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# COMMUNITY COMPOSITION AND STRUCTURE ALONG THE ENVIRONMENTAL GRADIENTS OF *LARIX GMELINII* FOREST IN NORTHEAST CHINA

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**Abstract**

*Larix gmelinii* forest is one of the most important cold-temperate conifer forests which plays a crucial role on national ecological security in China. Understory plants of *Larix gmelinii* forest has different distribution and ecological strategy. This paper quantitatively explored the relationship between community composition and environmental factors in natural *Larix gmelinii* forest in Northeast China. The regional sample plots (n=175, size=30 m×30 m) were classified into 6 plant associations by two-way indicator species analysis (TWINSPAN), and different plant associations showed different habitat preferences. Species richness and diversity showed a similar trend. Both of them had significantly negative correlation with elevation, isothermality, temperature seasonality, showing significantly positive correlation with mean annual temperature and annual precipitation. Species evenness had significantly negative correlation with mean annual temperature and annual precipitation, showing significant positive correlation with elevation and isothermality. Species richness and diversity in Asso.II (*Larix gmelinii-Spiraea chamaedryfolia* + *Corylus heterophylla-Eriophorum vaginatum*) and Asso.VI (*Larix gmelinii-Carex Larix gmelinii-Sorbaria sorbifolia-Geranium wilfordii*) showed higher index than others. However, species evenness in Asso.III (*Larix gmelinii-Ledum palustre+Vaccinium vitis-idaea-Deyeuxia angustifolia*) and Asso.IV (*Larix gmelinii-Rhododendron dauricum-Pyrola dahurica*) showed higher index than others. Canonical correspondence analysis (CCA) claimed that mean annual temperature, annual precipitation and elevation were primary environmental factors affecting species association distribution. The study can be used as a reference for *Larix gmelinii* forest ecosystem protection and a theoretical basis for scientifically sustainable management in similar areas.

**Key words:** Species diversity, Plant association, Two-way indicator species analysis, Canonical correspondence analysis, Environmental gradient.

## Introduction

Plant community assembly is always a focus issue for understanding species coexistence and biodiversity maintenance in community ecology (Wang *et al.*, 2018). The heterogeneity of light, water, and temperature drives plant species distribution, community assembly and complex landscape heterogeneity (Vassilev *et al*., 2011). *Larix gmelinii* forest is used to growing in harsh climate and it is one kind of dominant trees with economic value in China (Hu *et al.*, 2017a). Coniferous forests with single species composition and mono structure are likely to suffer soil fertility degradation, outbreak of disease, regeneration problems after overexploitation (Hu *et al*., 2017b; Nan & Guo, 2021; Yang *et al*., 2018). Understanding ecological function and habitat characteristics are the foundation for sustainable development of boreal forests (Hao *et al.*, 2007).

Understanding how forest plants respond to the environment is conductive to forest versatility. A recent experimental study has recognized that four-fifth of the species in tropical forests are associated with topographical habitats (Gunatilleke *et al.*, 2006). Canopy density is also an important structural trait determining species composition, besides large forest gaps are generally beneficial for light-demanding plant regeneration (Senécal *et al.*, 2018). Environmental heterogeneity is inherently spatially auto-correlated, and thus the use of spatially variables helps to account for its variation at different spatial scales (Legendre *et al.*, 2009). Comparisons between ecological groups and taxonomic groups are necessary to gain a more comprehensive understanding of diversity patterns (Lan *et al.*, 2011). Quantitative analysis can be used to quantify the relative importance of environmental drivers on community composition and structure (Zhao *et al.*, 2017).

In the study, climate, topography and canopy density were considered as environmental factors. TWINSPAN and CCA were used to analyze plant association distribution along environmental gradients. The study was designed to answer the following questions: (1) what was the present situation in terms of species composition and community structure of natural *Larix gmelinii* forest? (2) Which environmental factors mainly limited different plant association distribution patterns in natural the forests? Based on the two questions, we expected to find out variation trends of community composition and structure along environmental gradients and to provide important guidance for managing and protecting *Larix gmelinii* forest.

## Materials and Methods

**Study area:** The study was conducted in the Khingan Mountains of Northeast China (118.83°E - 135.09°E, 38.72°N - 53.56°N) (Fig. 1). The survey region is cold temperate continental monsoon climate zone, with elevation ranging from 200 to 1300 m above sea level (a.s.l.). The mean annual temperature changes from -4°C to 11.5°C and mean annual precipitation is from 400mm to 1100 mm. The annual sunshine duration is 2300-3000 h and frost-free period is 100-160 d. The zonal vegetation types in the area are forest, shrub, grassland, wetland meadow, marsh, and aquatic vegetation. The most common tree species are *Larix gmelinii*, *Pinus pumila*, *Betula platyphylla*, *Populus davidiana*. *Pinus pumila* shrubs. The soil types are brown coniferous forest soil, meadow soil and boggy soil (Jiang *et al.*, 2016).

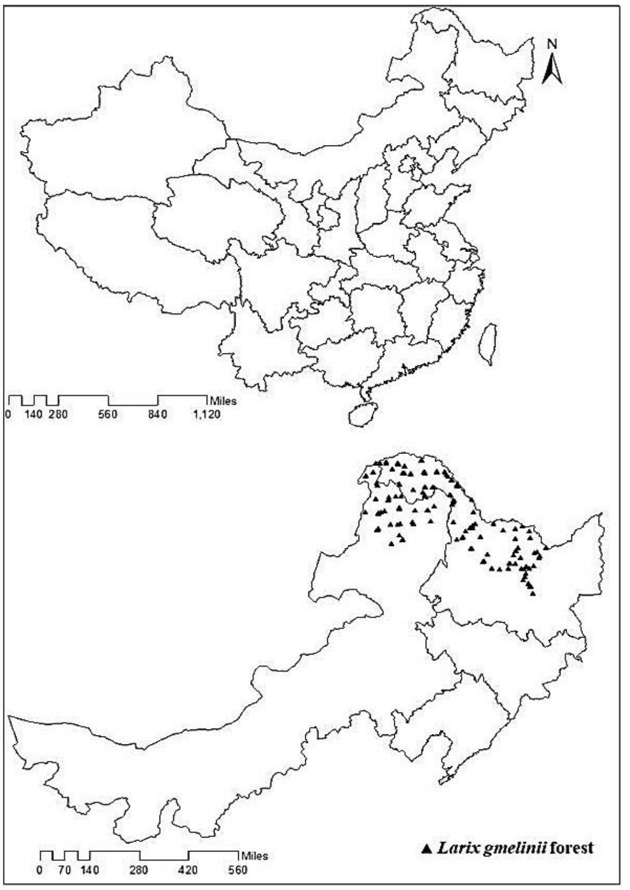


Fig. 1. Sample plot sites of *Larix gmelinii* forest in Northeast China.

**Data collection:** A total of 175 *Larix gmelinii* forest plots were investigated within 3 months in 2018 (from July to September). The size of forest plots was 900 $m^2$ (30 m×30 m), and consisted of nine 10 m×10 m subplots (Yuan *et al*., 2018). The plots basically covered the total distribution range of *Larix gmelinii* forest in Northeast China. Species name, diameter at breast height (DBH), and height of all individual trees with a DBH＞2.5 cm were investigated in each plot. Two of the nine subplots were selected for a survey of the shrub layer at the cross corners. Species abundance and average height of all woody individuals with DBH＜2.5 cm (including sapling trees) were recorded. Five 1 m×1 m herbaceous quadrats within each subplot were set up. Average coverage and height of each vascular species occurring in the herbaceous quadrats were recorded.

Climatic data that contained 19 bioclimatic variables with 30s (ca.1 km) spatial resolution was obtained from the World Climate Database (www.worldclim.org). Detrended canonical correspondence analysis suggested that mean annual temperature, annual precipitation, isothermality, temperature seasonality, precipitation seasonality as climatic variables were more appropriate than others. Habitat factors were recorded, including altitude, slope, aspect, canopy density. Ultimately, nine environmental factors that mainly influenced species distribution of *Larix gmelinii* forests were added to modeling statistics.

### Statistical analysis

The species data matrix functions consisted of importance values of 423 species in 175 natural *Larix gmelinii* forest plots (423×175). Species importance value (IV) was used in a multivariate analysis of forests and species diversity.

$IV_{tree}$ = (relative abundance + relative dominance + relative height)/3
$IV_{shrub\ and\ herb}$ = (relative coverage + relative height)/2
Species richness (Patrick index): $R=S$
Species heterogeneity (Shannon-Wiener index): $H = -\sum_{i=1}^{S}\frac{N_i}{N}ln\frac{N_i}{N}$
Species evenness (Pielou's index): E=*H*/*ln*(*S*)

where $N_i/N$ is the relative importance value of species *i*, $N_i$ is the importance value of species *i*, *N* is the sum of importance values for all species in a plot, and *S* is the species number present in a plot.

Plant associations were named after indicator species in the tree layer, shrub layer and herb layer. TWINSPAN were used to divide the sample plots into different association groups (Jan *et al.*, 2009). CCA were used to analyzing community species composition along environmental variation. Forward selection was used to compute the most parsimonious model based on significant explanatory variables. Monte Carlo 1000 permutations text assessed the significance of F-values of environmental variables in CCA (Bai & Zhang, 2018; Song *et al.*, 2017).

## Results

**Association classification and species diversity patterns:** There were totally 423 species, belonging to 212 genera, 79 families in all the forest plots. 175 forest plots were classified into 6 association groups by TWINSPAN, including Asso.I (*Larix gmelinii-Betula fruticosa- Carex meyeriana*), Asso. II (*Larix gmelinii-Spiraea chamaedryfolia + Corylus heterophylla-Eriophorum vaginatum*), Asso. III (*Larix gmelinii- Ledum palustre + Vaccinium vitis- idaea-Deyeuxia angustifolia*), Asso.IV (*Larix gmelinii-Rhododendron dauricum-Pyrola dahurica*), Asso.V (*Larix gmelinii-Carex*), Asso.VI (*Larix gmelinii-Carex Larix gmelinii-Sorbaria sorbifolia-Geranium wilfordii*). Different plant associations and habitats were detailedly described in the table (Table 1).

Species richness ranged from 17.07 to 28.18, the Shannon-Wiener index ranged from 1.98 to 2.46, and evenness ranged from 0.69 to 0.81 in natural forest (Fig. 2). Asso. II and Asso.VI had higher Patrick and Shannon-Wiener index than others. However, species evenness in Asso. III and Asso. IV showed higher index than others. Species richness and diversity showed a similar trend in different associations, but species evenness had no obvious trends.

**The response of different associations to main environmental gradients:** In the CCA analysis, the Monte Carlo permutation test indicated significant eigenvalues for all canonical axes ($p < 0.001$). The species-environment correlations of CCA axes respectively were 0.942, 0.813, 0.778, 0.749 for the first four UV interactions respectively. The cumulative percentage variance of the species-environment relationship for CCA axes was 69.8% in natural forest (Table 2). CCA ordination performed well in plant association distribution along environmental gradients and there was only 30.2% unconstrained fraction.

Asso.I was used to distributing with relatively more precipitation seasonality, middle-high elevation, abundant annual precipitation, semi-sunny or semi-shady slope, lower canopy density. Asso.II had higher correlation with temperature seasonality and canopy density, lower precipitation seasonality and annual precipitation. Asso.III distributed with higher temperature seasonality and isothermality, steep slope, lower annual precipitation. Asso.IV distributed in the left bottom of two-dimensional CCA ordination diagram usually with higher elevation, isothermality and precipitation seasonality, lower mean annual temperature and canopy density. Asso.V distributed in the top right corner usually with higher mean annual temperature and canopy density, lower elevation, relatively gentle slope. Asso.VI was immensely limited by annual precipitation and aspect, and it used to distribute in sunny slope and low-middle elevation (Fig. 3).

**The main limiting environmental factors in *Larix gmelinii* forest:** Species richness showed highly significant negative correlation with elevation, isothermality, temperature seasonality, but highly significant positive correlation with mean annual temperature and annual precipitation (Table 3). Species evenness showed highly significant negative correlation with mean annual temperature and annual precipitation, but significant positive correlation with elevation, slope, isothermality. Species diversity showed significant negative correlation with elevation, aspect, isothermality, temperature seasonality, precipitation seasonality, but highly significant positive correlation with mean annual temperature and annual precipitation.

Forward selection was conducted by 9 environmental variables in turn until there was no obvious explanatory variable (Table 4). Environmental variable ranking of marginal effect in order was mean annual temperature, annual precipitation, isothermality, elevation, temperature seasonality, precipitation seasonality, aspect, canopy density, slope. Eight environmental factors had significant marginal effects on community distribution ($p<0.001$). Environmental variable ranking of conditional effect in order changed. Removing the collinearity of leading factors, only 3 environmental factors past through significance test ($p<0.001$). The conditional effect order of environmental factors was mean annual temperature, annual precipitation and elevation.

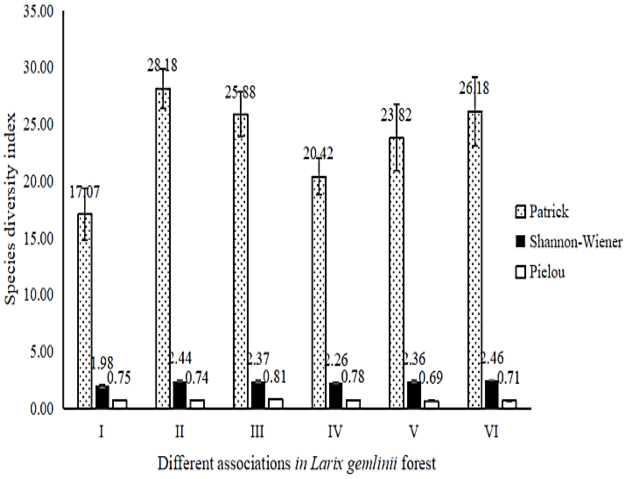


Fig. 2. Species diversity variation in different associations in *Larix gmelinii* forest.

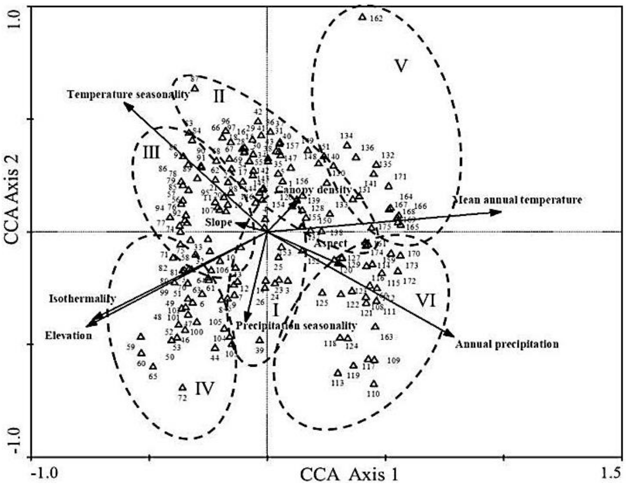


Fig. 3. Two-dimensional CCA ordination diagram of 175 plots and 9 environmental factors in *Larix gmelinii* forest (plots serial number is indicated by number. The length of an environmental vector indicates the degree of correlation).

## Discussion

*Larix gmelinii* forest is so ecological adaptable that it can grow in arid barren mountains or wet marshland (Dong *et al.*, 2016; Aert & Honnay, 2011). Based on filed investigation, all the forest plots were classified into six plant associations. The results showed that Asso.I had obvious preferences for precipitation seasonality gradient. It also implied that *Spiraea chamaedryfolia* usually distributed in semi-shady and moist slope. Asso.II and Asso.III had habitat preferences for temperature seasonality, slope, canopy density. *Spiraea chamaedryfolia* and *Corylus heterophylla* appeared in Asso.II with higher species richness. *Ledum palustre* and *Vaccinium vitis-idaea* usually appeared in the stable community of semi-sunny or shady slope. Community spatial distribution of Asso.IV showed positive correlation along elevation and isothermality. It was in accordance with previous study that *Rhododendron dauricum* was partial to middle hill distribution (Wakui *et al.*, 2017; Liu & Yang., 2014). Asso. V and Asso.VI respectively had obvious preferences for mean annual temperature and annual precipitation. The results were consistent with some studies that environmental filtering might drive community structure and make closely species to occur in the same community (Harrison *et al.*, 2006; Qin *et al*., 2017).

Species diversity was frequently used as an indicator of forest dynamics, composition and structure. Spearman correlation test showed that Patrick index and Shannon-Wiener index had a similar trend, showing significantly positive correlation with mean annual temperature and annual precipitation. Many researchers have pointed out that species richness was often strongly correlated with climate, and most of the previous studies at a large scale were based on natural environment and association types (Swenson, 2011; Wang *et al.*, 2016). Plant community would like to regulate itself to maintain appropriate biodiversity in succession. Species evenness had significantly negative correlation with mean annual temperature and annual precipitation, but significantly positive correlation with elevation and isothermality. Stands at early successional stage were typically dominated by shade intolerant, nutrient demanding and fast-growing species due to the availability of abundant resources, so that species richness and diversity showed higher index in Asso.II and Asso.VI than others (Liu *et al.*, 2018). Late-successional community was more often dominated by shade tolerant species due to competitive exclusion so that species evenness in Asso.III and Asso.IV showed higher index than others (Letcher *et al.*, 2012). Such transformation has been generally attributed to shifts in community assembly processes, from environmental filtering to competitive exclusion (Purschke *et al.*, 2013). Species diversity in natural forest was more stable, higher coverage might limit light availability and enhance interspecific competition (Feng *et al.*, 2008).

Climate change had strong effects on composition and structure of understory community in natural forest. The strong correlations among the environmental factors could produce unstable regression coefficients of the explanatory variables in the model (Wang *et al.*, 2017). Five climatic variables (mean annual temperature, annual precipitation, isothermality, temperature seasonality, precipitation seasonality) and four habitat factors (altitude, slope, aspect, canopy density) ultimately were added to model operation in order to reduce the number of explanatory variables and avoid strong collinearity among variables (Wilson *et al.*, 2017). Most studies had shown that the patterns and underlying mechanisms of woody plants and herbaceous plants were different due to the different response patterns (Hawkins *et al.*, 2009). The Monte Carlo permutation test in our results suggested that significant species-environment correlations with the CCA axes (Alexander *et al.*, 2011). In our results, cumulative percentage variance of species-environment relation jointly explained 69.8% of the total variance. The environmental variables affected species diversity and plant distribution in natural forest (Khatiwada *et al.*, 2019). Marginal effect and conditional effect provided importance ranking of environmental variables with forward selection model (Fang *et al.*, 2013; Achat *et al.*, 2015). Mean annual temperature, annual precipitation and elevation were the primary environmental drivers of species association distribution by CCA analsis and forward selection model.

**Table 1. Classification results of *Larix gmelinii* forest by TWINSPAN.**

| | Association | Plot serial number | Habitat |
|---|---|---|---|
| I. | *Larix gmelinii-Betula fruticosa-Carex meyeriana* | 2, 3, 4, 7, 8, 9, 10, 12, 13, 14, 23, 24, 25, 26, 39, 45, 103, 104, 152, 153 | Elevation: 420-730 m, high-middle hills. Aspect: semi-sunny or semi-shady slope. Slope: 17-31°. Canopy density 0.5-0.72. Shrub species: sparse. Herb species: sparse. |
| II. | *Larix gmelinii-Spiraea chamaedryfolia+Corylus heterophylla-Eriophorum vaginatum* | 1, 5, 15, 16, 17, 18, 27, 28, 29, 30, 31, 34, 35, 36, 37, 38, 40, 41, 42, 43, 54, 55, 66, 67, 68, 69, 83, 84, 87, 96, 97, 126, 128, 137, 138, 139, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 154, 155, 156, 157, 158 | Elevation: 338-560 m, middle hills. Aspect: sunny or semi-shady slope. Slope: 10-31°. Canopy density 0.64-0.82. Shrub species: abundant. Herb species: sparse. |
| III. | *Larix gmelinii-Ledum palustre+Vaccinium vitis-idaea-Deyeuxia angustifolia* | 11, 19, 20, 21, 22, 32, 33, 56, 57, 62, 74, 76, 77, 78, 79, 85, 86, 88, 89, 90, 91, 92, 93, 94, 95, 98, 106, 107 | Elevation: 458-753 m, middle or high-middle hills. Aspect: semi-sunny or shady slope. Slope: 21-33°. Canopy density 0.45-0.71. Shrub species: abundant. Herb species: sparse. |
| IV. | *Larix gmelinii-Rhododendron dauricum-Pyrola dahurica* | 6, 44, 46, 47, 48, 49, 50, 51, 52, 53, 58, 59, 60, 61, 63, 64, 65, 70, 71, 72, 73, 75, 80, 81, 82, 99, 100, 101, 102, 105 | Elevation: 618-803 m, high hills. Aspect: semi-sunndy, shady or sunny slope. Slope: 19-28°.Canopy density 0.43-0.76. Shrub species: abundant. Herb species: sparse. |
| V. | *Larix gmelinii-Carex* | 130, 131, 132, 133, 134, 135, 136, 140, 141, 162, 164, 165, 166, 167, 168, 169, 171, 175 | Elevation: 180-450 m, low hills. Aspect: semi-sunny and sunny slope. Slope: 8-18°. Canopy density 0.6-0.8. Shrub species: sparse. Herb species: abundant. |
| VI. | *Larix gmelinii - Sorbaria sorbifolia - Geranium wilfordii* | 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 127, 129, 159, 160, 161, 163, 170, 172, 173, 174 | Elevation: 220-530 m, low-middle hills. Aspect: sunny slope. Slope: 5-21°. Canopy density 0.63-0.85. Shrub species: abundant. Herb species: abundant. |

**Table 2. Eigenvalues and species-environment correlations of CCA ordination.**

| Item | CCA | | | |
|---|---|---|---|---|
| | Axis1 | Axis2 | Axis3 | Axis4 |
| Eigenvalues | 0.435 | 0.196 | 0.134 | 0.130 |
| Species-environment correlations | 0.942 | 0.813 | 0.778 | 0.749 |
| Cumulative percentage variance of species data | 3.7 | 5.3 | 6.5 | 7.6 |
| Cumulative percentage variance of species-environment relation | 33.9 | 49.2 | 59.7 | 69.8 |

**Table 3. Spearman correlation coefficients between species diversity and environmental factors.**

| Index | Elevation | Slope | Aspect | Canopy density | Mean annual temperature | Isothermality | Temperature seasonality | Annual precipitation | Precipitation seasonality |
|---|---|---|---|---|---|---|---|---|---|
| Richness | -0.519 ** | -0.085 | 0.071 | 0.048 | 0.667** | -.0.499** | -0.330** | 0.501** | -0.106 |
| Evenness | 0.295** | 0.174* | 0.057 | -0.109 | -0.395** | 0.338** | 0.093 | -0.274** | -0.104 |
| Diversity | -0.381** | -0.014 | -0.159* | 0.013 | 0.447** | -0.306** | -0.245** | 0.324** | -0.217** |

**Significance at the 0.01 level (2-tailed); * Significance at the 0.05 level (2-tailed)

**Table 4. Ranking of environmental variables in order of importance in *Larix gmelinii* forest.**

| Order | Marginal effect | | | | Order | Conditional effect | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Environmental variable | Canonical eigenvalue | F value | P | | Environmental variable | Canonical eigenvalue | F value | P |
| 1 | Mean annual temperature | 0.426 | 6.42 | 0.001 | 1 | Mean annual temperature | 0.426 | 6.42 | 0.001 |
| 2 | Annual precipitation | 0.333 | 4.976 | 0.001 | 2 | Annual precipitation | 0.175 | 2.662 | 0.001 |
| 3 | Isothermality | 0.31 | 4.621 | 0.001 | 3 | Elevation | 0.138 | 2.11 | 0.001 |
| 4 | Elevation | 0.301 | 4.484 | 0.001 | 4 | Temperature seasonality | 0.12 | 1.851 | 0.051 |
| 5 | Temperature seasonality | 0.257 | 3.805 | 0.001 | 5 | Precipitation seasonality | 0.117 | 1.815 | 0.088 |
| 6 | Precipitation seasonality | 0.138 | 2.021 | 0.001 | 6 | Aspect | 0.084 | 1.306 | 0.080 |
| 7 | Aspect | 0.126 | 1.844 | 0.001 | 7 | Canopy density | 0.077 | 1.19 | 0.084 |
| 8 | Canopy density | 0.094 | 1.378 | 0.005 | 8 | Isothermality | 0.072 | 1.119 | 0.161 |
| 9 | Slope | 0.071 | 1.044 | 0.339 | 9 | Slope | 0.072 | 1.11 | 0.296 |

## Conclusions

The results demonstrated that plant association distribution and community structure of natural *Larix gmelinii* forest were affected by multiple environmental factors and showed habitat preference. Combined utilization of TWINSPAN and CCA established an objective method for analyzing composition and structure of forest community along environmental gradients. The primary environmental driving factors of plant association distribution were mean annual temperature, annual precipitation and elevation. Our results provided a theoretical basis for scientific conservation and restoration of *Larix gmelinii* forest in Northeast China.

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