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Diversity and composition of plant functional groups in mountain forests of the Lishan Nature Reserve, North China

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ABSTRACT. Canonical correspondence analysis (CCA) was used to characterize the composition and distribution of forest vegetation within the Lishan National Nature Reserve (LNNR), Shanxi Province, China. The LNNR is located at E111º05'43"-111º56'29", N35º29'07"-35º23'10", and is part of the Zhongtiao mountain range. Forest vegetation was sampled from 58, 10 m × 20 m plots along an elevation gradient from 1,400 to 2,100 m. Floristic and environmental data of different functional groups, such as trees, shrubs, saplings and herbs, were analyzed using CCA; and the changes of species richness, diversity and evenness of different functional groups were analyzed in relation to environmental variables. Overall, all the functional groups of forest vegetation showed a statistically significant correlation with elevation and soil Cu. Responses to other environmental gradients differed among the four groups of plants analyzed. Tree layer showed a correlation with soil P, shrubs and herbs showed a correlation with soil organic matter and N, while saplings showed a correlation with slope and aspect. Elevation was the most important variable in terms of variations in species diversity. Species richness, evenness, and diversity of different functional groups showed a similar responding model to changes in elevation, i.e. the maximum diversity occurring at intermediate elevations. Of the functional groups analyzed, trees were most important in maintaining species evenness within communities, while shrubs and herbs were significant in maintaining species richness within communities of the LNNR.

Keywords: CCA; Functional groups; Ordination; Soil variables; Species diversity; Topographic factors; Vegetation-environment relationship.

INTRODUCTION

Mountain forest communities perform an array of important ecosystem functions, including water and soil conservation (Wang, 1991; Molles, 2002), the provision of important animal and wildlife habitat, maintenance of biological diversity (Wu, 1982; Sparks, 1995), and the development of ecotourism (Cheng and Zhang, 2003). In North China, most natural forests can only be found in mountainous areas. The virgin forests of North China occur only in the Lishan National Nature Reserve (LNNR), Shanxi province (Jiang, 1986). The conservation of mountain forest communities in this reserve is significant and of wide interest (Liu, 1984; Fu and Zheng 1994; Zhang et al., 1997; Zhang, 2003).

In China, the need for proper characterization of natural forests is important in light of the mandates of the National Conservation Project for Natural Forests of 1999 (State Forestry Administration, 1999) and recent efforts to pursue ecosystem management, both of which require the use of effective quantitative approaches to ensure that management practices maintain the integrity and biodiversity of forest ecosystems (Zhang, 2002). Many studies of mountain forests have used multivariate statistical techniques to characterize vegetation patterns (Zhang, 1995; Zhang et al., 1997; Loreau et al., 2001; Leps and Smilauer, 2003; Zhang and Chen, 2004), but few studies have attempted to incorporate other vegetation layers in the evaluation of vegetation patterns and underlying environmental gradients using quantitative methods (Mi and Zhang, 1995; Lyon and Sagers, 2002).

One approach to addressing the complexity of mountain forests is functional analysis. Plant species can be classified into functional groups based on a variety of characteristics. Each functional group potentially will partition the environmental gradient differently (Smith and Huston, 1989; Austin, 1990; Dale, 1998; Lyon and Sagers, 2002). Thus, spatial and temporal changes in environmental resources will also affect functional groups.

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The use of vertically stratified growth forms or vegetation layers as a means of separating species functional groups has a sound ecological and physiological basis (Grime, 1993; Box, 1996). However, information concerning the differential responses of different forest layers to environmental gradients is limited in the literature (Pausas, 1994; Zhang, 2003; Lyon and Sagers, 2002). The hypothesis of species diversity-elevation gradient has been tested many times (e.g. Stevens, 1992; Dolezal and Srutek, 2002), but information concerning the responses of functional group species diversity to environmental gradient is limited (Lomolino, 2001; Kessler, 2001; Austrheim, 2002).

The LNNR was established in the 1970s to protect its virgin forest communities. Vegetation within the reserve is typical of warm temperate deciduous broadleaved forest in China. Previous studies have examined the flora (Liu, 1984), vertical distribution of vegetation (Zhang et al., 1997), and plant resources (Liu, 1984; Fu and Zheng, 1994) of the reserve. However, the relationships between forest functional groups and environments have not been studied. The objectives of this study were to evaluate the roles of species functional groups in the forest communities, determine if different functional groups exhibit different responses to the same suite of environmental variables, and determine the patterns of species diversity in different functional groups.

MATERIALS AND METHODS

Study area

The LNNR is located at E111º05’43”-111º56’29”, N35º29’07”-35º23’10”, and is part of the Zhongtiao mountain range in Southern Shanxi, China. Elevation within the reserve varies from 1,000 to 2,358 m. The reserve lies on the southern edge of the Loess Plateau and is within a transitional area from a warm-temperate zone to a subtropical zone (Wu, 1982). The climate of the area is warm temperate and semi-humid, with continental characteristics and controlled by seasonal winds. Annual mean temperature is 13.3°C, the monthly mean temperatures of January and July are -0.5°C and 27.5°C, respectively, and the annual accumulative temperature in excess of 10°C is 2,100°C. Annual mean precipitation varies from 667.6 mm to 900.0 mm in the mountain regions, with 70% of annual precipitation during July and September. The dominant soil types are drab (cinnamon) soil, mountain drab soil, brown forest soil and mountain meadow soil according to Chinese soil classification system (Liu, 1992). The study area of Zhuweigou is the main valley within the LNNR. Its elevation varies from 1,400 to 2,358 m. Most of the valley is forested, while a small area close to the mountain tops is covered by mountain shrub-lands and meadows. This study dealt with all forests distributed from 1,400 to 2,100 m elevation. The vegetation communities are mainly broad-leaved deciduous forests (Zhang et al., 1997).

Vegetation sampling

We established 8 eight transects within Zhuweigou valley at intervals of 100 m in altitude along an elevation gradient from 1,400 to 2,100 m. These transects cut across the valley and were oriented parallel to topographic contours. Four to eight sites along each transect were established randomly; the number of sites along each transect was determined based on the transect length. The plot size was 10 m × 20 m, based on the minimum community area of 128 m^2 in this area (Mi and Zhang, 1995). A total of 58, 10 m × 20 m plots were sampled during our survey in July, 2002.

We categorized plants as trees (>2 cm dbh, height 5-15 m), tree saplings (<2 cm dbh, height 2-5 m), shrubs (height <2 m) and herbs (height <0.5 m). Correspondingly, we segregated the vegetation into four *a priori* defined functional groups: tree layer species, tree sapling species, shrub layer species, and herb species. The criteria for division into functional groups were the height layers of plants; tree saplings and shrubs were separated because saplings are generally much taller than shrubs and have special roles in forest regeneration, and adult trees and saplings for the same species may have different roles in the forest (Grime, 1993; Loreau et al., 2001). The cover, height, diameter at 1.3 m height (dbh), basal area, and individual number for tree species were measured in each 10 m × 20 m plot. Three 4 m × 4 m and four 2 m × 2 m subplots within each 10 m × 20 m plot were used to record shrubs and herbs, respectively; the cover and height for shrubs and tree saplings were measured in each 4 m × 4 m subplot, and that for herbs was measured in each 2 m × 2 m subplot. We calculated the mean values of cover for shrub, sapling and herb in the three 4 m × 4 m or four 2 m × 2 m subplots, and the mean values of heights for species in the subplots. The cover of plants was estimated visually, and the heights were measured using tree-finder for trees and saplings, and tape-ruler for shrubs and herbs. The db h diameters and basal diameters of trees were measured using calipers and were used to calculate stem and basal areas.

Environmental attributes

Each study plot was characterized by three physical factors: elevation, slope, and aspect. The elevation for each plot was measured by altimeter, while the slope and aspect were measured by compass. The 8 classes of aspect of 1 (337.6°-22.5°), 2 (22.6°-67.5°), 3 (292.6°-337.5°), 4 (67.6°-112.5°), 5 (247.6°-292.5°), 6 (112.6°-157.5°), 7 (202.6°-247.5°), 8 (157.6°-202.5°) were used in the analysis (Zhang, 2004). We collected soil samples at 20 cm depth from five locations chosen randomly within each 10 m × 20 m plot using a soil cylindered core sampler. The five samples were thoroughly mixed and one quarter of the mixture was collected for laboratory chemical analysis. Soil samples were dried at 70°C for over 48 h to a constant weight and analyzed in terms of soil pH, conductivity, organic matter, total nitrogen, total phosphorus, K, Cu, Mn, and Zn. These variables were selected because some, such as N, P, K, and organic matter, are the most important nutrient elements, while others, such as the micronutrient elements Cu, Mn, and Zn, are deficient in soils of the area (Liu, 1992). A 1:2.5 ratio of soil to distilled water suspension was used to measure pH and conductivity using a Whatman pH sensor meter and a conductivity meter, respectively. Total nitrogen was estimated using Kjeldahl extraction, and total phosphorus was measured via the $HClO_4$-H_2SO_4 colorimetric method (molybdovanadate method). Organic matter was measured using $K_2Cr_2O_7$-capacitance. The elements K, Cu, Mn, Zn were determined using an atomic absorption spectrophotometer (Page, 1982).

Data analysis

We used the importance value (IV) of each species as data in ordination analysis and the calculation of diversity indices. The IV was calculated using the following formulae (Zhang, 1995, 2004):

$$IV_{Tree} = \text{Relative cover} + \text{Relative dominance} + \text{Relative height} \quad [1]$$

$$IV_{Tree\ sapling,\ Shrub\ or\ Herbs} = \text{Relative cover} + \text{Relative height} \quad [2]$$

where the dominance refers to the sum of the basal areas for each tree species within a plot; relative cover, relative dominance and relative height refer to the percentages of one species cover, dominance and mean height over the sum of all species cover, dominance and mean height within a plot respectively.

Canonical correspondence analysis (CCA) was conducted on plant species-environmental variable matrices using the software CANOCO 4.5 (ter Braak and Šmilauer, 2002). The square root transformation of environmental data was used, but no transformation of species data (IVs) was applied in the analysis. To determine if different functional groups exhibited differential responses to the same suit of environmental variables, separate CCA ordinations were performed on the four functional groups, i.e. tree layer, sapling layer, shrub layer and herb layer.

To determine the patterns of species diversity, we employed three species diversity indices: species richness, species diversity (diversity), and species evenness:

Species number (as a richness index):

$$D = S. \quad [3]$$

Shannon-Wiener diversity index:

$$H' = -\sum P_i \ln P_i. \quad [4]$$

Pielou evenness index:

$$E = (-\sum P_i \ln P_i)/\ln S. \quad [5]$$

where P_i is the relative importance value of species i, and S is the number of species within a plot (Pielou, 1975; Zhang, 1995; Tóthmérész, 1995). Calculation of species diversity indices was performed for the four functional groups.

Linear and non-linear (quadratic curves) regression methods were used to analyze the relationships between the CCA axes of the four functional groups, and between species diversity indices and environmental variables. The regression analyses were performed using SPSS (SPSS Inc. 2000), and the regression diagrams were plotted using Microsoft Excel.

RESULTS

Ordination analysis of functional groups

We performed CCA ordinations on trees, shrubs, tree saplings and herbs respectively. In all CCA ordinations, the Monte Carlo permutation test indicated that the eigenvalues for the first four axes were all significant ($P<0.05$; Ter Braak, 1986). The species-environment correlations with the CCA axes for all functional groups were significant (Table 1), however, the relationships between species and environmental variables differed for different plant groups (Figures 1-4, Table 1, Table 2).

Nine of the twelve environmental variables are significantly correlated with tree species distribution (Figure 1, Table 2). The dominant environmental variables correlated with the first axis were soil Cu and elevation (Figure 1, Table 2). Elevation, P and Mn showed a strong correlation with the second axis, while slope and aspect showed a correlation with the third axis. The plots at high elevation that contain *Betula albo-sinensis, Populus davidiana, Salix pseudotangii*, and *Pinus armandii* are located in the upper left quadrant of the CCA triplot (Figure 1). Species that are characteristic of low-elevation plots, such as *Pinus tabulaeformis, Juglans cathayensis,*

Table 1. Comparison of eigenvalues and species-environment correlations produced by CCA ordinations on the four functional groups in the Lishan Nature Reserve, China.

	Eigenvalues				Species-environment correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Trees	0.784	0.470	0.394	0.235	0.925	0.837	0.834	0.82
Scrubs	0.644	0.481	0.356	0.233	0.962	0.866	0.893	0.791
Tree sapling	0.838	0.602	0.506	0.440	0.946	0.841	0.798	0.810
Herbs	0.535	0.371	0.323	0.282	0.928	0.858	0.843	0.829

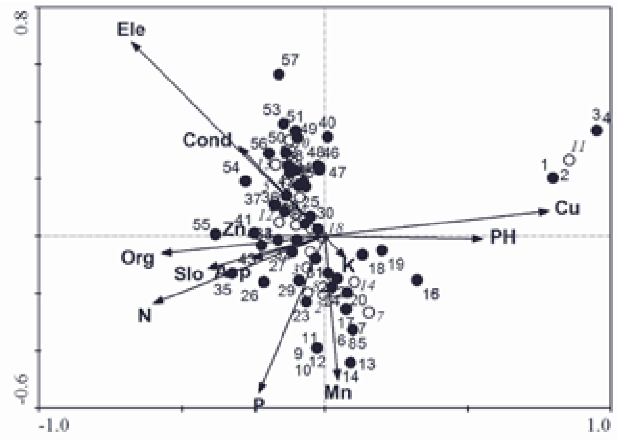

Figure 1. CCA ordination of 58 plots and 18 tree species (> 2 cm dbh) with 12 environmental variables in the Lishan Nature Reserve, China. Biplot vectors shown represent the major explanatory environmental variables. Ele: Elevation; Slo: slope; Asp: aspect; Org: organic matter content; Cond: conductivity. ● and regular font numbers represent plots, ○ and italic numbers represent tree species. 1, *Carpinus turczaninowii*; 2, *Carpinus turczaninowii* var. *stipulata*; 3, *Ulmus lamellosa*; 4, *Acer davidii*; 5, *Sorbus pohuashanensis*; 6, *Quercus liaotungensis*; 7, *Juglans cathayensis*; 8, *Betula platyphylla*; 9, *Betula albo-sinensis*; 10, *Pinus armandii*; 11, *Pinus tabulaeformis*; 12, *Salix pseudotangii*; 13, *Populus davidiana*; 14, *Toxicodendron verniciflum*; 15, *Acer mono*; 16, *Rhus chinensis*; 17, *Tilia mongolica*; 18, *Quercus aliena.*

Carpinus turczaninowii var. *stipulata*, *Carpinus turczaninowii,* plot in the right-hand quadrants. Species that prefer fertile soil and that occur in mid-elevation plots, such as *Acer davidii*, *Quercus liaotungensis, Acer mono* and *Toxicodendron verniciflum*, plot in the lower left quadrant.

As with the CCA ordination of trees, shrubs showed a strong correlation between the first axis and elevation and soil Cu (Table 2, Figure 2). Soil organic matter, N and pH were also important to the first axis. The dominant environmental variables that correlate with the second axis were P and N, while the dominant variables that correlate with the third axis were slope and aspect. The high-elevation plots contained *Abelia biflora*, *Spiraea pubescens, Philadelphus incanus* and *Lonicera chrysantha* plot in the upper left quadrant of the CCA triplot (Figure 2). Species characteristic of low-elevation plots, such as *Vitex negundo* var. *heterophylla* and *Rosa xantheana* plot in the upper right quadrant, while species that prefer fertile soil and that occur in mid-elevation plots, such as *Philadelphus incanus, Forsythia suspensa* and *Sambucus williamsii*, plot in the lower quadrants.

For tree saplings, the dominant variable correlated with the first axis was slope, while aspect and elevation were also significantly correlated with the first axis (Table 2, Figure 3). The dominant variables correlated with the second and third axes were slope and elevation respectively. Cu was also significantly correlated with the first three axes. Saplings were unevenly distributed in the study area; 18 plots do not have any saplings.

Herbaceous species showed strong correlations between the first axis and elevation, Cu, organic matter and N (Table 2, Figure 4), similar to the trees and shrubs ordinations. Zn, pH and conductivity were also important to the first axis. Zn, pH, and P showed a significant correlation with the second axis, while aspect and slope showed a strong correlation with the third axis. The

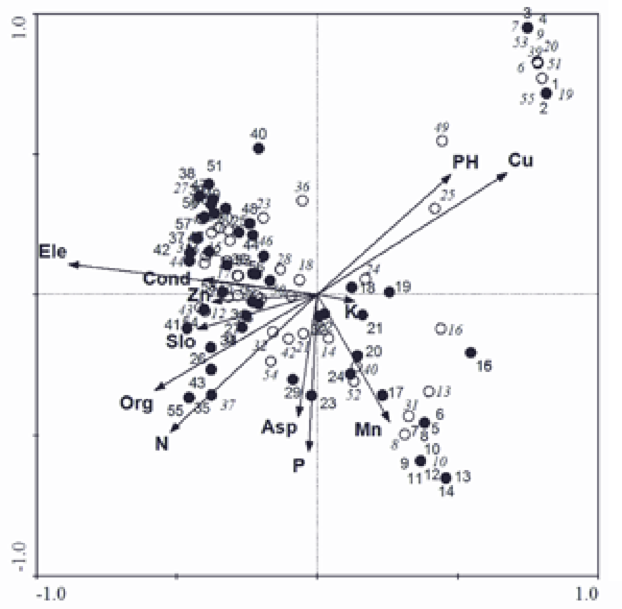

Figure 2. CCA ordination of 58 plots and 55 shrub species with 12 environmental variables in the Lishan Nature Reserve, China. Biplot vectors shown represent the major explanatory environmental variables. Ele: Elevation; Slo: slope; Asp: aspect; Org: organic matter content; Cond: conductivity. ● and regular font numbers represent plots, ○ and italic numbers represent shrub species. 1, *Staphylea holocarpa*; 2, *Swida alba*; 3, *Cerasus polytricha*; 4, *Euodia rutaecarpa*; 5, *Crataegus kansuensis*; 6, *Cornus bretschneideri*; 7, *Koelreuteria paniculata*; 8, *Syringa reticulata* var. *mandshurica*; 9, *Pyrus betulaefolia*; 10, *Malus honanensis*; 11, *Hydrangea bretschneideri*; 12, *Celastrus orbiculatus*; 13, *Forsythia suspensa*; 14, *Lonicera chrysantha*; 15, *Lonicera hispida*; 16, *Lonicera ferdinandii*; 17, *Lonicera microphylla*; 18, *Spiraea pubescens*; 19, *Spiraea trilobata*; 20, *Vitex negundo* var. *heterophylla*; 21, *Sambucus williamsii*; 22, *Abelia biflora*; 23, *Cotoneaster multiflorus*; 24, *Rubus crataegifolius*; 25, *Lespedeza bicolor*; 26, *Schisandra chinensis*; 27, *Cotoneaster acutifolius*; 28, *Sorbaria sorbifolia*; 29, *Philadelphus incanus*; 30, *Acanthopanax gracilistylus*; 31, *Acanthopanax senticosus*; 32, *Euonymus alatus*; 33, *Euonymus nanoides*; 34, *Ribes mandshuricum*; 35, *Viburnum betulifolium*; 36, *Viburnum schensianum*; 37, *Viburnum opulus* var. *calvescens*; 38, *Smilax china*; 39, *Rosa xanthina*; 40, *Rosa davurica*; 41, *Rosa bella*; 42, *Hydrangea bretschneideri*; 43, *Berberis amurensis*; 44, *Syringa microphylla*; 45, *Ribes bruejense*; 46, *Pyrus betulaefolia*; 47, *Myripnois dioica*; 48, *Daphne odora*; 49, *Sophora flavescens*; 50, *Rhamnus davurica*; 51, *Elaegnus pungens*; 52, *Celastrus orbiculatus*; 53, *Elsholtzia stauntoni*; 54, *Crataefus pinnatifida*; 55, *Diospyros lotus.*

high-elevation plots that contain species *Thalictrum squarrosum*, *Polygonum convolvulus, Cimicifuga foetida, Dryopteris laeta* and *Maianthemum bifolium* plot in the left quadrants. Plots with N-rich soils were found in the lower left quadrant, while plots with Zn-rich soils were located in the upper left quadrants. The low-elevation plots contained the species *Patrinis jeterophylla*, *Carex lanceolata*, *Phlomis umbrosa*, *Artemisia lavandulaefolia* and *Dryopteris laeta* plots were in the right quadrants; their soils were rich in Cu with comparatively high pH.

Species diversity of functional groups

Elevation was one of the most significant variables that correlate with vegetation and species functional groups from the CCA ordination analyses (Table 2, Figures 1-4). Therefore, we examined variations in species diversities of functional groups along the elevation gradient (Figure 5). Species richness, diversity and evenness of the three main functional groups, trees, shrubs and herbs, varied throughout the study area (diversity of saplings was not considered separately because saplings were not found in more than 30% plots). Species richness of trees and herbs

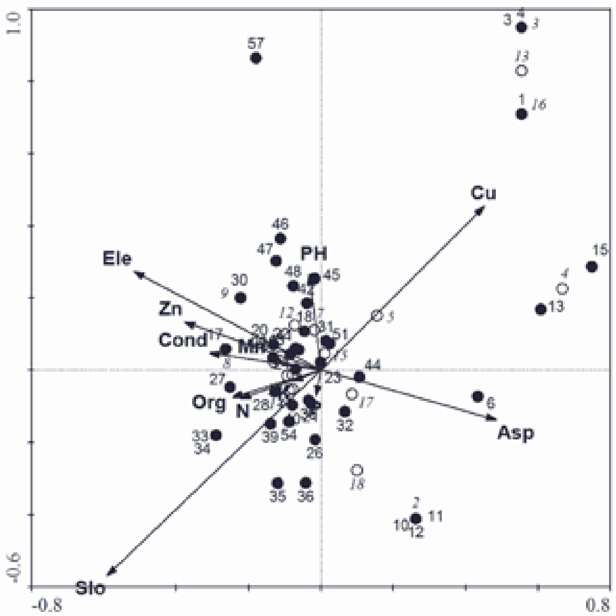

Figure 3. CCA ordination of 58 plots and saplings of 20 tree species (< 2 cm dbh) with 12 environmental variables in the Lishan Nature Reserve, China. Biplot vectors shown represent the major explanatory environmental variables. Ele: Elevation; Slo: slope; Asp: aspect; Org: organic matter content; Cond: conductivity. ● and regular font numbers represent plots, ○ and italic numbers represent sapling species. 1, *Pinus tabulaeformis*; 2, *Ulmus lamellose*; 3, *Koelreuteria paniculata*; 4, *Juglans cathayensis*; 5, *Cornus bretschneideri*; 6, *Pinus armandii*; 7, *Carpinus turczaninowii* var. *stipulata*; 8, *Toxicodendron verniciflum*; 9, *Quercus liaotungensis*; 10, *Acer davidii*; 11, *Acer mono*; 12, *Carpinus turczaninowii*; 13, *Ailanthus altissima*; 14, *Sorbus pohuashanensis*; 15, *Tilia mongolica*; 16, *Fraxinus chinensis*; 17, *Populus davidiana*; 18, *Syringa reticulata* var. *mandshurica*; 19, *Salix pseudotangii*; 20, *Swida alba.*

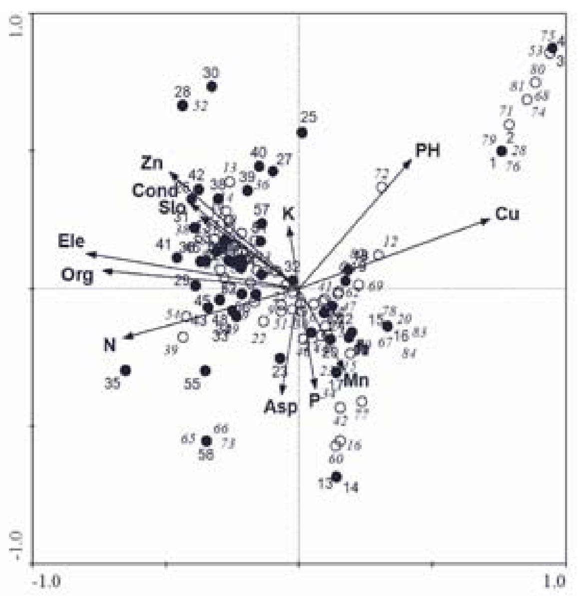

Figure 4. CCA ordination of 58 plots and 85 herbaceous species with 12 environmental variables in the Lishan Nature Reserve, China. Biplot vectors shown represent the major explanatory environmental variables. Ele: Elevation; Slo: slope; Asp: aspect; Org: organic matter content; Cond: conductivity. ● and regular font numbers represent plots, ○ and italic numbers represent herb species. 1, *Smilacina japonica*; 2, *Phlomis umbrosa*; 3, *Veratrum nigrum*; 4, *Paris verticillata*; 5, *Triosteum pinnatifidum*; 6, *Astilbe chinensis*; 7, *Cacalia hastata*; 8, *Cystopteris fragilis*; 9, *Dryopteris laeta*; 10, *Aquilegia viridiflora*; 11, *Vicia unijuga*; 12, *Patrinia heterophylla*; 13, *Dioscorea nipponica*; 14, *Polygonatum odoratum*; 15, *Galium verum*; 16, *Arisaema erubescens*; 17, *Epimedium grandiflorum*; 18, *Saussurea japonica* var. *alata*; 19, *Aconitum carmichaeli*; 20, *Aconitum barbatum*; 21, *Ajuga ciliata*; 22, *Ligularia intermedia*; 23, *Viola prionantha*; 24, *Viola varietata*; 25, *Viola biflora*; 26, *Artemisia lavandulaefolia*; 27, *Artemisia argyi*; 28, *Artemisia brachyloba*; 29, *Pedicularis resupinata*; 30, *Thalictrum petaloideum*; 31, *Thalictrum squarrosum*; 32, *Achyranthes bidentata*; 33, *Rubia cordifolia*; 34, *Serratula chinensis*; 35, *Pimpinella thellungiana*; 36, *Hylotelephium verticillatum*; 37, *Polygonatum involucratum*; 38, *Pertya sinensis*; 39, *Polygonum convolvulus*; 40, *Lamium album*; 41, *Carpesium cernuum*; 42, *Glycine soja*; 43, *Chrysosplenium pilosum*; 44, *Polygonatum verticillatum*; 45, *Lactuca tatarica*; 46, *Lonicera tragophylla*; 47, *Kalimeris lautureana*; 48, *Heracleum hemsleyanum*; 49, *Maianthemum bifolium*; 50, *Cimicifuga foetida*; 51, *Sedum aizoon*; 52, *Pyrrosia lingua*; 53, *Lespedeza davurica*; 54, *Cardamne tangutorum*; 55, *Aster tataricus*; 56, *Angelica dahurica*; 57, *Paeonia obovata*; 58, *Convallaria keiskei*; 59, *Hypericum erectum*; 60, *Cirsium teo*; 61, *Poa annua*; 62, *Arundinella hirta*; 63, *Dendranthena lavandulifolium*; 64, *Polygonum viviparum*; 65, *Cynanchum ascyrifolium*; 66, *Allium senescens*; 67, *Potentilla chinensis*; 68, *Leontopodium leontopodioides*; 69, *Carex lanceolata* var. *subpeditormis*; 70, *Carex rigescens*; 71, *Carex arnellii*; 72, *Viola yedoensis*; 73, *Iris tenuifolia*; 74, *Anemone tomentosa*; 75, *Leibnitzia anandria*; 76, *Cleistogenes serotina*; 77, *Geum urbanum*; 78, *Stellaria media*; 79, *Dendranthema cavandulifolium*; 80, *Vitis amurensis*; 81, *Ixeris sonchifolia*; 82, *Duchesnea indica*; 83, *Akebia quinata*; 84, *Cacalia farfaraefolia*; 85, *Clematis macropetala.*

Table 2. A comparison of intraset correlations between environmental variables and CCA ordination axes for plant functional groups in the Lishan Nature Reserve, China.

Environmental	Trees			Shrubs			Saplings			Herbs		
variables	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Elevation	-0.625^{***}	0.568^{***}	0.182	-0.851^{***}	0.093	-0.270^{*}	-0.489^{***}	0.230	-0.505^{***}	-0.739^{***}	0.109	-0.140
Slope	-0.379^{**}	-0.094	-0.681^{***}	-0.412^{***}	-0.107	0.306^{*}	-0.559^{***}	-0.478^{***}	0.155	-0.344^{**}	0.226	0.488^{***}
Aspect	-0.233	-0.067	0.482^{***}	-0.065	-0.376^{**}	-0.607^{***}	0.458^{***}	-0.115	-0.266^{*}	-0.062	-0.331^{**}	-0.677^{***}
PH	0.510^{***}	-0.008	-0.440^{***}	0.457^{***}	0.369^{***}	0.021	-0.030	0.223	0.035	0.390^{**}	0.403^{**}	-0.161
Organic matter	-0.529^{***}	-0.051	-0.232	-0.556^{***}	-0.300^{*}	0.202	-0.231	-0.063	-0.123	-0.683^{***}	0.055	-0.026
Conductivity	-0.277^{*}	0.263^{*}	0.004	-0.388^{**}	0.046	-0.093	-0.291^{*}	0.040	-0.347^{**}	-0.379^{**}	0.266^{*}	-0.160
N	-0.555^{***}	-0.198	-0.222	-0.505^{***}	-0.423^{***}	0.269^{*}	-0.210	-0.067	-0.114	-0.611^{***}	-0.154	0.059
P	-0.213	-0.458^{***}	0.038	-0.029	-0.483^{***}	0.266^{*}	-0.013	-0.060	0.344^{**}	0.057	-0.312^{*}	0.342^{**}
K	0.068	-0.065	-0.131	0.128	-0.021	-0.130	-0.074	-0.026	0.169	-0.036	0.194	0.043
Cu	0.725^{***}	0.073	0.165	0.649^{***}	0.374^{**}	0.062	0.427^{***}	0.382^{**}	0.354^{**}	0.666^{***}	0.217	-0.092
Mn	0.043	-0.420^{***}	-0.250^{*}	0.247	-0.391^{**}	0.146	-0.140	0.025	0.291^{*}	0.156	-0.255^{*}	0.226
Zn	-0.250^{*}	0.001	-0.334^{**}	-0.360^{**}	-0.022	0.273^{*}	-0.357^{**}	0.112	-0.060	-0.451^{***}	0.363^{**}	-0.036

Note: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

showed a significant correlation with elevation, but the relationship between shrub richness and elevation was not significant (Figure 5). Tree richness showed a quadratic increase with increasing elevation and reached a maximum value at 1,900-2,000 m. In contrast, herb richness decreased with increasing elevation, and reached a lowest value at 1,750-1,800 m, before it increased again at higher elevations. The species richness rank of functional groups is herbs > shrubs > trees (Figure 5).

The species heterogeneities (diversities) (Shannon-Wiener index) of functional groups showed a distinct correlation with elevation (Figure 5). Heterogeneities of trees, shrubs and herbs all showed a quadratic curve: the value increased at low elevations to a maximum value before decreasing at high elevation. The diversity curve of shrubs reached a maximum value at 1,850 m (Figure 5). Similar to richness, the species diversity rank of functional groups is herbs > shrubs > trees.

The relationship between species evenness of functional groups and elevation is unimodal with a peak at intermediate elevations (Figure 5). The evenness of trees, shrubs and herbs reached maximum values at elevations of 1,850 m, 1,800 m and 1,900 m, respectively. The variation of tree evenness was smaller than that of shrubs and herbs in the study area. The species evenness rank of functional groups is trees > shrubs > herbs, which is different to that of species richness and diversity.

DISCUSSION

A variety of plant characteristics, including morphology, physiology, reproductive, competitive status or location in a successional sere could be used to define functional groups (Grime, 1993; Zhang, 2005). We separated forest plants into four functional layers, trees, saplings, shrubs and herbs, based on their height, which reflected importance of community structure (Zhang, 1999; Lyon and Sagers, 2002). The heights varied from 5 m to 15 m, 2 m to 5 m, and < 2 m for trees, saplings and shrubs respectively in LNNR, and the heights of herbaceous species were usually below 0.5 m. Correspondingly, the depth of their root system varied greatly (Begon et al., 1990; Molles, 2002; Zhang, 2003). Therefore, the responses of these functional layers to environmental variables may differ and should be studied. This work demonstrated the distinctive responses of different functional groups to environmental gradients and confirmed the necessity of this kind of study.

Forest vegetation and their functional groups in the LNNR responded directly or indirectly to several important variables, including elevation, soil Cu, soil organic matter, soil N, slope and aspect. The responses of woody vegetation to these gradients have been observed in other studies (Nigh et al., 1985; Lyon and Sagers, 1998; Verburg and van Eijk-Bos, 2003; Chen et al., 2004), however, these previous studies usually focused on the distribution of canopy species within a forest. Lyon and

Sagers (2002) investigated the responses of all trees and shrubs to environmental gradients, and identified specific relationships between environmental variables and woody vegetation. A more detailed approach, incorporating all species groups (trees, shrubs, saplings and herbs), reveals some of the specific interactions between environment and forest communities.

The differences in responses to environmental gradients between functional groups were clear in the LNNR forests. Elevation and soil Cu are dominant variables in affecting trees, shrubs and herbs, whereas slope is most important to tree saplings. In addition to elevation and Cu, soil P is important to trees, while organic matter and N are significant to shrubs and herbs. Herbs also show close relationship to pH and Zn. The relationship between elevation and vegetation in the LNNR has been noted in previous studies (Liu, 1984; Fu and Zheng, 1994; Zhang et al., 1997). The Cu content of soils of the LNNR is high compared with other mountain areas, but Cu distribution is uneven in the study area (Liu, 1992); some communities were Cu-deficient. Therefore, Cu is significant to forest communities in the LNNR (Wu, 1982). Organic matter, N and P are basic nutrient resources for plants, however, their concentrations vary markedly with elevation (Liu, 1984; Zhang et al., 1997) and therefore their effects on vegetation and species were significant. These variables were more significant to shrubs and herbs (Table 1-2, Figure 2 and Figure 4), because these variables were richer in shallow soil than in deep soil, and the root systems of shrubs and herbs were shallower than those of trees (Nangendo et al., 2002). Variations in slope were obvious, and its effects on saplings were apparent because it affected the maintenance and germination of seeds in soils. For instance, the number of seeds of *Quercus variabilis* within soil decreases with increasing slope in the Zhongtiao Mountains (Fu and Zheng, 1994; Zhang, 2004). Steep slopes make it difficult for seeds to stay at the soil surface, to move within the soil, and to absorb sufficient water (Zhang et al., 1997). These relationships must be considered when investigating the regeneration of forest in the LNNR.

Although differences in response to environmental gradients among functional groups were obvious, their similarities were clear from the CCA ordination results. Figure 6 shows the correlations of the first two CCA axes of one functional group with that of the other. All the axes show a significant correlation with other axes, similar to other studies (Franklin et al., 2001; Lyon and Sagers, 2002; Nangendo et al., 2002). Different functional groups

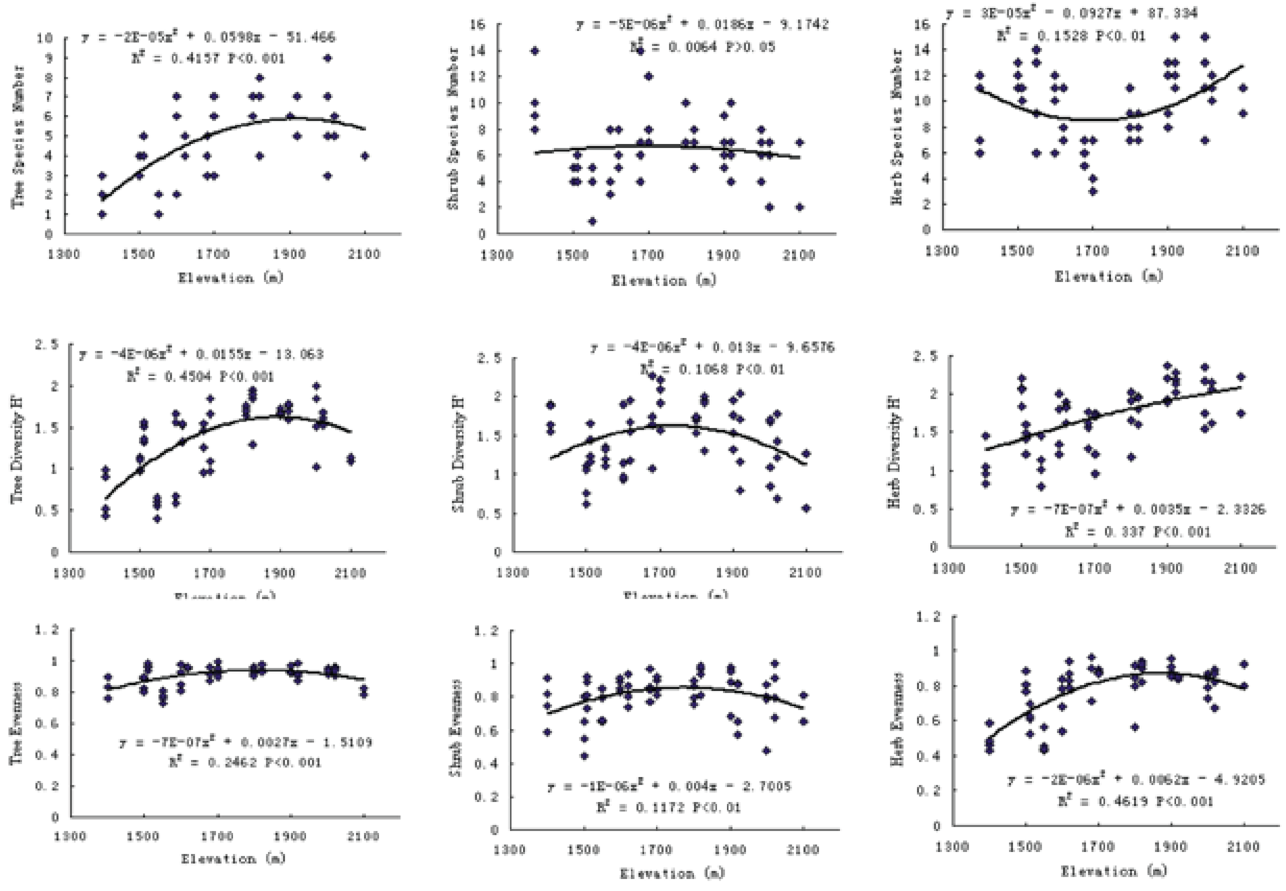

Figure 5. Variations of species diversity of functional groups along elevational gradient in the Lishan Nature Reserve, China.

in a community share the same complex of environmental variables, and therefore, it is easy to understand that they are similar in their responses to environmental gradients. This indicates that the functions and roles of species groups in communities are closely related to each other (Whitaker, 1967; Zhang, 2003; Nummelin and Zilihona, 2004). Although different plant groups show similar patterns of species diversity in response to elevation, those elevations with the maximum diversity values are different from each plant group (Figure 5); this is due to interactions between functional groups (Figure 5). The effects of trees on the diversity of shrubs and herbs are significant because tree canopies affect the distribution of resources such as light, water-conditions and temperature available to shrubs and herbs (Kessler, 2001; Zhang, 2003; Nummelin and Zilihona, 2004). Among trees, shrubs and herbs, trees were most important in maintaining species evenness of communities, and shrubs and herbs were significant in maintaining species richness of communities in the LNNR (Zhang and Chen, 2004). All the functional groups were important in maintaining species diversity (Loreau et al., 2001; Verburg and van Eijk-Bos, 2003), because species diversity is related to both species richness and evenness (Zhang, 1995). To protect species diversity and forests, the conservation of all functional layers should be emphasized. Elevation gradient is one key variable that affects the variation of species diversity in communities and is frequently studied (Lyon and Sagers, 2002; Zhang, 2002). The patterns of species diversity of functional groups along the elevation gradient were very similar; the species richness, diversity and evenness of different plant groups all show a significant correlation with elevation, with most being unimodal, consistent with the hypothesis of maximum diversity at intermediate elevations (Lomolino, 2001; Zhang and Chen, 2004). One exception was the richness of herbs, which had a minimum richness at intermediate elevations.

The distribution patterns of vegetation and species diversity are often correlated with patterns of resource variation and resource gradients, which have been well established in vegetation science (Whittaker, 1967; Austin, 1990; Zhang, 2002). Different plant functional groups may have different resource-use strategies, physiologies, and competitive abilities (Lyon and Sagers, 2002). In the literature, many vegetation studies avoid complexity by over-emphasizing a single type of plant group, typically a group of canopy tree species (O'Neill et al., 1986). In the present study, an analysis of all species, including canopy trees, understory shrubs, saplings and herbs, emphasized the importance of the structure of complex forest ecosystems. The inclusion of different functional groups in multivariate analysis provides more detailed and comprehensive information on the spatial variation of vegetation and species diversity and the response of plant species to underlying gradients (Lyon and Sagers, 2002; Zhang, 2004). Furthermore, vegetation functional group analyses can be used in a management and conservation context to identify vegetation and landscape characteristics (Lyon and Sagers, 2002; Verburg and van Eijk-Bos, 2003).

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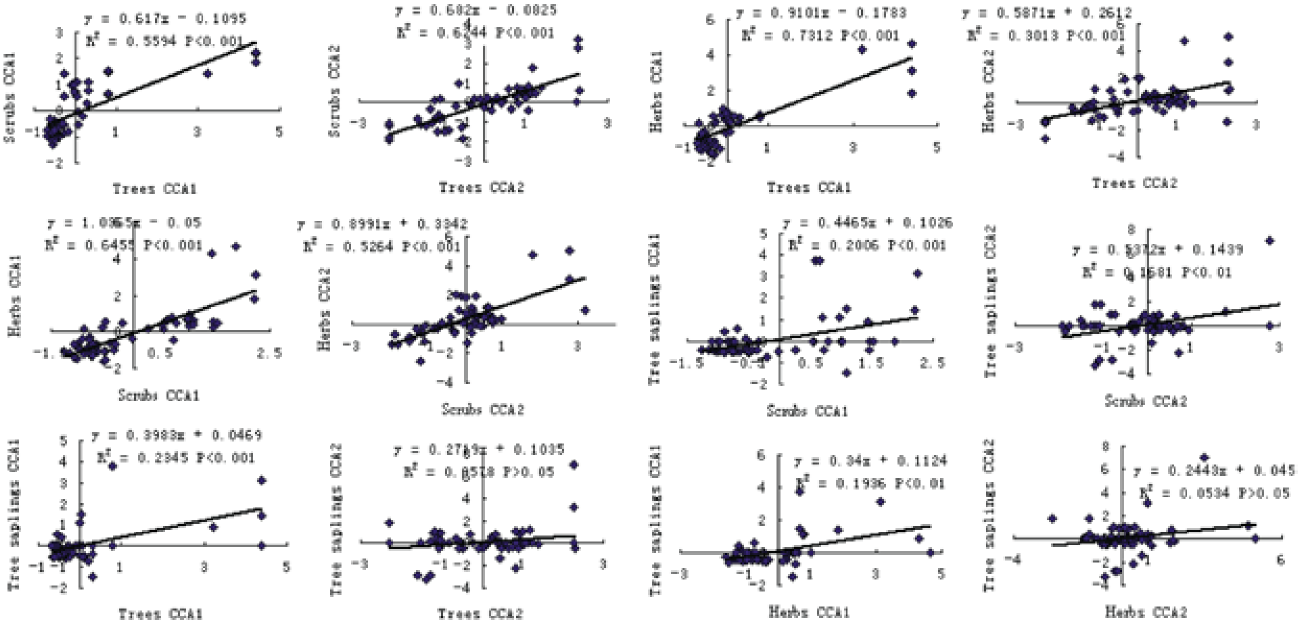

Figure 6. Relationships of the first two CCA ordination axes of one functional group with the other functional group in the Lishan Nature Reserve, China.

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中國曆山自然保護區森林群落植物功能群的組成與多樣性

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用典範對應分析 (CCA) 研究了中國山西曆山自然保護區森林植被的組成與分佈。曆山自然保護區位于東經 111º05’43”-111º56’29”，北緯 35º29’07”-35º23’10”，是中條山系的一部分。從海拔 1,400 到 2,100 米，我們設立了 58 個 10 m × 20 m 的樣方。群落的組成和環境資料用 CCA 按植物功能群比如喬木，灌木，幼樹和草本分別進行分析；同時進行各功能群的物種豐富性、多樣性和均匀性與環境因數間的關係分析。結果表明，森林群落所有功能群都與海拔和土壤 Cu 含量顯著相關，而對其他環境因數，各功能群有不同的關係。喬木層與土壤 P 含量相關，灌木和草本與土壤有機質和 N 含量相關，而幼樹與坡度和坡向相關。海拔是影響物種多樣性的最重要的因數，各功能群的豐富性、均匀性和多樣性沿著海拔梯度的變化符合同一模型，即最大的多樣性出現在中等海拔。喬木對維持群落的均匀性最重要，而灌木和草本對保持群落的豐富性最重要。

關鍵詞：典範對應分析；排序；功能群，植被和環境關係；物種多樣性；土壤因數；地形因數。