Population dynamics of *Betula ermanii* in response to climate change at the Changbai Mountain treeline, China

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To elucidate the mechanisms underlying the population dynamics of *Betula ermanii* in response to climate change over temporal and spatial dimensions, 310 quadrats were systematically sampled in 7 plots located in the upper treeline region on the north-facing slopes of Changbai Mountains. IKONOS images were used to identify the spatial distribution of *Betula ermanii* with the aid of a digital elevation model (DEM). Meteorological data were recorded in the field throughout the study area and collected from a nearby long-term weather station, to reconstruct the temperature and precipitation changes. We collected tree-ring samples from a total of 1197 *Betula ermanii* trees. The correlation coefficients between 14 eco-climate parameters (from 1953 to 2008) and the aggregated annual indices of population dynamics for each quadrat (totaling 310 quadrats) in the corresponding years were calculated via statistical analysis facilitated by GIS technology. The results show that the *Betula ermanii* population is more sensitive to changes in air temperature, than to change in precipitation. During the period when air temperatures increased at a slower pace, the *Betula ermanii* population steadily expanded via asexual reproduction and showed higher survival rate. During the period when air temperatures increased rapidly, the *Betula ermanii* population responded via rapid sexual reproduction and produced a large number of progeny.

Keywords. *Betula ermanii* population dynamics, climate change, Changbai Mountains, treeline shift, tree-ring analysis.

THE Alpine treeline is highly sensitive to climate variations, and its dynamics has often been regarded as critical indicator of climate change[1,2]. Temperature and precipitation are often considered the controlling factors, underlying the process of treeline dynamics[3,4]. According to the Sink limitation hypothesis, low temperatures limit tree growth at treelines[5]. The composition of sub-alpine communities and the elevation of the upper treeline are especially sensitive to the length of the growing season and relative warmth[6]. Temperature variations in late spring and throughout the growing season, clearly influenced the tree growth at the treeline in northern Quebec, Canada[7]. Precipitation and moisture conditions are also believed to be important factors shaping the structure and composition of the forest at the treeline in the front range of the European Alps[8]. The position of a treeline has long been recognized as primarily temperature driven[9]. The mean annual temperature and precipitation show the strongest connection to tree height at the upper treeline in the Andes, from Venezuela to central Argentina[10]. Moreover, the spatial pattern of treeline populations shows significant variation in response to temperature and precipitation changes[11].

The Changbai Mountains stretch along the border between China and North Korea (41°31′–42°28′N, 127°9′–128°55′E). In recent decades, the shift of treeline upward has been more evident on the north-facing slopes of the Changbai Mountains than that on other sides[12,13]. The relationship between *Betula ermanii* forest growth (in terms of population density and diameter at breast height (DBH)) and climate factors, such as temperature and precipitation, have been intensively studied via traditional quadrat surveys, and the results indicate that climate is the controlling factor of treeline dynamics in the region[14]. Changes in treeline were simulated using ecological models and GIS technology[15]; the area of *Betula ermanii* forest was estimated to increase from approximately 10,000 ha in the 1990s to 32,000 ha by 2050 (ref. 16), and the treeline was estimated to advance from 2070 m above sea level in the 1990s to 2110 m by the year 2290 (ref. 17). The dynamics of the *Betula ermanii* population at the treeline of the Changbai Mountains, actively responded to climate change according to tree-ring analyses and the sporopollen record[18]. Annual stem recruitment of the *Betula ermanii* population presents a significant response to the increase of air

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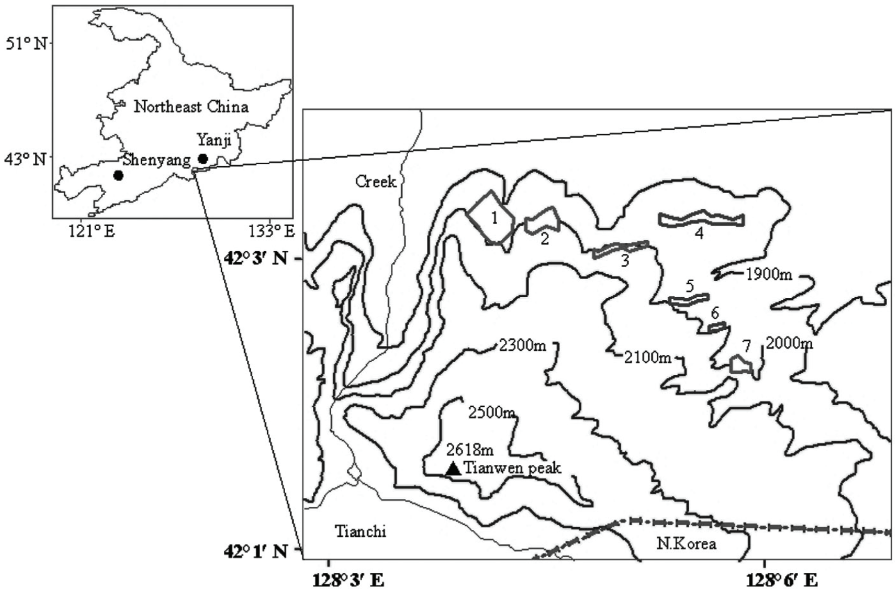

Figure 1. Sampling plots in the treeline on the north-facing slopes of the Changbai Mountains; 1, 2, 3, 4, 5, 6, and 7 denote the plot numbers and locations.

Table 1. Location of plots along the treeline on the north-facing slopes of the Changbai Mountains

Plot	Longitude (E)	Latitude (N)	Altitude (m)	Slope (°)	No. of transects	No. of quadrates	No. of trees
1	128.0658–128.0696	42.0522–42.0546	1972–2010	10–20	7	24	104
2	128.0725–128.0763	42.0530–42.0558	1968–2032	8–28	5	75	289
3	128.0803–128.0864	42.0502–42.0519	1994–2048	7–25	9	61	246
4	128.0880–128.0972	42.0539–42.0553	1938–1968	3–10	9	66	268
5	128.0891–128.0932	42.0448–42.0458	1963–1989	16–40	4	19	89
6	128.0937–128.0952	42.0418–42.0425	1970–1986	14–36	3	14	56
7	128.0962–128.0984	42.0371–42.0387	1979–2024	12–48	4	51	145

temperature, which leads to upward shift of treeline along with a population expansion[19]. As summer temperatures continue to rise and growing seasons have lengthened in recent years, the treeline upward shift and *Betula ermanii* expansion at the treeline are expected to continue[20].

However, limited research has been performed on the mechanisms underlying the expansion and growth strategy of *Betula ermanii* population dynamics in response to climate change[21,22]. This study aims to examine the mechanism underlying the spatial and temporal expansion of *Betula ermanii* at the treeline by analysing historical changes in the diameter structure of *Betula ermanii* trees sampled from 310 quadrats within 7 typical *Betula ermanii* forest stands and by evaluating the relationships between the diameter and climate change. The main objectives are to (1) reconstruct the historical record of age groups of *Betula ermanii* from diameter using tree-ring data and aggregate indices of yearly population dynamics from 1953 to 2008 based on field sampling data; (2) simulate 14 eco-climate parameters from 1953 to 2008 using meteorological data obtained from Tianchi station as reference; (3) evaluate the population dynamics responses to climate change over temporal and spatial dimensions using statistical analyses and spatial interpolations based on the relationships between the 14 eco-climate parameters and the aggregated indices of population dynamics; and (4) explore the spatial and temporal patterns of population dynamics in response to climate change.

Materials and methods

Remotely sensed data and topographic maps

We adopted the multispectral composite (Band 3 (0.63–0.70 μm), Band 1 (0.45–0.52 μm), Band 2 (0.51–0.60 μm)) of IKONOS imagery with a spatial resolution of 2.5 m of the Changbai Mountains treeline dated 1 October 2007. The images were geometrically and atmospherically corrected, before being georeferenced to the coordinate system of Beijing 54. More than 40 ground

Table 2. Age (y), diameter (x) and height (t) relationships among *Betula ermanii* in the 7 plots

	+HLJ KW•		Height <1.5 m	
Plot number	Shrubs	Trees	Shrub	Trees
1	$y = \exp(2.5736 + 0.1089x)$	$y = \exp(2.5732 + 0.1098x)$	$y = 6.4614t^{0.9258}$	$y = 6.4784t^{0.8510}$
2	$y = \exp(2.5745 + 0.0960x)$	$y = \exp(2.5833 + 0.1311x)$	$y = 7.0317t^{0.8116}$	$y = 6.5988t^{0.8516}$
3	$y = \exp(2.5642 + 0.1247x)$	$y = \exp(2.5427 + 0.1181x)$	$y = 7.3700t^{0.9142}$	$y = 6.5685t^{0.8590}$
4	$y = \exp(2.5838 + 0.1189x)$	$y = \exp(2.4983 + 0.1207x)$	$y = 5.9737t^{0.9358}$	$y = 6.6519t^{0.8674}$
5	$y = \exp(2.4998 + 0.1287x)$	$y = \exp(2.4562 + 0.1087x)$	$y = 6.6227t^{0.8740}$	$y = 6.8635t^{0.8612}$
6	$y = \exp(2.5828 + 0.1161x)$	$y = \exp(2.5442 + 0.1073x)$	$y = 6.1461t^{0.9060}$	$y = 6.4197t^{0.8390}$
7	$y = \exp(2.4762 + 0.1175x)$	$y = \exp(2.5578 + 0.1027x)$	$y = 6.2078t^{0.8614}$	$y = 6.5821t^{0.8533}$

control points (GCPs) were selected for the ground-truth survey. Supervised classification using the maximum likelihood method was applied to the images by establishing training areas using ENVI 5.1 image processing software. According to the ground-truth data, the overall classification accuracy was 85%. We identified 54.4 sq. km of *Betula ermanii* forest and 7.69 sq. km of tundra in the study area. By extracting contour lines from the topographic maps of the region at 1 : 10,000 scale, we established a digital elevation model (DEM) using the Triangular Irregular Network (TIN) function of ArcGIS10 (ESRI). The DEM was then processed to calculate the slopes and aspects of the region. We overlaid the slope and aspect maps on the map of *Betula ermanii* derived from the IKONOS images and extracted the distribution of *Betula ermanii* on the north-facing slopes with a slope <70°. The results show that *Betula ermanii* is primarily distributed between elevations of 1534 and 2098 m, whereas tundra is primarily distributed between 1948 and 2538 m.

Field sampling

Field surveys were conducted along 41 transects within 7 typical forest stands of *Betula ermanii* on the north-facing slopes of the Changbai Mountains between 2 July and 28 September 2009. The area of each stand varied from 6100 sq. m to 27,700 sq. m. Within each of the 7 stands, various transects, 30–40 m apart, were set-up perpendicular to the contour lines at the treeline. Depending on the length, each transect was divided into several 10 × 10 sq. m quadrats. The samples were collected from a total of 310 quadrats, which included 75 quadrats of shrubs, 97 quadrats of trees, and 138 quadrats of mixed trees and shrubs (Figure 1, Table 1).

Betula ermanii is the dominant species in the study area[23] and has two different forms: single-trunk tree (T) and shrub (S). For each tree in a quadrat, we recorded the DBH (approximately 1.2 m above the ground) and tree height. DBH was measured using a tape to a precision of 0.1 cm. Tree heights were measured with a tape to a precision of 0.01 m for trees ≤2 m. For trees higher than 2 m, the height was estimated with the plane table to a precision of 0.1 m. In addition, we recorded the geographic location, slope and altitude of each quadrat. The geographic location and altitude were determined by a TATO 108 GPS unit. The slope was measured with a DL-155V digital inclinometer (Table 1).

Tree-ring analyses

A total of 1197 trees/shrubs were selected for sampling for the tree-ring analysis (Table 1). Two or three samples were taken every one centimetre apart near the DBH of each tree to ensure that we had enough samples of good quality. Two cores were extracted from each sampling location on these trees/shrubs using increment borers. For trees or shrubs with DBH <3 cm and height ≤1.5 m, we collected the base disks 0.3 m above the ground from the tree/shrub recently damaged by various factors, such as wind, wildlife or accidental breakage caused by human activities. After eliminating the damaged samples, we collected a total of 546 cores and 830 disks for tree-ring analysis. All the cores and disks were dried at room temperature, mounted and polished using progressively fine sandpapers until growth ring boundaries were clearly visible. The samples were read by the LA-S Tape of Plant Growth Ring (0.2 billion pixels), an image-analysis system, and then cross-dated by the program COFFCHA[24,25]. To estimate the age of these sampled trees, regression analyses were conducted to establish the relationship between age and DBH for trees taller than 1.5 m and the relationship between age and height for trees shorter than 1.5 m according to *Betula ermanii* biological growth traits[26] using the classification methods described by Zhou *et al.*[23]. These relationships allowed us to reconstruct historic age structures for both trees and shrubs (Table 2). The annual stem recruitment of the *Betula ermanii* population from 1953 to 2008 was calculated from the field data (Figure 2).

Measurement and simulation of air temperature

We simulated temperature data based on meteorological records for 56 years (1953–2008) from the Tianchi station (2624 m altitude) located approximately 4 miles

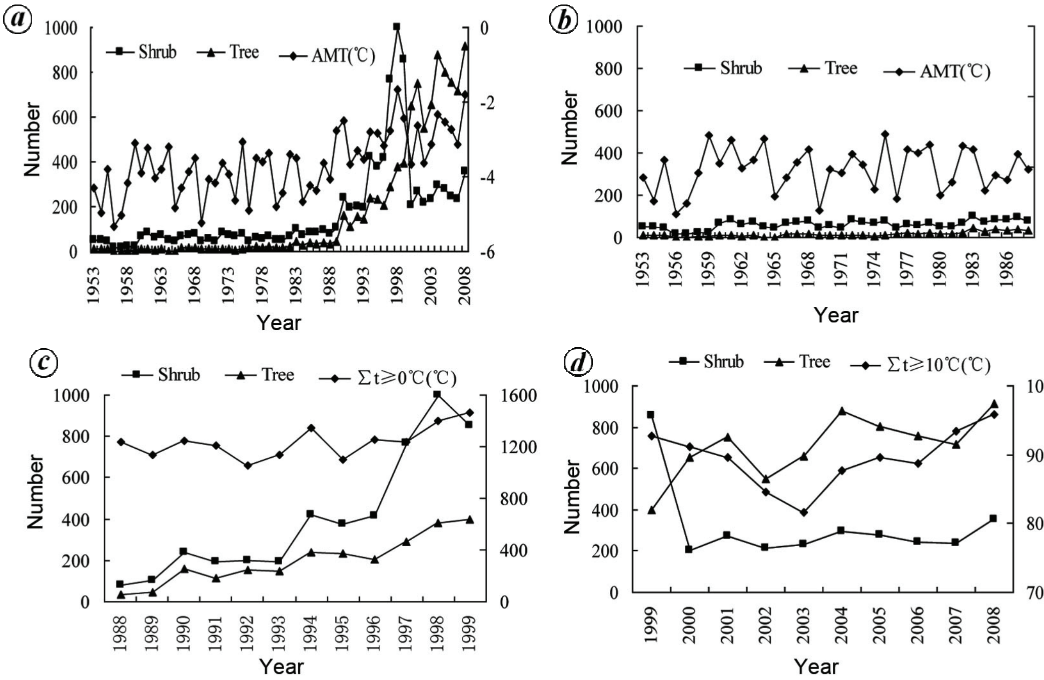

Figure 2. Annual stem recruitment of shrubs and trees for the periods from (***a***) 1953–2008, (***b***) 1953–1986, (***c***) 1988–1999 and (***d***) 1999–2008.

north of the study area. The annual mean lapse rate of air temperature on the north-facing slopes of Changbai Mountains were 0.32°C per $100\ \mathrm{m}^{-1}$ in January and 0.62°C in June (ref. 27). The following 14 eco-climate parameters were simulated using meteorological records of Tianchi station as a reference, including annual mean temperature (AMT); monthly mean temperature in January (MMTJA), May (MMTM), July (MMTJ) and September (MMTS); the precipitation in May (PM), July (PJ) and September (PS); precipitation from May to September (PMS), precipitation from June to August (PJA), accumulative temperature ($\sum t$) at 10°C and $\sum t$ at 0°C; warmth index (WI); and humidity index (HI). WI and HI were used to represent the moisture and heat conditions.

Statistical analysis

An aggregated index (I) was selected to describe the population dynamics. I was calculated as

$$I = S^2/\bar{x} - 1,$$

where S^2 is the variance of age structures and $\bar{x}$ is the mean of age structures.

The relationships between the 14 eco-climate parameters and the Annual I index (AII) from 1953 to 2008 were quantified using Pearson correlation coefficients for each of the two *Betula ermanii* forms for the 310 quadrats. Scatter diagrams of the correlation coefficients (Figures 3 and 4) were created, and the results were assessed for statistical significance. Specifically, the number of significant relationships ($P < 0.05$) and the number of extremely significant relationships ($P < 0.01$) were counted for each of the two life forms. The percentage of significant relationships and extremely significant relationships was calculated to quantify the closeness of the relationships between population dynamics and each of the eco-climate parameters (Table 3).

A Kriging interpolation was applied in ArcGIS to create two raster layers, one for shrubs and one for the trees, of the correlation coefficients for the AMT and AII from all the quadrats. We examined the spatial correlation between the distribution of the coefficients of AMT and AII and altitude by overlaying the two rasters with the DEM (Table 4).

An auto-correlation analysis was conducted by calculating Moran's I coefficients for each of the two raster layers (Table 4). Then, the correlation analysis was applied between the Moran's I coefficient and the slopes at the 7 plots. The correlation coefficients of the AMT and AII for shrubs and trees were classified into the following 6 different groups based on the level of significance of the coefficients: 1 (–0.54 to –0.37 ($P < 0.01$)), 2 (–0.37 to 0.27 ($P < 0.05$)), 3 (–0.27 to 0 (negative correlation)), 4 (0 to 0.29 (positive correlation)), 5 (0.29 to 0.37 ($P < 0.05$)) and 6 (0.37 to 0.62 ($P < 0.01$)). The total area and percentage of area for each group were calculated to determine the spatial scale of the population expansion (Table 5).

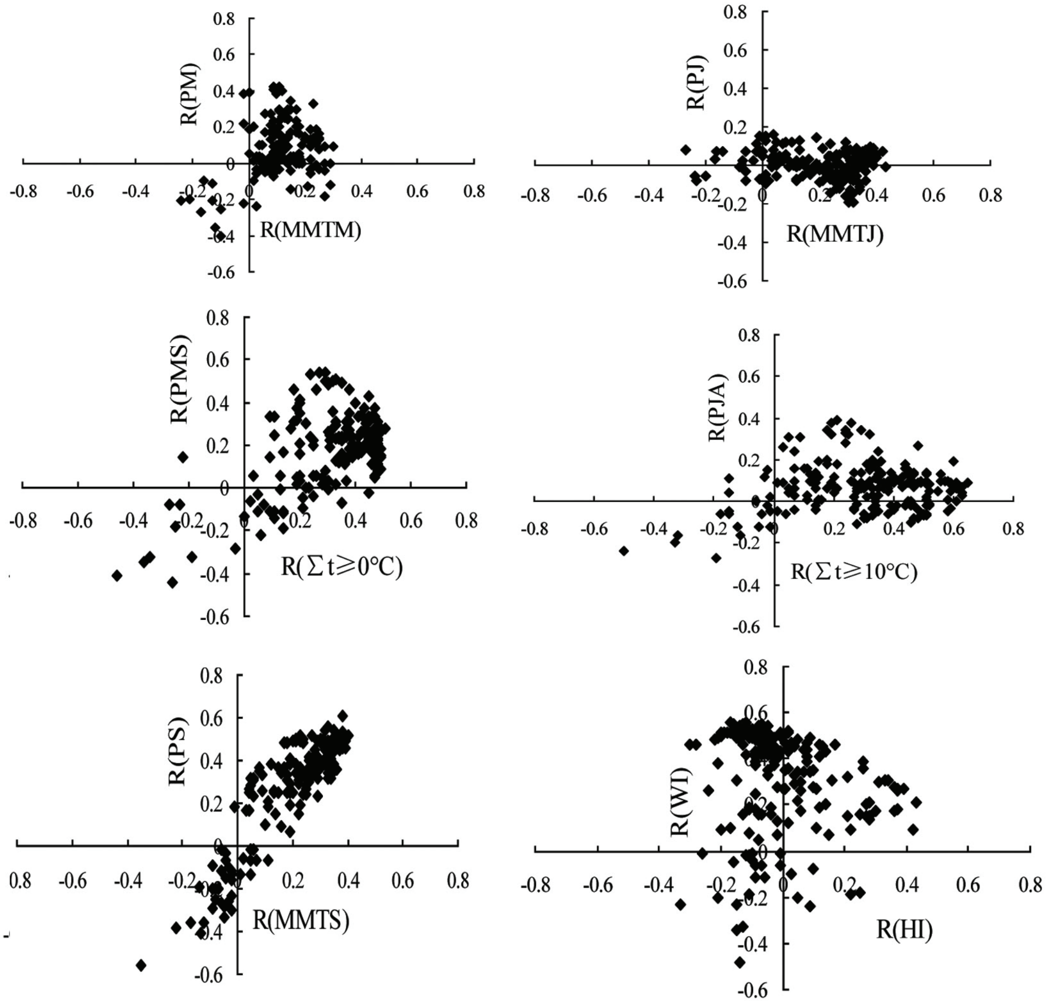

Figure 3. Scatter diagram of correlation coefficients between the AII for shrubs and the eco-climate preferences, including the monthly mean temperature in May R(MMTM), monthly mean temperature in July R(MMTJ), monthly mean temperature in September R(MMTS), precipitation in May R(PM), precipitation in July R(PJ), precipitation in September R(PS), precipitation from June to August R(PJA), precipitation from May to September R(PMS), warmth index R(WI), and humid index R(HI).

Results

Climate factors

The number of statistically significant coefficients ($P < 0.05$) between the temperature parameters and AII is higher than that between the precipitation parameters and AII (Table 3), which demonstrates that the population dynamics of the species were better correlated with temperature variation than precipitation variation. The most important temperature factor is AMT for trees, because 95% of the correlation coefficients are statistically significant ($P < 0.05$), whereas cumulative temperature ($\sum t \geq 0°C$) is the most important factor for shrubs, because 79% of the correlations are significant (Table 3). The numbers in Table 3 also show that the temperatures in July (MMTJ) and September (MMTS) are more important for trees than for shrubs, whereas September's precipitation (PS) is critical for both. These results clearly indicate that species population expansion is sensitive to both temperature and precipitation during their reproductive season in late summer, especially for trees.

Compared to shrubs, the AII of *Betula ermanii* trees respond differently to growing season's cumulative temperature. For trees, 95% of the relationship between $\sum t \geq 10°C$ and AII are statistically significant, whereas for *Betula ermanii* shrubs, only 64% of these relationships are significant (Table 3). On the other hand, 79% of the relationships between $\sum t \geq 0°C$ and AII are significant for shrubs, but only 66% are significant for trees (Table 3). These findings show that sexual reproduction is more sensitive than vegetative propagation to temperature variation during summer, whereas vegetative propagation or asexual reproduction of the shrubs is more sensitive to the cumulative heat condition throughout the entire growing season.

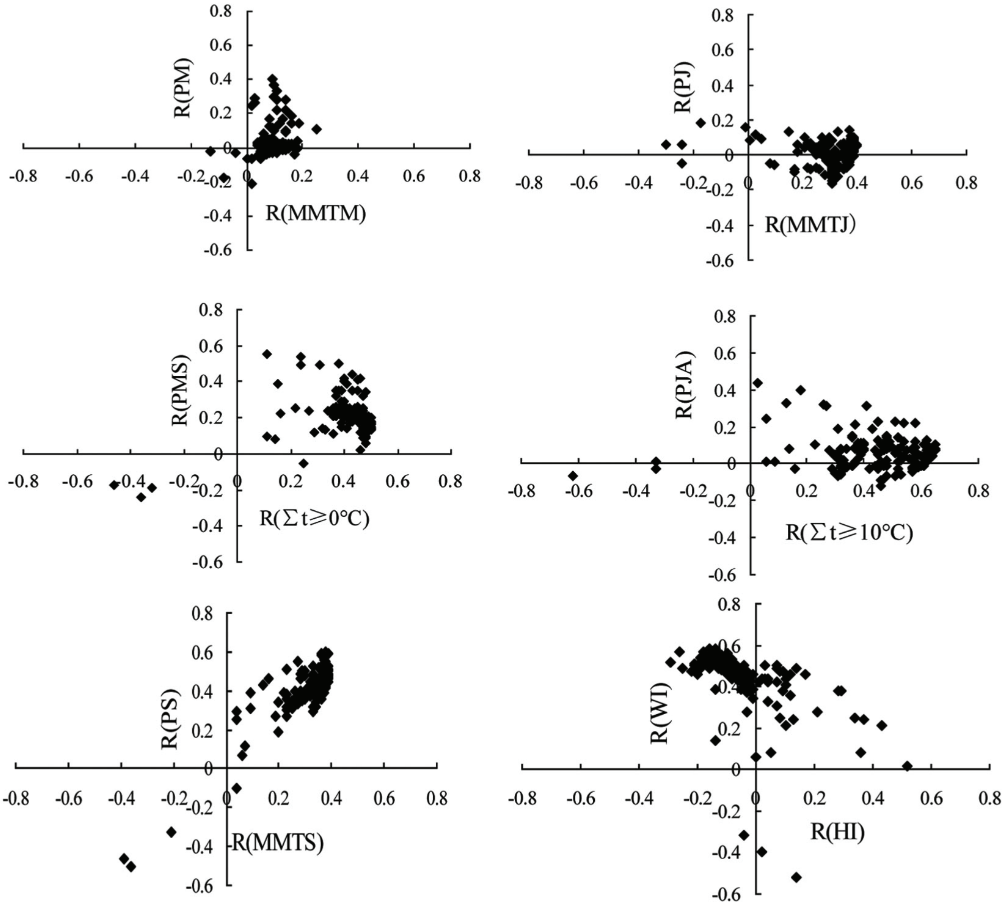

Figure 4. Scatter diagram of the correlation coefficients between the AII for trees and the eco-climate preferences, including R(MMTM), R(MMTJ), R(MMTS), R(PM), R(PJ), R(PS), R(PJA), R(PMS), R(WI), and R(HI).

Asynchronous responses to climate change from 1953 to 2008

The AMT gradually increased at 0.007°C/year between 1953 and 1988. The rising temperature accelerated from 1989 to 1999 at 0.034°C/year. Subsequently, AMT rose even faster (0.07°C/year) from 1999 to 2008 (Figure 2 *d*). Both tree and shrub populations gradually expanded, as the AMT slowly increased from 1953 to 1988 (Figure 2 *b*). However, shrubs reproduced faster than trees during this period. As AMT increased from 1988 to 1999, the *Betula ermanii* shrub populations expanded ten-fold while the tree population increased eight-fold during the same period (Figure 2 *c*). Since 1999, the shrub population decreased to nearly the same level as that observed a decade before, whereas the tree population increased as AMT continued to quickly rise from 1999 to 2008 (Figure 2 *d*).

Expansion along altitudinal and slope gradients

For the entire study area, the correlation coefficient (C–C) between altitude and AMT and AII is –0.15 ($P < 0.01$) for trees and –0.08 ($P < 0.01$) for shrubs (Table 4), which means that higher altitude may weaken the response of *Betula ermanii* to increase in AMT. The expansion of trees appears to be significantly hindered by higher altitude, with increases in slope from 22° to 48°. However, steeper slopes at higher elevation actually promote the response of shrubs to increases in AMT, as shown by their strong positive correlation (Table 4).

The results of auto-correlation analysis reveal strong spatial agglomeration of the population expansion for both *Betula ermanii* trees and shrubs according to the Moran's *I* coefficient (Table 4), which demonstrates that expansion generally occurs from parent plants at diferent rates in all directions. The spatial dispersal of shrubs generally shows stronger spatial auto-correlation than trees, because Moran's *I* is 0.95 for shrubs and 0.89 for trees. Along the slope gradient, shrubs exhibit extreme closeness to the parent plants at gentler slopes, especially at slopes from 10° to 22°, and become much more scattered and diminished as they move up the steeper slopes. Trees, on the other hand, continually showed strong family ties with increases in altitude along steeper slopes.

Slope itself exhibits a significant impact on *Betula ermanii*'s response to rising AMT. As steepness increases,

Table 3. Correlation coefficients between the aggregated indices of the diameter-class distribution and eco-climate parameters

Factor	Life form	Mean	STD	PPC (%)	PNC (%)	PSC (%)	PESC (%)
PM	S	0.08	0.15	78	22	11	7
	T	0.03	0.08	76	24	3	1
PJ	S	0	0.07	58	42	0	0
	T	0.01	0.07	69	31	0	0
PS	S	0.28	0.25	82	18	72	52
	T	0.43	0.13	98	2	97	83
PMS	S	0.17	0.17	86	14	25	11
	T	0.22	0.1	98	2	11	6
PJA	S	0.07	0.11	73	27	6	1
	T	0.06	0.08	81	19	3	1
MMTJA	S	0.11	0.09	92	8	1	0
	T	0.09	0.05	98	2	0	0
MMTM	S	0.11	0.09	94	6	1	0
	T	0.08	0.05	98	2	0	0
MMTJ	S	0.22	0.15	91	9	42	13
	T	0.28	0.1	97	3	51	20
MMTS	S	0.21	0.15	86	14	41	11
	T	0.32	0.1	100	0	81	30
AMT	S	0.32	0.18	95	5	72	54
	T	0.4	0.11	99	1	95	66
™W • °C	S	0.31	0.21	91	9	64	46
	T	0.44	0.18	99	1	94	68
™W • °C	S	0.37	0.24	94	6	79	69
	T	0.36	0.16	99	1	66	55
WI	S	0.32	0.22	88	12	67	56
	T	0.44	0.13	99	1	95	92
HI	S	–0.01	0.15	37	63	8	3
	T	–0.05	0.12	15	85	3	2

PPC, The percentage of positive correlations; PNC, The percentage of negative correlations; PSC, The percentage of significant correlation ($P < 0.05$); PESC, The percentage of extremely significant correlation ($P < 0.01$); MMTM, Monthly mean temperature in May; MMTJ, Monthly mean temperature in July; and MMTS, Monthly mean temperature in September.

Table 4. Correlation coefficients of the altitude and relationship between AMT and AII (C–C) and Moran's *I* along the slope gradient

			Slope			
	Life form	Entire study area	1–10°	10–22°	22–28°	28–48°
C–C	S	–0.08**	–0.13**	0.13**	0.31**	0.55**
	T	–0.15**	–0.23**	–0.20**	–0.22**	–0.55**
Moran's *I*	S	0.95**	0.90**	0.94**	0.25**	0.25**
	T	0.89**	0.88**	0.89**	0.78**	0.64**

the expansion of trees or shrubs significantly decreases. In Figure 5, each dot represents a quadrat of shrubs (*a*) or trees (*b*), in the study area. The highest densities of these dots in Figure 5 are located at slopes between 10° and 20°, which indicates that *Betula ermanii* survived best along gentler slopes, where trees showed the most positive response to rising AMT, although shrubs did not necessarily show positive responses. In areas with slopes lower than 30°, many of the shrubs negatively responded to rising AMT, but only a few trees exhibited the same behaviour. This finding reveals that shrubs showed significant shrinkage along the gentler slopes, which may indicate that they were outcompeted by tree expansion. The positive response of trees to increases in AMT was even stronger on steeper slopes with slope greater than 40° (Figure 5).

Spatial scales of the population expansion

The spatial scales of the population expansion were measured by the percent area covered by each of the 6 correlation groups of AII in response to AMT (Table 5).

Table 5. Percentage of the area covered by each of the 6 correlation groups of the AII in relation to the AMT for shrubs and trees

			Plot#						
Life form	Group	Study area	1	2	3	4	5	6	7
S	1	0.5	0	0.23	0	0	0	0.84	3.29
	2	0.5	0	0.6	0	0	0	0.84	2.47
	3	5.34	0	9.94	0.88	0	0	10.08	14.4
	4	21.43	27.23	31.33	15.86	9.47	2.8	58.82	27.98
	5	10.3	12.05	8.96	8.96	10.87	13.08	13.45	12.96
	6	61.93	60.71	48.95	74.3	79.66	84.11	15.97	39.09
T	1	0.02	0	0	0	0.09	0	0	0
	2	0.02	0	0	0.15	0	0	0	0
	3	0.22	0	0	0.3	0.19	0.63	0	0
	4	27.82	33.79	36.3	39.55	18.53	20.69	2.52	16.53
	5	19.79	14.61	20.78	26.27	19.66	2.19	63.87	12.19
	6	52.13	51.6	42.92	33.73	61.53	76.49	33.61	71.28

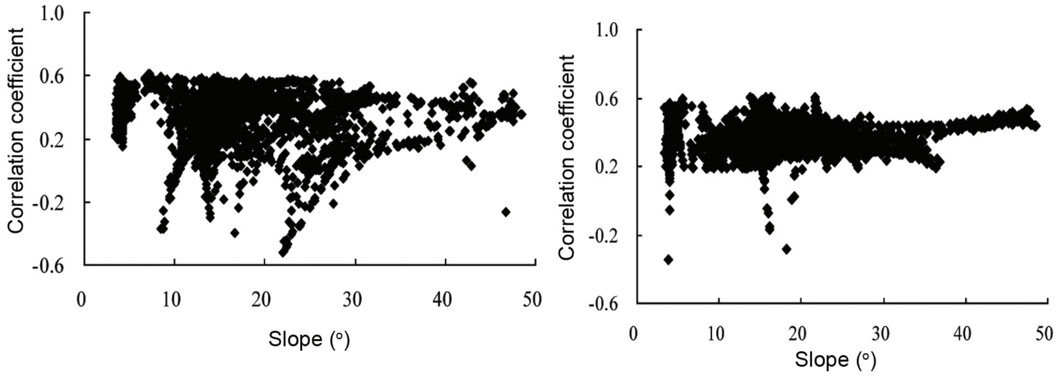

Figure 5. Correlations between AMT and AII along the slope gradient.

Betula ermanii shrubs and trees responded highly positively (groups 5 and 6) to AMT in more than 72% of the study area. Few negative correlations between AII and AMT are observed in the entire study area. In 61.93% of the area, the expansion of shrubs responded to AMT extremely well, whereas this value was only 52.13% for trees. Among the plots with different slopes, the percentage of area covered by each group of relationships varied, although with a similar pattern, with a positive response to AMT dominating the study area across the plots for both trees and shrubs. The only exception is the relatively even spatial coverage of these relationships in plot 7 with the steepest slope, which was a shrub-only quadrat.

Discussion

Many previous studies have shown that the Changbai Mountain treeline has shifted up in recent decades, especially on the north side of the mountains[14,16–18], because *Betula ermanii* is sensitive to both temperature and precipitation, especially during the growing season[15]. Our study shows that *Betula ermanii* expands as summer temperature and precipitation increases, by adjusting its reproductive strategies to adapt to the rate of climate change and overcome environmental resistance. This capability of *Betula ermanii* appears to be responsible for its wave-like expansion over time and space as the dominant species in the Changbai Mountain treeline.

Temporal patterns in response to climate change

An important finding of this study is that *Betula ermanii* trees are better correlated with $\sum t \geq 10°C$, whereas *Betula ermanii* shrubs respond better to $\sum t \geq 0°C$. Although total precipitation is not as important as overall temperature, September precipitation is critical for both trees and shrubs, because, it affects the reproduction of *Betula ermanii* at the critical phase of seed maturation and nutrient storage. Although studies have suggested that January temperature may affect the survival rate of the species[28] and that precipitation is also a controlling factor[4], we found that neither the January temperature nor July precipitation were important. We believe that the limited influence of winter temperatures on the survival of seeds or seedlings has been in gradual decline over the recent decades, because of the warming trend. July precipitation in the study area, which accounts for 44% of the annual total precipitation, meets the reproduction requirements of *Betula ermanii*.

Because of the different response of *Betula ermanii* shrubs to the increase in temperature over the past 7 decades, this life form spread slightly faster and wider than trees as the temperatures rose from 1953 to 1988. Asexual reproduction dominated because, shoots survived better than did individual tree seedlings in the cold winters during that period, because they were protected by the parent plants. Shrubs thrived with the rapid increase in temperature from 1988 to 1998 and expanded like ‘wild fire’ under the most favourable heat and moisture conditions (Figure 2 *c*). *Betula ermanii* trees also began to expand by producing large numbers of high-quality seeds under the same favourable physical conditions; moreover, winter cold was no longer a widespread threat to tree seedling survival. Seedlings are more competitive than are shrub shoots, because they do not rely on the parent plants for physical protection or nutritional support. Because of competition, the *Betula ermanii* shrub population crashed, while tree seedlings began to take over and became the dominant expansion force with the increases in temperature since 1999, as shown in Figure 4 *d*. In other words, *Betula ermanii* switched its reproductive strategy from asexual to sexual as the temperature rapidly rose.

Spatial patterns in response to topographic resistance

Topography has definitely complicated the positive response of *Betula ermanii* expansion to rising temperature. Higher altitudes hinder the expansion of trees more than the shrubs, and steeper slopes further amplify the difference (Table 4). Therefore, *Betula ermanii* shrubs show a more dominant expansion along the upper edges of the treeline at a higher elevation since vegetative propagation of shrubs can overcome low winter temperatures, because of physical protection by parent plants. However, behind the front lines, *Betula ermanii* trees leap and hold the gaps, especially in areas with steep slopes, because of their stronger seed dispersal flexibility and the increasing survival rate of seedlings under rising AMT. Trees not only occupy the gaps, but also spread by outcompeting the *Betula ermanii* shrubs around them, which explains the negative response of shrubs to rising AMT in areas with slopes lower than 30°. This finding may also explain why trees responded more positively to increases in AMT than the shrubs in the areas with lower elevation and steeper slopes (Figure 5). The pioneering role played by shrubs may account for the carpet style expansion along the upper edges of the treeline, because they can overcome the environmental resistance better than trees at a higher elevation. By exploiting the dispersal flexibility and high survival capability of seeds, the leap-and-hold expansion style of trees relies even more on rapid temperature increases, especially during summers, when seeds are maturing.

Vertical stratification has been reported as the epitome of horizontal zonation[29], and the results of this study suggest that the ecotone would widen as the ecosystem moves along altitudinal or latitudinal gradients with further increases in temperature, which may lead to a broader distribution of certain species that present different life forms and/or other species go extinct due to niche competition.

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