Peterson & Peterson, 2001; Deslauriers, Morin & Begin, 2003).

In Jezo spruce, growth was strongly and negatively correlated with spring precipitation both at the species' lower limit and at the middle of its distribution range (Table III; Figure 4). Two mechanisms could explain this relationship. First, since the snow starts to melt in April, higher precipitation during this period could cause waterlogging in the soil associated with a decrease in soil oxygen content and an increase in carbon dioxide concentration, reducing soil redox potential and subsequently limiting root and photosynthetic activity (Armstrong, Jackson & Brändle, 1994; Stokes, 2008). Jezo spruce requires higher soil drainage levels and has lower tolerance to waterlogged conditions as compared to Korean pine and Manchurian fir (Andersson, 2005). Second, the pattern might be due to the fact that precipitation in April falls as snow and heavier snowfalls would

imply delayed onset of both the budburst (Worrall, 1983; Hansen-Bristow, 1986) and the growing period (Kramer & Kozlowski, 1979). In general, our results were consistent with previous studies that showed a negative relationship between spring precipitation and Jezo spruce growth at the middle and lower limit of its distribution range on Changbai Mountain (Yu *et al.*, 2006; Gao, Wang & Zhao, 2011).

EFFECTS OF CLIMATE CHANGE ON DISTRIBUTIONS OF CANOPY DOMINANTS AND DYNAMICS OF THE BKSFE

Future climate conditions will likely be warmer in northeastern China. The PRECIS regional climate model has predicted increases in spring (3.1 °C), summer (4.7 °C), and autumn (3.6 °C) temperatures and minor increases (2%, 1%, and 0%, respectively) in precipitation during these seasons (Xu *et al.*, 2006). Climate changes would likely lead to shifts in the elevational positions of the climate optima for tree growth and subsequent changes in species and ecotone ranges. At their respective upper limits, growth of Manchurian fir may benefit from warming during autumn and spring, while warmer summers would likely enhance the growth of Korean pine and Jezo spruce. At their lower limits, the autumn climate may become less favourable for growth of the studied trees, since an increase in temperature and little change in precipitation would make this period drier, causing more severe drought stress.

The effects of future climate on regeneration may differ among species. Future drier summers may be important in limiting regeneration of Jezo spruce at its lower distribution limit. It is still unclear how changing climate would affect regeneration of Korean pine and Manchurian fir at their lower limits. The relatively high regeneration densities of these 2 species across the studied gradient (Figure 2a) suggests that their recruitment may be more resilient than growth to future climate variability.

Climate-driven shifts of the distribution range of dominants in the BKSFE (Korean pine and Jezo spruce) would result in an upward shift of the BKSFE. Our results provide empirical support of simulation studies that predict migration of the dominant conifer species on Changbai Mountain to higher elevations (Shao, 1996; He *et al.*, 2005). We speculate that in the future the elevational gradient currently covered by BKSFE is likely to contain a higher proportion of broadleaved species such as Amur linden (*Tilia amurensis*) in the main canopy and maples in the sub-canopy (e.g., *Acer barbinerve* and *Acer tegmentosum*), which are generally limited by low temperatures (Xu *et al.*, 2004).

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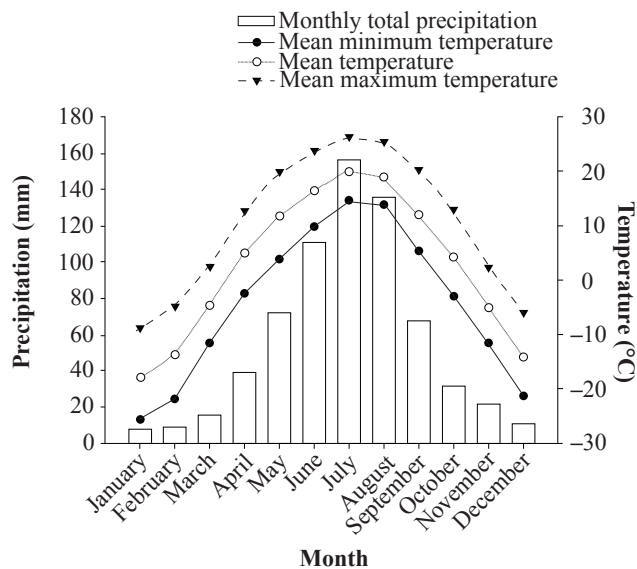
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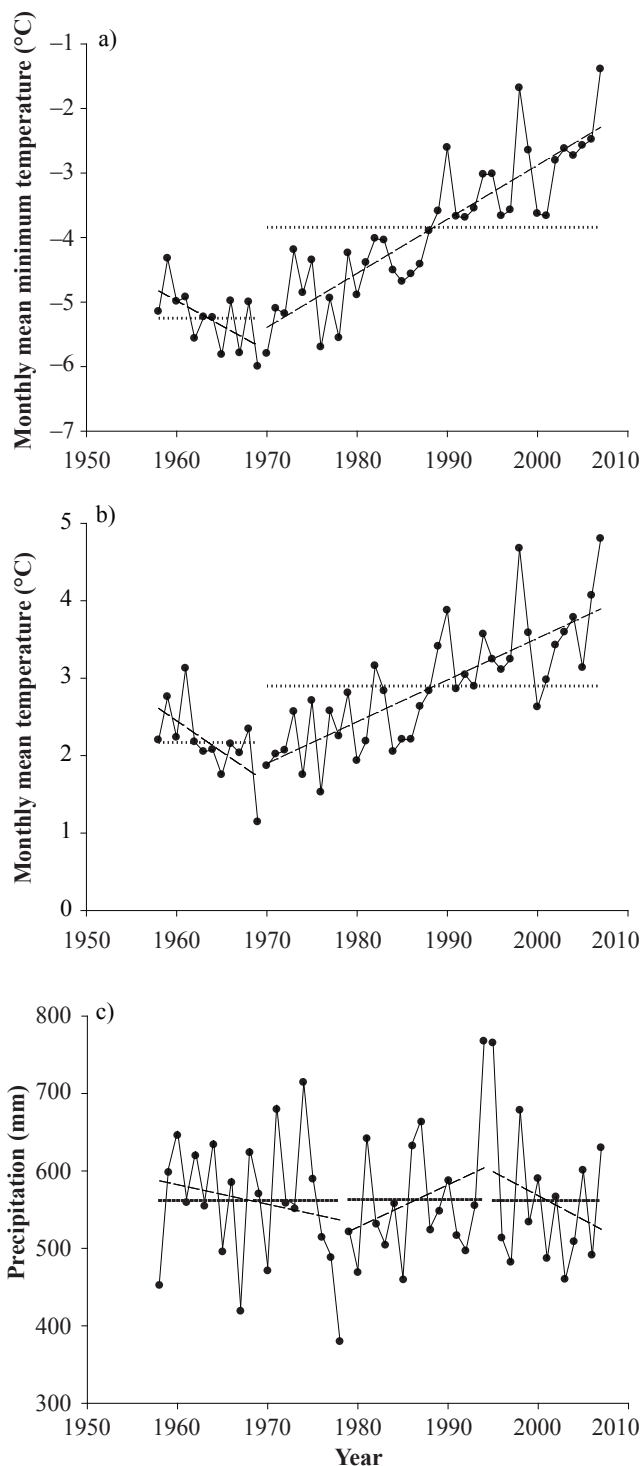
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Appendix I

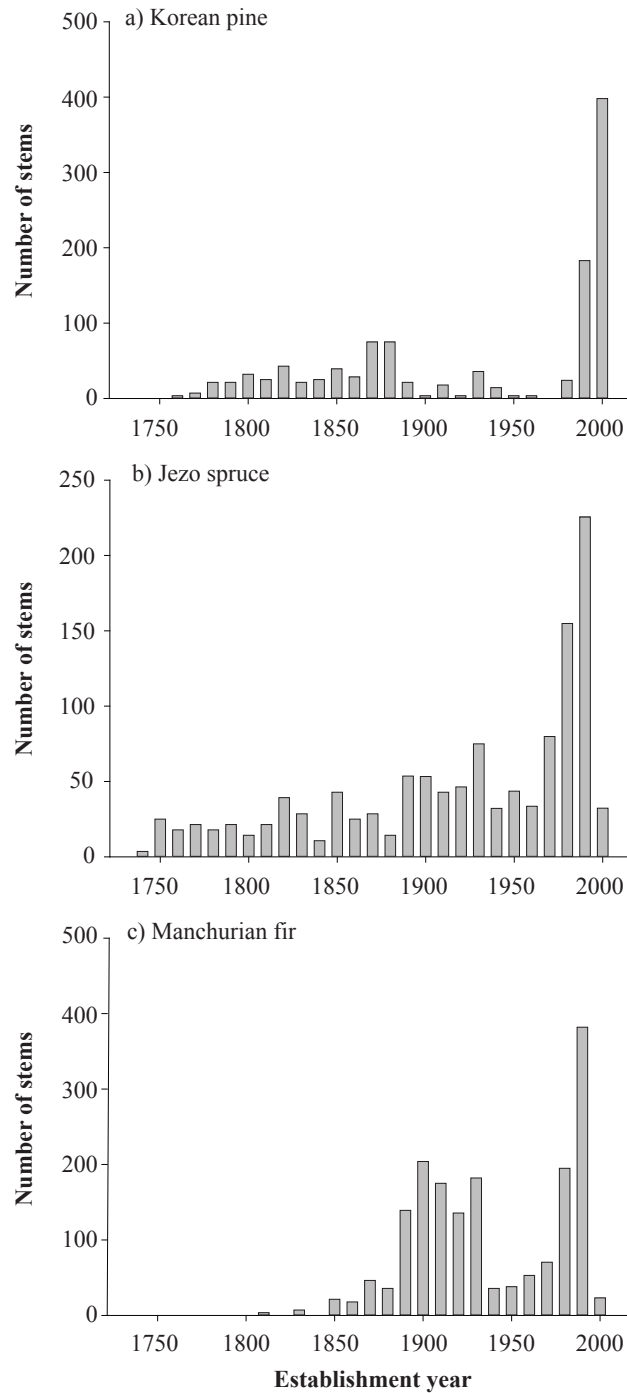


APPENDIX I, FIGURE 1. Long-term (1958–2007) patterns of precipitation and temperature at the Songjiang station in the Changbai Mountain, Northeastern China.



APPENDIX I, FIGURE 2. Dynamic of a) annual mean minimum temperature, b) annual mean temperature, and c) annual total precipitation from 1958 to 2007. Dashed line indicate climate trend. Break points were estimated by piecewise linear regression algorithm.

Appendix II



APPENDIX II, FIGURE 1. Age structure of the three species in the broadleaved-Korean pine/spruce-fir forest ecotone (BKSF) (Zhang *et al.*, 2014).

Appendix III

APPENDIX III, TABLE I. Chronology statistics for the studied species on the northern slope of the Changbai Mountain. Statistics refer to the residual chronologies and include mean ring width (MRW), mean sensitivity (MS), standard deviation (SD), signal-to-noise ratio (SNR), express population signal (EPS), and variance explained by the first principal component (PC1, %).

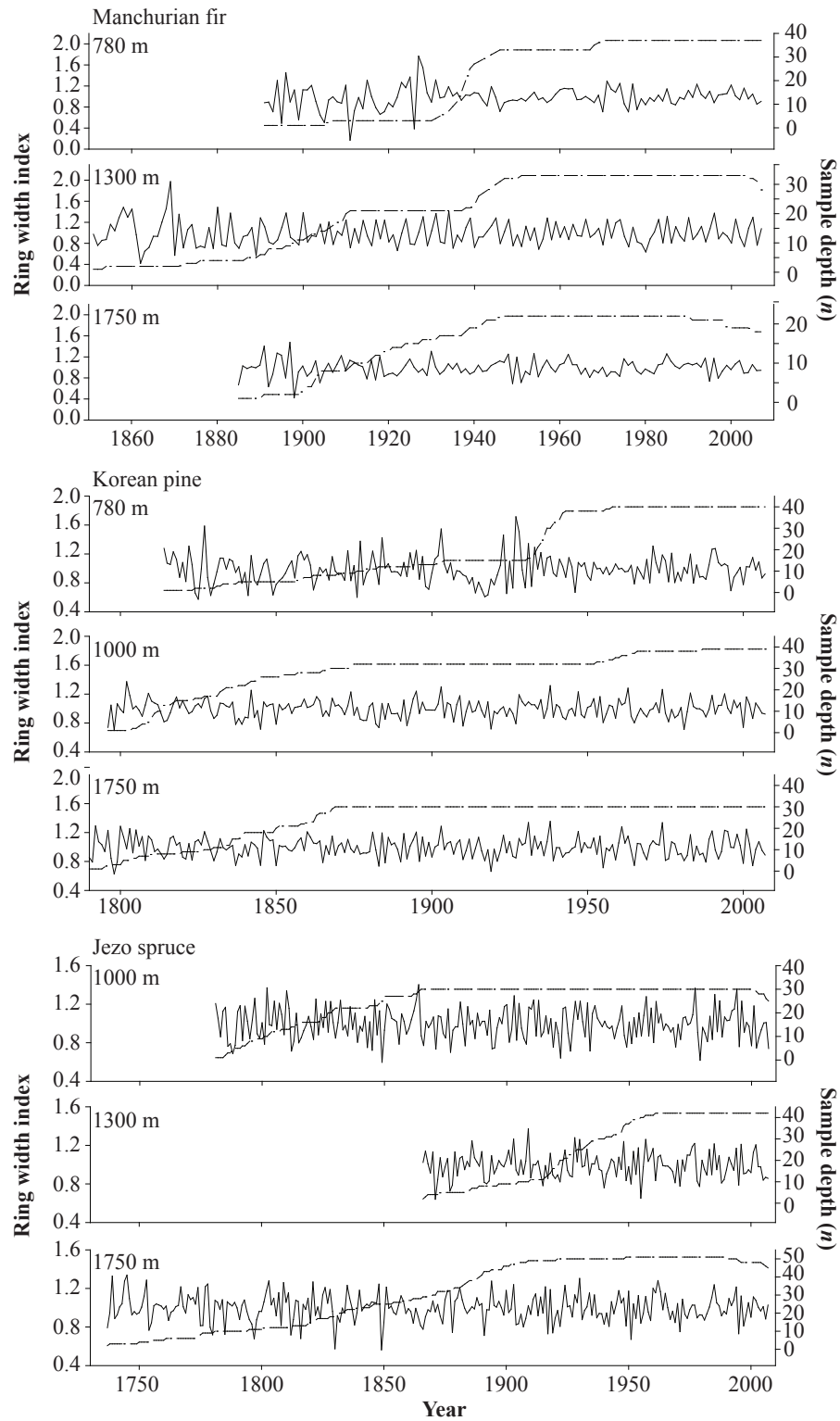
Site no	Species	Cores/trees	Chronology length	MRW (mm)	MS	SD	Common interval analyses for the period 1958–2007					
							EPS \geq 0.85	Mean correlation	Core/stem	SNR	EPS	PC1
1	<i>A. nephrolepis</i>	37/20	1889–2011	0.31	0.22	0.21	1936–2011	0.349	33/18	17.68	0.95	37.72
3	<i>A. nephrolepis</i>	33	1850–2007	0.48	0.22	0.23	1890–2007	0.480	28	25.80	0.96	40.38
4	<i>A. nephrolepis</i>	22/14	1884–2008	0.32	0.14	0.12	1922–2009	0.258	18/12	6.25	0.86	30.18
1	<i>P. koraiensis</i>	40/21	1810–2011	0.36	0.20	0.18	1929–2011	0.277	40/21	15.34	0.94	30.96
2	<i>P. koraiensis</i>	33	1795–2007	1.18	0.20	0.27	1814–2007	0.311	33	13.99	0.93	34.39
3	<i>P. koraiensis</i>	30	1788–2007	0.70	0.15	0.13	1829–2007	0.357	30	16.62	0.94	38.80
2	<i>P. jezoensis</i>	30	1780–2007	0.61	0.22	0.19	1796–2007	0.384	25	15.55	0.94	41.00
3	<i>P. jezoensis</i>	34	1865–2007	1.05	0.21	0.29	1917–2007	0.294	34	14.99	0.94	32.70
4	<i>P. jezoensis</i>	51/27	1654–2008	0.30	0.18	0.17	1780–2009	0.318	45/24	20.95	0.95	34.40

Appendix IV

APPENDIX IV, TABLE I. Soil gravimetric composition in two plots at the studied sites.

Site no	Survey year	Elevation (m)	Soil (plot 1/2)			
			Sand	Clay	Silt	pH
1	2012	780	78/54	10/22	12/24	4.3/4.1
2	2008	1000	72/76	14/13	14/11	4.0/4.8
3	2008	1300	70/74	16/12	14/16	3.1/3.4
4	2009	1750	74/70	16/14	10/16	3.8/3.8

Appendix V



APPENDIX V, FIGURE 1. Residual chronologies of the 3 species at each elevation and corresponding replications (number of trees sampled).

Appendix VI

APPENDIX VI, TABLE I. Post-hoc comparisons of regeneration density, mean basal area increment (BAI) in recent 10 y, and mean diameter growth rate of the 3 species among 3 elevations. For each species, contrasts marked with the same letters (a–c) are not significantly different (LSD test for *post hoc* pairwise comparisons, $p \geq 0.05$).

Variable	<i>A. nephrolepis</i>			<i>P. koraiensis</i>			<i>P. jezoensis</i>		
	780 m	1300 m	1750 m	780 m	1000 m	1300 m	1000 m	1300 m	1750 m
Regeneration density (trees·ha ⁻¹)	737 ± 441 a	1048 ± 197 a	565 ± 176 a	1000 ± 530 a	1050 ± 234 a	965 ± 231 a	221 ± 46 a	1446 ± 449 b	987 ± 109 b
BAI (cm ²)	0.59 a	1.9 b	0.58 a	0.65 a	15.03 b	4.87 c	2.37 a	7.22 b	0.73 c
Mean diameter growth rate (mm)	0.31 a	1.0 b	0.34 a	0.45 a	2.85 b	1.24 c	0.75 a	1.86 b	0.57 c