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Slope Gradient Effect on Microhabitat and Small Rodents in a Tree Thinned Japanese Larch Plantation

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ABSTRACT

Slope gradient affects the development of vegetation. Because vegetation serves as food and shelter for wildlife, information about the effect of slope gradient on vegetation is important for managing wildlife and their habitats. We examined the effects of slope gradient on small rodent populations and their microhabitat conditions from May to November 2015 in a tree-thinned Japanese larch (*Larix kaempferi*) plantation in South Korea. Study animals were captured using Sherman live traps. We surveyed slope gradient and microhabitat conditions at multiple trapping points. We focused on two rodent species for statistical analysis, the striped field mouse (*Apodemus agrarius*) and the Korean field mouse (*A. peninsulae*). *A. agrarius* preferred microhabitat with dense ground vegetation, whereas *A. peninsulae* preferred understory vegetation. Ground vegetation was reduced as slope gradient increased, but understory vegetation was not affected by slope gradient. The results highlight that the *A. agrarius* population was influenced indirectly by the negative effect of slope gradient on ground vegetation because ground vegetation serves as food and shelter for *A. agrarius*. Thus, slope gradient had a negative effect on *A. agrarius*, but not on *A. peninsulae*. This study suggests that habitat management, especially in tree-thinned habitats where ground vegetation develops explosively, should be accomplished by considering slope gradient for both creating suitable microhabitats for small rodents and encouraging biodiversity.

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Authors' Contribution
JKL and SJR designed the study and wrote the manuscript. HSH, TKE, and DHL performed field work and analyzed the data.

Key words
***Apodemus agrarius*, *Apodemus peninsulae*, Ground vegetation, Slope gradient, Thinned habitat.**

INTRODUCTION

Forest ecosystems are among the most diverse of all terrestrial ecosystems (Larocque, 2016). Within the forest ecosystems, animals select their habitats based on habitat resources, such as food, water, cover, and space (Czech, 2000). The availability of resources can be modified by various and complex interactions between biotic factors, such as intra- and interspecific competition, and abiotic factors, such as climate and topography (Lewis *et al*., 2017). These factors therefore directly or indirectly affect the distributions and abundances of animals and plants (Martin, 2001). Furthermore, the relative influence of biotic and abiotic factors on the distribution and abundance of organisms is species- and habitat-specific (Katz *et al*., 2017).

Habitat heterogeneity arises in part from topographic factors, such as altitude, slope aspect and slope gradient, as these affect the nature of the vegetation (Wang *et al*., 2016; Eom *et al*., 2019). In particular, slope gradient is associated with vegetation survival and growth because a steep slope is strongly conducive to soil erosion and landslide under conditions of heavy rain (Xu *et al*., 2013; Piacentini *et al*., 2018). Erosion of soil results in its loss and in degradation characterized by reduced water-holding capacity and altered organic matter composition (Jiao *et al*., 2009; Cerdan *et al*., 2010; Duan *et al*., 2016); erosion may also exacerbate pollution damage (Garcia-Fayos *et al*., 2010; Keesstra *et al*., 2016).

Vegetation is an important habitat element, providing food and shelter resources to wildlife (Kearney *et al*., 2007; Lee *et al*., 2008). Small rodents generally prefer to forage and travel under vegetation cover, such as grasses and shrubs, where they are hidden from predators (Loggins *et al*., 2019). Habitat with dense ground vegetation therefore tends to contain more abundant small rodent populations (Smit *et al*., 2001). Further, microhabitat use by small rodents can vary at the species level in relation to ground vegetation (Lozada *et al*., 2000).

The order Rodentia is the most diverse mammalian group, and its smaller members are crucial components in terrestrial ecosystems (Mohammadi *et al*., 2019; Šálek *et al*., 2020). They influence plant population dynamics through seed predation and dispersal (Smit *et al*., 2001), and their distribution and abundance affect the populations of the terrestrial and flying predators that prey on them (Orrock and Connolly, 2016). Small rodents can therefore function as keystone species throughout diverse ecosystems (Davidson and Lightfoot, 2006; Nikolic *et al*., 2019).

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Ground vegetation affects small rodent populations positively (Carrilho *et al*., 2017; Crego *et al*., 2018; Lee *et al*., 2019). Unfortunately, erosion due to slope gradient can affect vegetation negatively, in terms of seedling emergence rate, plant survival and growth, and seed production (Guerrero-Campo and Montserrat-Marti, 2000; Espigares *et al*., 2011; Yuan *et al*., 2019). Although the relationships between slope gradient, vegetation, and small rodent populations have critical effects on various ecosystems and provide insight into ecological mechanisms, the relationships between these three elements are not well studied (Lee *et al*., 2020). Therefore, research is needed to study the indirect effect of slope gradients on small rodent populations.

Our aim was to test the effects of slope gradient on small rodent populations and their microhabitat conditions in a tree-thinned Japanese larch (*Larix kaempferi*) plantation in South Korea. Habitat management, such as clearcutting and thinning, provides wildlife with suitable habitats by modifying vegetation structure (Ausden, 2007). Tree thinning can induce explosive development of ground vegetation, such as grass, because of increasing sunlight on the ground level by removing standing trees (Lee *et al*., 2018). We conducted a three-step analysis to assess the three relationships between microhabitat conditions and small rodent populations, between slope gradient and vegetation, and between slope gradient and small rodent populations. Our standing hypotheses were (i) that small rodent populations prefer microhabitat conditions with dense ground vegetation; (ii) that coverage of ground vegetation is decreased as slope gradient increases; and (iii) that slope gradient has an indirect and negative effect on small rodent populations.

MATERIALS AND METHODS

Study area

This study was conducted from May to November 2015 in a Japanese larch plantation (37°40′03″-37°40′17″N; 127°52′07″-127°52′13″E) on Mt. Maehwa, Hongcheon, South Korea. Elevation ranges from 170 to 260 m above sea level. The mean temperature and annual precipitation were 12.2°C and 740.0 mm, respectively (Korea Meteorological Administration, 2016). Seasons were defined as spring (March to May), summer (June to August), fall (September to November), and winter (December to February).

The study area was dominated by Japanese larch planted in 1960 and thinned in January 2015 (Lee *et al*., 2019). We found a diversity of mammals, including the Korean hares (*Lepus coreanus*), the raccoon dogs (*Nyctereutes procyonoides*), the Siberian weasels (*Mustela sibirica*), the water deer (*Hydropotes inermis*), and the wild boar (*Sus scrofa*) (Hwang *et al*., 2014). Also present were amphibians, including the black-spotted frogs (*Pelophylax nigromaculatus*) and the Dybowski's frogs (*Rana dybowskii*), and reptiles, including the steppe rat snakes (*Elaphe dione*) (Park *et al*., 2016). The main predators of small rodents were the Siberian weasels and the steppe rat snakes.

Experimental design and data collection

We randomly selected two 90 m × 90 m (0.81 hectare) study plots in the study area. The study plots were separated by 200 m to avoid movements of small rodents between plots based on the movement distances reported by Lee and Rhim (2016). All individuals remained within their study plots. Within each study plots, a 7 × 7 grid with 15 m intervals between points provided 49 trapping stations per plot, and thus 98 trapping stations in total.

We measured slope gradient and microhabitat conditions in 5.64 m radius circles, centered on each trapping station, in July 2015. Slope gradients measured by laser rangefinder (Forestry Prom Nikon Vision Co., LTD., Tokyo, Japan) were transformed into standardized slope gradients (SP; %): Slope gradient (°) / 90 × 200 (Chai and Wang, 2016). Microhabitat conditions were characterized by measurement of the following: the proportions of ground vegetation, woody debris, stone, and bare ground (to total 100%); the coverage of understory vegetation (1–2 m tall); the coverage of overstory vegetation (> 2 m tall); the number of standing trees; and the number and volume of downed trees. Vegetation coverage variables were categorized into four grades: 0 (0%), 1 (1–33%), 2 (34–66%), and 3 (67–100%) (Kang *et al*., 2013).

Sherman live traps were used for capture–recapture of small rodents. We conducted trapping over three consecutive nights in each month from May to November 2015. Each trap was baited with peanuts and placed in a trapping station (n = 98). Traps were checked each morning to record captured individuals and replace baits. Upon initial capture, we clipped a toe for identification purposes. We recorded species, trap location, sex, whether adult or juvenile, weight, individual ID, and reproductive and release condition of each captured individuals clipped a toe for identification, and immediately released the animal at the trapping station. Experimental protocols describing the treatment and care of animals were reviewed and approved under the guidelines of the local ethics committee (Institutional Animal Care and Use Committee, Chung-Ang University; approval number: CAU 2014-005).

Data analysis

The normality of all variables was tested using the

Shapiro-Wilk test prior to analysis. Multicollinearity between independent variables was removed using the Spearman rank sum test. We selected one variable in each highly correlated pair ($r \geq 0.6$), that had a higher correlation with dependent variables or more ecological meaning (Carrilho *et al*., 2017; Lovera *et al*., 2019). The proportion of woody debris and number of downed trees were removed during this process.

Table □.- Generalized linear mixed models (GLMMs) having the corrected Akaike information criterion (ΔAIC*c*) of < 2 that explain the relationship between microhabitat conditions and abundances of two small rodent species, the striped field mouse (*Apodemus agrarius*) and the Korean field mouse (*A. peninsulae*).

Species / Models	AIC*c*	ΔAIC*c*	w_i
A. agrarius			
[Intercept + %VEG]	297.63	0.00	0.44
[Intercept + %VEG + %ST]	299.22	1.58	0.20
[Intercept + %VEG + UV]	299.28	1.65	0.19
[Intercept + %VEG + OV]	299.54	1.91	0.17
A. peninsulae			
[Intercept + %ST + UV]	155.30	0.00	0.29
[Intercept + %ST + UV+ OV]	156.00	0.69	0.20
[Intercept + UV]	156.50	1.18	0.16
[Intercept + %ST + UV + OV + NST]	157.10	1.73	0.12
[Intercept + %VEG + %ST + UV]	157.20	1.84	0.11
[Intercept + %ST + UV + NST]	157.20	1.87	0.11

w_i, Akaike weight; %VEG, proportion of ground vegetation; %ST, proportion of stone; UV, understory vegetation coverage; OV, overstory vegetation coverage; NST, number of standing trees.

All statistical analyses were carried out using the program R (R Development Core Team, 2017). We used generalized linear model (GLM) or generalized linear mixed model (GLMM) procedures to assess three hypotheses at a trapping station ($n = 98$) level. First, the relationship between microhabitat conditions and small rodent populations was evaluated by the GLMM procedure with trap ID as the random effect in a global model relating abundance of small rodent populations to proportion of ground vegetation, proportion of stone, proportion of bare ground, coverage of understory vegetation, coverage of overstory vegetation, number of standing trees, and volume of downed trees. We selected models based on the corrected Akaike information criterion (AIC*c*; ΔAIC*c*<2) and Akaike weight (w_i), and carried out model averaging (Bartoń, 2016). Second, the GLM procedure was conducted to assess the slope gradient-dependent differences in vegetation, which are closely associated with small rodent populations. We discovered this association because GLMM was not appropriate for the complicated random effect. Third, we tested the relationship between standardized slope gradient and small rodent populations using the GLM procedure. We used the 'lme4' and 'ggplot2' packages to run the GLM or GLMM procedures and for graph production, respectively (Bates *et al*., 2015; Wickham, 2016).

RESULTS

The three small rodent species captured during the study period were the striped field mouse (*Apodemus agrarius*; 136 captures of 90 individuals), the Korean field mouse (*A. peninsulae*; 39 captures of 22 individuals), and the red-backed vole (*Myodes regulus*; 16 captures of 14 individuals) during the study period. In total, we observed 191 captures of 126 individuals. We excluded *M. regulus* data from the statistical analyses because the number of captured individuals was insufficient for the tests.

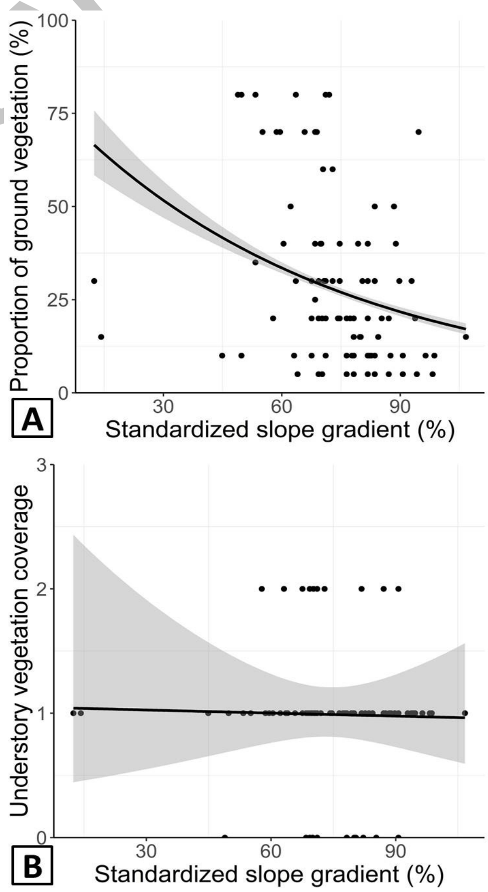

Fig. 1. Relationship between standardized slop gradient (%) of the local habitat land and proportion of ground vegetation and understory vegetation coverage, obtained with the generalized linear model (GLM).

Table II.- Model averaging results from the generalized linear mixed model (GLMM) explaining the relationship between microhabitat conditions and abundances of two small rodent species, the striped field mouse (*Apodemus agrarius*) and the Korean field mouse (*A. peninsulae*).

Species	Variables	B	SE	Z	P	95% CI	
						Lower	Upper
A. agrarius	Intercept	0.2533	0.0805	3.146	0.002	0.0955	0.4111
	%VEG	0.2600	0.0621	4.178	<0.001	0.1383	0.3816
	%ST	-0.0748	0.1004	0.745	0.456	-0.2715	0.1219
	UV	0.0678	0.0951	0.713	0.476	-0.1186	0.2543
	OV	0.0470	0.0923	0.509	0.611	-0.1339	0.2278
A. peninsulae	Intercept	-1.7347	0.3710	4.675	<0.001	-2.4619	-1.0074
	%VEG	-0.1394	0.2389	0.584	0.559	-0.6076	0.3288
	%ST	-0.6205	0.3697	1.687	0.093	-1.3451	0.1041
	UV	0.6152	0.2210	2.779	0.005	0.1813	1.0491
	OV	-0.3027	0.2384	1.270	0.204	-0.7699	0.1645
	NST	0.2128	0.2564	0.830	0.407	-0.2899	0.7154

w_i, Akaike weight; %VEG, proportion of ground vegetation; %ST, proportion of stone; UV, understory vegetation coverage; OV, overstory vegetation coverage; NST, number of standing trees.

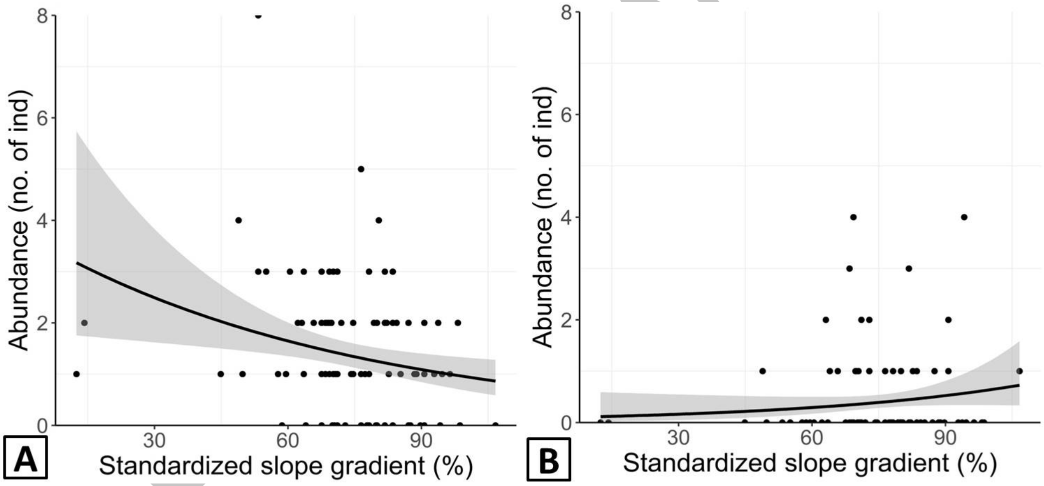

Fig. 2. Relationship between standardized slop gradient (%) of the local habitat land and abundances of two small rodent species, the striped field mouse (*Apodemus agrarius*) and the Korean field mouse (*A. peninsulae*), obtained with the generalized linear model (GLM).

Relationship between microhabitat conditions and small rodent populations

The GLMM models relating microhabitat conditions and small rodent populations that had $\Delta AICc < 2$ are shown in Table I with four models for *A. agrarius* and six models for *A. peninsulae*. The four models for *A. agrarius* included four microhabitat variables: the proportion of ground vegetation, the proportion of stone, the coverage of understory vegetation, and the coverage of overstory vegetation. The six models for *A. peninsulae* included five microhabitat variables: the proportion of ground vegetation, the proportion of stone, the coverage of understory vegetation, the coverage of overstory vegetation, and the number of standing trees. The proportion of ground vegetation had a positive effect on the *A. agrarius* population ($\beta = 0.2600$, Z = 4.178, $P < 0.001$; Table Ⅱ). In contrast, the coverage of understory vegetation was highly related to the *A. peninsulae* population ($\beta = 0.6152$, Z = 2.779, P = 0.005).

Relationship between slope gradient and vegetation

We tested the effects of slope gradient on the proportion of ground vegetation and coverage of understory vegetation, which were highly correlated with *A. agrarius* and *A. peninsulae*, respectively. The proportion of ground vegetation was decreased as standardized slope gradient increased (β = –0.0144, Z = –13.120, P < 0.001; Fig. 1). However, the coverage of understory vegetation was not affected by slope gradient (β = –0.0008, Z = –0.119, P = 0.905).

Relationship between slope gradient and small rodent populations

The standardized slope gradient of trapping stations that captured (n = 71) and did not capture (n = 27) *A. agrarius* was 71.83 ± 1.84% and 79.93 ± 2.05%, respectively. The standardized slope gradient of trapping station that captured (n = 24) and did not capture (n = 74). *A. peninsulae* was 73.09 ± 1.79% and 77.07 ± 2.55%, respectively. Slope gradient had a negative effect on the abundance of *A. agrarius* population (β = –0.1379, Z = –2.770, P = 0.006; Fig. 2), in contrast to that of *A. peninsulae,* which was not affected by slope gradient (β = 0.0196, Z = 1.556, P = 0.120).

DISCUSSION

In this study, we revealed the three relationships between slope gradient, vegetation, and small rodent populations. First, *A. agrarius* and *A. peninsulae* populations preferred microhabitats with dense ground vegetation and understory vegetation, respectively. Second, slope gradient had a negative effect on ground vegetation, but not on understory vegetation. Third, the population of *A. peninsulae* was not affected by slope gradient, whereas the population of *A. agrarius* decreased as slope gradient increased. We thus demonstrated that slope gradient had an indirect and negative effect on *A. agrarius* abundance via the negative impact of slope gradient on ground vegetation in a tree thinned habitat.

Small rodents select their habitats based on quality and quantity of available food and shelter resources (Ecke *et al*., 2002), preferring dense ground or understory vegetation. Such vegetation provides resources suitable for these animals (Sunyer *et al*., 2016; Jacques *et al*., 2017; Teixeira *et al*., 2017) and fundamental to the success of small rodents (Gasperini *et al*., 2016). In this study, we found that *A. agrarius* and *A. peninsulae* differed in their microhabitat use. Whereas, *A. agrarius* was dominant locally and preferred microhabitats with dense ground vegetation, *A. peninsulae* mainly occupied microhabitats with dense understory vegetation. Interspecific competition for resources between sympatric species is typically density-dependent (Morris *et al*., 2000). However, niche partitioning by individuals is a strategy to avoid competition (Casula *et al*., 2019). These two processes are likely to be linked to the difference in microhabitat preferences between these two sympatric species.

This study area underwent tree thinning in January 2015. This procedure reduces competition among plants (Chase *et al*., 2016). Accordingly, ground vegetation was very well-developed following the increase in available sunlight, soil nutrients, and water (Bauhus *et al*., 2001; Lee *et al*., 2018). Although ground vegetation was as substantial as expected, its early development varied depending on slope gradient in this study. This phenomenon is closely related to the negative effect of soil erosion on soil nutrients, water, and organic matter (Cosentino *et al*., 2015). However, the understory coverage was similar for all slope gradients. This may be related to the deeper and longer roots of understory vegetation compared to ground cover, because these roots contribute to the plants' stability of understory plant when threatened by soil erosion (Edmaier *et al*., 2014).

Ground vegetation and understory vegetation were key food and shelter resources for *A. agrarius* and *A. peninsulae* populations, respectively. Steeper slopes had a negative effect on the development of ground vegetation, but not on understory vegetation. As a consequence of poorer quality ground vegetation essential to its success, the *A. agrarius* population was affected indirectly and negatively by steeper slope gradient. To further examine the effects discovered in the present short-term study, we anticipate conducting a long-term study that investigates the relationship between slope gradient, vegetation, and small rodents in tree-thinned habitats over time.

CONCLUSIONS

Our data indicated that support the three hypothesized close relationships between slope gradient, vegetation, and small rodent populations. Ground vegetation and understory vegetation were key resources for *A. agrarius* and *A. peninsulae* populations, respectively. Slope gradients negatively influenced the development of the ground vegetation needed by *A. agrarius*. Accordingly, fewer *A. agrarius* were captured as slope gradient increased, confirming the indirect negative effect of slope gradient on this species. This study suggests that habitat management, especially in tree thinned habitats, should take slope gradient into account when creating suitable microhabitats for small rodent populations and, more generally, when encouraging biodiversity.

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Statement of conflict of interest

The authors declare that there is no conflict of interest.

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