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# Empirical Evaluation of the Elevational Rapoport's Rule: The Species Richness Patterns for Vascular Plants on Seorak Mountain, Korea

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## Abstract

Research on species abundance patterns and the advanced elevational Rapoport rule (ERR) has been widespread in recent years; however, for the temperate mountainous regions in northeast Asia, such research is lacking. Here, we collected plant species from the Seorak Mountain in northeast Asia through field surveys. The species were divided into 11 groups according to the life-form types and phytogeography affinities of each species. The ERR was tested using Steven's method and by examining the species abundance patterns of each group. The species abundance patterns revealed a positive multimodal pattern along the elevation gradient, but phytogeography affinities (increasing trend) and life-form (unimodal) exhibited different patterns. The elevation gradients (1350 m for the mean elevation-range relationships), which are affected by the boundary effect and different life-forms, did not consistently support the ERR. However, herbs as well as rare, endemic, and red list species showed consistent support for the ERR, which can be influenced by phytogeography affinities. Thus, the results from Seorak Mountain showed that the ERR was not consistent for different plant life-forms in the same area. The result of our field survey revealed that life-forms in the plant species did not support ERR, whereas phytogeography affinities could support and explain ERR.

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Abstract: Research on species abundance patterns and the advanced elevational Rapoport rule (ERR) has been widespread in recent years; however, for the temperate mountainous regions in northeast Asia, such research is lacking. Here, we collected plant species from the Seorak Mountain in northeast Asia through field surveys. The species were divided into 11 groups according to the life-form types and phytogeography affinities of each species. The ERR was tested using Steven's method and by examining the species abundance patterns of each group. The species abundance patterns revealed a positive multimodal pattern along the elevation gradient, but phytogeography affinities (increasing trend) and life-form (unimodal) exhibited different patterns. The elevation gradients (1350 m for the mean elevation-range relationships), which are affected by the boundary effect and different life-forms, did not consistently support the ERR. However, herbs as well as rare, endemic, and red list species showed consistent support for the ERR, which can be influenced by phytogeography affinities. Thus, the results from Seorak Mountain showed that the ERR was not consistent for different plant life-forms in the same area. The result of our field survey revealed that life-forms in the plant species did not support ERR, whereas phytogeography affinities could support and explain ERR.

Keywords: Elevation gradient, Seorak Mountain, Elevational Rapoport rule, Species diversity, Phytogeography

Introduction

Biodiversity is expected to decrease globally over time, which will result in widespread changes to the benefits that it currently provides and directly impact humans and animals (Sala et al., 2000). In terrestrial ecosystems, it was found that the main cause of biodiversity decline is anthropogenic habitat loss due to land use changes (Sala et al., 2005). At the level of biomes such as tundra, desert, northern coniferous forests, and cold forests, alterations are caused by environmental changes rather than by artificial habitat destruction (Sala et al., 2005).

Among the various theories on biodiversity patterns, Steven's (1992) elevational Rapoport rule (ERR) remains widely debated (Almeida-Neto et al., 2006; Colwell & Hurtt, 1994; Fleishman, Austin & Weiss, 1998; Ogwu et al., 2019). Although this approach has attracted the attention of ecologists and biogeographers worldwide, there is considerable controversy regarding the ERR because of the high level of variability supporting the hypothesis. For example, some studies showed strong support for the ERR (Chan et al., 2016; Feng et al., 2016; Luo et al., 2011; Rohner et al., 2015; Sanders, 2002), whereas in others, little or no support was found (Bhattarai & Vetaas, 2006; Fleishman, Austin & Weiss, 1998; Guerrero, Durán & Walter, 2011; Kwon et la., 2014; Külköylüoğlu et al., 2012; McCain & Bracy Knight, 2013). Altitude range shifts due to climate change can increase the risk of extinction for range-restricted species (Elsen & Tingley, 2015; Freeman & Freeman, 2014; Harte & Shaw, 1995; McCain & Colwell, 2011; Sorte & Jetz, 2010). Therefore, the accumulation of research and information on ERR in various regions helps to increase not only our understanding of the rule, but also the conservation of species with particularly narrow distributions, thus helping to maintain and promote biodiversity.

An important prediction of the ERR is the positive relationship between range-size and elevation (Stevens, 1992). The pattern in the altitude range-size may differ for each taxon (Feng et al., 2016; Gaston, 1996), suggesting that the range altitude relationship varies depending on the ecological characteristics and physiological adaptations to the climate or microenvironment along the altitude slope. Temperate taxa show a wider altitude range-size than tropical taxa, as they may have experienced higher variability in environmental factors during their evolutionary and geographic history (Oommen & Shanker, 2005; Wang, Tang & Fang, 2007). Therefore, information from various regions is required to determine the link between ecological and physiological properties and biogeographic affinity.

Another hypothesis made using the ERR is that species diversity decreases as altitude increases. However, the results of previous studies have been inconsistent (Feng, 2016; Zhou et al., 2019). For ERR, a multimodal trend other than unimodal decreases has been observed worldwide, and thus further surveys are required. Species with tropical affinities can migrate their habitats along warm climate zones (Bergamin et al., 2020; Feeley, Rehm & Machovina, 2012). This suggests that biogeographic affinity is capable of differentiated adaptation to environmental factors including the altitude of different taxa. Species with different biogeographic affinities may exhibit varying patterns of abundance with altitude, which may explain the differences in support for the abundance-altitude hypothesis of the ERR (Feng et al., 2016; Zhou et al., 2019).

In this study, (1) the ERR was applied to Seorak Mountain (1708 m), which is relatively lower than the world's highest mountains (e.g., Himalayas at 8848 m or Andes at 6961 m); (2) we determined the plant distribution pattern according to the boundary effect and plant geographical affinity; and (3) information regarding the species range-size distribution patterns on the Seorak Mountain area was obtained.

Materials and Methods

2.1 Study area

The Seorak Mountain (128°18'N, 38deg05'E) is in eastern Korea and covers an area of approximately 398 $km^2$ (Figure 1a). The main peak of Seorak Mountain is Daecheongbong (1708 m), and it is the second highest mountain in Korea. The climate of the region is temperate, with a mean annual temperature of 3.05degC and mean annual precipitation of 1537.39 mm (Kim, Lim & Yun, 2019). Its temperate forests comprise*Pinus densiflora* or *Abies holophylla* in the lowlands and*Betula ermanii* , *Pinus koraiensis* , *Quercus mongolica* , and *Abies nephrolepis* in the highlands. There are also dwarf tree species near the peak and in the highlands, including*Pinus pumila* , *Taxus caespitosa* , and *Thuja koraiensis* , as well as arctic-alpine plants, such as *Arctous ruber* , *Crataegus komarovii* , and *Vaccinium uliginosum* . To evaluate the relationship between elevation range-size and species richness of vascular plants along the elevation gradients, the elevation range (500–1708 m) of our study area was divided into 13 elevation bands (100 m bands, Figure 1b).

2.2 Data collection

A list of 238 plant taxa including varieties and subspecies belonging to 163 genera and 70 families was compiled for Mount Seorak based on field data collected during vegetation surveys in this region from 2016 to 2020 at the most favorable season for plant flowering (i.e., when most plants could be identified). For this field survey, the study area was divided into 13 elevation bands, each with 100 m line transects established on the mountain along elevational gradients using the Misiryeong, Hangyeryeong, Danmokryeong, and Osaek trails centered on Daecheongbong, which is the highest peak.

The lengths of the Misiryeong, Hangyeryeong, Danmokryeong, and Osaek trails are approximately 15.4, 9.5, 15.5, and 10.3 km, respectively. The four line transects were divided into 13 elevational bands at 100 m intervals from 500 to 1708 m, and 228 plots were randomly investigated in every elevation band of the line transects. A 400 $m^2$ survey zone within each transect was set to conduct plant surveys at controlled points. For surveys within each plot, the cover-abundance scale and plant species were recorded using a previously described vegetation survey method (Braun-Blanquet, 2013). The location of each plot was recorded using Garmin Montana 64s GPS equipment (Garmin, Olathe, KS, USA).

2.3 Plant life-forms and taxonomy

Following the Raunkiaer system (Raunkiaer, 1934), each species was classified as tree, shrub, liana, herb, pteridophyte, or woody species (including trees, shrubs, and lianas) based on the species descriptions in the illustrated plant books by Lee (2003) and KNA (2008, 2010). Species were classified as common species, rare, or endemic to Korea (Lee, 2003; KNA, 2008; KNA, 2010; KFS, 2010a; KFS, 2010b). In addition, rare plants were classified into different groups based on the red list in IUCN 2020. The rare and red list species found in Mountain Seorak have phytogeographic affinities (e.g., *Pinus pumila* ,*Leontopodium leiolepis* , *Arctous ruber* , and*Thalictrum coreanum* ).

2.4 Species richness

Species richness was defined as the total number of species in randomly selected plots within the 100 m elevation bands, referred to as gamma diversity. That is, a species was defined as being present in every 100 m band between its upper and lower elevational limits (Bhattarai & Vetaas, 2006; Feng et al., 2016; Stevens, 1992; Vetaas & Grytnes, 2002; Zhou et al., 2019). We calculated the species richness for the distribution patterns of the total plant species; each life-form; and each rare, endemic, and red list species (IUCN 2020).

2.5 Elevation range-size

To compare the elevation patterns of the different components using the same standard, Steven's method was used to estimate the elevation range of each species (Stevens, 1989). We identified the minimum and maximum elevation for the distribution of each plant species in every 100 m elevation band. A range of 100 m was provided for species found only on a single plot and was included in the analysis.

We used our own field observations based on Steven's method and generalized additive models to explore the range of diversity (Feng et al., 2016; Zhou et al., 2019). The elevation range-size for each species was estimated using the distribution patterns between the minimum and maximum elevations, and a cubic smooth spline was used to evaluate the significance of specific trends in the elevation range-size and species richness (Feng et al., 2016; Hastie & Tibshirani, 1990; Zhou et al., 2019). These analyses were carried out using R 3.6.3 (R Core Team, 2020).

## Results

### 3.1 Patterns of species richness along the elevation gradient

A total of 238 plant taxa, 163 genera, and 70 families were reported to be growing from elevations of 500 m up to the tree line on the Seorak Mountain (above 1500 m). The total species richness exhibited a positively multimodal pattern along the elevation gradient, with a pronounced mid-peak at 1008.4 m above sea level (a.s.l.). At this peak, 41 taxa were identified in each band (Figure 2a). After rare and endemic species were excluded, the results were similar to those of the pronounced mid-peak at 1004.1 m a.s.l; 39 taxa were observed at the peak (Figure 2b). For the different life-form groups, there were decreases in tree species at 927.3 m, shrub species at 932.7 m, and climber species at 937.4 m (Figure 2c, d, f). In contrast, the multimodal pattern exhibited decreased herb species at 1435.5 m, pteridophytes at 1104.1 m, and woody species (including trees, shrubs, and lianas) at 1004.8 m (Figure 2e, g, h).

### 3.2 Mean elevation range-size for the distribution of life-form groups

The mean elevation range size for total species richness exhibited a pronounced downward trend after the mid-peak at 1291.7 m (Figure 3a). The mean elevation range-size of excluding rare, endemic, and red list species showed a downward trend at 1292.7 m in the elevation regions (Figure 3b), as observed for total species richness. Similarly, trees, shrubs, lianas, and woody groups exhibited a sharp downward trend after the mid-peak. Pteridophytes exhibited a gentle downward trend at 1061.7 m, but no trend was detected for herbs (Figure 3).

### 3.3 Elevation patterns of the rare, endemic, and red list species (IUCN)

Rare, endemic, and red list species with phytogeographic affinities intermittently appeared on the Seorak Mountain from 500 m; in contrast to the elevation patterns of the life-forms or total species, the rare species increased continuously from 1613.3 m (Figure 4a), and endemic species exhibited a positive unimodal pattern at 1430 m (Figure 4b). Red list species showed similar elevation patterns as rare species (Figure 4c). Furthermore, rare and endemic species were almost absent from the Seorak Mountain below 800 m (Figure 4). The mean revolution range was slightly adjusted to the range-size compared to species richness and was similar to the species richness elevation pattern.

## Discussion

The results of the empirical data collected were similar to those found in previous studies for various taxa (e.g., birds, land snails, and fish), as they were observed to decrease in abundance along the elevation slopes (Carvajal-Quintero et al., 2015; Liew, Schilthuizen & Lakim, 2010; Pan et al., 2016). Although Seorak Mountain is a low mountain with an altitude of 1708 m, its treeline begins at 1500 m, above which characteristic dwarf and arctic-alpine plants appear (Kim, Lim & Yun, 2019).

Mount Seorak is home to a temperate climate zone forest. In tropical and subtropical mountains, unimodal patterns of organisms are common, and are more likely to appear because of peak diversity below the mid-point of elevation (Cirimwami et al., 2019; Feng et al., 2015; Guo et al., 2013; Rahbek, 2005; Zhou et al., 2019). Mountains always exhibit a larger altitude range and longer climatic slopes, and thus they generally have unimodal patterns. In this study, we conducted surveys in multiple elevation bands to minimize the possibility of bias due to uneven sampling. Field surveys were conducted using the same sampling intensity via a phytosociology-based line transect survey method.

The maximum species abundance of vascular plants on Seorak Mountain was found to have a multimodal pattern, with a mid-peak at 1008.4 m a.s.l., along the elevation gradients (Figure 2a). By excluding rare and endemic species, the abundance patterns were found to decrease above 1004.1 m a.s.l. (Figure 2b). Although the different life-forms groups and vegetation species composition were similar, the total species showed a slightly adjusted range-size pattern depending on the elevation. The abundance of each component varies greatly along the elevation gradients (Figure 3). The height of plants, such as trees and shrubs, showed a high level of diversity at lower elevations, and the herbaceous and pteridophytes patterns were combined with those of woody plants (i.e., trees, shrubs, and lianas), significantly reducing the maximum species abundance (Figure 2a). The significant decrease in the proportion of woody plants in relatively low mountain areas, including Mount Seorak, reflects their physiological adaptations. The unimodal pattern of these woody plants suggests that a strong boundary effect can result in a pattern of decreasing species density (Colwell, Rahbek & Gotelli, 2005; Feng et al., 2016; Grytnes & Vetaas, 2002).

Furthermore, the presence or absence of rare and endemic species (maximum peaks at 1613.3 and 1430 m, respectively; Figure 4) greatly influences the altitude patterns of the total species abundance (elevation 900 to 1100 m; Figures 2a, b). For species abundance, when rare and endemic species were excluded, the rule of decreasing species abundance from approximately 1000 m above sea level and with higher altitudes was confirmed. This is likely because of the shorter growing seasons, lower temperatures, lower mass circulation, and treeline-like environments (i.e., physical environments such as hard rock formations and physiological constraints due to extreme climatic conditions). The region around the Daecheongbong Peak of Mount Seorak has a strong wind and rocky terrain; this will benefit species with a small distribution range such as rare or endemic species (Kim et al., 2017; Kim, Lim & Yun, 2019).

In the Himalayas (Bhattarai & Vetaas, 2006; Feng et al., 2016; Vetaas & Grytnes, 2002), Andes (Cuesta et al., 2017; Hutter, Guayasamin & Wiens, 2013), and various African mountain ranges (Cirimwami et al., 2019; Zhou et al., 2019), the species abundance of rare and endemic species continuously increased at higher altitudes, a pattern similar to that of most mountains. In the Himalayan Mountains of Nepal, endemic species increase with elevation gradients to an altitude of 4200 m (Vetaas & Grytnes, 2002), and rare and endemic species in Korea's Seorak (maximum peak 1708 m) increased to 1613.3 and 1430 m, respectively (Figure 4). Because of the physiological adaptations of the plants, the range-size of endemic species or rare species may have been reduced differently compared to that of general species, particularly in the lowlands. Therefore, endemic and rare species may peak at altitudes that are higher than those for the total species.

Tropical or endemic species exhibited a small elevation range-size (Zhou et al., 2019). Similarly, on Mount Seorak, most rare or endemic species remaining after the interglaciation showed a small elevation range-size (Figure 4). As altitude increases, the range-size of species in the assembly is explained as the result of individuals having to withstand extreme climatic conditions at higher altitudes (Feng et al., 2016; Gaston, 1996; Gaston & Chown, 1999; Morin & Lechowicz, 2011). Thus, even if the overall elevation range is small, a species pool has a similar shape (ecosystem), and an adjusted range-size can be predicted for each species.

This elevation pattern also affects the mean elevation range of the total species (Figure 2c, d). The mean elevation range for total species was skewed along the elevation slope at 1291.7 m (Figure 2c), and the mean elevation range excluding rare and endemic plants was found to have the same elevation gradients at 1292.7 m (Figure 2d). Strong support for the range-elevation relationship predicted by the ERR was observed in herbs, rare, endemic, and red list species (Figure 3e; Figure 4a–c). According to the boundary effect, the decreasing trend in the average altitude range at high altitudes may be affected by environmental or climatic conditions (Bhattarai & Vetaas 2006; Feng et al., 2016; Vetaas & Grytnes, 2002). Considering that this study showed support for the ERR as an increasing trend in the elevation relationship of the range-size of herbs, rare, endemic, and red list species, the boundary effect did not appear to have a strong effect. The proportion of endemic and rare species increasing along the elevation gradient can affect the relationship between the mean elevation range and elevation of species assemblages (Pottier et al., 2013; Vetaas & Grytnes, 2002). On Mount Seorak, rare and endemic species were distributed continuously and appeared at high elevation gradients (species included *Adenophora grandiflora* , *Weigela subsessilis* , *Lonicera subsessilis* ,*Viola diamantiaca* , *Syringa wolfii* , *Rodgersia podophylla* , *Smilacina bicolor* , *Patrinia saniculifolia* , and *Pinus pumila* , which were from different life-form groups).

Conclusions

A field survey of plant diversity from the lowland forests of Mount Seorak to its maximum peak was conducted, and the plants identified were divided into their different components to test the ERR. The altitude range of the herbs, rare, endemic, and red list species was significantly higher than that of woody plants. Particularly, the rare, endemic, and red list species can withstand extreme climatic conditions through physiological adaptations, as their ranges reached the highest elevation, and therefore can be applied to the ERR. However, the hard boundary effect in this region consistently supported different life-forms (i.e., trees, shrubs, lianas, pteridophytes, and woody species). Overall, the ERR was inconsistent between plants of different life-forms in the same region.

Data accessibility statement

All data for analysis are available at Dryad (https://doi.org/10.5061/dryad.d51c5b02x).

Competing interest statement

The authors declare that they have no competing interests.

Author contributions section

Ji-Dong Kim: Conceptualization (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (lead); Software (equal); Writing-original draft (equal). Mi-Hyun Lee: Data curation (equal); Formal analysis (equal); Software (equal); Visualization (lead); Writing-original draft (equal). Ju-Hyeon Song: Investigation (equal); Writing-review & editing (equal). Seong-Yeob Byeon: Formal analysis (equal); Investigation (equal). Jeong-Eun Lee: Data curation (equal); Investigation (equal). Ho-Jin Kim: Investigation (equal); Writing-review & editing (equal). Seung-Beom Chae: Investigation (equal); Visualization (equal). Chung-Weon Yun: Funding acquisition (lead); Project administration (equal); Resources (equal); Supervision (lead).

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Figure Legends

**FIGURE 1** (a) Location of the Seorak Mountain (peak 1708 m) in Korea; (b) 100 m vertical elevation bands of the Seorak Mountain. The survey route was: Misiryeong, Hangyeryeong, Danmokryeong, and Osaek.

**FIGURE 2** Elevation patterns of species richness of vascular plants on the Seorak Mountain. Total species richness (a); species richness excluding rare, endemic, and red list species (b); and species richness of trees (c); shrubs (d); herbs (e); lianas (f); pteridophytes (g); and woody species (h).

**FIGURE 3** Mean elevation range-size of different of life-form groups along the elevation gradient of the Seorak Mountain: (a) total plants; (b) total plants excluding rare, endemic, and red list species; (c) trees; (d) shrubs; (e) herbs; (f) lianas; (g) pteridophytes; and (h) woody species.

**FIGURE 4** Elevation patterns in species richness and mean elevation range of (a) rare species, (b) endemic species, and (c) red list (IUCN) species on the Seorak Mountain.

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