



Altitudinal patterns and determinants of plant species richness on the Baekdudaegan Mountains, South Korea: common versus rare species

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Abstract

Altitudinal patterns of plant species richness and the effects of area, the mid-domain effect, climatic variables, net primary productivity and latitude on observed richness patterns along the ridge of the Baekdudaegan Mountains, South Korea were studied. Data were collected from 1,100 plots along a 200 to 1,900 m altitudinal gradient on the ridge. A total of 802 plant species from 97 families and 342 genera were recorded. Common and rare species accounted for 91% and 9%, respectively, of the total plant species. The altitudinal patterns of species richness for total, common and rare plants showed distinctly hump-shaped patterns, although the absolute altitudes of the richness peaks varied somewhat among plant groups. The mid-domain effect was the most powerful explanatory variable for total and common species richness, whereas climatic variables were better predictors for rare plant richness. No effect of latitude on species richness was observed. Our study suggests that the mid-domain effect is a better predictor for wide-ranging species such as common species, whereas climatic variables are more important factors for range-restricted species such as rare species. The mechanisms underlying these richness patterns may reflect fundamental differences in the biology and ecology of different plant groups.

Keywords: altitudinal gradient, climatic variables, different plant groups, hump-shaped pattern, mid-domain effect

INTRODUCTION

Mountains are important habitats for a diversity of organisms in continental ecosystems. The altitudinal gradients formed in mountain ecosystems are an important physical factor that influences biodiversity and species distribution patterns because altitude affects temperature and precipitation, thus influencing the ecological and physiological adaptation of plants, mammals, birds and invertebrates (Lomolino 2001). Therefore, mountains represent a remarkable, distinctive system valuable for

evaluation of ecological and biogeographical patterns and theories of species diversity (Körner 2000, Grau et al. 2007).

Many studies have documented the altitudinal richness patterns of plants (Lee et al. 2012), mammals (Rowe 2009), birds (McCain 2009) and invertebrates (Liew et al. 2010). Observed patterns have differed among taxa and regions. Three main types of richness pattern in relation to increasing altitude are reported: (1) a monotonic

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decrease, (2) a plateau at low altitudes, and (3) a hump-shaped distribution with high richness at intermediate altitudes (Rahbek 2005). Of these patterns, the hump-shaped pattern is reported to be the most common. Although the mechanisms underlying altitudinal richness patterns are still subject to debate, typical explanations include the influence of variables such as climate, area, geometric constraints or the mid-domain effect (MDE), productivity and evolutionary history (McCain 2009). Climatic variables are considered to be the most widely supported predictors of worldwide species richness (Rowe 2009), because they directly limit a species' distribution when the physiological tolerance of the species is exceeded and indirectly affect photosynthetic activity and other biological processes. Previous studies indicate that the area of altitudinal bands explains a large proportion of the variation in species richness (Karger et al. 2011), in a similar manner to the well-known species–area relationships. Species–area predictions posit that a larger area provides increased habitat diversity, which may harbor a larger number of species, and an increase in area is accompanied by both a decrease in the extinction rate and an increase in speciation or colonization (Rosenzweig 1995). Recent studies suggest that the MDE, or geometric constraints, is also highly effective at explaining altitudinal patterns of species richness (Kluge et al. 2006, McCain 2009). The MDE postulates that geometric constraints on species ranges within a bounded domain yield a mid-domain peak in richness regardless of ecological factors (Colwell and Lees 2000). The MDE is abiotic and stochastic, and is founded on the premise that the spatial distribution of species richness is constrained by the shape of landmasses and by species range size. Under these conditions, random replacement of species ranges within a bounded domain creates an overlap of species ranges and thus a peak of species richness toward the center of the geographical domain (Colwell and Hurr 1994, Colwell and Lees 2000). Productivity is an additional variable that may influence species richness patterns. Although the relationship between species richness and productivity is controversial, with disagreement over whether productivity controls or is controlled by species richness (Loreau et al. 2001), productivity is frequently cited as a fundamental determinant of species richness (Chalcraft et al. 2004). Waide et al. (1999) reviewed productivity–species richness relationships and identified four types of relationship: negative, positive, unimodal, and no relationship.

Despite increased interest in altitudinal patterns of species richness in recent years, few studies have comprehensively analyzed the underlying mechanisms of rich-

ness patterns along altitudinal gradients. Moreover, recent rigorous comparative studies suggest that, although area, MDE, climatic variables, and productivity are frequently cited in studies of species richness on mountains, a single variable cannot fully explain the species richness patterns among different groups in a single taxon along altitudinal gradients, and that different variables may drive such patterns among different groups in mountain ecosystems (Wang et al. 2007, Watkins et al. 2006, Lee et al. 2013).

In this context, we examined the distribution of terrestrial plants along an altitudinal gradient on the ridge of the Baekdudaegan Mountains (hereafter 'the Baekdudaegan'), South Korea. Using data from field surveys, we aimed to (1) explore the altitudinal patterns of species richness for total, common and rare plant species along the ridge of the Baekdudaegan; (2) evaluate the effects of area, MDE, two climatic variables (mean annual precipitation and temperature), and productivity on the altitudinal patterns of plant species richness; and (3) examine whether species richness patterns are related to latitude.

MATERIALS AND METHODS

Study area

The study transect covered the main ridge of the Baekdudaegan (35°15'N to 38°22'N, 127°28'E to 129°3'E) in South Korea (Fig. 1). The Baekdudaegan consists of about 487 mountains, hills and peaks along the Korean Peninsula and is a major resource for forest biodiversity (Korea Forest Research Institute 2003). The protected area of the Baekdudaegan was designated in September 2005 by the Korea Forest Service; the total protected area, including the main ridge, covers 2,634 km² (1,712 km² core area and 922 km² buffer zone). The main ridge extends about 650 km from Hyangnobong Peak of 1,287 m above sea level (a.s.l.) to Mt Jiri of 1,917 m a.s.l. in South Korea. One can travel along the ridgelines without crossing any rivers or streams. The altitudinal gradient of the main ridge extends from 200 to 1,909 m a.s.l. as indicated by a digital elevation model generated using a mosaic of 1:25,000 topographical maps produced by the National Geographic Information Institute that cover the study area (Fig. 1a).

The Baekdudaegan in South Korea belongs to a mountain ecoregion, and temperate deciduous and mixed forest biome (Korea Forest Research Institute 2003). The soil consists of granite, granite gneiss, and highly deformed and recrystallized sedimentary rocks (Shin 2002). Although the natural environment of the Baekdudaegan

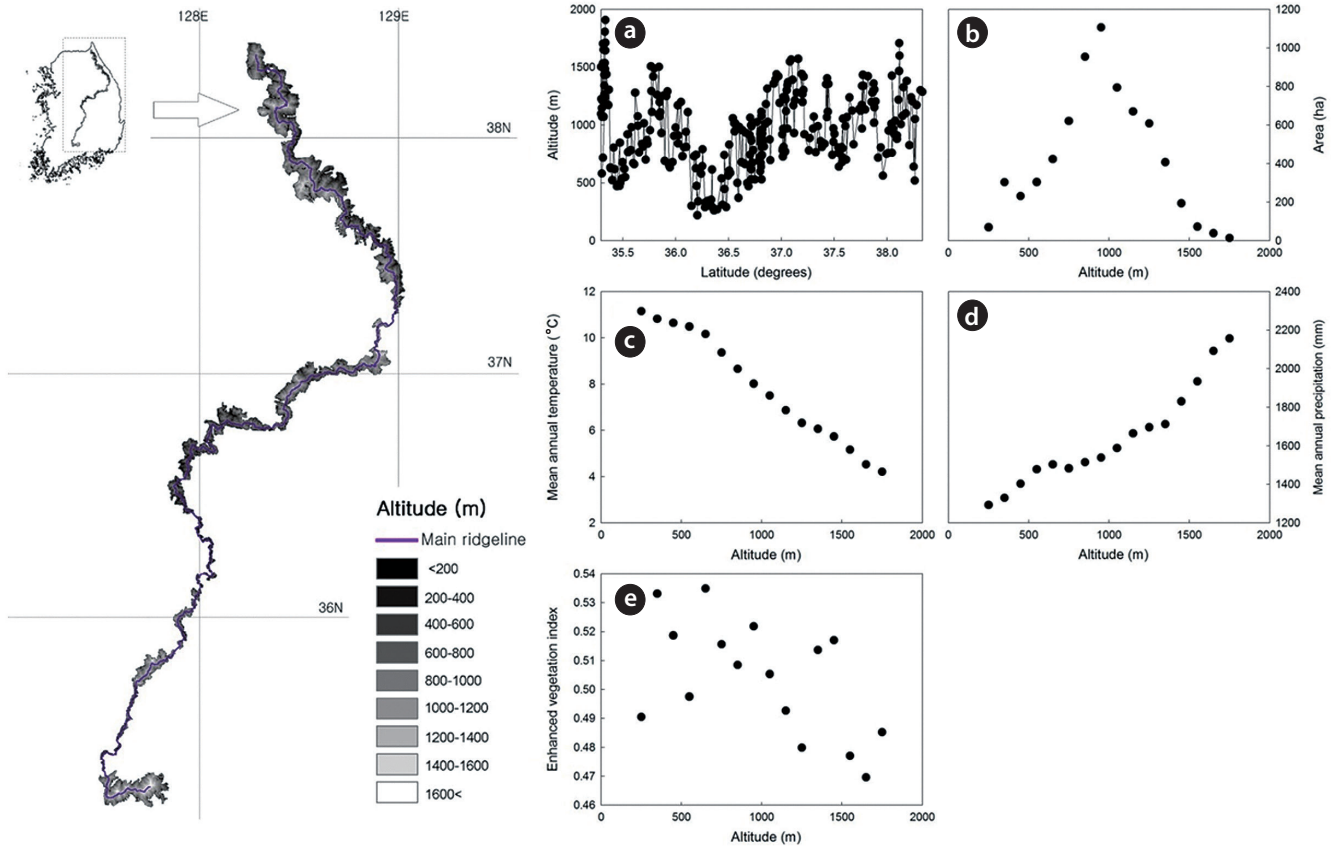


Fig. 1. Location, topography and explanatory variables recorded in the study area along the ridge of the Baekdudaegan Mountains in South Korea. The relationships are shown between altitude and followings; (a) latitude, (b) area, (c) mean annual temperature (MAT), and (d) annual precipitation (MAP) and (e) enhanced vegetation index (EVI).

is poorly known because of insufficient survey data, the Baekdudaegan contains many biodiversity hotspots and offers natural habitats for abundant and varied fauna and flora. A total of 1,477 plant species are distributed on the Baekdudaegan (Korea Forest Research Institute 2003), which accounts for 35.2% of the vascular plant diversity on the Korean Peninsula.

The vegetation on the Baekdudaegan can be categorized into 49 communities, including seven planted communities (e.g., the *Larix kaempferi* community) and 42 natural vegetation communities (e.g., the *Quercus mongolica* community). The Korea Forest Research Institute (2003) divided the Baekdudaegan in South Korea into three regions on the basis of characteristic plant community groups: (1) the northern region, characterized by *Acer komarovii* and *Betula ermanii*, (2) the central region, characterized by *Acer pseudosieboldianum* and *Fraxinus rhynchophylla*, and (3) the southern region, characterized by *Abies koreana* and *Fraxinus mandshurica*. The vegetation on the Baekdudaegan can also be divided into four major zones along an altitudinal gradient. These altitudinal

vegetation zones include (1) temperate (montane) deciduous broad-leaved and pine forest (<550 m a.s.l.) dominated by *Pinus densiflora* and *Rhus tricocarpa*, (2) temperate deciduous broad-leaved and coniferous mixed forest (550 to 1,100 m a.s.l.) dominated by *Q. mongolica*, *Q. serrata*, *P. koraiensis*, and *Abies holophylla*, (3) subalpine coniferous forest (1,100 to 1,600 m a.s.l.) dominated by *Taxus cuspidata*, *A. koreana*, and *Abies nephrolepis*, and (4) alpine forest (>1,600 m a.s.l.) dominated by *B. ermanii* and *P. pumila* (Kong 2007).

Plant survey data

For field sampling, an imaginary 100-meter-wide transect was established in a north–south direction along the ridge of the Baekdudaegan, and the ridge was divided into 16 altitudinal bands each of 100 m altitude from 200 m a.s.l. to >1,700 m a.s.l.. Although sampling extended to 1,900 m a.s.l., the 1,700 m and higher range was treated as a single band because only a small number of plots were sampled and few plant species were observed above 1,700

m a.s.l. Data on the plant species present within each altitudinal band of the transect were recorded from May 2005 to August 2009. Vegetation sampling was performed to cover the most common and specific physiognomic vegetation types in each 100 m altitudinal band. Data were obtained for a total of 1,100 plots of 400 m². Within each plot, plants were surveyed in accordance with the method of Braun-Blanquet (1965).

We divided the altitude range into 100 m bands to examine the relationship between plant species diversity and altitude. Plant data for the same altitudinal band were pooled and the number of species observed in each band was considered to be a measure of richness. Plant species were classified into three groups including total, common and rare plant species based on the Rare Plants Data Book of Korea (Lee 2009). The plant species checklists for each altitudinal band are available in Lee et al. (2013).

Explanatory variables

Two space-related variables, area and MDE, were investigated in relation to species richness. To test species-area relationships, we calculated the area of each altitudinal band along the 100-meter-wide transect. Calculations were performed using a digital elevation model with the 3D Analyst extension in ArcGIS. The MDE null model was used to test the influence of geometric constraints on the spatial patterns of species richness along the altitudinal gradient. We used a novel, discrete MDE model based on Colwell and Hurtt's (1994) continuous Model 2, which does not require the use of interpolated ranges (Fu et al. 2006). RangeModel ver. 5 software (Colwell 2006) was used for simulation. The simulation process was repeated 5,000 times and expected mean richness and its 95% confidence intervals were used to assess the effects of geometric constraints on the altitudinal gradient. Unlike many recent studies, we did not use interpolated species richness modified from actual distribution records. The justification for interpolation is that undersampling creates gaps in altitudinal distribution (Kluge et al. 2006). However, three problems with interpolation are reported (Grytnes and Vetaas 2002, Diniz-Filho et al. 2003, Kluge et al. 2006). First, it disrupts the crucial control of sampling area and intensity as species are added that were not, in fact, present in the plots. Second, interpolation might artificially increase richness to a higher degree at intermediate altitudes, because gaps are filled only between the lower and upper range limits; this essentially assumes that no individuals of a species have been missed beyond the observed range limits, but that individuals have been

missed at sampling points within the range limits. Third, species richness at nearby altitudes is more similar than at distant altitudes, and the resulting spatial autocorrelation inflates Type I errors. The spurious effects of autocorrelation increase when using interpolated distribution data. However, many studies on altitudinal richness patterns use interpolated data and comparisons of such studies with our non-interpolated results might be difficult. Therefore, we also calculated the interpolated richness for total, common and rare plant species. Observed and interpolated richness patterns showed the same pattern along the altitudinal gradient and were strongly correlated (total species, $R^2 = 0.92$; common species, $R^2 = 0.92$; rare species, $R^2 = 0.93$; $P < 0.001$ in each comparison). Thus, we only present results derived from the observed richness values without interpolation in this study.

The two climatic variables used in this study were mean annual temperature (MAT) and precipitation (MAP). We used digital climate maps produced by the Korea Meteorological Administration and National Center of Agrometeorology to extract the meteorological parameters for each altitudinal band (Yun 2010). The MAT data were dated from 1971 to 2008 and the MAP data were dated from 1981 to 2009. The spatial resolution of the raster data was 30 m for MAT and 270 m for MAP. The MAT and MAP were calculated for each altitudinal band in the transect.

As a proxy for aboveground net primary productivity we used the enhanced vegetation index (EVI), which is preferred over the normalized difference vegetation index because it is insensitive to soil or atmospheric effects and adjusts the red wavelength as a function of the blue wavelength to minimize brightness-related soil effects (Adhikari et al. 2012). MODIS-driven EVI images, composited at 16-day intervals, were downloaded in tiles for the period from January 2004 to December 2009 and mosaicked together using the MODIS reprojection tool. The averaged annual EVIs were used to assess the relationship between the diversity indices and productivity.

Statistical analysis

The relationships between species richness and the explanatory variables were analyzed for each individual variable using a simple linear regression. Such a linear model tests only for a linear relationship between the potential explanatory variable and species richness, but several scenarios under which a unimodal model is more biologically reasonable are plausible (Kluge et al. 2006). Therefore, we also used a polynomial regression model to detect curvilinear relationships by including a quadratic

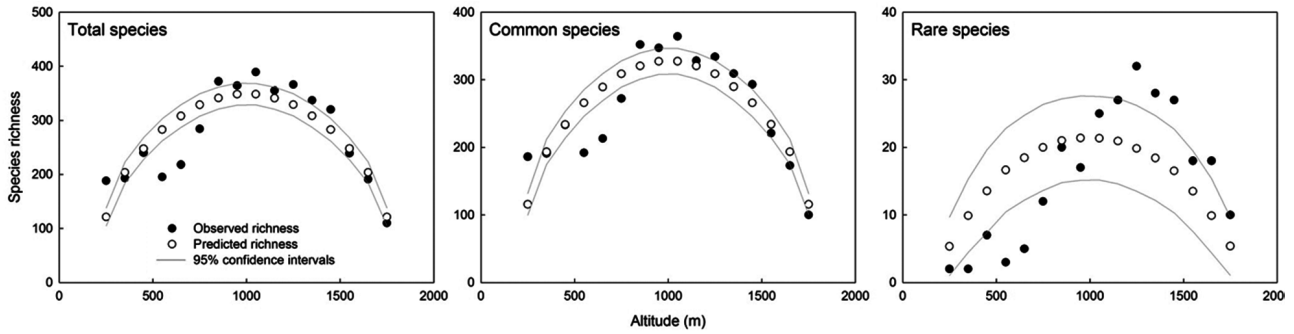


Fig. 2. Observed and predicted species richness and 95% confidence intervals for the predicted mid-domain effect richness as a function of altitude for total, common, and rare plant species along the ridge of the Baekdudaegan Mountains, South Korea.

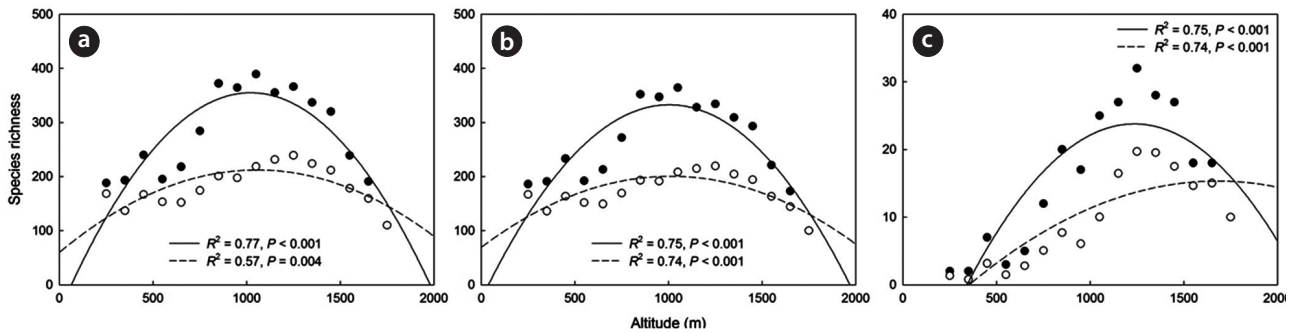


Fig. 3. Relationship between altitude and species richness for (a) total, (b) common, and (c) rare plant species along the ridge of the Baekdudaegan Mountains, South Korea. Solid and hollow circles indicate observed and rarefied species richness, respectively.

term in the regression function. In addition, we used forward stepwise multiple regression models to establish the relative importance of area, MDE, MAT, MAP and EVI as explanatory variables for species richness. Forward stepwise multiple regressions were used to find a set of independent variables that together provided the best fit for diversity indices by minimizing the sum of squared residuals. All linear and quadratic terms for the explanatory variables were used in forward stepwise multiple regressions. Simple and forward stepwise multiple regression models were analyzed with S-PLUS ver. 8.0 (Insightful Corp., Seattle, WA, USA). All possible analyses were conducted for each of the three plant groups.

RESULTS

General description

A total of 802 plant species belonging to 97 families and 342 genera were recorded from the 1,100 plots along the altitudinal gradient (Table 1). More than half of these species were herbaceous (69%; 62 families, 249 genera, and

554 species) and woody plants accounted for 31% of the species (47 families, 99 genera, and 248 species). Common and rare species accounted for 91% and 9%, respectively, of the total plant species.

With increasing altitude, the area of the altitudinal bands increased sharply and then decreased above the 900 to 1,000 m band, thus showing a hump-shaped pattern (Fig. 1b). The MAT declined monotonically with increasing altitude (Fig. 1c), whereas the MAP increased along the altitudinal gradient (Fig. 1d). The EVI generally declined with increasing altitude (Fig. 1e). The MDE null model showed deviation of the observed species richness from simulated richness (Fig. 2). The analysis revealed that for total, common and rare plant species, 56%, 63% and 63% of the data points, respectively, were outside the 95% confidence intervals of the values predicted by the MDE null model.

Altitudinal richness patterns and range size

The richness of total and common plant species each showed a hump-shaped pattern with maximum richness recorded between 1,000 and 1,100 m (Fig. 3a and 3b),

whereas the richness of rare plant species peaked in the altitudinal band between 1,200 and 1,300 m and the maximum richness peak was higher than those of total and common species (Fig. 3c). The patterns of rarefied species richness were similar to the observed richness patterns for all three plant groups. Overall, species richness for all plant groups showed a distinctly hump-shaped pattern in relation to altitude, even though the absolute altitudes of the peaks differed somewhat among the plant groups.

Most plant species in the Baekdudaegan showed very narrow altitudinal ranges (Fig. 4). The altitudinal range was ≤ 200 m for 29% of total plant species, 27% of common plant species, and 43% of rare plant species. No species was present in every altitudinal band. The relative proportion of rare species declined more rapidly than for total and common species with increasing range size (i.e., the altitudinal range of total and common species tended to be greater than that of rare species).

Determinants of altitudinal richness patterns

Simple linear regressions showed that total species richness and common species richness were strongly correlated with area and the MDE, whereas rare species richness was correlated with the MDE and MAT (linear model in Table 2). The results for quadratic models differed

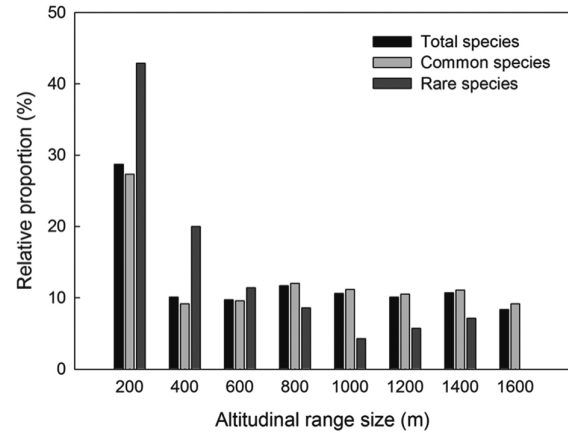


Fig. 4. Range size distribution of plant species observed along the altitudinal gradient along the ridge of the Baekdudaegan Mountains, South Korea. X-axis values represent the upper boundary of 200 m altitudinal bands.

somewhat from those for simple linear models (quadratic model in Table 2) in that climatic variables were also significant predictors for species richness of total and common plants. Considering the multiple regression models, the results for models that included all linear and quadratic terms were similar to those that included only the linear terms (Table 3). The forward stepwise multiple regression models showed that the MDE was the most im-

Table 1. Observed richness among total, common and rare plant species for different altitudinal bands along the ridge of the Baekdudaegan Mountains, South Korea

Lower boundary of altitudinal band (m)	No. plots	Total species			Common species			Rare species		
		Total	Woody	Herbaceous	Total	Woody	Herbaceous	Total	Woody	Herbaceous
200	36	188	86	102	186	86	100	2	0	2
300	64	193	93	100	191	93	98	2	0	2
400	64	240	106	134	233	105	128	7	1	6
500	46	195	88	107	192	87	105	3	1	2
600	61	218	101	117	213	100	113	5	1	4
700	93	284	126	158	272	123	149	12	3	9
800	117	372	138	234	352	135	217	20	3	17
900	113	364	127	237	347	127	220	17	0	17
1000	103	389	133	256	364	128	236	25	5	20
1100	72	355	118	237	328	110	218	27	8	19
1200	70	366	114	252	334	107	227	32	7	25
1300	68	337	111	226	309	103	206	28	8	20
1400	75	320	109	211	293	99	194	27	10	17
1500	54	239	86	153	221	75	146	18	11	7
1600	38	191	73	118	173	63	110	18	10	8
1700	26	110	39	71	100	33	67	10	6	4
All bands pooled	1100	802	248	554	732	233	499	70	15	55

portant predictor of total and common species richness, whereas climatic variables such as MAT and MAP were the most powerful predictors of rare species richness.

A simple linear regression showed no significant correlation between species richness and latitude for all plant groups (Fig. 5). These analyses do not support the presence of latitudinal effects on plant species richness patterns along the ridge of the Baekdudaegan.

Latitudinal effect

Table 2. Simple linear and quadratic models for explanatory variables and species richness along the ridge of the Baekdudaegan Mountains, South Korea

Plant group	Variable	Linear model			Quadratic model		
		F	R ²	P	F	R ²	P
Total species	Area	25.87	0.65	<0.001	13.64	0.68	<0.001
	MDE	39.21	0.74	<0.001	23.78	0.79	<0.001
	MAT	0.18	0.01	0.676	67.50	0.91	<0.001
	MAP	0.44	0.03	0.516	17.80	0.73	<0.001
	EVI	0.41	0.03	0.534	1.68	0.21	0.224
Common species	Area	32.13	0.70	<0.001	17.22	0.73	<0.001
	MDE	42.92	0.75	<0.001	27.10	0.81	<0.001
	MAT	0.02	<0.01	0.895	73.06	0.92	<0.001
	MAP	0.92	0.06	0.353	18.39	0.74	<0.001
	EVI	0.72	0.05	0.41	1.99	0.23	0.176
Rare species	Area	2.26	0.14	0.155	1.14	0.15	0.351
	MDE	6.36	0.31	0.024	3.04	0.32	0.083
	MAT	12.05	0.46	0.004	40.13	0.86	<0.001
	MAP	3.28	0.19	0.092	17.60	0.73	<0.001
	EVI	1.23	0.08	0.285	1.04	0.14	0.382

MDE, mid-domain effect; MAT, mean annual temperature; MAP, mean annual precipitation; EVI, enhanced vegetation index.

Table 3. Forward stepwise multiple regression models for explanatory variables, including all linear and quadratic terms and diversity indices, along the ridge of the Baekdudaegan Mountains, South Korea

Plant group	Variable	t	P	Model F, R ² , P
Model A				
Total species	Intercept	0.15	0.882	F = 39.21, R ² = 0.74, P < 0.001
	MDE	6.26	<0.001	
Common species	Intercept	0.21	0.840	F = 42.92, R ² = 0.75, P < 0.001
	MDE	6.55	<0.001	
Rare species	Intercept	7.60	<0.001	F = 43.23, R ² = 0.87, P < 0.001
	MAT	-8.22	<0.001	
	MAP	-6.36	<0.001	
Model B				
Total species	Intercept	4.15	0.001	F = 48.36, R ² = 0.78, P < 0.001
	MDE ²	6.95	<0.001	
Common species	Intercept	4.51	<0.001	F = 54.30, R ² = 0.80, P < 0.001
	MDE ²	7.37	<0.001	
Rare species	Intercept	11.68	<0.001	F = 82.70, R ² = 0.93, P < 0.001
	MAT ²	-11.82	<0.001	
	MAP ²	-8.11	<0.001	

Model A included only linear terms for explanatory variables, whereas Model B included all linear and quadratic terms for explanatory variables. The magnitude of the t-value indicates the relative importance of each variable in the models. MDE, mid-domain effect; MAT, mean annual temperature; MAP, mean annual precipitation; EVI, enhanced vegetation index.

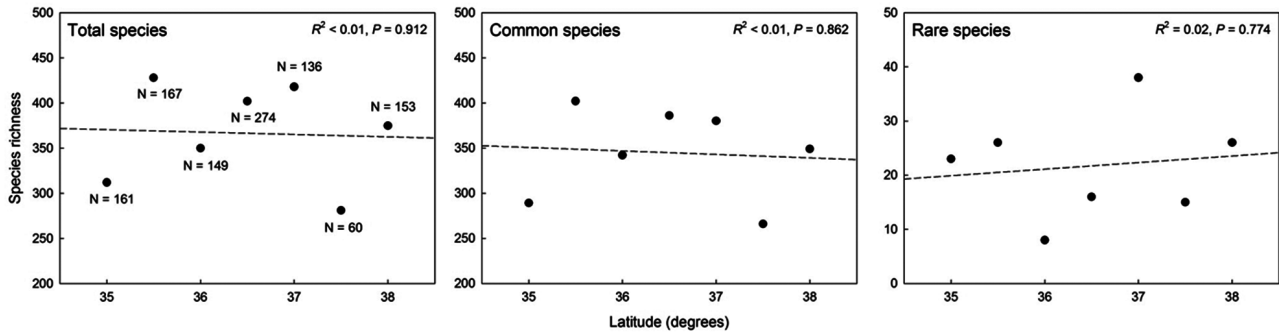


Fig. 5. Relationship between latitude and species richness for total, common, and rare plant species along the ridge of the Baekdudaegan Mountains, South Korea. N represents the number of sample plots in each latitudinal band.

DISCUSSION

In this study, we examined plant species richness patterns in relation to an altitudinal gradient and explored the underlying causal mechanisms of those patterns using primary data at a regional scale from the ridge of the Baekdudaegan, South Korea. Previous studies that demonstrate the existence of a relationship between altitude and species richness can be classified as representing either local or regional datasets (Romdal and Grytnes 2007). Many previous studies aimed to explain mechanisms at broad regional scales, such as countrywide or continental scales (Jetz and Rahbek 2002, Grau et al. 2007, McCain 2009, Alexander et al. 2011), using secondary distribution data derived from the literature. Studies focused at regional scales cover large areas and large fractions of the total biota as they combine data from numerous sources (Karger et al. 2011). In general, regional-scale studies, including the present study, presume that when examined at broad scales, mountain massifs are bounded with respect to macroecological processes. Therefore, such large-scale studies focus on altitudinal effects and consider that latitudinal effects on species diversity are either insignificant or extremely small (Marini et al. 2011). Indeed, in the current study, plant species richness did not show a significant relationship with latitude for any of the plant groups. This result supports the assumption that latitude is not a significant determinant of plant species richness patterns, at least on the basis of data from the Baekdudaegan ridge. Moreover, most previous analyses of the relationship between species richness and latitude used data from wide latitudinal bands ($>10^\circ$) and at continental or hemispheric scales (Stevens 1989, Buckley et al. 2003, Cruz et al. 2005).

The cause of altitudinal richness patterns is a contro-

versial topic in ecology and biogeography (Wang et al. 2007). Rahbek (2005) identified three main patterns of altitudinal species richness: (1) a monotonic decline with increasing altitude, (2) a plateau at low altitudes, and (3) a 'hump-shaped' distribution with peak richness at intermediate altitudes. The present study showed that species richness in all plant groups peaked at intermediate altitudes along the Baekdudaegan ridge, even though the absolute altitudes of the richness peaks differed somewhat among the three plant groups. At the most general level, the present results contribute to the growing body of evidence that, in mountainous regions, hump-shaped distributions of plant species richness predominate.

Altitudinal richness patterns are considered to reflect an optimal combination of space-related variables, such as area and the MDE (Wang et al. 2007), climatic variables including temperature and precipitation (Bhattarai and Vetaas 2003, Kluge et al. 2006), and productivity (Chalcraft et al. 2004). On the ridge of the Baekdudaegan, we observed that space-related variables (area and the MDE) strongly influence altitudinal patterns of total and common plant species richness as determined by simple linear models, and that climatic variables (MAT and MAP) also contribute significantly to the altitudinal patterns as determined by quadratic models. However, MDE and MAT were significant predictors of rare species richness pattern in simple linear models and only climatic variables contributed significantly to the altitudinal pattern of rare plant species in quadratic models. These results for the linear models were similar to those obtained with multiple regression models. In multiple regression models, the MDE was selected as the most powerful determinant of richness patterns in total and common plant species, whereas climatic variables were selected as the most powerful determinants of rare plant species rich-

ness pattern. The relative influence of each of these determinants on species richness may vary among regions and taxa. Below, we discuss how area, the MDE, climatic variables, and productivity may contribute to altitudinal patterns of plant species richness along the ridge of the Baekdudaegan.

The important influence of the MDE on species richness patterns along altitudinal gradients is well documented (Liew et al. 2010, Acharya et al. 2011, Lee et al. 2012). The MDE is a stochastic abiotic hypothesis that is based on the premise that spatial distributions of species richness are constrained by the shapes of geographical domains and by species range sizes. Under these conditions, the random replacement of species ranges within a bounded domain results in overlapping species ranges, with a greater number of overlapping ranges towards the center of the domain than at the margins; thus, higher species richness occurs in the central region of geographical domains than at the periphery (Colwell and Lees 2000). However, we also observed a deviation of diversity distributions from the MDE null hypothesis for all plant groups. Recent work in the eastern Himalayas indicates that tree species richness patterns strongly deviate from those predicted by the MDE null model (Acharya et al. 2011), as do species richness patterns for other plant groups (Kluge et al. 2006, Ah-Peng et al. 2012). The deviations may be caused by the presence of relatively large numbers of species with narrow altitudinal ranges (i.e., those present in only one or two bands); as in the present study, Ah-Peng et al. (2012) recorded a relatively large number of species with a small altitudinal range, which comprised species present in only one or two altitudinal bands. Therefore, we suggest that narrowly distributed species are likely to result in large deviations from the MDE null model for all plant groups. The degree of deviation from the MDE null model may also explain the influence of factors such as ecology, history, and evolution on observed distribution patterns (Acharya et al. 2011).

Area is also an important predictor of total and common plant species richness in both simple linear and quadratic regression models; however, area is a weak predictor of richness patterns in multiple regression models in which the MDE is one of the variables. This result may reflect the strong correlation between the MDE and area ($R^2 > 0.55$, $P < 0.001$ for all plant groups), such that the MDE has a stronger influence on species richness than does area in multiple regression models. Therefore, we speculate that the effect of area is masked by the dominance of the MDE, at least in relation to plant species richness.

The present regression analyses indicated that the cli-

matic variables were the most powerful predictors for rare plant species. In general, rare species characteristically have a narrow geographical range and highly restricted habitat preferences compared with common species (Bevill and Louda 1999). Moreover, most rare species on the Baekdudaegan ridge are distributed at higher altitudes than common species (Cho et al. 2004). Indeed, climatic variables are indicated to be more important than space-related variables for range-restricted species such as rare species, whereas space-related variables are more important than climatic variables for wide-ranging species such as common species (Jetz and Rahbek 2002, Brehm et al. 2007, Lee et al. 2013). Although we excluded climatic variables from the simple linear and multiple regression models for total and common plant species richness, climatic variables still might play an important role as determinants of richness patterns for such plant species. Parabolic patterns of species richness in relation to climatic variables are best described using a quadratic function. If climatic variables contribute to observed patterns of total and common plant species richness, optimal ranges of temperature and precipitation are likely to occur at intermediate altitudes, and favorable climatic conditions at intermediate altitudes may lead to higher total and common plant species richness in these areas. Intermediate altitudes may provide optimal combinations of temperature and moisture levels for plant growth, and consequently higher resource availability to support the coexistence of a greater number of species (Kluge et al. 2006).

Remote sensing-based vegetation indices used as surrogates of primary productivity provide evidence for significant productivity–richness relationships, both linear and unimodal, which indicates that productivity estimates can be used to evaluate plant species richness patterns (Rowe 2009), albeit at different spatial scales depending on the taxonomic group under study (Hurlbert and Haskell 2003). However, we found little evidence that productivity (as measured by EVI) influences species richness patterns along the altitudinal gradient on the Baekdudaegan ridge. This finding indicates that the relationship between productivity and plant richness may be more complex than previously thought. Furthermore, poor support in the present study for a productivity–richness relationship questions the energy–diversity hypothesis for vascular plants, at least along the altitudinal gradient on the ridge of the Baekdudaegan. Energy input is indicated to be a strong predictor of richness only in far northern portions of the globe, and precipitation or the interaction between energy input and moisture shapes

large-scale worldwide biodiversity patterns (Hawkins et al. 2003). However, the results presented here provide weak support for the productivity–diversity hypothesis and suggest that the relationship between productivity and richness at smaller spatial scales (e.g., that of a mountain range) may be incongruent with that found at larger spatial scales. Furthermore, Adler et al. (2011) intensively reviewed relationships between productivity and species diversity in mountainous areas across the globe and observed that a non-significant relationship is predominant between the two variables.

CONCLUSION

Although the absolute altitudes of the richness peaks vary among total, common and rare plant species, species richness patterns on the Baekdudaegan ridge show ‘hump-shaped’ patterns for each plant group. Regression analyses show that the MDE and climatic variables are the best predictors of altitudinal patterns of plant species richness on the Baekdudaegan ridge. The MDE is the most important explanatory variable for total and common species richness, whereas climatic variables are significant predictors for rare species richness. Our results are consistent with many previous studies, which indicate that the MDE is more important for wide-ranging species such as common species, whereas climatic variables are better predictors for range-restricted species such as rare species. Latitudinal effects are not supported as a determinant of species richness in the present study. Even though the MDE and climatic variables are the primary predictors in the best simple and multiple regression models, discrimination among these variables may not be possible by simple comparisons of regression coefficients because the MDE and climatic variables are strongly correlated with plant species richness. Altitudinal species richness patterns can be influenced by a number of climatic, spatial, and historical variables (Rahbek 2005, Acharya et al. 2011, Lee et al. 2013). In the present study, we examined the relationships between major explanatory variables and altitudinal patterns of plant species richness. However, we did not consider evolutionary or historical variables in our analysis. Further study into the influence of evolutionary history, including historical contingencies and niche conservatism, with spatial, climatic, and energy-related variables may provide insights into the factors that determine the altitudinal distribution of plant communities at macroecological scales.

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LITERATURE CITED

- Acharya BK, Chettri B, Bijayan L. 2011. Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India. *Acta Oecol* 37: 329–336.
- Adhikari D, Barik SK, Upadhya K. 2012. Habitat distribution modelling for reintroduction of *Ilex khasiana* Purk., a critically endangered tree species of northeastern India. *Ecol Eng* 40: 37–43.
- Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Harpole WS, O’Halloran LR, Grace JB, Anderson M, et al. 2011. Productivity is a poor predictor of plant species richness. *Science* 333: 1750–1753.
- Ah-Peng C, Wilding N, Kluge J, Descamps-Julien B, Bardat J, Chuah-Petiot M, Strasberg D, Hedderson TAJ. 2012. Bryophyte diversity and range size distribution along two altitudinal gradients: continent vs. island. *Acta Oecol* 42: 58–65.
- Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium. 2011. Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proc Natl Acad Sci USA* 108: 656–661.
- Bevill RL, Louda SM. 1999. Comparisons of related rare and common species in the study of plant rarity. *Conserv Biol* 13: 493–498.
- Bhattarai KR, Vetaas OR. 2003. Variation in plant species richness of different life forms along a subtropical elevational gradient in the Himalayas, east Nepal. *Global Ecol Biogeogr* 12: 327–340.
- Braun-Blanquet J. 1965. *Plant sociology: the study of plant communities*. Hafner Publishing Company, New York.
- Brehm G, Colwell RK, Kluge J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecol Biogeogr* 16: 205–219.
- Buckley HL, Miller TE, Ellison AM, Gotelli NJ. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecol Lett* 6: 825–829.
- Chalcraft DR, Williams JW, Smith MD, Willig MR. 2004.

- Scale dependence in the species-richness-productivity relationship: the role of species turnover. *Ecology* 85: 2701–2708.
- Cho HJ, Lee BC, Shin JH. 2004. Forest vegetation structure and species composition of the Baekdudaegan Mountain Range in South Korea. *J Korean For Soc* 93: 331–338.
- Colwell RK. 2006. RangeModel: A Monte Carlo simulation tool for assessing geometric constraints on species richness. Version 5. User's Guide and application published at: <http://viceroy.eeb.uconn.edu/rangemodel>. Accessed 26 July 2012.
- Colwell RK, Hurtt GC. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *Am Nat* 144: 570–595.
- Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol Evol* 15: 70–76.
- Cruz FB, Fitzgerald LA, Espinoza RE, Schulte JA 2nd. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J Evol Biol* 18: 1559–1574.
- Diniz-Filho JAF, Bini LM, Hawkins BA. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol Biogeogr* 12: 53–64.
- Fu C, Hua X, Li J, Chang Z, Pu Z, Chen J. 2006. Elevational patterns of frog species richness and endemic richness in the Hengduan Mountains, China: geometric constraints, area and climate effects. *Ecography* 29: 919–927.
- Grau O, Grytnes JA, Birks HJB. 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *J Biogeogr* 34: 1907–1915.
- Grytnes JA, Vetaas OR. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am Nat* 159: 294–304.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.
- Hurlbert AH, Haskell JP. 2003. The effect of energy and seasonality on avian species richness and community composition. *Am Nat* 161: 83–97.
- Jetz W, Rahbek C. 2002. Geographic range size and determinants of avian species richness. *Science* 297: 1548–1551.
- Karger DN, Kluge J, Krömer T, Hemp A, Lehnert M, Kessler M. 2011. The effect of area on local and regional elevational patterns of species richness. *J Biogeogr* 38: 1177–1185.
- Kluge J, Kessler M, Dunn RR. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecol Biogeogr* 15: 358–371.
- Kong WS. 2007. *Biogeography of Korea Plants*. GeoBook Publishing Company, Seoul. (In Korean)
- Korea Forest Research Institute. 2003. *Ecological aspects of Baekdu Mountains in Korea and delineation of their management and conservation area*. Korea Forest Research Institute [report no. 198], Seoul. (In Korean)
- Körner C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol Evol* 15: 513–514.
- Lee BC. 2009. *Rare plants: Data book of Korea*. Korea National Arboretum, Pocheon.
- Lee CB, Chun JH, Cho HJ, Song HK. 2012. Altitudinal patterns of plant species richness on the ridge of the Baekdudaegan Mountains, South Korea: area and mid-domain effect. *For Sci Technol* 8: 154–160.
- Lee CB, Chun JH, Song HK, Cho HJ. 2013. Altitudinal patterns of plant species richness on the Baekdudaegan Mountains, South Korea: mid-domain effect, area, climate, and Rapoport's rule. *Ecol Res* 28: 67–79.
- Liew TS, Schilthuizen M, bin Lakim M. 2010. The determinants of land snail diversity along a tropical elevational gradient: insularity, geometry and niches. *J Biogeogr* 37: 1071–1078.
- Lomolino MV. 2001. Elevational gradients of species-density: historical and prospective views. *Global Ecol Biogeogr* 10: 3–13.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294: 804–808.
- Marini L, Bona E, Kunin WE, Gaston KJ. 2011. Exploring anthropogenic and natural processes shaping fern species richness along elevational gradient. *J Biogeogr* 38: 78–88.
- McCain CM. 2009. Global analysis of bird elevational diversity. *Global Ecol Biogeogr* 18: 346–360.
- Rahbek C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett* 8: 224–239.
- Romdal TS, Grytnes JA. 2007. An indirect area effect on elevational species richness patterns. *Ecography* 30: 440–448.
- Rosenzweig ML. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rowe RJ. 2009. Environmental and geometric drivers of small mammal diversity along elevational gradients in

- Utah. *Ecography* 32: 411–422.
- Shin JH. 2002. Ecosystem geography of Korea. In: *Ecology of Korea* (Lee DW, Jin V, Choe JC, Son YW, Yoo SJ, Lee HY, Hong SK, Ihm BS, eds). Bumwoo Publishing Company, Seoul, pp 19–46.
- Stevens GC. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am Nat* 133: 240–256.
- Waide RB, Willing MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R. 1999. The relationship between productivity and species richness. *Ann Rev Ecol Syst* 30: 257–300.
- Wang Z, Tang Z, Fang J. 2007. Altitudinal patterns of seed plant richness in the Gaoligong Mountains, south-east Tibet, China. *Divers Distrib* 13: 845–854.
- Watkins JE Jr, Cardelús C, Colwell RK, Moran RC. 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. *Am J Bot* 93: 73–83.
- Yun JI. 2010. Agroclimatic maps augmented by GIS technology. *Korean J Agric For Meteorol* 12: 63–73.