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Earth surface processes and environmental sustainability in China

Separation of environmental effects on community variation of a larch forest in north China

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ABSTRACT: Pangquangou National Nature Reserve is well known as 'the distribution centre of Prince Rupprecht's larch (*Larix principis-rupprechtii*)' in China. Community variation in Prince Rupprecht's larch forest provides habitat heterogeneity for animals, especially for the endemic and endangered brown-eared pheasant (*Crossoptlon mantchuricum*). In this study a total of 120 quadrats (each 10 × 10 m) were established to measure and record species composition and six environmental variables to examine the underlying variables that control community variation. We applied a multivariate regression tree analysis to detect community variation, and used redundancy analysis-based variation partitioning to separate the effects of environmental variables on community variation. The results show that Prince Rupprecht's larch forest in the Pangquangou National Nature Reserve can be represented by eight community types. The amount of total species variability captured by all environmental variables was 20.6 %, and the cumulative percentage variance of species–environment relationships was 95.8 %. However, analyses with a conditional effect approach revealed that elevation, aspect and litter thickness contribute the most to community variation. The pure and joint effects of these three explanatory variables were separated with variation partitioning analyses. The results highlight that the effect of elevation accounts for the largest fraction of community variation in Prince Rupprecht's larch forest.

KEY WORDS: nature reserve, Prince Rupprecht's larch forest, variation partition, vegetation–environment relationships.

A nature reserve is a protected area for conserving endemic species or special ecosystems, and is designed to protect relationships between endemic species and their natural habitat (Liu *et al*. 2001). The Pangquangou National Nature Reserve (PNNR) was established in 1986 to protect the endemic and endangered brown-eared pheasant (*Crossoptlon mantchuricum*) and its high-quality habitat: Prince Rupprecht's larch (*Larix principis-rupprechtii*) forest (Zhang *et al*. 2006a, b, c; Zhang & Yang 2008). Owing to the wide distribution of Prince Rupprecht's larch, the PNNR is well known as 'the distribution centre of Prince Rupprecht's larch' in China. Prince Rupprecht's larch forest plays significant roles in the PNNR, such as conservation of soil and water, and carbon fixation (Zhang *et al*. 2010). In addition, the community variation within Prince Rupprecht's larch forest provides more ecosystem diversity and habitat heterogeneity for animals and, thus, increases species diversity, especially for forest interior and resident birds (Tews *et al*. 2004). Yang & Li (1995) reported that bird species diversity in the PNNR has increased by 30.1 % since its establishment. Moreover, habitat use by animals changes with seasons (Wilson *et al*. 1997; Li *et al*. 2012), and, therefore, habitat heterogeneity is commonly proposed to explain the increase in population density (Gorini *et al*. 2012; Krüger *et al*. 2012). In the PNNR, brown-eared pheasants prefer mixed conifer and broadleaved forests with abundant shrubs as habitat in the autumn, utilising the plentiful fruit of species such as *Ribes burejense*, *Rosa bella* and *Crataegus wilsonii*. However, in the winter they prefer coniferous forests with low canopy density and abundant sunlight (Liu *et al*. 1991).

Studies on soil seed reserves under the canopy (Guo *et al*. 1998), distribution patterns (Liu *et al*. 2007) and simulation of population dynamics (Zhang *et al*. 2010) have been carried out within the nature reserve for both sustainable development of Prince Rupprecht's larch forest and conservation of suitable habitats for animals. However, no studies have determined the community variation associated with the major environmental variables in the area. Both stochastic and deterministic processes have been proposed to explain community structure and assembly. In some cases, modelling of stochastic processes has successfully predicted species abundance (Chave 2004), suggesting that species dissimilarity is not needed to generate the observed patterns of diversity in nature. However, Adler *et al*. (2010) suggest that species coexistence within communities cannot be understood without considering deterministic processes. On the one hand, deterministic processes impose ecological filters that select individual species from a regional

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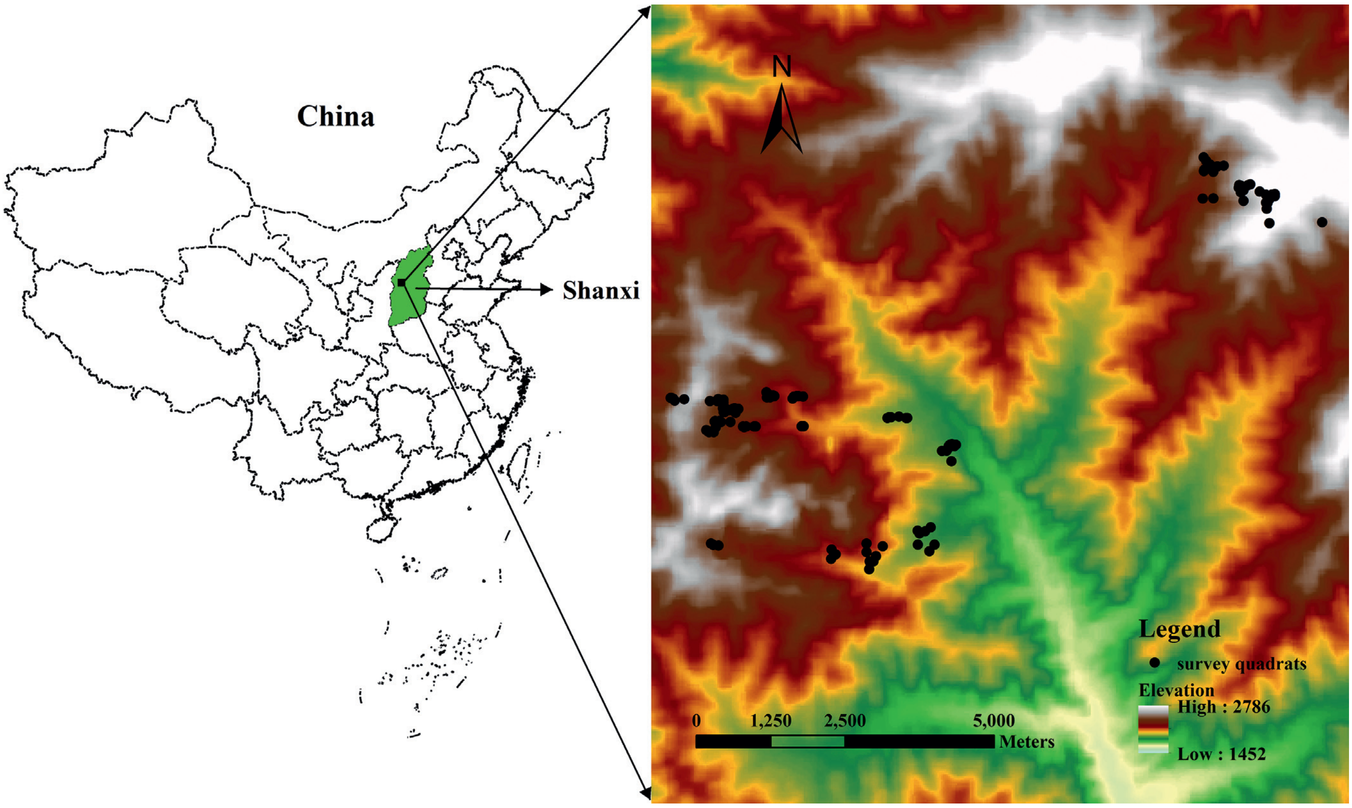

Figure 1 Location of the study area. Points show distribution of 120 survey quadrats in Pangquangou National Nature Reserve based on a digital elevation model provided by International Scientific & Technical Data Mirror Site, Computer Network Information Center, Chinese Academy of Sciences (http://www.gscloud.cn).

pool because they possess specific traits suitable for a given habitat (Keddy 1992). On the other hand, deterministic processes also enhance the complementarity of species coexistence by niche differentiation (Maire *et al.* 2012). As plant abundances determine how species respond to environmental gradients and also how they affect local resources, it has been proposed that a species' position within an ordination space can represent its niche (Sabo & Whittaker 1979). Therefore, gradient analysis can be used to explore community variation and test the relationships between communities and the environment (Zhang *et al.* 2013). In this study, we analysed community variation within Prince Rupprecht's larch forest and the relationships with environmental variables by gradient analysis. The specific objectives were to (1) determine the community variation in Prince Rupprecht's larch forest of the PNNR and (2) assess the relative importance of the measured environmental variables on community variation.

1. Study area and methods

1.1. Study area

The PNNR [37°45′–37°55′ N, 111°22′–111°33′ E] is in the middle of the Lüliang Mountains in west Shanxi Province, and at the eastern margin of the Loess Plateau (Fig. 1). The climate of this area is temperate and semi-humid with continental characteristics, and is controlled by seasonal winds. The annual mean temperature is 3–4°C and the annual mean precipitation is 830.8 mm, 70 % of which falls from July to September. The growing season lasts about 105 days. Soil types range from mountain brown soils, mountain alfisols to mountain cinnamon soil along with the decrease in elevation. The PNNR has a total area of >10,000 ha and its elevation varies from 1600 to 2670 m. Based on the national vegetation system, the zonal vegetation in the PNNR is a warm temperate deciduous broad-leaved forest. The vegetation zones change from deciduous broadleaved forest, needle–broad-leaved mixed forest, cold–temperate coniferous forest to sub-alpine scrub-meadow along with increasing elevation. The dominant zone is the cold-temperate coniferous forest, which consists mainly of Prince Rupprecht's larch (Zhang & Yang 2008).

1.2. Data collection

One hundred and twenty quadrats (each 10 × 10 m, Fig. 1) were selected in different areas in July and August 2010. In each quadrat, species-related data were recorded from two 5 × 5 m sub-quadrats for shrubs and from four 1 × 1 m sub-quadrats for herbs. For individual trees, we measured height (by a height meter), diameter at breast height (DBH, by a caliper) and number. For shrubs, we estimated herbage cover (estimated by the naked eye), height (by a ruler) and abundance. Altogether 169 plant species were recorded in 120 quadrats. Sixty-four species were excluded to eliminate the influences of rare species, and, then, 105 frequently occurring species were chosen for the subsequent analysis.

We also recorded elevation (by GPS), slope and aspect (by compass), slope position (by eye), litter thickness (by a ruler) and soil depth using an iron probe in each quadrat. Slope aspect (clockwise from south), which is a circular variable, was expressed as cos (aspect) (Suriguga *et al.* 2011); a greater value indicates a sunnier and drier condition. All hillslopes were divided into three positions from top to bottom, and the upper, middle and bottom positions were recorded as 1, 2 and 3 respectively.

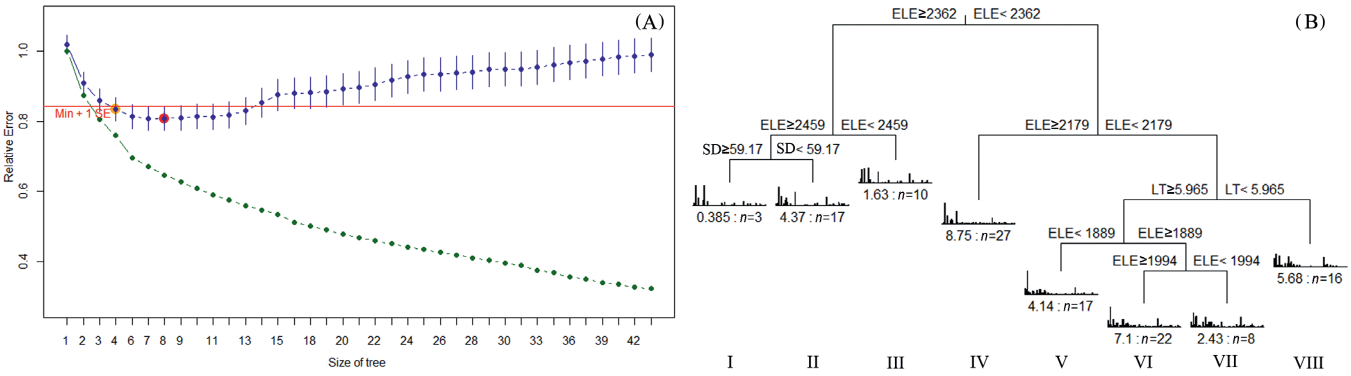

Figure 2 Multivariate regression tree (MRT) relating environmental variables to multispecies data. (A) Selection of MRT; (B) MRT of eight leaves predicted using elevation (ELE), litter thickness (LT) and soil depth (SD). The relative error (green points) decreases with tree size, whereas the cross-validated relative error (blue points) decreases to a minimum for a tree size of eight (big red point), and then increases. The red line indicates one standard error above the minimum cross-validated relative error and suggests a tree size of eight leaves.

The importance value (IV) of each species was used in multivariate analysis of communities and calculated as follows (Zhang *et al*. 2006a, b, c):

$$\mathrm{IV}_{\text{tree}} = \frac{\text{relative density} + \text{relative dominance} + \text{relative height}}{3}$$

$$\mathrm{IV}_{\text{shrubs and herbs}} = \frac{\text{relative coverage} + \text{relative height}}{2}$$

Relative density is the ratio of the density of a tree species to the density of the total tree species, relative dominance means the ratio of the basal area of a species to the sum of the basal area of all trees, relative height refers to the ratio of average height of a species to the sum of the average height of all species in the same layer, and relative coverage means the coverage ratio of a species to all species in the same layer. The species-related data were the IVs of 105 species in the 120 quadrats. The environmental data were the six variables, elevation, slope, aspect, position, litter thickness and soil depth.

1.3. Analytical methods

A multivariate regression tree (MRT) was constructed to identify community variation related with the environmental variables (elevation, slope, aspect, position, litter thickness and soil depth). The MRT is based on the same principles as Classification and Regression Trees (CART) but extended to more than one response variable (De'ath 2002). It can be used to explore, describe and predict relationships between multispecies data and environmental characteristics. We used MRT to determine clusters of sites by repeatedly splitting the data with each split defined by an environmental variable. The splits were chosen to minimise the dissimilarity of quadrats within clusters, and, hence, each cluster represents a community, whereas its environmental values define its associated habitat. The software package 'mvpart' package v1.6–2 of software R was used for the MRT analyses (R Core Development Team 2012).

To determine whether a linear or a unimodal model was best, detrended correspondence analysis (DCA) (Hill & Gauch 1980) was applied in advance to calculate the length of the first axis, which measures the total heterogeneity in the vegetation data. The first axis in Hill's scaling was 2.386, which indicated that the redundancy analysis (RDA) should perform reasonably well (Šmilauer & Lepš 2014). Given that multicollinearity among explanatory variables can hamper the identification of the most important variables, we performed the RDA with forward stepwise selection with the six explanatory variables ($P < 0.05$) to select the significant predictors that accounted for most of the variation in community patterns. Then, the significant variables were further analysed by a partitioning approach to determine the relative influences on community variation (Borcard *et al.* 1992). The variation was decomposed using (partial) regression analyses with RDA (Liu 1997). All of the RDAs were tested for significance with a Monte Carlo Permutation (MCP) test 1000 times. The DCA, RDA and partial RDA were all performed in CANOCO 5.0 (Šmilauer & Lepš 2014; Braak & Šmilauer 2015).

2. Results

2.1. Community variation

In the MRT analysis, the size of the tree was selected by cross-validation, with an eight-leaf tree clearly identified as having the minimum estimated predictive error (Fig. 2A). The clusters represent eight forest types with the splits based only on elevation, litter thickness and soil depth (Fig. 2B). The tree explained 24.1 % of the species variance. Briefly, the main characteristics of the eight forest types and their major composition species are displayed in Table 1. The eight forest types represented four vegetation succession stages: *Larix principis-rupprechtii* + *Populus maximowiczii* mixed forest (VII), *Larix principis-rupprechtii* + *Betula platyphylla* mixed forest (VIII), *Larix principis-rupprechtii* pure forests (I, II, IV, V and VI) and *Larix principis-rupprechtii* + *Picea wilsonii* mixed forest (III). This was related to the length of succession time and the change in dominant species, representing a striking dissimilarity in the dominant species in the tree layer. Pure forests could be divided into different community types and they were mainly different in dominant species in the shrub layer.

2.2. Relationships between community variation and environmental variables

The 120 quadrats and six environmental variables were analysed by RDA ordination (Fig. 3). The MCP indicated that the eigenvalues for all canonical axes were significant ($P < 0.001$). The eigenvalues of the first four RDA axes were 0.134, 0.045, 0.010 and 0.008 respectively; the species–environment correlations coefficients were 0.915, 0.560, 0.465 and 0.535 respectively; the amount of variation captured by all the explanatory variables was 20.6 %, and the cumulative percentage variance of the species–environment relation was 95.8 %. These results indicated that the RDA performed well in describing the

Table 1 The description of the main characteristics of eight communities of Prince Rupprecht's larch forest in PNNR, China.

	Forest type	Coverage (%)				Common species
		Total	Tree	Shrub	Herb	
I	*Larix principis-rupprechtii* forest	78 ± 6	73 ± 6	17 ± 3	55 ± 9	*Lonicera hispida*, *Carex lanceolata*
II	*Larix principis-rupprechtii* forest	79 ± 8	75 ± 9	28 ± 14	53 ± 14	*Lonicera tangutica*, *Carex lanceolata*
III	*Larix principis-rupprechtii* + *Picea wilsonii* mixed forest	78 ± 7	68 ± 10	26 ± 8	72 ± 9	*Ribes mandshuricum*, *Lonicera tangutica*, *Carex lanceolata*
IV	*Larix principis-rupprechtii* forest	88 ± 10	73 ± 18	23 ± 20	79 ± 16	*Lonicera chrysantha*, *Carex lanceolata*
V	*Larix principis-rupprechtii* forest	90 ± 6	47 ± 17	54 ± 14	83 ± 8	*Rosa bella*, *Crataegus wilsonii*, *Carex lanceolata*
VI	*Larix principis-rupprechtii* forest	91 ± 8	72 ± 19	40 ± 18	84 ± 12	*Lonicera chrysantha*, *Rosa bella*, *Carex lanceolata*
VII	*Larix principis-rupprechtii* + *Populus maximowiczii* mixed forest	96 ± 4	69 ± 14	75 ± 17	83 ± 19	*Corylus mandshurica*, *Carex lanceolata*
VIII	*Larix principis-rupprechtii* + *Betula platyphylla* mixed forest	63 ± 19	53 ± 25	42 ± 13	28 ± 14	*Corylus mandshurica*, *Carex lanceolata*

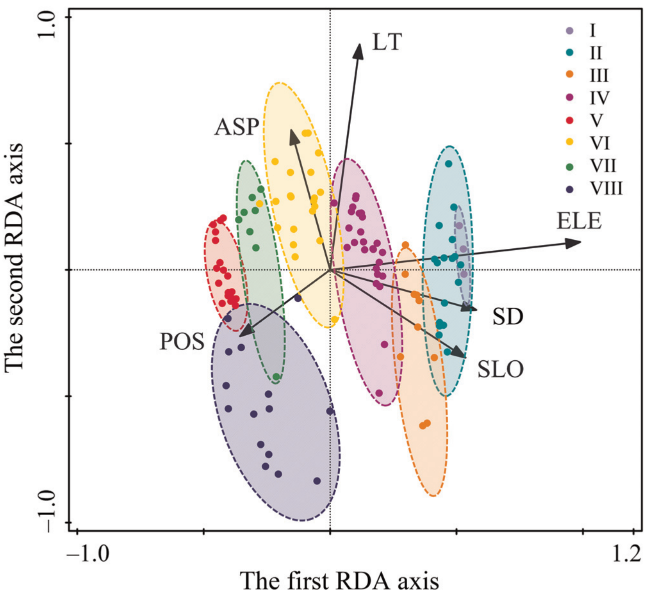

Figure 3 RDA ordination biplot of 120 quadrats and six environmental variables of Prince Rupprecht's larch forest in PNNR. The arrows refer to environmental variables, and the ellipses refer to the eight communities. Abbreviations: ASP = aspect; ELE = elevation; LT = litter thickness; POS = position; SD = soil depth; SLO = slope.

Table 2 Correlations between environmental variables and the first four RDA axis.

Environmental variable	Axis 1	Axis 2	Axis 3	Axis 4
Slope	0.5092***	−0.1937	0.5477***	0.4573***
Position	−0.4184***	−0.4160**	−0.2953***	0.6416***
Elevation	0.9816***	0.1326	−0.0939	0.0578
Soil depth	0.5572***	−0.008	0.6061***	−0.1611
Litter thickness	0.1179	0.6894***	−0.0413	−0.0636
Aspect	−0.2529**	0.7904***	−0.0302	0.2025

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

relationships among species, communities and environmental gradients.

The first RDA axis was significantly related to all environmental variables except litter thickness (Fig. 3; Table 2). This axis was positively correlated with elevation and topographical position and negatively correlated with soil depth, slope and aspect. The second RDA axis was significantly correlated with aspect, litter thickness and position. The third RDA axis was correlated with soil depth, slope and position, and the fourth axis was correlated only slope and position.

The distribution of plant communities on the ordination map is related to the environmental gradient (Fig. 3). Each community had its own distribution and specific species composition. The variation in communities on the ordination diagram showed a clear shift of communities along the first axis as elevation increased from left to right. Community V is at lower elevations (1800–1900 m) in the PNNR, while Community I occurs at the timberline (2550–2600 m). Besides the obvious altitudinal pattern, it was also found that the distribution was also related to other environmental factors, such as Community VI in sunny slopes with thick litter, Community VIII in lower slopes and Community II in steep slopes with thick soil.

Since some environmental variables may be significantly correlated with each other, forward selection was used to build a simpler model with fewer explanatory variables. The results are shown in Table 3. Regarding the marginal (independent) effects, elevation was the major factor for species composition, followed by slope, soil depth, aspect, position and litter thickness (Table 3). In summary, the independent effects of all environmental variables significantly affected community variation. However, after elevation was selected, the conditional (additional) effects of the other variables were reduced dramatically. Only slope aspect and litter thickness qualified for the final model when the probability threshold level for factor entry was set at 0.05, suggesting this set of environmental variables built a simpler model which still sufficiently explains the species composition patterns. Finally, elevation, aspect and litter thickness were included in the model. The last two variables had relatively small marginal effects, but were independent of elevation, because they added explanatory power to elevation. The amount of variation captured by all the significant explanatory variables decreased to 18.4 %.

2.3. Ecological variation partitioning of significant environmental variables

The overall variation in community pattern was decomposed into eight components: pure effect of elevation (ELE), pure effect of aspect (ASP), pure effect of litter thickness (LT), joint effect of elevation and aspect (ELE ∩ ASP), joint effect of elevation and litter thickness (ELE ∩ LT), joint effect of aspect and litter thickness (ASP ∩ LT), joint effect of the three variables (ELE ∩ ASP ∩ LT) and unexplained variation.

Table 3 Marginal and conditional effects of explanatory variables on vegetation patterns from forward selection.

Marginal effects			Conditional effects		
Environmental variable	**Canonical eigenvalue**	***P***	**Environmental variable**	**Canonical eigenvalue**	***P***
Elevation	0.157	0.001	Elevation	0.157	0.001
Slope	0.06	0.001	Aspect	0.039	0.001
Soil depth	0.147	0.001	Litter thickness	0.024	0.006
Aspect	0.116	0.001	Slope	0.011	0.206
Position	0.157	0.001	Position	0.011	0.178
Litter thickness	0.148	0.001	Soil depth	0.009	0.486

Table 4 Variance partitioning among the pure and joint effects of elevation (ELE), aspect (ASP) and litter thickness (LT) explaining variation in communities.

	Variable set	**R^2 (%)**	***P***
Pure effect	ELE	11.71	0.001
	ASP	2.23	0.001
	LT	1.94	0.001
Joint effect	ELE ∩ ASP	0.49	
	ELE ∩ LT	0.58	
	ASP ∩ LT	0.87	
	ELE ∩ ASP ∩ LT	–0.29	
Total variation explained		18.4	0.001
Unexplained variation		81.6	

R^2 = the amount of variation explained; P = P-value of MCP (1000 times). The joint effects were obtained by subtraction and could not be tested for significance.

The variation partitioning results indicated that all three variables had significant pure effects on the response variable (Table 4). Overall, community variation was best explained by elevation (13.1 %), but less by aspect (3.9 %) or litter thickness (3.7 %). The results also show large fractions of shared variation, such as variation that cannot be attributed to any particular group. Among these joint effects, the largest came from ASP ∩ LT. The negative value of the shared variation component due to ELE ∩ ASP ∩ LT (–0.3 %) indicated that the corresponding explanatory variables had opposite effects: one process hindered the contribution of the other in the joint regression model (Klimek *et al.* 2007).

3. Discussion and conclusions

Community variation is influenced by environmental variables with space and time heterogeneity, such as climate, topography, soil and human disturbance (Willis *et al.* 2010). In the PNNR, the variation within Prince Rupprecht's larch forest is closely related to all the tested environmental variables. The changes in plant communities in the RDA ordination space clearly illustrated the relationships between plant communities and environmental variables. Each community had a distribution area with a specific combination of environmental variables.

It is well established that strong correlations among environmental factors obscure the identification of causal mechanisms for community variation from field experiments (Zhang *et al.* 2006a, b, c, 2013). Community variation models can be fit to field data but suffer from ambiguity in parameter identification, and acceptable model structures emphasise different ecological processes. Therefore, their number should be reduced using forward selection of environmental variables in order to build a simpler model. According to the results of the conditional effects, elevation, aspect and litter thickness were selected sequentially. The fitness could not be significantly improved by the further addition of variables. Elevation was more important than the other environmental variables, because change of elevation leads to changes in humidity, temperature, soil type and other variables affecting community variation (Zhang *et al.* 2013). Changes in aspect may lead to changes in the duration of sunshine, humidity and temperature, all of which affect community development (Virtanen *et al.* 2010). Although litter thickness can be considered as a response variable in terms of its response to the species composition of a stand and the age of a stand, litter also supplies nutrients, moisture and a subclimate to the area (explanatory variable) (Blagoveshchenskii *et al.* 2006). Therefore, it can be also considered as an environmental factor affecting vegetation structure and organisation (Suriguga *et al.* 2011), consistent with this present study (Fig. 3, Table 3). Moreover, litter thickness was significantly and positively correlated with elevation (Table 4), possibly because litter decomposes more slowly as the mean temperature drops (Zhang 2005).

The decomposition of the explained variation in Prince Rupprecht's larch forest of the PNNR into pure and joint components indicates the relative importance of elevation, aspect and litter thickness. The variation partitioning results suggest that elevation is a crucial determinant for Prince Rupprecht's larch forest of the PNNR. Overall, we found a strong effect of elevation on vegetation patterns. These findings support the view that elevation has a strong influence on vegetation pattern in most mountains in the world (Doležal & Šrůtek 2002; Zhang *et al.* 2006a, b, c; Brinkmann *et al.* 2009), and is also a key factor affecting species diversity in mountains (Muhumuza & Byarugaba 2009; McVicar & Körner 2013). However, after partitioning the effects of elevation, there was still a significant amount of variation in the species data that could be attributed to the pure effects of aspect and litter thickness. In general, the variation partitioning results revealed a relatively moderate amount of explained variation in the vegetation pattern, suggesting that the spatial pattern of communities was structured mainly by these environmental factors. In addition, dispersal limitation is also expected to contribute to determining species composition (Chytrý *et al.* 2012), especially for large organisms. It assumes that the individuals are functionally equivalent and predicts that community similarity decreases with increasing geographic distance independent of any environmental variables (Hubbell 2001). The spatial patterns of community variation should also closely associate with geographic distance. Thus, the effect of environmental factors on community variation might be overestimated without regard to dispersal limitation in this study. However, the RDA was effective in revealing the deterministic processes. Furthermore, the unexplained variation may be caused by unmeasured environmental variables, such as soil chemical properties, which are important determinants of vegetation pattern in mountains (Navarro *et al.* 2011).

In conclusion our results indicate that Prince Rupprecht's larch forest of the PNNR clustered into eight groups using MRT, representing eight community types. The forward stepwise selection of the RDA presented here ranked both the marginal and conditional effects of six measured environmental factors on community variation. Furthermore, the results revealed that elevation, aspect and litter thickness contributed most to the variation in plant communities. The partitioning approach separated the pure effects and the shared effects of these three environmental factors and highlighted that elevation is the key factor in determining community variation in Prince Rupprecht's larch forest of the PNNR.

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5. Contributions by the authors

Qindi Zhang and Jintun Zhang conceived and designed the experiments; Qindi Zhang performed the experiments and wrote the paper. Zongshan Li, Lei Yang and Xing Wu reviewed and edited the manuscript. All authors read and approved the manuscript.

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