1 *Article*

2 # Hierarchical Environmental Factors affecting the

3 # Distribution of *Abies koreana* on the Korean

4 # Peninsula

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14 **Abstract:** Regional declines of the Korean fir (*Abies koreana*) have been observed since the 1980s on
15 the subalpine region. To explain this decline, it is fundamental to investigate the degree to which
16 environmental factors have contributed to plant distributions on diverse spatial scales. We applied
17 a hierarchical regression model to determine quantitatively the relationship between the abundance
18 of Korean fir (seedlings) and diverse environmental factors across two different ecological scales.
19 We measured Korean fir density and the occurrence of its seedlings in 102 (84) plots nested at five
20 sites and collected a range of environmental factors at the same plots. Our model included
21 hierarchical explanatory variables at both site-level (weather conditions) and plot-level (micro-
22 topographic factors, soil properties, and competing species). The occurrence of Korean fir seedlings
23 was positively associated with moss cover and rock cover but negatively related to dwarf bamboo
24 cover. On site-level, winter precipitation was significantly positively related to the occurrence of
25 seedlings. A hierarchical Poisson regression model revealed that Korean fir density were negatively
26 associated with slope aspect, topographic position index, *Quercus mongolica* cover, and mean
27 summer temperature. Our results suggest that drought and competition with other species are
28 factors which halt the survival of Korean fir. We can predict that the population of Korean fir will
29 continue to decline on the Korean Peninsula due to rising temperatures and seasonal drought, and
30 only a few Korean fir will survive on northern slopes or valleys where competition with dwarf
31 bamboo and *Q. mongolica* can be avoided.

32 **Keywords:** Korean fir; Hierarchical regression model; climate change; seedling survival; dwarf
33 bamboo; drought

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35 ## 1. Introduction

36   Environmental differences play a critical role in species establishment and their growth [1, 2].
37 Specifically in mountain areas, the heterogeneity of topographic factors can exert strong effects on a
38 wide variety of micro-habitats [3, 4, 5]. For example, different elevations, topographic position, and
39 slope aspects can create a mosaic of diverse microclimates, and this can affect the distribution and
40 diversity of species. Hence, ecological data are often hierarchically structured, and environmental
41 variables act in a hierarchical manner on different ecological scales [6, 7]. With regard to experimental
42 designs, ecological field data often involve random effects [8]. Common random effects in field
43 ecology data are blocks that are replicated across sites or times [9, 10]. When a hierarchical
44 relationship (or random effects) within explanatory variables is ignored, the true results can be
45 distorted or obscured because the assumption of independent errors is violated [8]. To quantify the

46 contributions of environmental factors to the distribution of Korean fir on different spatial scales, we
47 applied a multilevel/hierarchical generalized linear model, which is a more sophisticated and novel
48 statistical technique than a simple regression model [7, 8].
49   Korean fir is an endemic and rare species which grows in the subalpine regions of Mount Halla,
50 Jiri, Dukyu, and Gaya located in the southern part of the Korean Peninsula [11]. This tree endures
51 harsh environmental conditions, such as low temperatures, strong wind, and low soil nutrient levels
52 in its subalpine ecosystem [12, 13]. It is well known that relictual cold-adapted subalpine plant species
53 can be very sensitive to climate changes such as rising temperatures and drought [14, 15, 16]. Korean
54 fir, a subalpine cold-adapted tree, is categorized as an endangered species (EN) by the International
55 Union for Conservation of Nature (IUCN) [17]. Regional declines of the Korean fir population have
56 been observed since the 1980s, occurring for complex reasons, including rising temperatures, drought
57 stress, and competition with other species [12, 15, 18, 19, 20]. However, these studies conducted in
58 regional Korean fir forests, and did not consider diverse environmental factors on a hierarchical
59 spatial scale. Thus far, most studies only provide a description of local Korean fir forests without
60 reasonable statistical evidence. To explain the reason for the decline in the Korean fir population, it
61 is fundamental to investigate the degree to which different environmental factors contribute to the
62 distribution on diverse spatial scales. We considered a range of environmental factors, including
63 climatic factors, topographic factors, soil properties, and competition with other species. The
64 objective of this study was quantitatively to determine the relationship between the abundance of
65 Korean fir (seedlings) and diverse environmental factors across a range of ecological scales.
66 Additionally, we discuss future changes in Korean fir distribution patterns.

2. Materials and Methods

2.1. Study Sites

69   The sites chosen for this study were five Korean fir forests on Mt. Gaya, Mt. Jiri, and Mt. Halla,
70 all of which are located in the southern part of the Korean Peninsula (Figure 1).
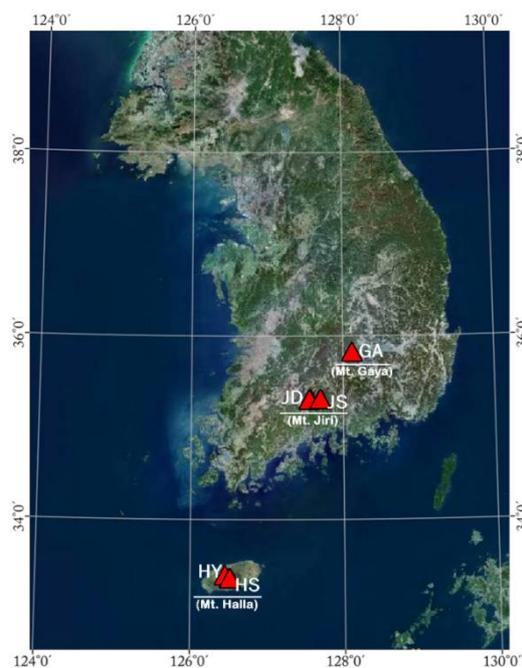
Figure 1. Distribution of the study sites located in the southern part of the Korean Peninsula. GA: Mt. Gaya; JD: Dweajiryeong of Mt. Jiri; JS: Sesuck of Mt. Jiri; HY: Youngsil of Mt. Halla; HS: Southern slope of Mt. Halla

The bedrock types at the Mt. Gaya and Mt. Jiri sites consist of granite and gneiss. Mt. Halla is a dormant volcano, and the surface in this region is composed of volcanic rock types such as andesite and basalt [21]. The altitude at the summit of Mt. Gaya is 1,430 m. Mt. Jiri is the second highest mountain (1,915 m), followed by Mt. Halla (1,947 m) in South Korea. The study sites experience low levels of winter precipitation, at about 2 – 5% of the total annual precipitation, and more than half of the annual precipitation falls in the summer. Mt. Halla had higher winter temperatures and annual precipitation rates than the other sites due to oceanic effects (Figure 2). Mt. Gaya and Mt. Jiri are dominated by Korean fir at higher elevations (> 1,300 m) and are mixed with *Quercus mongolica, Pinus densiflora, Betula ermanii,* and *Magnolia sieboldii* at lower elevations (< 1,300 m) (22, 23). Korean fir forests on Mt. Halla are found at elevations ranging from 1,400 to 1,800 m above sea level, with these trees mixed with *Taxus cuspidate, Betula ermanii, and Prunus sargentii* [19, 24].
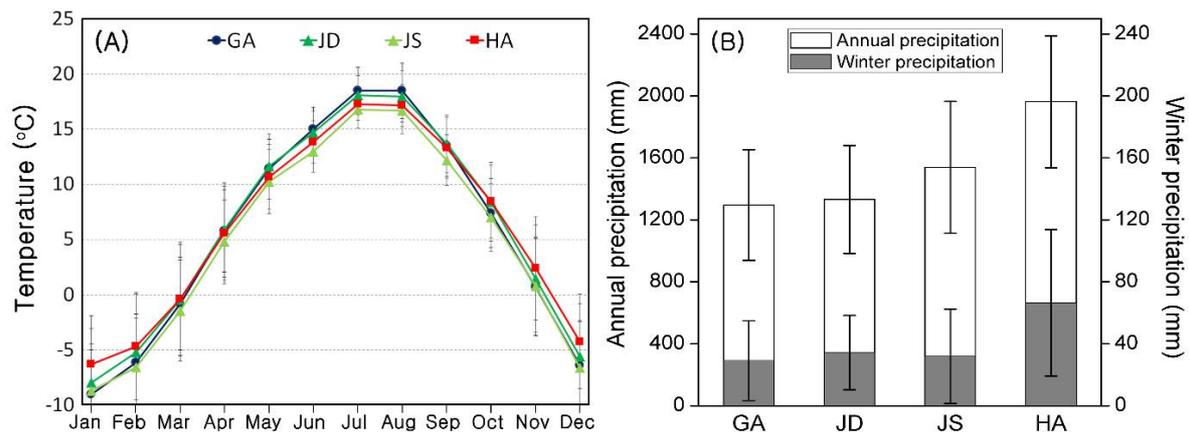
Figure 2. Monthly mean temperature (A) at the study sites during the period of June 2008 – June 2018. Temperatures are estimated value using the generalized least squares method considering time-series autocorrelation (Mean Absolute Error: 0.56 – 0.99). Annual and winter precipitation (B) during 1987 – 2017 (data from the nearest weather station of the Korea Meteorological Administration) GA: Mt. Gaya; JD: Dweajiryeong of Mt. Jiri; JS: Sesuck of Mt. Jiri; HY: Youngsil of Mt. Halla; HS: Southern slope of Mt. Halla

2.2. Sampling Design and Species Data Collection

We collected data at five Korean fir forest sites in September of 2015 and June of 2016 using a random sampling design. The sampling plots are nested in five sites. For each sampling plot, a 10 x 10 m and 1 x 1 m area was set to survey the density of Korean fir trees and its seedlings, respectively. We placed a total of 102 (84) plots over the five different sites (GA: 24, JD: 25, JS: 15, HY: 23 (5), HS: 15) and recorded the coverage or the density of all vascular plants and bryophytes within the plots. A handheld GPS unit (Garmin, GPSMAP 64s, USA) was used to record the longitude and latitude of each plot.

2.3. Environmental Data Collection

We assumed that the weather conditions are the main environmental variables on the site-level. We selected four seasonal mean temperatures (T_{sp}, T_{su}, T_{au}, T_w) and the average annual precipitation (P_{an}) and winter precipitation (P_w) to investigate the association between the Korean fir distribution and the weather conditions. Due to elevation differences between the study sites and weather stations used in this study, we could not use temperature data from the weather stations, except in the case of Mt. Halla. Temperatures on Mt. Gaya and Mt. Jiri were estimated using a generalized least squares model considering time-series autocorrelation in the R package name (R version 3.4) (mean absolute error: 0.56 – 0.99) [25]. The response variables were the temperature datasets from field measurements from June of 2015 to October of 2016 using a HOBO data logger, and the explanatory variables are the temperature dataset and binary data of the rainfall status from the closest automatic weather

120 station in each case. We predicted the daily mean temperature for a time span of ten years. The
121 precipitation data were from the closest weather station (Korea Meteorological Administration from
122 1987 to 2017).

123   We selected four micro-topographic variables (elevation, slope, aspect, topographic position
124 index), four soil physicochemical variables (rock cover, pH, organic matter content, electrical
125 conductivity), and three biological variables (Sasa cover, moss cover, *Q. mongolica* cover) at plot-scale
126 (level 1). The topographic variables were derived from the DEM (10 m x 10 m) of the study area.
127 Elevations varied from 1306 m to 1715 m, and slopes varied from 0° to 45°. The topographic position
128 index was classified into one of the following categories: 1 = valley or lower slope, 2 = mid slope, and
129 3 = upper slope or ridge. The slope aspect was divided into the following four categories considering
130 the amount of solar radiation: 1 = 315° – 45°, 2 = 45° – 90° or 270° - 315°, 3 = 90° - 135° or 225° - 270°,
131 and 4 = 135° - 225°. To measure the soil physicochemical properties, soil samples were collected from
132 five randomly selected points in each plot (10 m x 10 m) after removing organic debris. This was
133 followed by thorough mixing to produce a composite sample for each sampling plot. The soil samples
134 were returned to the laboratory and the pH, EC, and OM values were calculated. The soil pH and
135 electrical conductivity (ratio of soil to distilled water, 1:5) values were measured using a pH meter
136 (Orion, model Star A211; USA) and an electrical conductivity meter (Orion, model Star A212; USA),
137 respectively. The soil organic matter was calculated according to the weight loss after the samples
138 were kept in a muffle furnace at 550℃ for four hours. Rock cover, moss cover, Sasa cover, and *Q.*
139 *mongolica* cover levels were measured as the percentage of ground covered in each plot with division
140 into six categories for further statistical analysis (0 = 0%, 1 = < 5%, 2 = 5 – 25%, 3 = 25 – 50%, 4 = 50 –
141 75%, 5 = 75 – 100%).

142 *2.4. Data Analysis*

143   We calculated the Pearson correlation coefficient using the plot scale-dataset to determine the
144 correlation and the degree of multicollinearity among the nine environmental variables.
145 Furthermore, sampling plots were grouped based on two-dimensional nonmetric multidimensional
146 scaling (NMDS) scores to present the associations between the groups and variables. NMDS
147 ordination plots were produced from the Euclidean distances. The goodness-of-fit of the NMDS
148 configuration was assessed by the loss of stress function. The stress value was 0.161 for the two-
149 dimensional solution, which is lower than the generally accepted maximum stress value: < 0.05 =
150 excellent, < 0.10 = good, and < 0.20 = usable [26]. NMDS ordination was conducted with the R package
151 'vegan' [27].

152   Hierarchical generalized regression models were applied to investigate the associations between
153 the abundance of Korean fir (seedlings) and the explanatory variables on the different spatial scales
154 [28]. This refers to a type of mixed model with datasets nested at more than one level [29]. Our model
155 provides a hierarchical framework for identifying the effects of site-level and plot-level explanatory
156 variables on the response variables. We combined the HY and HS sites into a single HA site for our
157 hierarchical regression model because the distance between the two sites is less than 2 km, and we
158 assumed that the two sites had similar weather conditions. To reduce the collinearity among the
159 explanatory variables and to improve the model performance, all explanatory variables were
160 centered by subtracting the mean of the explanatory variables χ from every value in χ [8].

161   Before constructing the explanatory regression models, we fitted an unconditional model
162 without introducing other explanatory variables but considering random intercepts to estimate the
163 baseline of the variance. This model can be expressed as follows:

$$Y_{ij} = \gamma_{00} + u_{oj} + e_{ij}$$

165   Here, Y_{ij} is the abundance of Korean fir (the Poisson distribution with the log link function) and
166 the occurrence of its seedlings (a Bernoulli distribution with the logit link function) at sample plot i
167 of site j, γ_{00} represents the overall average of the density of Korean fir at all sites, and u_{0j} is the
168 difference between the average density at the jth site from that overall mean. The variable e_{ij}
169 represents the difference between the density level at the plot and its mean at the site.

170 To ascertain the relationship between the abundance of Korean fir and each predictor variable
171 on the plot scale, we devised a univariate random coefficient model instead of a random intercept
172 model. The random coefficient model assumes that all groups have a different slope for a fitted
173 covariate, which can reduce Type Ⅰ and Type Ⅱ errors [8, 29]. Scatter plots also showed that the
174 slope of a predictor could vary considerably among the sites.

$$Y_{ij} = \gamma_{00} + \gamma_{p0}X_{pij} + u_{pj}X_{pij} + u_{0j} + e_{ij}$$

176 In this equation, the relationship between the Korean fir density and each explanatory variable
177 is partitioned into two components: (1) the across-site slope relating the tree's density to each
178 environmental variable (γ_{p0}) and (2) the difference between the slope of the within-site relationship
179 between tree's density and each explanatory variable (u_{pj}).

180 We extend this model by including multiple explanatory variables at both the plot-level and the
181 site-level. Specifically, our final model also includes site-level explanatory variables, in this case the
182 monthly mean temperature and the annual precipitation.

$$Y_{ij} = \gamma_{00} + \gamma_{p0}X_{pij} + \gamma_{0q}Z_{qj} + u_{pj}X_{pij} + u_{0j} + e_{ij}$$

184 The additional piece of the random coefficient model is $\gamma_{0q}Z_{qj}$, where γ_{0q} represents the fixed
185 effect of the site-level variable Z_{qj} on the response variables.

186 To find the best hierarchical linear model, we applied a stepwise selection method based on the
187 *p* values of the predictors and the information criterion (AIC and BIC). With the desired set of
188 predictors selected, we calculated the variance inflation factor (VIF) of each predictor, dropping
189 variables with a VIF higher than 3 to avoid collinearity among the predictor variables [29].

190 **3. Results**

191 *3.1. Comparison of Study Sites*

192 The descriptive statistics for the Korean fir density and environmental variables are shown in
193 Table 1.

194 **Table 1.** Descriptive statistics of the Korean fir density and environmental variables *.

|	N	GA	JD	JS	HY	HS	F value
Living *A. koreana*	102	7.2 ± 1.4[c]	12 ± 1.8[bc]	20.8 ± 2.5[a]	12.3 ± 1.1[bc]	15.5 ± 1.5[ab]	8.4***
Death *A. koreana*	84	0.2 ± 0.1[b]	4.6 ± 0.9[a]	4.3 ± 0.6[a]	4.61 ± 0.8[a]	2.5 ± 0.8[ab]	10.1***
A. koreana seedling	84	3.6 ± 1.0	2.1 ± 0.9	4.9 ± 1.7	6.0 ± 1.3	2.5 ± 1.2	1.2
Elevation (m)	102	1354.0 ± 4[e]	1401 ± 19[d]	1457 ± 19[c]	1615 ± 4[b]	1681 ± 5[a]	118***
Aspect (1–4)	102	2.3 ± 0.2[b]	1.9 ± 0.2[bc]	3.6 ± 0.1[a]	1.4 ± 0.1[c]	3.1 ± 0.2[a]	18.4***
Slope (°)	102	31.0 ± 1.9[a]	18.4 ± 0.5[b]	13.5 ± 1.4[c]	8.3 ± 0.7[d]	9.5 ± 0.7[cd]	64.1***
TPI (1–3)	102	2.1 ± 0.2[bc]	2.8 ± 0.1[a]	1.5 ± 0.2[c]	2.3 ± 0.1[ab]	1.9 ± 0.2[bc]	8.2***
Rock cover (0–5)	102	4.0 ± 0.3[a]	1.1 ± 0.2[b]	3.1 ± 0.4[a]	3.7 ± 0.2[a]	1.5 ± 0.4[b]	23.3***
pH	84	4.6 ± 0.1	4.6 ± 0	4.5 ± 0.1	4.3 ± 0.1	4.6 ± 0.0	1.4
OM (%)	84	36.3 ± 1.6[a]	17.5 ± 1.2[b]	18.4 ± 1[b]	20.1 ± 4.3[b]	14.0 ± 1.6[b]	37.5***
EC (dS/m)	84	0.8 ± 0.1[a]	0.4 ± 0.0[b]	0.5 ± 0.1[b]	1.0 ± 0.2[a]	0.7 ± 0.1[ab]	10.1***
Sasa cover (0–5)	102	0.7 ± 0.3[b]	1.2 ± 0.4[b]	1.1 ± 0.4[b]	3.2 ± 0.5[a]	4.8 ± 0.1[a]	16.9***
Moss cover (0–5)	102	2.3 ± 0.2[ab]	0.8 ± 0.2[c]	1.5 ± 0.3[bc]	2.9 ± 0.2[a]	0.8 ± 0.4[c]	14.6***
Qm cover (0–5)	102	1.8 ± 0.3[a]	1.5 ± 0.2[ab]	1.4 ± 0.3[ab]	0.6 ± 0.2[bc]	0.0 ± 0.0[c]	7.3***

195 * GA: Mt. Gaya; JD: Dweajiryeong of Mt. Jiri; JS: Sesuck of Mt. Jiri; HY: Youngsil of Mt. Halla; HS: Southern slope
196 of Mt. Halla; TPI: topographic position index; OM: organic matter; EC: electrical conductivity. Qm: Quercus
197 mongolica. Meaningful differences in each variable among the five sites are marked with *, **, and *** to

198 represent $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, based on the results from an analysis of variance (Tukey's
199 HSD).

200 Living Korean fir had the highest density in JS and the lowest density in GA among the five surveyed
201 sites. The proportion of dead Korean fir trees at the HY and JD sites was higher than those of the
202 other sites. We could not find significant differences in the density of Korean fir seedlings among the
203 five sites. Mean elevations with small variations were significantly different depending on the site.
204 Plots on Mt. Halla are located at higher elevations than the other mountains. Plots at JS had the lowest
205 TPI value compared to the other sites because they lie in a valley on Mt. Jiri. Ga and HY had higher
206 rock cover and moss cover levels than the other sites. The cover level of the genus Sasa was higher
207 on Mt. Halla than on Mt. Jiri and Mt. Gaya.

208 *3.2. The Relationship among Environmental Variables*

209   Pearson correlation coefficients of ten environmental variables are presented in Figure 3. Strong
210 positive correlations were observed between rock cover and moss cover levels, whereas rock cover
211 was negatively associated with Sasa cover (Figure 3A). Moss cover was higher on the north side slope
212 than on the southern slope, and moss cover was negatively correlated with Sasa cover (Figure 3A).
213 To determine the characteristics of each plot and site, we grouped 84 plots based on a matrix of the
214 ten selected environmental variables (Figure 3B). Surveyed plots were divided into three groups
215 according to the NMDS (stress: 0.161) and hierarchical clustering (average silhouette width: 0.43)
216 scores. Moss cover, rock cover, Sasa cover, and *Q. mongolica* cover were more critical factors with
217 regard to the grouping of each site compared to the other environmental factors. GA and HY had
218 similar environmental characteristics with higher moss cover and rock cover levels than the other
219 sites. GA and JD showed greater *Q. mongolica* cover; otherwise, HS had higher Sasa cover than the
220 other sites.

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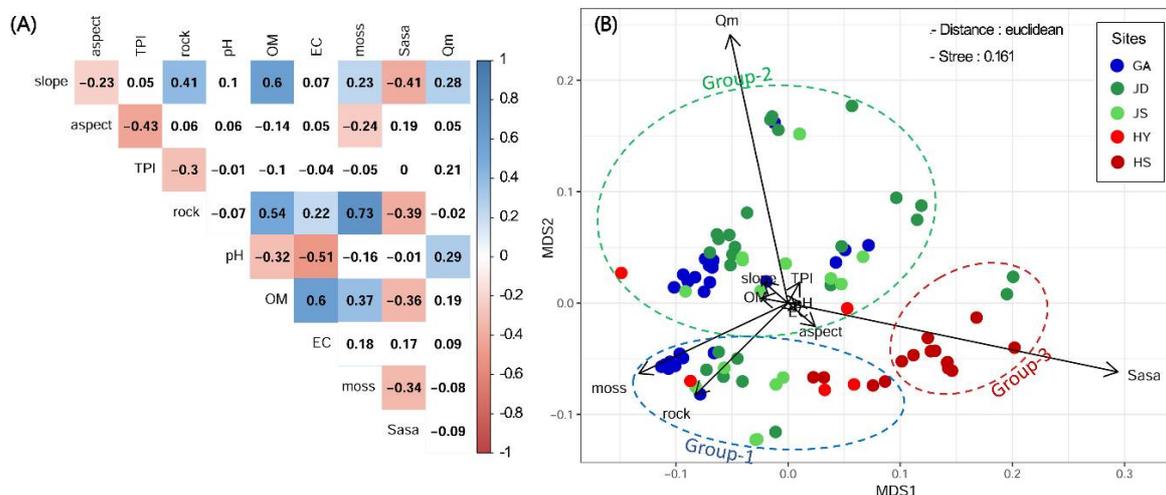
Figure 3. (A) Pearson correlation coefficient plot of combinations of environmental variables (n=84). Colored
boxes represent a significant correlation coefficient between the variables ($p < 0.05$). (B) The ordination of non-
metric multidimensional scaling (NMDS) based on the environmental variables matrix, showing the scores of
the environmental variables. Dots represent individual plots sampled from the five sites. Dotted ellipses
represent three groups based on hierarchical clustering of the NMDS points. GA: Mt. Gaya; JD: Dweajiryeong
of Mt. Jiri; JS: Sesuck of Mt. Jiri; HY: Youngsil of Mt. Halla; HS: Southern slope of Mt. Halla; TPI: topographic
position index; OM: organic matter; EC: electrical conductivity, Qm: *Quercus mong*olica

229 *3.3. Korean Fir Seedling – Environmental Factors Relationships*

230   Before constructing the explanatory models, we fitted the unconditional model of the occurrence
231 of Korean fir seedlings without introducing other explanatory variables but considering random

intercept across sites (Table 2, *upper*). The unconditional model showed a non-significant random intercept. This indicated that the occurrence of Korean fir seedlings within each site does not differ from the overall average. The results of the univariate random coefficient model showed that the occurrence of seedlings was primarily related to variations in the (4) rock cover, (8) moss cover, and (9) Sasa cover levels. Moss cover exerted more influence than rock cover in this study.

Table 2. Unconditional (*upper*) and Hierarchical logistic regression (*lower*) models of the occurrence of Korean fir seedlings (Y_{ij}) with plot-level explanatory variables (X_{ij}) and site-level explanatory variables (Z_j) using the maximum likelihood method (Laplace approximation)*.

	Parameter	Estimate	z value	*p*-value	Variance	AIC
			Unconditional model			
		$(Y_{ij} \sim Bernoulli(P_{ij})\,,\ Logit(P_{ij}) = \gamma_{00} + u_{oj} + e_{ij})$				
		Fixed effect			Random effect	
	Intercept	0.16	0.415	0.67	0.39	119
		Univariate random coefficient model				
		$(Y_{ij} \sim Bernoulli(P_{ij}),\ Logit(P_{ij}) = \gamma_{00} + \gamma_{p0}X_{pij} + u_{pj}X_{pij} + u_{0j} + e_{ij})$				
(1)	Intercept	- 0.50	- 1.27	0.20	0.001	110
	Slope	- 0.06	- 0.61	0.54	0.046	
(2)	Intercept	- 0.17	- 0.55	0.58	0.036	114
	Aspect	- 0.63	- 1.05	0.29	1.241	
(3)	Intercept	0.15	0.37	0.71	0.386	124
	TPI	- 0.01	- 0.04	0.97	0.008	
(4)	Intercept	0.03	0.36	0.92	0.240	111
	Rock cover	**0.48**[**]	2.30	< 0.05	0.078	
(5)	Intercept	0.15	0.39	0.69	0.407	123
	pH	- 0.50	- 0.40	0.69	1.961	
(6)	Intercept	0.16	0.45	0.65	0.256	121
	OM	0.03	1.13	0.26	0.001	
(7)	Intercept	0.31	0.74	0.46	0.371	120
	EC	0.02	0.01	0.99	7.052	
(8)	Intercept	- 0.13	0.39	0.72	0.195	104
	Moss cover	**1.01**[**]	2.27	< 0.05	0.514	
(9)	Intercept	0.31	0.50	0.62	0.889	109
	Sasa cover	**- 0.56**[**]	- 2.57	< 0.05	0.002	
		Final hierarchical logistic regression model				
		$(Y_{ij} \sim Bernoulli(P_{ij}),\ Logit(P_{ij}) = \gamma_{00} + \gamma_{p0}X_{pij} + \gamma_{0q}Z_{qj} + u_{pj}X_{pij} + u_{0j} + e_{ij})$				
	Intercept	**0.02**[*]	0.06	0.07	0.036	
	Moss cover	**0.76**[*]	1.82	0.06	0.406	97
	Sasa cover	**-0.68**[**]	- 2.53	< 0.05	-	
	P_w	**0.08**[**]	1.96	< 0.05	-	

240   * TPI: topographic position index; OM: organic matter; EC: electrical conductivity. Each significant each
241   parameter is marked with * (*p* < 0.1) and ** (*p* < 0.05), respectively.

242

243   Moss cover had greater random effect variation (0.514) than that of rock cover (0.078), indicating that
244   the relationship of moss cover to the occurrence of seedlings varies more across the sites than does
245   the impact of rock cover. The occurrence of seedlings was negatively related to Sasa cover, and Sasa
246   cover showed minor random effect variation compared to the other explanatory variables.
247   Based on univariate random coefficient model, we constructed final hierarchical logistic
248   regression model including the site-level explanatory variable (Table 2, *lower*). We dropped rock
249   cover owing to the degree of collinearity with moss cover. On the plot-level, moss cover was
250   positively related to the occurrence of seedlings. On the other hand, Sasa cover was negatively
251   associated with the occurrence of seedlings. On the site-level, winter precipitation was positively
252   related to the occurrence of seedlings.

253   *3.4. The Density of Korean Fir – Environmental Factors Relationships*

254   When we fitted the unconditional model of the density of Korean fir, this model showed significant
255   random intercept (Table 3). This indicates that the average of the Korean fir density level within each site
256   differed from the overall average. The univariate random coefficient model showed that the Korean fir
257   density levels were negatively related to aspect and TPI. Aspect had greater random effect variation (0.02)
258   than that of TPI (0.003), indicating that the relationship between aspect and the Korean fir density level
259   varies more across the sites than does the impact of TPI. We incorporated site-level explanatory variables
260   into the final model. The final hierarchical Poisson regression model revealed that the Korean fir density
261   levels were negatively associated with aspect, TPI, Qm cover, and the mean summer temperature at the
262   0.1 p-value level.

263   **4. Discussion**

264   This study revealed the hierarchical nature of the relationships between the Korean fir
265   distribution patterns and environmental conditions in various types of Korean fir forests. Our results
266   showed that Korean fir seedlings mainly occur at plots with higher levels of both rock cover and moss
267   cover and with lower levels of genus Sasa (dwarf bamboo) cover. At the site level, Korean fir
268   seedlings were frequently found in areas with higher rates of winter precipitation.
269   Earlier studies also noted that rock cover can have positive effects on the establishment and
270   growth of Korean fir seedlings [19, 30]. Rock covered areas usually have lower density levels of dwarf
271   bamboo and deciduous trees, indicating that Korean fir can receive higher levels of solar radiation in
272   rock-covered areas than under dwarf bamboo. Dwarf bamboo is the most dominant understory
273   species in Korean fir forests [19, 31]. Although interactions between high sunlight and water stress
274   can inhibit the growth and survival of fir seedlings in an alpine-treeline ecotone [32], the light
275   intensity may be too low for the survival of fir seedlings at sites with dense bamboo [33]. Moreover,
276   Korean fir seeds may stay for a long period of time in the gaps of rock, which can facilitate
277   germination [34]. Rock gaps usually have higher soil moisture, more organic matter, and longer
278   periods of time of snow cover than flatland areas, which can provide beneficial conditions for
279   seedling germination and survival [19, 35].
280   Korean fir seedlings are also frequently found in moss-covered plots. Moss cover is positively
281   associated with the humidity of the air [36, 37]. It is well known that stable moisture supply represent
282   an important factor for tree seedling survival [13, 38, 39]. Although the soil moisture and humidity
283   of the air were not included in our model as explanatory variables, we can speculate, especially in
284   the dry season, that a stable water supply is also a key factor for the survival of Korean fir seedlings.
285   Several studies also noted that dense dwarf bamboo can have a negative influence on not only Korean
286   fir seedlings but also on the establishment of seedlings of other trees [33, 40, 41, 42, 43]. Dwarf bamboo
287   is a broadleaf evergreen shrub; therefore, this species can continuously prevent light penetration into
288   Korean fir seedlings for all four seasons. Furthermore, a thick litter layer and the subterranean stems

289   of dwarf bamboo can negatively affect the germination of tree seeds [41, 42]. Our study shows that
290   winter precipitation is positively associated with the occurrence of Korean fir seedlings. Winter
291   precipitation is usually in the form of snow in subalpine areas. Snow cover can protect small tree
292   seedlings from freezing damage during the winter season [44]. In addition, higher levels of winter
293   precipitation can alleviate severe drought in the springtime.
294

295   **Table 3.** Hierarchical Poisson regression models of the density of Korean fir (Y_{ij}) with plot-level explanatory
296   variables (X_{ij}) and site-level explanatory variables (Z_j) using the maximum likelihood method (Laplace
297   approximation)*.

	Unconditional model				
	$(Y_{ij} \sim Poisson(\lambda_{ij}), \quad Log(\lambda_{ij}) = \gamma_{00} + u_{oj} + e_{ij})$				
	Fixed effect			Random effect	
Parameter	Estimate	z value	*p*-value	Variance	AIC
Intercept	**2.59*****	16.1	< 0.001	0.13	757
	Univariate Random coefficient model				
	$(Y_{ij} \sim Poisson(\lambda_{ij}), \quad Log(\lambda_{ij}) = \gamma_{00} + \gamma_{p0}X_{pij} + u_{pj}X_{pij} + u_{0j} + e_{ij})$				
(1)	Intercept **2.34*****	7.35	< 0.001	0.39	729
	Slope 0.006	0.42	0.67	0.001	
(2)	Intercept **2.56*****	9.57	< 0.001	0.27	734
	Aspect **- 0.17***	- 2.05	< 0.05	0.02	
(3)	Intercept **2.54*****	13.92	< 0.001	0.13	754
	TPI **- 0.11***	- 2.54	< 0.05	0.003	
(4)	Intercept **2.28*****	5.57	< 0.001	0.65	712
	Rock cover 0.07	0.57	0.56	0.07	
(5)	Intercept **2.55*****	12.47	< 0.001	0.16	738
	pH 0.03	0.08	0.95	0.62	
(6)	Intercept **2.34*****	6.32	< 0.001	0.53	699
	OM 0.02	0.87	0.38	0.002	
(7)	Intercept **2.78*****	9.21	< 0.001	0.33	727
	EC - 0.27	- 0.58	0.56	0.79	
(8)	Intercept **2.47*****	10.04	< 0.001	0.07	702
	Qm cover **- 0.17**·	- 1.89	0.06	0.03	
	Final hierarchical Poisson regression model				
	$(Y_{ij} \sim Poisson(\lambda_{ij}), \quad Log(\lambda_{ij}) = \gamma_{00} + \gamma_{p0}X_{pij} + \gamma_{0q}Z_{qj} + u_{pj}X_{pij} + u_{0j} + e_{ij})$				
Intercept	**2.66*****	46.79	< 0.001	0.006	
Aspect	**- 0.14****	- 3.25	< 0.01	-	
TPI	**- 0.11***	- 2.03	< 0.05	-	688
Qm cover	**- 0.17**·	- 1.78	0.08	0.022	
T_{su}	**- 0.30*****	- 5.13	< 0.001	-	

298   * TPI: topographic position index; OM: organic matter; EC: electrical conductivity, Qm: *Quercus mongolica*. Each
299   significant parameter is marked with • ($p < 0.1$), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$), respectively.
300

301
302
303 Our study also revealed that the abundance of Korean fir was significantly associated with the
304 aspect and topographic position index (TPI). Specifically, Korean fir trees were frequently found on
305 northern slopes and valleys than on southern slopes and ridges. Northern slope and valley sites
306 usually have higher air humidity, lower temperatures, lower solar radiation, and longer snow-
307 covered periods than the southern slope and ridge sites. At these sites, Korean fir can also avoid
308 competition with *Q. mongol*ica, which is a representative tree species competing with Korean fir at
309 high altitude areas [45]. Our model showed that the population of Korean fir can be affected by high
310 summer temperatures. Several molecular physiological studies also showed that Korean fir had
311 adapted to low-temperature environments. For example, Heat stress related genes of Korean fir were
312 expressed under heat stress conditions [46]. Similarly, an elevated air temperature (above 20℃) can
313 reduce the net photosynthetic rate and may contribute to the decline of Korean fir [47].

314 **5. Conclusions**

315 In the near future, the question arises of what changes in Korean fir forests are likely to occur.
316 Several reports have predicted that global climate change can lead to further increases in the
317 temperature on the Korean Peninsula as compared to other areas at similar latitudes [48, 49]. Rising
318 temperatures may increase high-temperature-induced photoinhibition and decrease the vitality of
319 Korean fir [14, 50]. In addition, increasing temperatures can cause heat-associated drought stress,
320 which can affect Korean fir [14]. With regard to water stress, the standard deviation of precipitation
321 may increase in East Asia [51], meaning that the Korean Peninsula may be affected by a slight increase
322 in seasonal drought. Seasonal drought and rising temperatures can be fatal to seedlings germinated
323 on southern slopes and ridges, and only a few Korean fir seedlings can survive in low-temperature
324 and high-humidity region of northern slopes and valleys. Furthermore, dwarf bamboo and *Q.*
325 *mongolica*, which are representative species competing with Korean fir, will move up to regions at
326 higher altitudes due to the increased temperatures. Based on our results and on climate change
327 forecasts, we can predict that the population of Korean fir will be continue to decline on the Korean
328 Peninsula, and only a few Korean fir can survive in northern slope or valley regions where the ground
329 is covered with rock and moss.

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