



Forest vegetation responses to climate and environmental change: A case study from Changbai Mountain, NE China

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ABSTRACT

The distribution of plant species has always been altered by changing climatic conditions. Nonetheless, the potential for species' range shift responses has recently become severely limited, as exceptionally fast temperature changes coincide with a high degree of anthropogenic habitat fragmentation. This study provides rare insights into the effects current temperature increases have on pristine temperate forest ecosystems, using the forests of Changbai Mountain, NE China, as a case study. On the northern slopes of the mountain at elevations between 750 and 2100 m, the composition of trees, shrubs and herbaceous species was recorded on 60 plots in 1963 and 2006/07. Multiple linear regression (MLR) and canonical correspondence analysis (CCA) were used to establish the response of plant diversity and plant distribution patterns to environmental conditions. Climatic factors proved important in explaining the spatio-temporal trends within the vegetation. The composition of dominant trees remained unchanged over the last 43 years, reflecting a very slow response of the forest canopy to environmental change. The composition of young trees, shrubs and herb species showed varied changes in the different forest types. A homogeneous species composition in the cohort of regenerating trees indicates an increased future uniformity in the mixed broadleaved and coniferous forest. The understorey vegetation of high elevation birch forests was invaded by floristic elements of the lower-elevation coniferous forests. Both these trends pose potential threats to forests plant diversity. Future research investigating climate change responses in forest canopy composition needs to be based on even longer timescales, while investigations in the near future need to pay particular attention to the changes in the distribution of rare and threatened herbaceous species.

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1. Introduction

Changes in climatic conditions and associated habitat patterns have always affected life on our planet (Kirilenko and Sedjo, 2007) and can even be seen as a key driver of evolution (Parmesan, 2006). During prehistoric times, plants could partly adjust to natural variations in temperature and precipitation by latitudinal and altitudinal shifts in their distribution ranges (Grayson, 2005; Tipping et al., 2008; Zenner and Berger, 2008). It was only with the onset of anthropogenic activities and the resulting strong increase in the fragmentation of natural habitats that the ability of plant species to adjust to changes in climatic conditions via shifts in their distribution ranges became severely limited (Liira et al., 2007; Malhi et al., 2008). Initially, fragmentation and isolation of habitats might protect their species from being out-competed by species better adapted to increases in temperature and precipitation

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changes (Kissling et al., 2008). Nonetheless, it can be expected that the fitness of many species will eventually decrease, leading to changes in the composition of the vegetation and to a decrease in local species diversity (Chust et al., 2006).

Changes in the vegetation can be expected to be particularly pronounced in forests, which represent not only the most phytodiverse terrestrial ecosystems (Kirilenko and Sedjo, 2007), but are also affected by drastic changes in their microclimatic conditions especially in small forest fragments (Rosenzweig, 1992). The effective long-term conservation of forest ecosystems therefore requires the protection of at least some large pristine forested tracts. These areas will not only allow the preservation of their unique flora and fauna, but can also form an important study base to gain insights into the inherent shifts in plant species compositions in reaction to climate change. These insights are crucial for the conservation and successful management of smaller forest patches, for example via the enrichment with rare species for which they provide suitable habitat conditions as a result of changed temperature and precipitation regimes (Lozano et al., 2007; Zenner and Berger, 2008). A thorough understanding of the reaction of forest

ecosystems to climate change is also of great importance in reforestation projects, for example in the selection of species suitably adapted to future climatic conditions (Harger, 1993).

Current anthropogenic changes in global temperatures are very rapid in comparison to most prehistoric temperature shifts (McCarty, 2001). It therefore remains unclear if and how well the vegetation can cope with these dramatic habitat alterations, even in areas where opportunities for range shifts are theoretically available. In comparison to plant formations dominated by herbaceous vegetation, forests are of particular concern due to the longevity of trees and the associated long timespan required for adaptations in the species composition of the forest canopy to take effect. This further underlies the importance of in-depth scientific research to assess the changes of forest ecosystems as a result of climate change.

A growing number of studies focus on long-term changes in the vegetation (Anderson and Inouye, 2001; Pauli et al., 2007) and associated changes in the carbon balance (Phillips et al., 1998; Clark, 2002) in reaction to climate change. Most of these studies nonetheless focus on the depleted flora of Europe or in the America, while long-term studies of vegetation change from the phyto-diverse Asian region remain very scarce. The Changbai Nature Reserve (CNR) in NE China on the border near North Korea provides a rare opportunity to conduct such an investigation. The reserve has been established in 1960 to protect China's last remaining large areas of pristine temperate forests, including mixed broad-leaved and Korean pine forest (Yang and Xu, 2003; Sang and Bai, 2009). The vegetation of the reserve was studied in detail in the early 1960s (Chen, 1963; Chen et al., 1964). As summer temperatures in Northeast China have increased by about 0.15 °C per decade over the last 50 years (Li et al., 2005), it is not surprising that changes were observed in plant diversity since this first survey (Bai et al., 2008; Wang et al., 2010). Using data collected during a re-surveying campaign in 2006 and 2007 of the plots and forest types sampled in the 1960s, we now aim to establish the nature and strength of links between environmental factors, including both climatic and edaphic parameters, and the spatial and temporal changes in the forest vegetation. In our research, we distinguish between the different forest types occurring on the northern slopes of Changbai Mountain and the different vegetation strata occurring in these forests.

2. Material and methods

2.1. Study area

The Changbai Nature Reserve is located in the Jilin Province, NE China. The climatic conditions within the CNR are influenced by monsoon rains. The vegetation in the reserve therefore experiences dry, windy springs, short rainy summers, cool autumns with a high frequency of fog, and long, cold winters. While the temperature decreases, the precipitation generally increases with increasing elevation (Chi et al., 1981).

Following this climatic gradient, the CNR is characterized by a clear altitudinal zonation of the vegetation (Chen et al., 1964; Zhao et al., 2004; Wang et al., 2010). Areas below 1100 m are covered in mixed coniferous and broad-leaved forests (MCBF) associated with a large variety of co-dominant tree species, including *Pinus koraiensis* Sieb. and Zucc. 1842, *Acer mono* Maxim. 1857, *Tilia amurensis* Rupr. 1869, *Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai 1932 and *Quercus mongolia* Fish. ex Ledeb. 1850. Between 1100–1500 m, mixed coniferous forest (MCF) dominated by *P. koraiensis*, *Picea jezoensis* Carr. var. *microsperma* (Lindl.) Cheng and Fu 1861, *Abies nephrolepis* (Trautv.) Maxim. 1866 and *Larix olgensis* Henry 1915 forms the main forest type. Sub-alpine coniferous forests (SCF) cover the slopes between 1500 and 1800 m. Dominant tree species in these forests are again *P. jezoensis*, *L. olgensis* and *A. nephrolepis*. The highest forests growing at altitudes between 1800 and 2100 m are birch forests (BF) dominated by *Betula ermanii* Cham. 1831. Elevations above 2100 m are covered in tundra vegetation composed of *Rhododendron aureum* Georgi 1772, *Rh. redowskianum* Maxim. 1859, *Vaccinium uliginosum* L. 1839 and other low shrub and grass species. This study focuses on changes in the forest vegetation, covering the entire range of forest communities between 800 and 2100 m on the Northern slopes of Changbai Mountain. Individual survey plots are located between 127°55'E and 128°08'E and 42° 03' N and 42° 23' N (Fig. 1).

2.2. Vegetation surveys

Detailed vegetation surveys were conducted in plots representing the four main forest types occurring in the study area. The

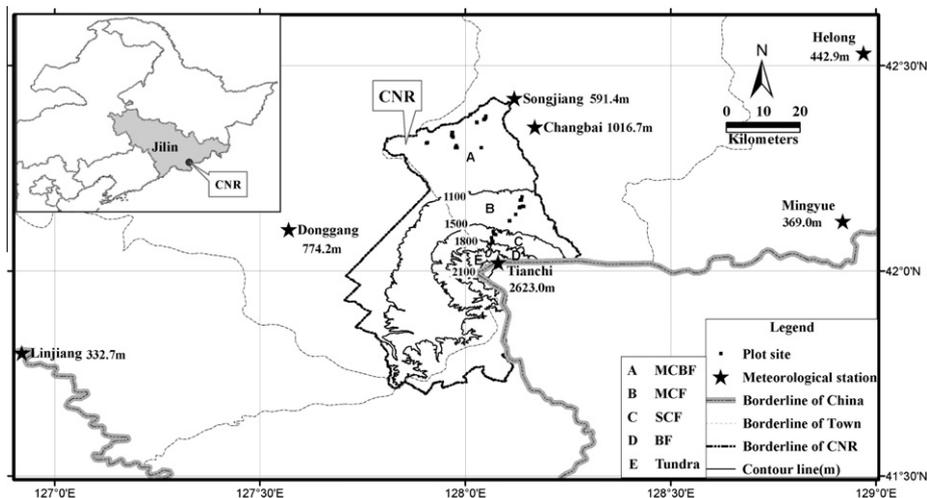


Fig. 1. Distribution of vegetation zones and sample plots on the northern slopes of the Changbai Nature Reserve (MCBF: mixed coniferous and broad-leaved forests; MCF: mixed coniferous forest; SCF: sub-alpine coniferous forest; BF: birch forests; D: alpine tundra). (A) mixed coniferous and broad-leaved forest zone (MCBF) (below 1100 m a.s.l.), dominated by *Pinus koraiensis*, *Acer mono*, *Tilia amurensis*, *Ulmus davidiana* var. *japonica*, *Quercus mongolia*, etc.; (B) mixed coniferous forest zone (MCF) (1100–1500 m a.s.l.), dominated by *P. koraiensis*, *Picea jezoensis* var. *komarovii*, *Abies nephrolepis*, *Larix olgensis* var. *changpaiensis* etc.; (C) sub-alpine coniferous forest zone (SCF) (1500–1800 m a.s.l.), dominated by *Picea jezoensis* var. *komarovii*, *Larix olgensis* var. *changpaiensis*, *Abies nephrolepis*; (D) birch forest zone (BF) (1800–2100 m a.s.l.), dominated by *Betula ermanii*; and (E) tundra zone (upon 2100 m a.s.l.), dominated by *Rhododendron aureum*, *Rh. redowskianum*, *Vaccinium uliginosum* var. *alpinum* etc.

survey methods closely follow the approach described in Chen (1963) and Chen et al. (1964) to allow a direct comparison of survey results between the different sampling periods. The first round of surveys had been completed between June and August 1963, while the second round of sampling was conducted between July and August in both 2006 and 2007. In the repeat sampling, all 20×20 m plots were located at the same elevation, landform, slope and exposition, and whenever possible at identical location to those in 1963 sampling. Of the 68 plots investigated in 1963, a total of 60 plots could be relocated with a high level of confidence. At least two plots were established at each 100 m altitudinal interval, with a minimum of eight plots located within each forest type.

All tree and shrub species were recorded on the entire plot. The shrub comprised all woody plant species reaching a maximum height of less than 3 m. To allow greater reliability of the vegetation surveys, all plots were divided into four 10×10 m subplots and results from these individual subplots were then combined. Living trees with a height of more than 1.3 m were recorded with their respective diameter at breast height (DBH). All trees with a DBH ≥ 8 cm were considered to belong to the main tree cohort, while young trees with a DBH < 8 cm were classified as the regenerating tree cohort (Hao, 2000). This differentiation allowed a separate analysis of the current forest structure represented by the composition of the mature trees, as well as future trends in the tree species composition.

The herbaceous vegetation was recorded on four sub-plots of 1×1 m, which were located randomly within each plot. In both shrub and herb layers, all vascular plant species were recorded with their abundance, coverage and average height.

2.3. Soil sampling and analysis

Three to four soil profiles were randomly located within the wider vicinity of the vegetation plots at each 100 m altitudinal interval. At these profiles, soil samples were taken in 10 cm depth intervals using metal rings to extract three mini-cores for each depth. The replicate samples were then analyzed following the methods described by Chen (1963). The potassium dichromate method was used to evaluate the soil organic matter (SOM) content; the alkali N-proliferation method was used to analyse the amount of plant available nitrogen (N); and Mo–Sb colorimetric measurements established the plant-available phosphorus (P). For further analyses and to limit the effects of local heterogeneities, mean contents for SOM, N and P were calculated for each 100 m altitudinal level. Following Chen (1963), both mean values for the first 10 cm of the soil profile (SOM_{0–10}; N_{0–10} and P_{0–10}) and overall mean values over the entire depth of the soil profiles (SOM_{All}; N_{All} and P_{All}) were calculated separately.

2.4. Data analysis

2.4.1. Vegetation data

The vegetation survey data were transformed into altered importance values (AIVs). AIVs provide an indication of the relative contribution of each plant species towards each vegetation layer and plot (Ma et al., 1995). The sum of AIVs for all plant species per layer and plot equals 100%. AIV values comprise three measurements: cover (for trees: dominance, based on the DBH of each tree), abundance and mean height of each species in relation to the sum of cover (dominance), abundance and height of all species in the respective vegetation stratum. In the case of trees, the data were further differentiated into main and regenerating tree cohort.

The calculations for the altered importance value of species j of the s species per layer and plot were based on the following formula:

$$AIV_j = 100 \times \left[\left(\frac{\%C_j}{\sum_{j=1}^s \%C_i} \right) + \left(\frac{A_j}{\sum_{j=1}^s A_i} \right) + \left(\frac{H_j}{\sum_{j=1}^s H_i} \right) \right] / 3,$$

where %C = percentage cover (for tree species: dominance), A = abundance, H = height.

The number of species per plot (S) was used to represent the α -diversity in regression models. Again, differentiation was made between main trees and the tree regeneration cohort, as well as between the shrub and herb layer.

2.4.2. Climate data

As detailed climatic data from individual plots was unavailable for both survey periods, regression models based on the equations outlined in Chi et al. (1981) were employed to model the climatic conditions of individual plots. The data provided by three climatic stations in the vicinity of Changbai Mountain (Fig. 1) were used to establish the regression equations describing the changes in climatic conditions with increasing elevation.

In the calibrations of the original equations by Chi et al. (1981), the coefficients b (Table 1) were assumed to have remained constant, as the physical mechanisms underlying the altitudinal variations in climatic factors are unlikely to have changed. The coefficients a in the regression equations, which relate directly to the recorded changes in climatic conditions, were adapted using the 1958–1963 and 2001–2006 mean climatic conditions of the Songjiang meteorological station (591 m; $128^\circ 15' E$, $42^\circ 32' N$; see Fig. 1), respectively. This resulted in two separate sets of climate factor equations to calculate the mean temperature (T), annual precipitation (RIA) and cumulative temperature ($\geq 5^\circ C$) (ACT5, Table 1) in the years prior to both vegetation surveys. The two equations were validated using data from the Linjiang (333 m; $126^\circ 55' E$, $41^\circ 48' N$) and Donggang (774 m; $127^\circ 57' E$, $42^\circ 06' N$) climatic stations. As the resulting relative errors in the validation were below 7% (range: -6.65% to $+4.32\%$), we used these two regression equations as suitable approximations to model the changes in climatic conditions along the altitudinal gradient (Table 2).

2.4.3. Links between vegetation and environmental factors

Significant correlations within the set of predictors in multiple linear regressions and constrained ordinations distort the resulting models. To avoid this problem, we replaced the original environmental parameter set with principal components (PCs) based on a Principal Components Analysis (PCA) of all z -transformed environmental parameters. The links between plant diversity and the environmental parameters were analyzed using multiple linear regression models including the PCs as predictor variables and the number of plant species per plot in the different strata as dependent variables. Forward stepwise calculations were selected and steps calculated until all parameters significantly contributing towards the model were included.

In a second step, a set of Canonical Correspondence Analyses (CCA) was calculated to gain insights into the relationship between spatial and temporal plant species turnover and the environmental parameters. The CCA ordination only represents the proportion of the variation in distribution and abundance (AVI) of plant species which is explained by a set of environmental parameters. As the resulting ordination plot showing the relationship between plant species and environmental parameters is again based on an MLR, PCs rather than the original environmental parameters were used in this analysis, too. The CCA was carried out using ECOM 1.37 (Henderson and Seaby, 2001), while the MLR models were calculated in STATISTICA 6.1 (StatSoft, 1984–2003).

Table 1

Original (Chi et al., 1981) and revised regression equations used to model changes in climatic factors with increasing elevation.

| Climate factor | Regression equation type | Original <i>R</i> | Coefficient <i>b</i> | Coefficient <i>a</i> | | | Relative error (%) | |
|----------------|----------------------------|-------------------|----------------------|----------------------|-----------|-----------|--------------------|-------|
| | | | | Original | 1960s | 2000s | 1960s | 2000s |
| TEM | $\bar{T} = a + bH$ | -0.9798 | -0.005115 | 6.4085 | 5.5350 | 6.5950 | -5.71 | -5.63 |
| RIA | $R = ae^{bH}$ | 0.9965 | 0.0003536 | 530.2589 | 562.9845 | 504.9523 | -4.23 | -6.65 |
| ACT5 | $\sum \bar{T}_5 = ae^{bH}$ | -0.9807 | -0.0007359 | 4117.2969 | 4027.9516 | 4380.4321 | -2.11 | 2.46 |
| HUM | $K_W = a + bH$ | 0.9996 | 0.003048 | -0.02281 | -0.3426 | -0.7226 | 4.20 | 4.32 |

TEM: annual mean temperature, RIA: annual precipitation, ACT5: cumulative temperature ($\geq 5^\circ\text{C}$), HUM: humid index, H: altitude (m).**Table 2**

Change in climate factors with increasing altitude on the northern slope of Changbai Mountain.

| Elevation | Temp | RIA | ACT5 | HUM | Bulk density | SOM | N | P | SOM | N | P |
|-----------|----------------------|--------|----------------------|------|----------------------------|-------------------------------------|-------------------------------------|-------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| (m) | ($^\circ\text{C}$) | (mm) | ($^\circ\text{C}$) | | (g/cm^3) | (0–10) (g/m^3) | (0–10) (g/m^3) | (0–10) (g/m^3) | (all) (g/m^3) | (all) (g/m^3) | (all) (g/m^3) |
| 1963 | | | | | | | | | | | |
| 800 | 1.44 | 747.1 | 2235.7 | 2.1 | 0.88 | 10030 | 36.75 | 9.39 | 9475 | 38.50 | 19.91 |
| 900 | 0.93 | 773.9 | 2077.1 | 2.4 | 0.88 | 14987 | 71.97 | 7.35 | 10789 | 42.90 | 10.67 |
| 1000 | 0.42 | 801.8 | 1929.7 | 2.71 | 0.88 | 17834 | 53.08 | 8.98 | 12135 | 42.17 | 16.56 |
| 1100 | -0.09 | 830.7 | 1792.8 | 3.01 | 0.81 | 5700 | 14.58 | 6.25 | 4124 | 11.00 | 5.38 |
| 1200 | -0.6 | 860.6 | 1665.6 | 3.32 | 0.81 | 12419 | 28.13 | 5.63 | 7858 | 17.97 | 10.19 |
| 1300 | -1.11 | 891.5 | 1547.4 | 3.62 | 0.81 | 3820 | 27.08 | 3.17 | 2803 | 10.67 | 5.60 |
| 1400 | -1.63 | 923.6 | 1437.6 | 3.92 | 0.81 | 2595 | 12.50 | 3.75 | 3159 | 19.50 | 4.67 |
| 1500 | -2.14 | 956.9 | 1335.6 | 4.23 | 0.73 | 3339 | 28.13 | 3.38 | 3875 | 21.90 | 6.02 |
| 1600 | -2.65 | 991.3 | 1240.9 | 4.53 | 0.73 | 10182 | 14.67 | 2.48 | 7217 | 18.86 | 3.81 |
| 1700 | -3.16 | 1027 | 1152.8 | 4.84 | 0.73 | 8753 | 5.63 | 3.38 | 7765 | 18.25 | 6.69 |
| 1800 | -3.67 | 1063.9 | 1071.1 | 5.14 | 0.67 | 2164 | 24.00 | 2.40 | 2177 | 32.24 | 4.05 |
| 1900 | -4.18 | 1102.2 | 995.1 | 5.45 | 0.67 | 9658 | 12.00 | 3.60 | 10063 | 10.05 | 3.91 |
| 2000 | -4.70 | 1141.9 | 924.5 | 5.75 | 0.67 | 8832 | 42.00 | 1.92 | 5449 | 20.10 | 4.80 |
| 2006 | | | | | | | | | | | |
| 800 | 2.5 | 670 | 2431.3 | 1.72 | 0.88 | 10162 | 40.75 | 5.59 | 8841 | 38.06 | 8.63 |
| 900 | 1.99 | 694.2 | 2258.8 | 2.02 | 0.88 | 13181 | 63.87 | 10.30 | 9692 | 51.89 | 11.74 |
| 1000 | 1.48 | 719.2 | 2098.6 | 2.33 | 0.88 | 10377 | 62.71 | 8.66 | 10657 | 41.35 | 14.85 |
| 1100 | 0.97 | 745 | 1949.7 | 2.63 | 0.81 | 3432 | 22.68 | 2.54 | 2868 | 12.69 | 7.87 |
| 1200 | 0.46 | 771.9 | 1811.3 | 2.94 | 0.81 | 6793 | 7.60 | 4.22 | 4718 | 5.11 | 6.61 |
| 1300 | -0.05 | 799.6 | 1682.8 | 3.24 | 0.81 | 6476 | 16.43 | 4.25 | 4950 | 7.35 | 5.01 |
| 1400 | -0.57 | 828.4 | 1563.4 | 3.54 | 0.88 | 6977 | 32.85 | 2.19 | 7391 | 14.98 | 1.92 |
| 1500 | -1.08 | 858.2 | 1452.5 | 3.85 | 0.73 | 6799 | 34.61 | 4.15 | 7804 | 37.88 | 4.90 |
| 1600 | -1.59 | 889.1 | 1349.5 | 4.15 | 0.73 | 6863 | 9.75 | 2.68 | 8449 | 12.16 | 4.07 |
| 1700 | -2.1 | 921.1 | 1253.7 | 4.46 | 0.73 | 7836 | 22.45 | 3.83 | 9365 | 31.75 | 6.02 |
| 1800 | -2.61 | 954.3 | 1164.8 | 4.76 | 0.67 | 5946 | 20.78 | 3.02 | 5353 | 21.40 | 4.45 |
| 1900 | -3.12 | 988.6 | 1082.1 | 5.07 | 0.67 | 8466 | 31.20 | 3.38 | 6759 | 25.62 | 4.13 |
| 2000 | -3.64 | 1024.2 | 1005.4 | 5.37 | 0.67 | 8552 | 34.66 | 3.68 | 7870 | 31.77 | 4.38 |

TEM: annual mean temperature, RIA: annual precipitation, ACT5: cumulative temperature ($\geq 5^\circ\text{C}$), HUM: humid index, SOM: Soil organic matter content, N: plant-available nitrogen, P: plant-available phosphorus, (0–10): first 10 cm soil depth, (all): entire soil profile.

3. Results

In 1963, a total of 213 vascular plant species representing 63 families was recorded. The respective species lists comprise 37 trees, 32 shrubs and 144 herbaceous species. In 2006/07, the plant diversity had decreased to 190 vascular plant species which represented 59 families. The decrease in diversity was limited to herb layer, which decreased to 119 species, while trees and shrubs actually increased by one species, each, in comparison to the 1963 dataset.

3.1. Environmental parameters and principal components

A high degree of correlations was observed within the environmental parameter dataset, and accordingly, the PCA (Fig. 2) produced only two PCs with Eigenvalues >1 . The first PC already explained 68.6% of the overall variance in the environmental dataset. It chiefly represented the changes in climatic conditions with increasing elevation. Both temperature and ACT showed a strong

positive loading (0.97 and 0.96, respectively), while precipitation and humidity loaded highly negative (both -0.96) on the first principal component.

The second PC explained a further 17.2% of the original variance. It mainly represented changes in SOM contents (factor loading of 0.90 for both SOM_{0–10} and SOM_{All}) and, to a lesser degree, in soil N (factor loading 0.81 and 0.78, respectively for N_{All} and N_{0–10}).

3.2. Environmental parameters and plant diversity

Multiple linear regression models were calculated for all different vegetation strata as dependent parameters and the two PCs as predictors. The different vegetation strata were also used in linear regression models including elevation as sole predictor, since altitudinal change is the basic factor underlying the highly interrelated climatic parameters.

In the model explaining the diversity of all plant species, both PCs were included in the 1963 and 2006/07 regression models (1963: $F_{2,57} = 46.4$, PC1 $\beta = 0.70$, $p < 0.0001$; PC2 $\beta = 0.27$, $p = 0.002$;

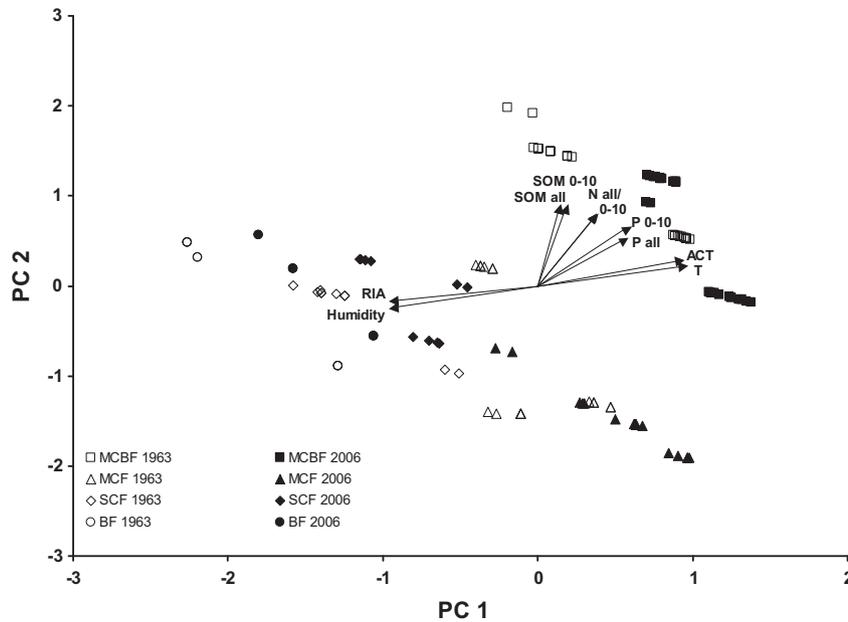


Fig. 2. PCA ordination plot showing the factor loading of individual environmental parameters on the two principal components and the associated spread of sampling plots representing different forest types (MCBF: mixed coniferous and broad-leaved forests; MCF: mixed coniferous forest; SCF: sub-alpine coniferous forest; BF: birch forests; SOM: soil organic matter, N: soil nitrate, P: soil phosphate; RIA: mean annual precipitation; T: mean temperature; ACT5: cumulative temperature ≥ 5 °C).

2006/07: $F_{2,57} = 15.7$; PC1 $\beta = 0.57$, $p < 0.0001$, PC2 $\beta = 0.2$, $p = 0.044$, see Fig. 3a and b). Both models indicate that climatic conditions are the main factor related to overall plant species richness, with soil conditions also contributing significantly, but to a lesser degree, towards the explained variance. In both years, elevation was a better predictor of plant diversity than any of the PCs on their own (1963: $F_{1,58} = 90.7$, $\beta = -0.78$, $p < 0.0001$; 2006/07: $F_{1,58} = 33.6$, $\beta = -0.61$, $p < 0.0001$).

With regard to the main tree cohort, both PCs were again included in the 1963 model, but only PC1 in the 2006/07 model (1963: $F_{2,57} = 132.5$, PC1 $\beta = 0.75$, $p < 0.0001$; PC2 $\beta = 0.25$, $p = 0.002$; 2006/07: $F_{1,58} = 70.2$, PC1 $\beta = 0.74$, $p = 0.0001$, see Fig. 3c and d). This shows that climatic conditions are a more important factor explaining tree species richness in the models, while soil conditions play a substantially smaller role. In both years, elevation was again a better predictor of plant diversity than the PCs (1963: $F_{1,58} = 132.5$, $\beta = -0.83$, $p < 0.0001$; 2006/07: $F_{1,58} = 70.2$, $\beta = -0.74$, $p < 0.0001$).

In models explaining the species richness of the regenerating tree cohort, only the first PC was included (1963: $F_{1,58} = 14.6$, PC1 $\beta = 0.45$, $p = 0.0003$; 2006/07: $F_{1,58} = 26.7$, PC1 $\beta = 0.56$, $p < 0.0001$, see Fig. 3e and f). Again, elevation on its own was a strong predictor of plant diversity, performing better than PC1 in the 1963 model (1963: $F_{1,58} = 21.7$, $\beta = -0.52$, $p = 0.0002$; 2006/07: $F_{1,58} = 22.7$, $\beta = -0.53$, $p = 0.0001$).

The 1963 model describing species richness in the shrub layer included both PCs ($F_{2,57} = 110.4$, PC1 $\beta = 0.76$, $p < 0.0001$; PC2 $\beta = 0.36$, $p < 0.0001$), while only PC1 was included in the 2006/07 model ($F_{1,58} = 58.0$, PC1 $\beta = 0.71$, $p < 0.0001$, see Fig. 3g and h). Elevation was again a superior predictor to either of the PCs (1963: $F_{1,58} = 204.1$, PC1 $\beta = -0.88$, $p < 0.0001$; 2006/07: $F_{1,58} = 71.7$, $\beta = -0.74$, $p < 0.0001$).

For the herb layer, PC1 again contributes significantly towards the species richness model in 1963 ($F_{1,58} = 11.7$, PC1 $\beta = 0.41$, $p < 0.001$), whereas neither of the two PCs contributed significantly ($p = 0.05$) towards the species richness model in 2006/07 (Fig. 3i and j). Instead, SOM showed a significant correlation with herb species richness ($F_{1,58} = 13.0$, $\beta = 0.43$, $p = 0.0007$) in the 2006/07 model.

3.3. Temporal and spatial plant species turnover

A set of canonical correspondence analyses was conducted combining the complete vegetation data of each vegetation stratum for 1963 and 2006/07, as well as the two PCs as environmental constraints. All ordination plots traced the altitudinal gradient along the first axis. In all cases, the first axis therefore correlated with PC1, which represented an increase in temperature and a decrease in precipitation. The second canonical axis was more closely aligned with changes of PC2 values, representing shifts in SOM and plant-available nutrients.

The main tree composition showed a clear grouping of the three forest types below the birch forest, with only minor overlap between these groups (Fig. 4a). Some of the plots classified as birch forest were located within the cluster of SCF plots, whereas most of the plots representing high-elevation birch forests were situated on top of each other in the ordination diagram and well separated from all other plots. The main tree cohort at these plots consisted entirely of *B. ermanii*. It appeared that there had been little change in the tree composition between the two survey periods, reflecting the long lifespan of the main forest trees.

Indications for change were more pronounced in the regenerating tree cohort. Again, the change in elevation between forest types was clearly reflected in the ordination plot, but with clusters of MCF and SCF plots less separated (Fig. 4b). Both plots representing BF and MCBF showed a clear differentiation with regard to species composition between 1963 and 2006/07, apparently reflecting the increase in temperature over this period.

Mixed coniferous and broad-leaved forests were also clearly separated from the other forest types in relation to the composition of their shrub layer (Fig. 3c). Furthermore, MCBF again showed a shift in species distribution following the increase in temperature between 1963 and 2006/07. The remaining forest types were less well separated with regard to their shrub species composition, and no clear temporal trend was apparent in the ordination biplot for these forest types.

The herb layer showed a clearly separation in species composition both according to forest type and survey period (Fig. 3d). It appeared that on many BF plots, the forest undergrowth in 2006/

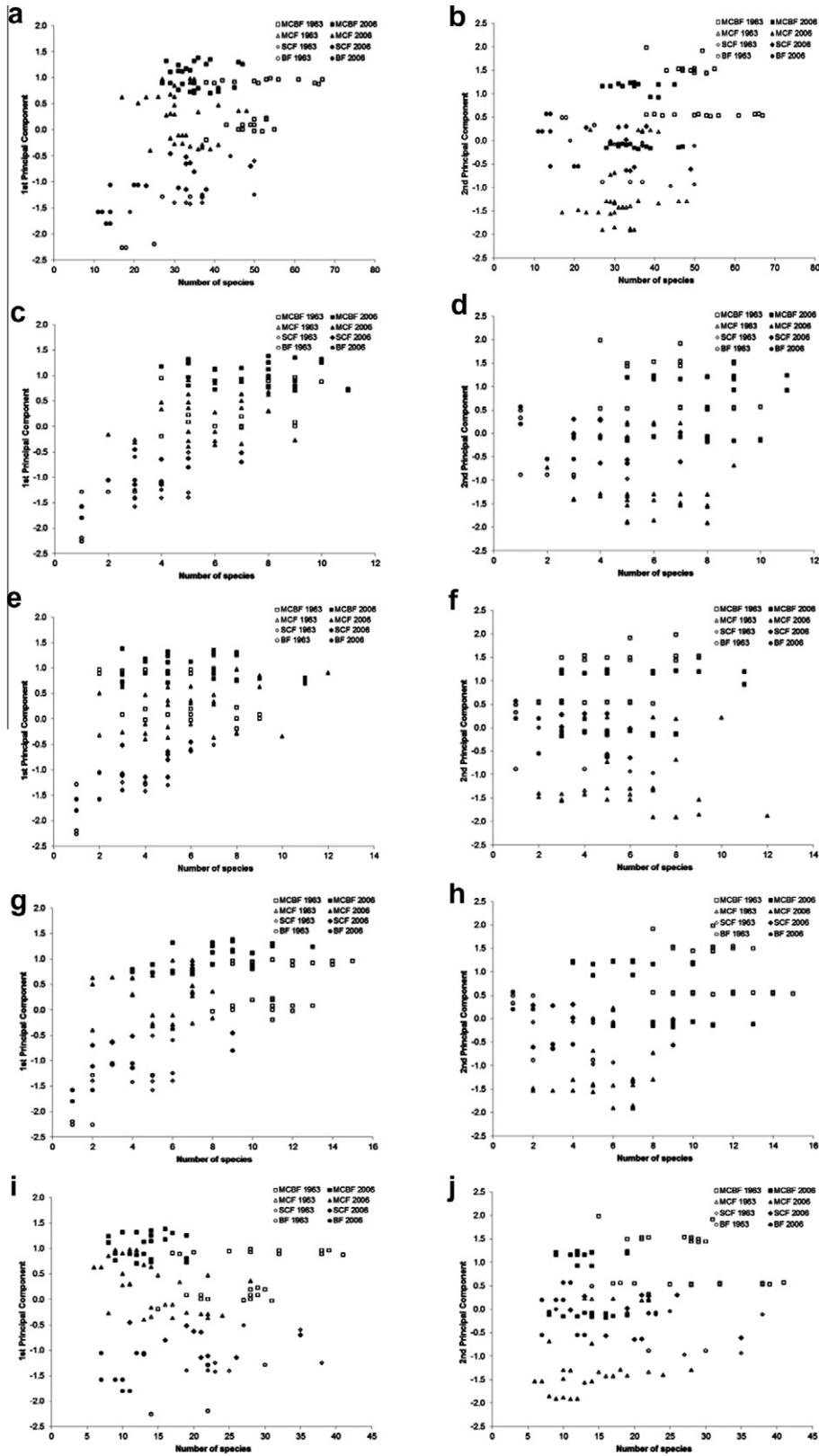


Fig. 3. Scatterplots showing the relationships between plant diversity and the two principal components (a and b: all plant species, c and d: main tree cohort, e and f: young tree cohort, g and h: shrub layer, i and j: herb layer).

07 resembled the undergrowth vegetation found at the SCF forests much more closely than it had done in 1963. The distinctiveness of

the undergrowth vegetation has increased in both MCF and MCBF forest plots over the last four decades. The species composition in

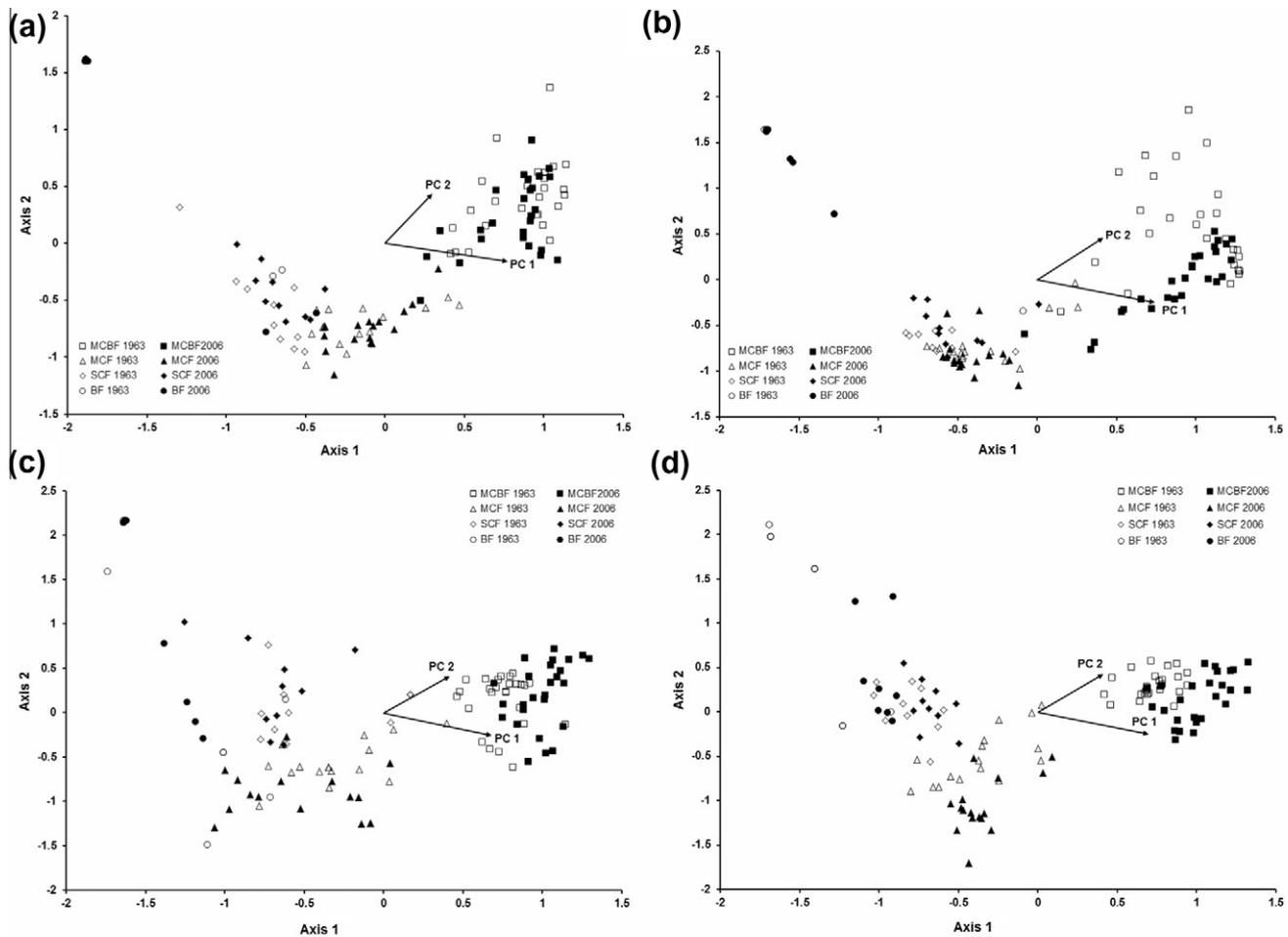


Fig. 4. Canonical Correspondence Analysis triplots reflecting the changes in vegetation composition between the four forest types and two sampling periods, constrained by the two principal components for the four vegetation layers, (a): species richness within the dominant tree cohort; (b): species richness in the understory cohort; (c): species richness in the shrub layer; (d): species richness in the herb layer (MCBF: mixed coniferous and broad-leaved forests; MCF: mixed coniferous forest; SCF: sub-alpine coniferous forest; BF: birch forests).

MCBF plots seems furthermore to reflect the increase in temperature and decrease in humidity and precipitation according to their shift in position in relation to PC1.

4. Discussion

4.1. Links between plant diversity patterns and environmental factors

At Changbai Mountain, the key driver of changes in overall plant diversity, as well as in the plant species density of individual strata is the change in elevation, which is closely associated with both changes in temperature and precipitation. This is coherent with reports that plant diversity particularly within woody vegetation is strongly altered in relation to changes in moisture and heat energy not only at large geographic scales (Pianka, 1966; Qian et al., 1998; Kreft and Jetz, 2007), but also along steep altitudinal gradients (Eeley et al., 1999; Sánchez-González and López-Mata, 2005; Odland, 2009).

The observed weaker link between elevation and diversity in the herb layer, which is particularly pronounced in the 2006/07 survey, has also been observed in studies of the tundra vegetation on Changbai Mountains (Zhao et al., 2004) and from the forests of Dongling Mountain near Beijing (Ren et al., 2006). One hypothesis for such a pattern is that more stable microclimatic conditions are experienced by herbaceous plants under the closed canopy of the

woody vegetation, which somewhat buffers the changes in temperature and humidity affecting the more exposed tree and shrub layers. Accordingly, other environmental parameters such as nutrient availability become more important for the diversity of the herb layer. A strong link between herbaceous plant diversity and soil parameters associated with the availability of nutrients has indeed been reported in previous studies (Ramovs and Roberts, 2003; Chust et al., 2006; Marks et al., 2008). Nonetheless, it could also be argued that the observed patterns in herbaceous plant diversity represents a state of transition within these plant communities, with different herbaceous species adapting to changes in the climatic conditions at different rates, so that the influence of temperature and precipitation originally observed in the 1963 dataset becoming hidden as a result of the non-equilibrium state within this component of the forest vegetation (Watson, 1980; Shmida and Wilson, 1985; Keeley et al., 2005).

Contrary to the trends within the herb layer, the importance of soil chemical characters in explaining the diversity in the woody vegetation appears to have decreased, as the regression models for 2006/07 only include the component representing altitudinal change/climatic factors as significant contributor. As the woody vegetation generally consists of long-lived species and must therefore not be expected to change significantly within a 40-year time-frame, it can be argued that the current state and composition of the woody vegetation does not fully reflect the changes which have occurred both in climatic and edaphic factors. A response

especially in the tree layers might further be delayed due to a buffering of adaptations towards altered environmental conditions by dominant species, which has been observed in a range of ecosystems (Vojta, 2007; Öster et al., 2009).

4.2. Changes in the plant species composition in relation to climate and environmental change

Mountain vegetation belts are reportedly shifting upwards along mountain slopes as a result of increasing temperatures (Grabherr et al., 1994; Lenoir et al., 2008). At Changbai Mountain, this trend does not become apparent in the dominant tree cohort, which remains very stable in relation to its composition. This could be related to the longevity of trees and the respective long turnover rates in the forest canopy. There are on the other hand indications of an upwards shift of some plant species in sections of the lower vegetation strata. Nonetheless, this trend is not uniform across the different forest types. The birch forest vegetation appears to show the strongest change throughout its strata. It has to be taken into consideration that in these forests with their very species-poor woody vegetation components, even small alterations like the colonization of an additional tree or shrub species can cause significant changes in this forest's plant community structure. This can partly explain the observed strong shifts in plot positions in the ordination diagrams. It is nonetheless apparent that the much more species-rich undergrowth vegetation in some of the birch forest plots in 2006/07 has also undergone significant changes. On a number of birch forest plots, the undergrowth now more closely resembles species assemblages found in the sub-alpine coniferous forests than in birch forests in 1963. This is a clear indication that at least some of the undergrowth plant species which were formerly characteristic of the sub-alpine coniferous forest are migrating upwards into areas previously occupied by distinct birch forest undergrowth communities. This indicates a potential threat to these communities, which appear to be pushed increasingly towards the uppermost limits of the birch forest.

The second forest type showing strong temporal alterations both in the woody and herbaceous plant communities is the mixed coniferous and broad-leaved forest growing on the lower slopes of the Changbai Mountain. The trend observed in the regenerating tree cohort is in this regard particularly interesting, as our results suggest that this group is becoming increasingly homogeneous in its composition. This has important potential implications for the future development of these forests, as a more homogeneous species composition in the future forest canopy is also likely to lead to an overall homogenization of the forest structure, potentially decreasing available niche space for both flora and fauna in these forests (Miles et al., 1983; Jin et al., 2005).

The species composition of both shrub and herb layers within the MCBF furthermore becomes more distinct from the other forest types. The underlying change in species composition reflects a shift towards a community better adapted to higher temperatures and dryer conditions. These shifts can possibly be attributed to different evolutionary strategies amongst the taxa present in the different forest strata (Lozano et al., 2007; Bryant et al., 2008). Both the capability of trees to buffer environmental changes (Kissling et al., 2008) and their delayed reaction towards altered environmental conditions have already been mentioned. Understory strata on the other hand have been reported to react more sensitively towards modifications in moisture and energy dynamics (Zhang et al., 1994; Ramovs and Roberts, 2003). While it was hypothesized earlier that in forests, the canopy of trees and shrubs might actually buffer the herbaceous vegetation against such modifications, the actual changes in species composition, in contrast to changes in species density, indicate that this initial hypothesis was incorrect. This is further supported by the observed changes in the

two conifer-dominated forest types. In these, the species composition in the woody vegetation appears least affected by the changes in environmental conditions over the 40-year interval. Nonetheless, distinct changes are again apparent in the herbaceous plant assemblages forming the undergrowth of the mixed coniferous forests, which also increased in their distinctiveness over time.

Overall, our results suggest that climatic conditions are a key factor determining the current distribution as well as changes in the forest vegetation of Changbai Mountain. This becomes even clearer when considering that climatic conditions do not only affect the vegetation directly, but also exert a strong influence on soil conditions and further environmental factors characterizing the local environment (Sarr and Hibbs, 2007; Xia et al., 2009). They hence exert further, indirectly controls over plant communities. Effects of climate change on soil parameters are complex, with changes in both precipitation and temperature for example leading to altered soil moisture and litter decomposition rates (Turetsky et al., 2008; Lindedam et al., 2009).

Despite the pristine condition of many parts of the Changbai forest ecosystems, there are also some direct anthropogenic pressures which potentially alter the composition of the vegetation. These mainly affect the understory vegetation and relate to the impacts of tourism, the collection of medicinal plants and pine nuts (Bai et al., 2008). These uncontrolled human activities have been related to a significant decrease in herbaceous plant diversity in sections of the Changbai forests and have potentially also affected the nutrient availability near the soil surface (Marks et al., 2008).

Potential threats to the future plant diversity and plant community structure of the Changbai forests are diverse, ranging from the decreasing area of typical high-elevation birch-forest herb and shrub communities to an increasing homogeneity of the mixed broad-leaved and coniferous forests covering the lower slopes of Changbai Mountain. It also appears that the canopy species composition remains widely constant despite the significant increase in temperatures at Changbai Mountain. Species sensitive to climate change could therefore be lost if conditions within their current distribution range became unsuitable for their successful reproduction before they have shifted into areas more congruent to their niche requirements. Our results also indicate that even the 43-year period is insufficient to provide a definite picture of the future changes in temperate forest ecosystems in reaction to climate change, and further research covering even longer time-spans is required. What is already obvious is that the response patterns in different vegetation strata and individual plant species is highly complex, and special attention must be given in particular to the reactions of rare, threatened plant species in future investigations.

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