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Original article

## Environmental correlates of plant diversity in Korean temperate forests

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## ABSTRACT

Mountainous areas of the Korean Peninsula are among the biodiversity hotspots of the world's temperate forests. Understanding patterns in spatial distribution of their species richness requires explicit consideration of different environmental drivers and their effects on functionally differing components. In this study, we assess the impact of both geographical and soil variables on the fine-scale (400 m<sup>2</sup>) pattern of plant diversity using field data from six national parks, spanning a 1300 m altitudinal gradient. Species richness and the slopes of species–area curves were calculated separately for the tree, shrub and herb layer and used as response variables in regression tree analyses. A cluster analysis distinguished three dominant forest communities with specific patterns in the diversity–environment relationship. The most widespread middle-altitude oak forests had the highest tree richness but the lowest richness of herbaceous plants due to a dense bamboo understory. Total richness was positively associated with soil reaction and negatively associated with soluble phosphorus and solar radiation (site dryness). Tree richness was associated mainly with soil factors, although trees are frequently assumed to be controlled mainly by factors with large-scale impact. A U-shaped relationship was found between herbaceous plant richness and altitude, caused by a distribution pattern of dwarf bamboo in understory. No correlation between the degree of canopy openness and herb layer richness was detected. Slopes of the species–area curves indicated the various origins of forest communities. Variable diversity–environment responses in different layers and communities reinforce the necessity of context-dependent differentiation for the assessment of impacts of climate and land-use changes in these diverse but intensively exploited regions.

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## 1. Introduction

Species diversity is one of the most important features of biotic communities. It is closely related to other parameters of ecosystem functioning such as productivity, temporal variability, invasion resistance and complexity of interactions (Brosfokske et al., 2001; Härdtle et al., 2003; Zhang et al., 2006; Jiang et al., 2007; Acharya

et al., 2011). One of the most important properties of diversity is its spatial variation (Rahbek, 2005; Qian et al., 2007; Stohlgren, 2007). Environmental determinants play a key role in the spatial distribution of diversity at broad geographic extents, while biotic interactions and species life-history strategies govern the distribution of diversity at local scales (Magurran, 2004; Palmer, 2007). Only a handful of field studies have examined how abiotic constraints modulate species diversity in complex forest communities at a broader spatial scale (e.g., in larger areas).

Local-scale patterns of plant diversity are the outcome of multiple interacting factors such as competition and facilitation. These depend upon local environmental constraints such as resource availability and heterogeneity or small-scale disturbances (Doležal and Šrůtek, 2002; Callaway, 2007; Tamme et al., 2010).

Abbreviations: SAR, Species–area curve; PADIR, Potential Annual Direct Incident Radiation.

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Local-scale variation in diversity can be expressed as the species–area relationship (SAR) than can be approximated, for example, by the Arrhenius power function (Magurran, 2004). Existing theories predict that SAR slopes (i.e., heterogeneity of vegetation) increase with resource availability/heterogeneity and decrease with environmental stress (Lepš and Štursa, 1989; He and Legendre, 2002; Dengler, 2009). The slope of SAR curves for specific vegetation types may also provide clues about community assembly rules (Yodzis, 1978; Lepš and Štursa, 1989). In theory, slopes of SAR curves for dominance-controlled communities are lower than those for founder-controlled communities (Yodzis, 1978). The former communities are composed predominantly of species that are tolerant to stress, whereas the latter are disturbance-driven and consist predominantly of species with competitive-ruderal strategies (Lepš and Štursa, 1989). We can assume that founder-controlled communities are more frequent at higher altitudes because the environment there is harsher (Bellingham and Sparrow, 2000; Körner, 2003).

Biodiversity research benefits from being performed in regions with a rich biota (Stohlgren, 2007). Mountainous areas of the Eastern Asian phytogeographic zone, including those in the Korean Peninsula, are among those that sustain the highest biodiversity within the world's temperate forests (Qian and Ricklefs, 1999). The forest flora of the Korean Peninsula is, for example, more diverse than that of comparable forests in Europe and North America (Ellenberg, 1986; Qian and Ricklefs, 2000). The Korean flora consists of 160 families comprising 883 genera, 3070 species and 550 varieties. No less than 800 of the species are physiognomically important woody plants (Park, 2007). Most biodiversity studies published for Korea are rather descriptive and sampled on the local scale without a broader ecological context. Nevertheless, recent analyses performed elsewhere have revealed differential covariance between environmental correlates and biodiversity parameters that are based on the whole species composition and functionally or structurally differing subsets or layers (Hutchinson et al., 1999; Small and McCarthy, 2002; Ren et al., 2006; Gonzalez et al., 2009).

This study aims to explain fine-scale (400 m<sup>2</sup>) spatial patterns of diversity of near-natural South Korean forests using two diversity measures – species richness and the slope of the species–area curve – and sets of both geographical and soil variables. We treated our vegetation dataset as a whole and then classified it into three subsets corresponding to vegetation types previously described in Korea (Byun et al., 1998; Song et al., 2003; Park et al., 2006). The reason is that we anticipated different diversity–environment patterns to emerge in individual vegetation types. Subsequently, we were able to search for relationships shared by all the datasets. We tested several hypotheses concerning the pattern of plant diversity in Korean forests: (a) Diversity of the herb layer is positively correlated with the openness of the tree and shrub canopies; (b) Soil fertility is associated with an increase in species diversity in all vegetation layers; (c) Species richness generally increases with increasing availability of solar energy along the topographical and latitudinal gradient; and (d) Species richness is strongly correlated with altitude and less so with soil factors; the opposite would be valid for the SAR slope.

## 2. Methods

### 2.1. Study areas and vegetation

The study sites are located in six South Korean mountain ranges (national parks, see Appendix), five on the mainland and one on Jeju Island (Fig. 1). These mountain ranges are interconnected ranges in a north–south direction and mostly covered by (semi-) natural forests. Mixed forests of evergreen conifers and broad-

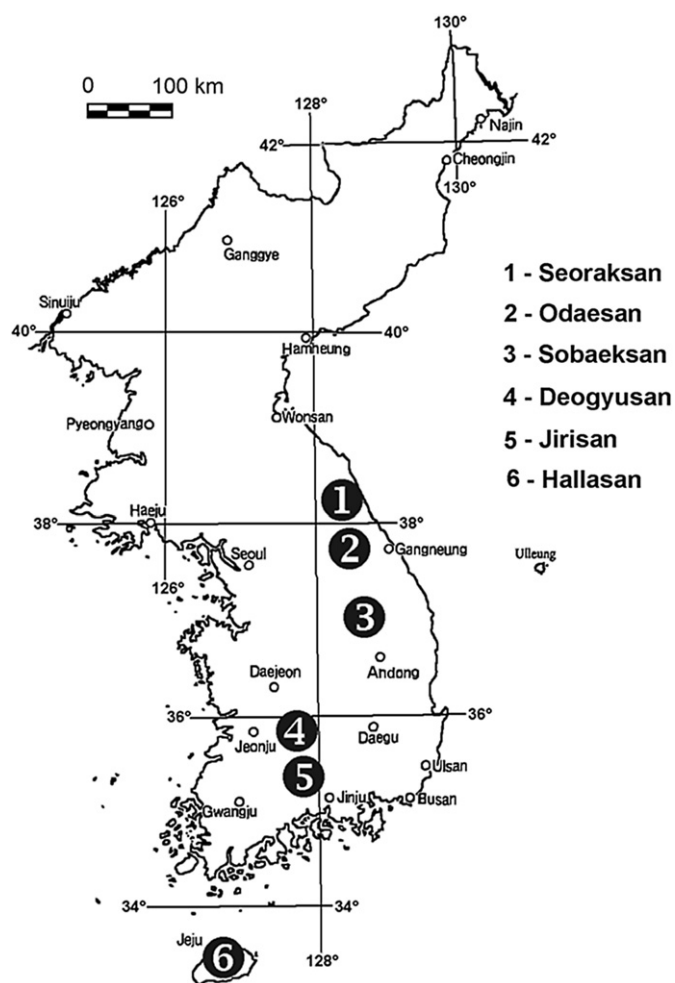


Fig. 1. Distribution on the Korean Peninsula of the national parks in which forest plots were studied.

leaved deciduous trees prevail in the central and higher parts of mountain slopes, dominated by the tree and shrub genera *Quercus*, *Abies*, *Acer*, *Carpinus*, *Lindera*, *Magnolia*, *Styrax*, *Pinus* and *Rhododendron*. At lower altitudes, there is a semi-deciduous forest in which the dominant genera of trees and shrubs are *Quercus*, *Zelkova*, *Rhus*, *Viburnum* and *Callicarpa*, *Quercus mongolica* being the most prevalent (Šrútek et al., 2003). The selected stands were close-to-nature old-growth forests which have not been recently subjected to major disturbances (as indicated, e.g., by groups of fallen logs). On the mainland of the regions under study, the mean annual air temperature varies between 9.9 and 12.7 °C, and mean annual precipitation varies between 1220 and 1400 mm. On Jeju Island, the mean annual climatic values are 15.9 °C and 1650 mm, respectively (averages for the period 1971–2000; Park et al., 2005).

### 2.2. Vegetation sampling

We studied the floristic composition and species abundances by establishing permanent 20 m × 20 m forest plots ( $N = 50$ ) during the summers 2005–2007. The plots were selected at sites covered with typical close-canopy forests (i.e., with no apparent indication of any human influence) which were uniform in soil, vegetation and stand characteristics. Each plot was divided into four subplots (10 m × 10 m), which we surveyed separately using the standard Braun-Blanquet nine-degree cover-abundance scale (Westhoff and

van der Maarel, 1978). At each plot, we measured its altitude (using a Garmin 60CSx GPS receiver) inclination, aspect and the cover of exposed rock (boulders, outcrops). Also, the percent coverage of all vegetation layers (trees, shrubs and herbs) was visually estimated and the cover of tree layer was further used as a variable describing the canopy openness.

To study species–area relationships, we established two sequences of nested square subplots with increasing size (0.25–1–9–25–49–100–200–400 m<sup>2</sup>) within each 20 m × 20 m plot. These sequences were laid out in opposite directions along a diagonal of each large plot (see Fig. 2). We calculated the mean number of species for every corresponding pair of subplots. This design was chosen to reduce the effect of the starting position on the sampling.

### 2.3. Soil sampling and analyses

Within each plot, we collected a mixed sample of soil consisting of eight systematically distributed subsamples (two per 10 m × 10 m subplot) from the Ah horizon. We measured the thickness of the Ah horizon. The collected soil was air-dried, ground in a ceramic mortar and sieved through a 2 mm mesh. The remaining soil gravel was weighed and removed. The following standardized analyses were performed: soil reaction (active in water solution and exchangeable in KCl solution), total carbon and nitrogen content, soluble phosphorus (as phosphate) in sodium carbonate solution, exchangeable calcium and magnesium content in ammonium acetate solution. The C/N ratio was then calculated.

### 2.4. Statistical analyses

To assign plots (10 m × 10 m) to vegetation types, we employed the cluster analysis algorithm of the SYN-TAX programme (Podani, 2001); details are described in Supplementary material I. Using the resulting dendrogram, we established three vegetation groups based on the similarity analysis in the Juice programme (Tichý, 2002). In addition, Juice programme also calculated the Potential Annual Direct Incident Radiation Index (Equation (3); McCune and Keon, 2002; PADIR) for each plot. The calculation employs slope, aspect and latitude as the entry parameters only. Aspect has to be 'folded' prior to calculation, to make this variable linear and symmetrical about the north–south axis. In this respect, PADIR strongly influences the habitat temperature and may serve as a proxy for evaluating site dryness or water availability in terrestrial vegetation under the normal water supply (i.e., in mesic conditions, which holds true for our plots). Since the calculation does not give account to cloud cover, regional differences in the atmospheric transmissivity or shading by adjacent topography/vegetation, it is rather approximative but still an efficient method how to capture the solar energy input into habitats.

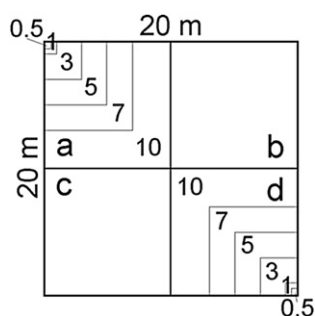


Fig. 2. Layout of the permanent 20 m × 20 m plots and the design of the subplots used for recording phytosociological relevés and assessing the species–area relationships. The numbers refer to the lengths of the edges of the respective squares in metres.

We calculated the parameters of the species–area curve using the number of species in each quadrant of successively increasing size. The power function was used to estimate  $z$ , which measures the rate of species increase:

$$S = cA^z$$

where  $S$  is the number of species,  $A$  is the plot area and  $c$  a constant. The model is an accurate means of describing the plant species richness of small and intermediate sample sizes (Rosenzweig, 1995; Zhang et al., 2006). The parameter  $z$  was fitted on untransformed data by ordinary least-squares regression. The power function described the data extremely well, with the medians of the coefficient of determination  $R^2 = 0.99$  for all species and  $R^2 = 0.97$  for the herbaceous understorey.

To select the explanatory variables that have good predictive power, we constructed regression trees. Since traditional regression trees suffer from serious problems due to the variable selection bias and over-fitting, we employed the modified technique of Conditional Inference Trees (Hothorn et al., 2006). Species richness (Magurran, 2004) and the slopes of the SAR curves were used as the dependent variables. These calculations were performed using the 'party' package (Hothorn et al., 2006) in the R statistical software (version 2.11.0). To test for environment–diversity patterns in data subsets partitioned according to the type of vegetation, we developed parsimonious models using multiple linear regressions in R (the number of observations was too low for the running regression tree procedure). The explanatory variables were visually assessed for normality prior to analysis by plotting normal–probability graphs and transformed, when needed, to approach a normal distribution (Table 1). Important correlations between variables are summarized in Table 2. Altitude and solar radiation are treated as geographical variables, all other factors as canopy structure or soil variables. Altitude was recorded and its quadratic term determined for testing the curvilinear relationship.

All the primary data are placed as a Supplementary material II.

## 3. Results

### 3.1. Vegetation characteristics and the environment

Our cluster analysis of taxonomic data distinguished three main types of forest named after the diagnostic tree/shrub species (see Supplementary material I.). The type with *Q. mongolica* and *Lindera obtusiloba* is representative of the climax forest in the study area (for nomenclature see Park, 2007). These stands had the highest tree richness but the lowest richness of herbs (Table 1). The soils in these stands had an intermediate content of the macronutrients nitrogen and carbon (Table 1). The type with *Acer pseudosieboldianum* and *Rhododendron schlippenbachii* is representative of upper montane forests, which grow on steeper slopes with soils poorer in nutrients (Table 1). This forest type had the highest total species richness of all. The type with *Carpinus tschonoskii* and *Abies koreana* occurs on the volcanic Jeju Island. Stands were sampled on moderate slopes with nutrient-rich soils almost lacking gravel (Table 1). The values of total, tree and herb plant richness were also intermediate (Table 1). All forest types occupied predominantly acidic soils, with water pH rarely exceeding 6. All analysed soils were humus-rich, covered mainly by acidic litter and had an increased calcium and magnesium content. The exchangeable acidity of most soils was relatively high. Organic content and the C/N ratio were very favourable. The values of the latter fluctuated above 10. The B-horizon usually reached the depth of 70 cm, exceptionally up to 85 cm (*Quercus*–*Lindera* and *Carpinus*–*Abies* types, see Table 1).

**Table 1**  
Means and ranges of the values of the variables investigated in the three forest types. Variables in bold denote significant differences among group means ( $\alpha = 0.05$ , Tukey's post-hoc test for unequal N), group means not mutually different are followed by the same superscript letter. DW means dry weight.

	Abbreviation	Forest type								
		<i>Quercus mong.–Lindera obtus.</i> n = 24 <sup>h</sup>			<i>Acer pseudo.–Rhododendron schl.</i> n = 15			<i>Carpinus tsch.–Abies koreana</i> n = 11		
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
<i>Explanatory variables</i>										
<i>Geographical variables</i>										
<b>Altitude (m)</b>	<b>altit</b>	<b>383</b>	<b>953<sup>a</sup></b>	<b>1474</b>	<b>823</b>	<b>1160<sup>ab</sup></b>	<b>1492</b>	<b>949</b>	<b>1337<sup>b</sup></b>	<b>1768</b>
<b>Aspect<sup>c</sup> (°)</b>	<b>aspect</b>	<b>12.5</b>	<b>85.3<sup>a</sup></b>	<b>180</b>	<b>5</b>	<b>85.3<sup>a</sup></b>	<b>158</b>	<b>25</b>	<b>96.3</b>	<b>180</b>
<b>Inclination (°)</b>	<b>slope</b>	<b>10</b>	<b>30<sup>a</sup></b>	<b>46</b>	<b>18</b>	<b>32<sup>a</sup></b>	<b>43</b>	<b>4</b>	<b>15</b>	<b>28</b>
PADIR <sup>d</sup> (MJ cm <sup>-2</sup> yr <sup>-1</sup> )	PADIR	1.818	2.268	2.945	1.631	2.212	2.895	1.980	2.519	2.818
Cover of exposed rock (%) !	rock	0	25	96	0	11	75	2	17	44
<i>Canopy structural variables</i>										
Cover of tree layer (%)	cover3	48	76	91	35	68	84	3	65	88
Cover of shrub layer (%) !	cover2	7	30	64	7	47	88	9	31	76
Cover of herb layer (%) !	cover1	5	53	99	11	48	89	9	60	93
<i>Soil variables</i>										
<b>Gravel in A horizon (%) !</b>	<b>gravel</b>	<b>0.1</b>	<b>9.7<sup>a</sup></b>	<b>33.5</b>	<b>2.0</b>	<b>6.0<sup>a</sup></b>	<b>29.6</b>	<b>0.1</b>	<b>0.4</b>	<b>1.3</b>
<b>A horizon depth (cm) !!</b>	<b>thick A</b>	<b>1</b>	<b>10<sup>a</sup></b>	<b>42</b>	<b>3</b>	<b>7<sup>a</sup></b>	<b>11</b>	<b>4</b>	<b>33</b>	<b>60</b>
<b>Total carbon (% DW) !</b>	<b>C</b>	<b>7.57</b>	<b>13.01<sup>a</sup></b>	<b>22.53</b>	<b>5.39</b>	<b>12.69<sup>a</sup></b>	<b>21.44</b>	<b>14.57</b>	<b>21.44</b>	<b>27.53</b>
<b>Total nitrogen (% DW) !</b>	<b>N</b>	<b>0.432</b>	<b>0.907<sup>a</sup></b>	<b>1.808</b>	<b>0.339</b>	<b>0.812<sup>a</sup></b>	<b>1.330</b>	<b>0.997</b>	<b>1.420</b>	<b>1.698</b>
pH actual !!	pH <sub>act</sub>	4.13	4.68	6.08	4.12	4.55	5.17	3.93	4.39	4.83
Potential soil acidity <sup>e</sup>	$\Delta$ pH	0.48	0.69	0.85	0.54	0.75	0.93	0.57	0.75	0.90
Carbon/nitrogen ratio	C/N	10.55	14.86	18.94	11.42	15.58	20.22	13.45	15.03	16.97
Exchangeable P (ppm) !!	P	4.30	12.91	74.45	2.81	6.34	10.30	3.58	8.90	23.63
Soil Mg ions (ppm) !!	Mg	73	170	684	84	140	219	71	191	257
Soil Ca ions (ppm) !!	Ca	226	1622	10,080	256	1244	2303	179	696	1951
<i>Response variables</i>										
<b>R<sub>total</sub><sup>f</sup></b>		<b>16</b>	<b>38<sup>a</sup></b>	<b>71</b>	<b>25</b>	<b>53<sup>b</sup></b>	<b>79</b>	<b>21</b>	<b>41<sup>ab</sup></b>	<b>82</b>
R <sub>tree</sub> <sup>f</sup>		4	9.3	16	2	6.6	10	1	7.2	12
<b>R<sub>shrub</sub><sup>f</sup></b>		<b>7</b>	<b>13.8<sup>a</sup></b>	<b>22</b>	<b>6</b>	<b>13.9<sup>a</sup></b>	<b>24</b>	<b>6</b>	<b>9.4</b>	<b>12</b>
<b>R<sub>herb</sub><sup>f</sup></b>		<b>1</b>	<b>16.4<sup>a</sup></b>	<b>37</b>	<b>5</b>	<b>32.9</b>	<b>65<sup>b</sup></b>	<b>7</b>	<b>23.8<sup>ab</sup></b>	<b>62</b>
SSAR <sub>total</sub> <sup>g</sup>		0.28	0.40	0.51	0.24	0.37	0.43	0.31	0.38	0.44
SSAR <sub>herb</sub> <sup>g</sup>		0.08	0.33	0.62	0.21	0.39	0.58	0.23	0.35	0.41

!, !! arcsin or log transformation, respectively.

<sup>c</sup> Linearized on 0–180° scale along NE-SW line, i.e., to approximate a heat load (McCune and Keon, 2002).

<sup>d</sup> Potential Annual Direct Incident Radiation (McCune and Keon, 2002 – Equation (3); also see Methods).

<sup>e</sup> Computed as pH actual – pH exchangeable.

<sup>f</sup> Number of species occurred in a sample/subordinate vegetation layer of 20 m × 20 m plots.

<sup>g</sup> Slope of the species–area curve for all species/herbs only in 20 m × 20 m plots.

<sup>h</sup> Number of 20 m × 20 m plots sampled.

### 3.2. Species richness

Total and tree richness was chiefly correlated with soil variables. By contrast, the richness of shrubs and herbs was correlated with geographical variables in the whole dataset (Fig. 3). One of the main factors positively correlated with total species diversity and richness was soil reaction, but only herb richness rose strongly with increasing soil reaction at higher altitudes (see Fig. 3). We found a strong effect of soluble phosphorus that was negatively associated with total richness (Fig. 3).

**Table 2**  
Correlation table with explanatory variables for those cases where the Pearson's coefficient is greater than 0.50.

X	Y	Corr (X,Y)
Slope	PADIR	–0.57
Cover1	cover2	–0.52
Rock	P	0.57
pH	Ca	0.64
Cover1	$\Delta$ pH	0.51
Ca	$\Delta$ pH	–0.54
C	N	0.94
Mg	N	0.60
Mg	P	0.57
Mg	Ca	0.69

A positive role of altitude, exposed rock, soil gravel and nitrogen and a negative role of soil carbon, phosphorus and solar radiation were proved to control the species richness of individual layers in *Quercus–Lindera* forests.

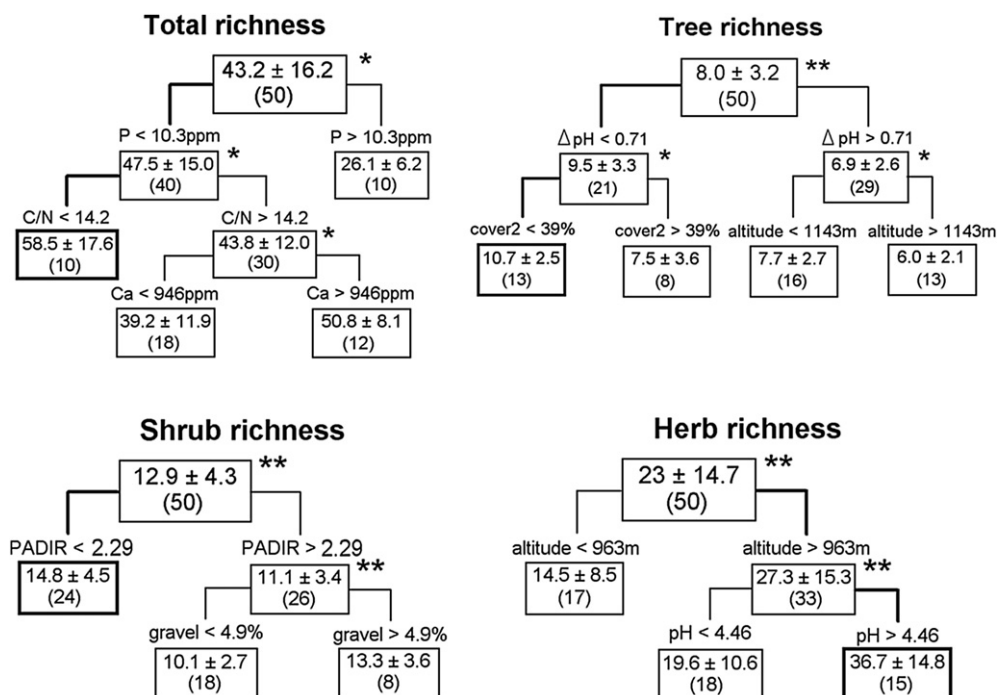
A different pattern emerged in upper montane forests, where soil carbon, nitrogen and the quality of the humus were important (Table 3, *Acer–Rhododendron* vegetation type). Total species richness was especially high at humus-rich sites and modest where the quality of the humus was inferior (indicated by a high C/N ratio).

Along the eastern slope of the Hallasan volcano (*Carpinus–Abies* vegetation type), only the richness of herbs appeared to be associated with altitude, exhibiting a curvilinear U-shaped relationship that was modified by the slope of the sites (Table 3).

### 3.3. Species–area relationships

The highest values for the SAR slope for the total composition were recorded for the dominant vegetation type (*Quercus–Lindera*, Table 1), the lowest for the mountain forest (*Acer–Rhododendron*). Assuming the SAR slopes for the herb layer, the results were the opposite.

Solar radiation played a fundamental role in both the total and the herbaceous SARs. The regression trees indicate that mesic forests at low altitudes reached the highest SAR slope (Fig. 4). Furthermore, a comparison of the vegetation subsets revealed



**Fig. 3.** Regression trees with species richness in different layers and of the total species composition of 20 m × 20 m forest plots. Each node is described by the splitting variable and its value. PADIR is given in unit MJ cm<sup>-2</sup> yr<sup>-1</sup>. In the boxes are the means and standard deviations of the species richness and number of plots assigned to that node (in parentheses). The thick lines in the terminal nodes indicate the indicator associated with the highest richness. Asterisks indicate the statistical significance of each split: \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.

a strong role of geographic and structural factors in *Quercus–Lindera* forests and a strong role of soil factors in *Acer–Rhododendron* and *Carpinus–Abies* forests in shaping SAR slopes (see Table 3).

A comparison between regression results for the dominant *Quercus–Lindera* forests with the SAR as a response variable and those with species richness as a response variable showed the same negative association with solar radiation (Table 3). Moreover, the

SAR for herbs along the altitudinal gradient was U-shaped. Within the *Acer–Rhododendron* and *Carpinus–Abies* forests, the soil reaction and the content of phosphorus and carbon correlated with the SAR slopes. These factors differed from those predicting species richness for the respective vegetation layers (Table 3).

## 4. Discussion

### 4.1. Vegetation characteristics and the environment

Both dominant forest types, *Q. mongolica–L. obtusiloba* and *A. pseudosieboldianum–R. schlippenbachii*, correspond to vegetation units distributed along an altitudinal gradient, which were distinguished in previous regional studies (Byun et al., 1998; Song et al., 2003; Park et al., 2006). The *C. tschonoskii–A. koreana* type occurring on the Hallasan volcano (Jeju Island) encompasses four altitudinal vegetation zones, where the corresponding associations along an altitudinal gradient have been described (details in Doležal et al., 2012). Ecological characteristics found for all forest types are in accordance with studies dealing with the forest environment of Korea (Byun et al., 1998; Song et al., 2003). In this way, our vegetation sample represents well the main bulk of Korean zonal forests.

### 4.2. Species richness

Environmental factors associated with total species composition differ from those associated with individual vegetation layers (Fig. 3). Tree richness is correlated with local soil variables. Shrub and herb richness is correlated with geographical variables. Thus, the pattern of the species–environment relationship does not agree with the assumption that it weakens from the lower to upper layer (Gonzalez et al., 2009).

**Table 3**

Results of multiple linear regressions using the environmental descriptors listed in Table 1 for determining the diversity parameters assessed separately for the tree, shrub and herb layer for the three types of vegetation considered. Only descriptors significant at α-level < 0.05 were selected for constructing the most parsimonious model. Positive relationships are indicated by descriptors in bold type; negative ones by standard type. Figures beneath the descriptors show the percentage of variability explained by each model together with the significance level of that linear model (\*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001), 'na' denotes no parsimonious model found.

Vegetation type	R <sub>total</sub>	R <sub>tree</sub>	R <sub>shrub</sub>	R <sub>herb</sub>	SSAR <sub>total</sub>	SSAR <sub>herb</sub>
<i>Quercus–Lindera</i> (24) <sup>a</sup>	<b>gravel</b> PADIR	<b>rock</b> P	<b>N</b> PADIR C	<b>altit</b> <b>gravel</b> PADIR	<b>Ca</b> PADIR pH <sub>act</sub> C	<b>altit2<sup>b</sup></b> altit
Multiple R <sub>adj</sub> <sup>2</sup>	42.8**	29.6**	24.5*	59.0***	45.2**	30.6**
<i>Acer–Rhododendron</i> (15)	<b>C</b> N	<b>N</b> <b>C/N</b> C/N	<b>C</b> slope <b>P</b> C	<b>altit</b> <b>rock</b> cover1 C	pH <sub>act</sub> C/N C PADIR C/N	<b>P</b>
Multiple R <sub>adj</sub> <sup>2</sup>	84.1***	72.8**	76.9***	90.8***	52.8**	65.2***
<i>Carpinus–Abies</i> (11)	<b>slope</b> <b>PADIR</b>	<b>thick A</b> <b>Mg</b> PADIR	na	<b>altit2</b> <b>slope</b> Altit	na	<b>pH<sub>act</sub></b> C PADIR
Multiple R <sub>adj</sub> <sup>2</sup>	92.4***	80.3**	–	93.4***	–	66.5*

<sup>a</sup> Number of 20 m × 20 m plots sampled in each subset.

<sup>b</sup> Quadratic term of altitude to test of non-linear relationship.

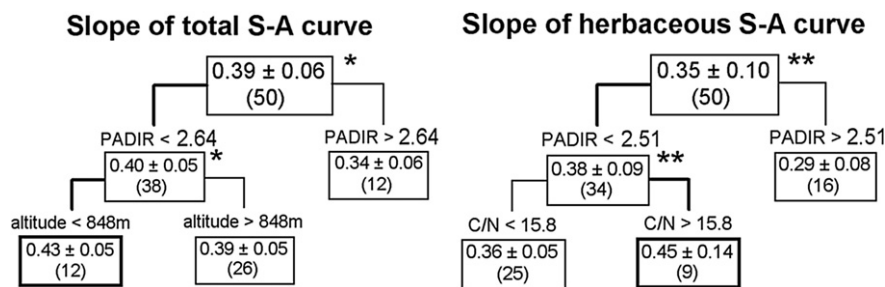


Fig. 4. Regression tree indicating the relatedness of the slopes of the species–area curves for all plants and for herbs only in 20 m × 20 m forest plots. For details see Fig. 3.

Soil reaction is one of the main factors that are positively correlated with total species diversity and richness in forest communities (Schuster and Diekmann, 2005; Chytrý et al., 2007). In our study, only the richness of herbs was found to be correlated with soil reaction in the case of plots at higher altitudes, a result indicating this predictor has a minor role (see Fig. 3). The aforementioned authors report that the strongest effect of soil reaction on species richness in forests occurs below pH 5.5, as recorded in the present study. This is presumably the result of more favourable growing conditions and greater resource availability with a slight increase in pH in predominantly acidic soils (Peet et al., 2003).

Especially noteworthy is the marked effect of soluble phosphorus, which is negatively associated with total richness (Fig. 3). This agrees with the results of Janssens et al. (1998) and Fu et al. (2004), who indicated that the threshold of soil phosphorus needed for the development of rich communities is below 10 ppm (compare Fig. 4). Han et al. (1995) report rather low amounts of PO<sub>4</sub> in forests dominated by *Q. mongolica*. This forest type is dominant in Korea and hosts most of its phytodiversity. This means that most forest plant species in Korea are adapted to low-phosphorus environments. Correlations repeatedly found for phosphorus indicate that its availability limits both productivity and decomposition in late successional stages, whereas nitrogen is a limiting element during early successional stages (Vitousek and Farrington, 1997). Results of long-term studies indicate that the availability of phosphorus, unlike that of nitrogen, can significantly affect the productivity of competitive plants, and thus diversity (Chytrý et al., 2009).

The situation is reversed in upper montane forests: soil carbon, nitrogen and humus quality all have an important role (Table 3, *Acer–Rhododendron* vegetation type). Total species richness is especially high at humus-rich sites and low where the humus has lower decomposability (indicated by a high C/N ratio), a fact also recognizable in other studies (Fu et al., 2004; Lenière and Houle, 2006). In addition, if the environment is harsh, the biota depends more on the availability of main macronutrients (Körner, 2003). In these habitats, succession is permanently maintained at an early stage by relatively frequent disturbances and subsequent rejuvenation (Bellingham and Sparrow, 2000). Nitrogen, not phosphorus, is therefore the limiting factor (Aber and Mellilo, 2001).

We did not find statistical evidence that rich herb layer is sustained under the conditions of increased light intake (open tree canopy), a phenomenon very often reported in forest studies. The reason can be found in niche dynamics. Härdtle et al. (2003) and Brosofske et al. (2001) show that high light intensities are only associated with herbaceous plant richness in oligotrophic conditions, whereas in nutrient-rich forests the number of herbaceous species increases with soil nutrient supply (i.e., Ah horizon thickness, pH or base cations as proxy variables). Chen (2006) found a positive correlation between tree carbon storage (which is positively related to tree foliage and hence shade) and tree species

richness. Thus, high understory richness may result from a diversification of the nutrient supply associated with a rich overstory layer. Such mechanism is supported by the proposed links between the number of individuals, number of species and the rate of net primary production NPP (Enquist and Niklas, 2001). NPP is determined by site productivity and regulates the total niche volume and consequently biological diversity.

Surprisingly for the solitary Jeju Island, there are no well manifested linear gradients along the eastern slope of the Hallasan Volcano. In fact, only the herb richness appeared to be associated with altitude, and this relationship was non-linear (U-shaped) even though a linear altitudinal decrease of this response also proved to be significant (Table 3, *Carpinus–Abies* vegetation type). Specifically, the alpine species pool becomes increasingly more important at high altitudes since stands close to the timber line are more open. If only closed stands are sampled throughout the altitudinal gradient, then the relationship between species diversity and altitude is unimodal due to the transitional character of the intermediate vegetation belt (Zhao et al., 2005; Jiang et al., 2007). Tree richness is well predicted by site productivity, being mainly associated with water availability (also Acharya et al., 2011), which makes altitude superfluous.

#### 4.3. Species–area relationships

Our assumption regarding the existence of founder-controlled communities at high altitudes are unequivocally corroborated by our data. Slope *z* of the SAR behaved in the opposite way between the forest types *Quercus–Lindera* and *Acer–Rhododendron* when comparing the results for the total species composition and for the herb layer only. This reversal may be explained by the fact that herbaceous and woody species are influenced by different regional processes. Herbs react relatively quickly to local disturbances, and their species pool is enriched at high altitudes due to the contribution of alpine habitats (Šrůtek and Doležal, 2003). The founder-controlled community assembly rule may therefore be the mechanism by which the slope of the SAR is increased. In addition, the herb layer in the oak forests is frequently dominated by *Sasa borealis*, a strong clonal competitor, which effectively suppresses other herbaceous plants (Doležal et al., 2009), leading to a uniform, dense understory (see further). On the other hand, the higher *z* found for the total plant composition within the *Quercus–Lindera* forests (Table 1) resulted from the abundance of woody species. Here the niche partitioning among large individuals of different taxa might have evolved in a more stable environment. This can be ascribed to higher net primary productivity, resulting in increased total niche volume (Enquist and Niklas, 2001).

We revealed a dominant negative association between solar radiation and SAR slopes for total plant composition and that of the herb layer, but this predictor was insignificant if richness was used as the diversity index (compare Figs. 3 and 4). In terms of the

diversity definition, we might therefore either assign a priority to this predictor or neglect it altogether. In spite of a linkage between species-rich vegetation and abundant moisture, an increase in solar radiation (site dryness) alone is not associated with a decrease in species richness in general, as documented by a positive regression between tree species richness and the high solar radiation and soil moisture in New Zealand (Leathwick et al., 1998). A linear relationship is assumed where the environmental gradient is short and where high temperatures and light intensities support community diversity (Small and McCarthy, 2002; Acharya et al., 2011). We, however, analysed the data on a broader scale, at which more complex interactions resulted in a unimodal relationship. This is likely since the inclusion of PADIR as a quadratic term into the parsimonious model significantly affected the slope of the total SAR (data not shown).

Regression results for the SAR of the dominant *Quercus–Lindera* forests are similar to those using species richness as a response variable. The U-shaped form of the SAR for herbs along the altitudinal gradient in these forests may be addressed by the negative PADIR-SAR correlation if solar radiation decreases towards the middle altitudes. But indeed, solar radiation rises towards the middle altitudes. Actually, the solar radiation rises along the whole altitudinal gradient, but the data are quite scattered and the trend is rather weak ( $r = 0.26$ ,  $p = 0.06$ ). Moreover, the rise of SAR values in high altitudes is quite pronounced. Another process, possibly responsible for this phenomenon, encompasses the role of immigration and dispersal (Rosenzweig and Ziv, 1999). This pattern can be caused by a positive effect of both lowland and alpine species pools. Within the *Acer–Rhododendron* and *Carpinus–Abies* forests, the SAR slope depends almost exclusively on soil productivity. Especially the role of phosphorus may indicate an enhanced clustering of species within nutrient-rich spots under harsher climatic conditions.

#### 4.4. Search for uniform predictors

Altitude, solar radiation and soil structure were most frequently correlated with community diversity patterns. Soil structure was often associated with a positive effect, solar radiation with a negative effect and altitude had a context-dependent effect. The dominance of altitude indicates its possible importance in shaping both geography-dependent species pools (Rosenzweig, 1995) and local environments through its effect on water supply and thermal regimes (Aber and Melillo, 2001). In a similar study from North Korea, the altitudinal gradient was of superior importance for the species richness pattern (Šrůtek et al., 2003). The mechanism underlying the negative role of solar radiation is that it has an indirect effect on nutrient dynamics by determining water availability at a site. The importance of soil structure is attributable to its effects on other components of soil quality such as aeration, humus formation or base status (Aber and Melillo, 2001).

It has frequently been reported that soil pH plays a major role (e.g., Brosofske et al., 2001; Härdtle et al., 2003; Chytrý et al., 2007). Our results, however, are less straightforward. For determining SAR slopes, in contrast to models incorporating species richness, the superiority of soil reaction may indicate that mainly soil cations sustain rich biotic interactions through effective niche partitioning (Wardle, 2002).

A strong and inverse association between soil phosphorus and total richness for the whole dataset might indicate its role in sustaining species accumulation. However, it may differently condition processes in the upper-montane forests, where phosphorus appears to be positively associated with diversity parameters. This nutrient seems to favour the co-existence of plants in harsher environments (Wardle, 2002).

The role of altitude might be explained by a mechanism driving species richness via the migration processes (Wilsey and Stirling, 2007; Zhang et al., 2011). Altitude can be used as a surrogate of migration under the assumption that neighbouring areas of land are a source of species colonizing the community under study. In the forests considered in our study, altitude was an important determinant only for richness of herbs. It seems that for mountain forests (*Acer–Rhododendron* and *Carpinus–Abies* types), the quality or supply of resources is a more important determinant of local species richness than migration.

The U-shaped relationship between herb richness and altitude on Jeju Island (*Carpinus–Abies* forests) as well as in the whole dataset can be explained in terms of the biology of the dominant dwarf bamboo (*S. borealis* and *Sasa palmata*). Bamboo only forms dense populations and competitively excludes other herbaceous plants at intermediate altitudes but is competitively weak at low and high altitudes (Kim and Yang, 1996; Doležal et al., 2009). Bamboo is disadvantaged in scree woodlands, especially at the bottoms of mountain slopes, by its inability to create an extensive rhizome system in shallow soils; likewise in upper montane woodlands, where it suffers frost damage during winters with a shallow snowpack (Doležal et al., 2009). This may account for the difference between the data for East Asian forests and global data on the herbaceous forest flora, for which the most frequent altitudinal patterns are hump-shaped or monotonically decreasing (Rahbek, 2005).

The strong association between plant co-existence and geographical and structural factors is corroborated by previous studies (Fu et al., 2004; He and Legendre, 2002; Houle, 2007). On the other hand, soil properties are strongly associated with species co-existence in individual forest communities in South Korea. A comparison of the associations of diversity criteria with geographical and soil factors revealed community-specific responses with hints on variable assembly mechanisms (Brosofske et al., 2001; Härdtle et al., 2003). Depending on the intensity of environmental stress, the important factors change from gross productivity (quantity of soil organic matter) to those characterizing the quality of the soil. The predictive capacity of the regression models for the diversity parameters used was comparable. Our understanding of the causes and mechanisms determining diversity patterns improves when we treat several diversity parameters together. Arguing about which diversity index works best is pointless because this depends on the context.

Even though gradients in geo-climatic factors reflected in the zonation of the vegetation exist across the Korean Peninsula (Park et al., 2005), they are not associated with concomitant changes in species saturation at the community level. Such changes can only be detected along longer or steeper gradients like, for example, those associated with geology or continentality (Chytrý et al., 2007).

## 5. Conclusions

The most important predictors of diversity of forest plants in this study were (1) altitude with variable effect, (2) solar radiation with negative effect and (3) soil gravel with positive effect. This applied to all layers of vegetation as well as individual ones. Taking the entire dataset into consideration, total species richness depended only on soil variables, phosphorus being the most important negative correlate. The strongest association was found between tree richness and soil factors. The diversity–environment relationship differed among the vegetation layers and also differed from the total diversity (apart from the herb layer, which makes up the main bulk of the community in terms of species richness). We found no correlation between the degree of canopy openness



and herb layer richness. The relative importance of individual predictors is most probably determined by environmental stress, which changes along the altitudinal gradient. Hence, the assumed universal role of soil fertility or solar energy shaping species richness was not proved. Also, soil factors were found to be weak predictors of SAR slopes, whereas the dominant role of altitude predicting the species richness was confirmed. Even though changes in the qualitative composition of the vegetation occur over a broad geographical scale due to shifts in geo-climatic factors, they are not associated with fine-scale changes in species co-existence (expressed in terms of diversity) within specific biome types.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2012.12.001>.

## Appendix

Brief characteristics of the national parks surveyed.

National park	Area (km <sup>2</sup> )	Peak (m)	Predominant geology <sup>a</sup>
Seoraksan	371	1708	Kenozoic granitic intrusives
Odaesan	291	1539	Precambrian migmatitic/porphyroblastic/leucocratic gneisses
Sobaeksan	320	1440	Precambrian migmatitic/porphyroblastic/leucocratic gneisses
Deogyusan	229	1614	Precambrian porphyroblastic/leucocratic granitic gneisses
Jirisan	441	1915	Precambrian granitic/pegmatitic gneisses
Hallasan	153	1950	Pliocene/quaternary basalts and trachytes

<sup>a</sup> After Lee, D.S. (Ed.) 1988. Geology of Korea, second ed. Geological Society of Korea, Kyohak-Sa, Seoul.

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