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Animal Biology 70 (2020) 203–213

Animal
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Cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem

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Submitted: July 11, 2019. Final revision received: September 9, 2019. Accepted: October 16, 2019

Abstract

In this study, we set out to determine the cascade effects of slope gradient on ground vegetation and small-rodent populations in a forest ecosystem. We focused on two forest-dwelling small rodents with different habitat requirements, the striped field mouse *Apodemus agrarius* (preferring dense ground vegetation) and the Korean field mouse *A. peninsulae* (dense forest and woodland). The study area comprised natural deciduous forests and Japanese larch *Larix kaempferi* plantations in South Korea. The abundance of *A. agrarius* but not that of *A. peninsulae* was related to slope gradient. There was a negative effect of slope gradient on ground vegetation coverage and a positive effect of ground vegetation on *A. agrarius* populations. Our results highlight that the population of *A. agrarius* was indirectly influenced by the negative effects of slope gradient on ground vegetation. Slope gradient can, therefore, be a limiting factor in the microhabitats occupied by small rodents. This study reveals a critical role for slope gradient since it can modify not only microhabitat conditions, but also small-rodent populations, and this finding can contribute to improved microhabitat management.

Keywords

Apodemus agrarius; *Apodemus peninsulae*; ground vegetation; slope gradient; small-rodents

Introduction

Forests form complex ecosystems, in which biotic assemblages and physicochemical environments interact (Pickett & Cadenasso, 2002). Within these ecosystems, the distribution and abundance of wildlife and vegetation are, therefore, closely linked to various and complex features of the climate and topography, promoting

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DOI 10.1163/15707563-20191192

various effects through the ecosystem (Monzón et al., 2011; Eom et al., 2018). Factors related to topography, such as elevation and location, direction, gradient of a slope, directly or indirectly affect habitat characteristics, such as solar radiation, temperature, water, and nutrients (Aguilar et al., 2010; Kunkel et al., 2011). A steep slope gradient facilitates soil erosion in conditions of heavy precipitation, with consequent negative effects on fine materials and soil nutrients in forest ecosystems (El Kateb et al., 2013; Sepúlveda & Carrillo, 2015). This process in turn negatively affects vegetation growth through changes to the soil water-holding capacity and soil nutrient content, such as nitrogen and phosphorus (Kapolka & Dollhopf, 2001; Jiao et al., 2009; Lou et al., 2016; Ma et al., 2016). Therefore, the unfertilized condition of the soil on steep slopes makes it difficult for vegetation to grow or survive decreases in vegetation coverage with increasing slope gradient (Parsakhoo et al., 2009).

This effect of slope gradient on vegetation cover has implications for the suitability of habitats for wildlife, as vegetation provides both food and shelter (Krebs, 2009). Different species form distinct habitat preferences based on vegetation characteristics. Ground vegetation, for example, provides important resources for small rodents, such as shelter from predators and a diverse range of food (Kang et al., 2013a). It is, therefore, a key factor influencing small-rodent populations, and the abundance and species richness of their populations can be regulated by vegetation characteristics in a particular habitat.

Small rodents are ubiquitous components in forest ecosystems, where they are an important part of the food web (Orrock & Connolly, 2016). They are prey to terrestrial and flying predators and consumers of fungi, invertebrates, plants, and seeds (Sullivan & Sullivan, 2001). They are also seed dispersers, through either larder- or scatter-hoarding (Campos et al., 2017). As a result, the species composition and abundance of plants in a particular habitat is influenced by the hoarding behaviors of small-rodent populations.

Various studies have considered the relationships between slope gradient and vegetation and between vegetation and small-rodent populations (Xu et al., 2008; Dong et al., 2014; Lee et al., 2019). However, there is a lack of studies focusing on the relationships between all three. Negative effects of soil erosion on vegetation succession have been reported in studies on the relationship between slope gradient and vegetation (Wang et al., 2015; Yuan et al., 2019). In contrast, other studies have reported a positive influence of ground vegetation on small-rodent populations in diverse environments because of its functions of providing food and cover resources (Coda et al., 2014; Crego et al., 2018; Lovera et al., 2019). In this study, we set out to determine the cascade effects of slope gradient on ground vegetation and small-rodent populations, given the possibility that slope gradient may negatively affect small-rodent populations indirectly because of its negative effects on ground vegetation.

We conducted three analyses to determine: (1) the characteristics of small-rodent populations according to their responses to habitat variables; (2) the effect of slope gradient on habitat variables preferred by small-rodent populations; and (3) the relationship between slope gradient and small-rodent populations. We used the analysis to test three hypotheses: (1) ground vegetation is a key factor for small-rodent populations; (2) slope gradient has a negative effect on ground vegetation; and (3) small-rodent populations are negatively influenced by slope gradient.

Materials and methods

Study area

This study was undertaken in 2014 (May to November) in natural deciduous forests and Japanese larch *Larix kaempferi* (Lamb.) Carrière plantations (37°35′11″-37°41′48″ N; 127°46′20″-127°55′37″ E; 170 to 340 m above sea level; area size, 7700 ha) in Mt. Maehwa, Hongcheon, South Korea. The values for annual mean temperature and annual precipitation were 11.8°C and 703.5 mm, respectively (Korea Meteorological Administration, 2014). The study area was dominated by oak species, such as sawtooth oak *Quercus acutissima* Carruth., Chinese oak *Q. variabilis* Blume, Mongolian oak *Q. mongolica* Fisch. ex Ledeb. and Japanese larch (Kang et al., 2013b).

Experimental design and data collection

Four study plots were randomly established to survey slope gradient, habitat variables and small-rodent populations. Each study plot was 90 × 90 m (0.81 ha) and contained a total of 49 trapping points set up at intervals of 15 m using a grid (7 × 7).

In July 2014, slope gradient and habitat variables were surveyed within circular subplots (radius, 5.64 m), centered on each trapping point. Slope gradient was determined using a laser measuring tool (Forestry Prom Nikon Vision Co., Ltd., Tokyo, Japan). The standardized slope gradient (SP) was evaluated according to $\mathrm{SP} = s/90 \times 200\%$, where s is slope gradient (Chai & Wang, 2016). We measured the following habitat variables: the proportion (%) of different categories of ground cover (ground vegetation, woody debris, bare areas; total 100%), coverage of each vertical layer of vegetation above 1 m diameter at breast height, number of standing trees, and number and volume of downed trees. The vertical layers were divided into three levels according to vegetation height: understory (1-2 m), midstory (2-8 m), and overstory (>8 m). Vegetation coverage was measured using four grades: 0 (coverage percentage = 0%), 1 (1-33%), 2 (34-66%), and 3 (67-100%) (Son et al., 2017).

Small-rodent data were collected using the capture-recapture method during three consecutive nights in each month from May to November, 2014. Sherman live traps (7.62 × 8.89 × 22.86 cm), baited with peanuts, were set up at all trapping points on each study plot. Each trap was checked every morning when traps were active. The following data were recorded for captured individuals: species and trap location. Each individual was given a specific identification (ID) using toe clipping, and this was also recorded. On the basis of the different species captured, we decided to focus on two: the striped field mouse *Apodemus agrarius* (Pallas 1771), and the field mouse *A. peninsulae* (Thomas 1907). After data recording was completed, captured individuals were immediately released at the capture point. We also recorded trapping points where no animals were captured, for input to the statistical analysis. The experimental protocols for the treatment and care of animals were reviewed and approved according to the guidelines of the local ethics committee (Institutional Animal Care and Use Committee, Chung-Ang University; approval number: CAU 2014-005).

Data analysis

We used whole data collected and merged from both natural deciduous forests and Japanese larch plantations for all statistical procedures. If small-rodent populations had a preference for stands, this might be a bias because small rodents could be affected by stands, and it might affect final results. Preferences of small rodents for stands, therefore, were evaluated using a Mann-Whitney U-test. As a result, there were no significant differences in the number of small rodents between natural deciduous forest and Japanese larch plantation (*A. agrarius*, $Z = 0.856$, $p = 0.392$; *A. peninsulae*, $Z = -0.263$, $p = 0.793$). The whole data set, therefore, was used for all statistical procedures.

To test the three relationships among slope gradient, ground vegetation, and small-rodent populations, we used a generalized linear mixed model (GLMM) and a Mann-Whitney U-test, after testing the normality of all variables using a Shapiro-Wilk test. Then, a Spearman rank sum test was performed to assess multicollinearity among all variables. In case of high correlation between two variables ($r \geqslant 0.7$), the variable more highly correlated with the dependent variables or with more ecological meaning was selected (Carrilho et al., 2017). As a result, two variables were removed from the analysis: the percentage of bare area and number of downed trees.

Thereafter, we performed three GLMM procedures with the stands and sites as random factors (R package: lme4; Bates et al., 2015), as follows. First, we evaluated the responses of small-rodent populations to ground cover percentage. We also evaluated responses to the volume of downed trees, which has been reported to have positive effects on small-rodent populations (Kang et al., 2013b). Second, we analyzed the responses of ground vegetation to the slope gradient. In addition, we added the percentage coverage of each vertical layer (>1 m) and number of standing trees to this second model because ground vegetation growth can be inhibited by light deprivation because of vegetation extent higher in the canopy (Bolen & Robinson, 2003). Third, we assessed the relationship between slope gradient and small-rodent populations (table 1) again using a Mann-Whitney U test, by measuring the gradient at traps where animals were captured, and those where they were not (slope gradient in the ‘capture trapping points’ versus ‘non-capture trapping points’). In each GLMM procedure, model selection was based on the corrected

Table 1.
Generalized linear mixed model (GLMM): procedures and variables used in the study.

Type	Dependent variables	Independent variables
Relationship between small-rodent populations and habitat variables (Hypothesis 1)	Small rodents	Percentage of ground vegetation Percentage of woody debris Volume of downed trees
Relationship between ground vegetation and slope gradient (Hypothesis 2)	Percentage of ground vegetation	Understory vegetation coverage Mid-story vegetation coverage Overstory vegetation coverage Number of standing trees Standardized slope gradient
Relationship between slope gradient and small-rodent populations (Hypothesis 3)	Small rodents	Standardized slope gradient

Akaike information criterion (AICc). We selected models according to ΔAICc $<$ 2, and then conducted a model averaging procedure (R package: MuMIn; Bartoń, 2016). All statistical analyses were performed using the R software program (R Core Team, 2017).

Results

In the study period, we achieved 50 captures of 47 individuals (striped field mouse, *A. agrarius*: 30 captures, 29 individuals; Korean field mouse *A. peninsulae*: 20 captures, 18 individuals) during 4116 trap-nights. To test hypothesis 1 (the relationship between small-rodent populations and habitat variables), different models (ΔAICc < 2) were constructed and tabulated: two for *A. agrarius* and six for *A. peninsulae* (table 2). The two *A. agrarius* models included two variables: the percentages of ground vegetation and woody debris. The six *A. peninsulae* models included three variables: the percentages of ground vegetation and woody debris, and the volume of downed trees. Ground vegetation was the only variable with positive effects on *A. agrarius* abundance (coefficient = 0.0228, $Z = 2.226$, $p = 0.026$), but had no impact on *A. peninsulae* (coefficient = 0.0184, $Z = 1.403$, $p = 0.164$; table 3).

Two models explaining hypothesis 2 (the relationship between ground vegetation and slope gradient) were selected using the GLMM procedure (table 4). These models incorporated five variables: standardized slope gradient, coverage of understory, mid-story, overstory vegetation, and number of standing trees. Three of these had significant effects on the percentage of ground vegetation (table 5). Ground vegetation decreased with increasing slope gradient (coefficient = −0.0145, $Z =$ 15.911, $p < 0.001$) and increasing understory vegetation (coefficient = −0.1189,

Table 2.
Results of generalized linear mixed model (GLMM) procedures explaining relationships between small-rodent populations (*Apodemus agrarius* and *A. peninsulae*) and habitat variables based on model selection (ΔAICc < 2).

Species	Model	AIC*c*	ΔAICc	Weight
A. agrarius	[Intercept + %VEG]	169.41	0.00	0.66
	[Intercept + %VEG + %WD]	170.69	1.29	0.34
A. peninsulae	[Intercept]	133.75	0.00	0.24
	[Intercept + %VEG]	133.94	0.18	0.22
	[Intercept + VDT]	134.41	0.66	0.17
	[Intercept + %VEG + VDT]	134.53	0.77	0.16
	[Intercept + %VEG + %WD]	135.21	1.46	0.12
	[Intercept + %VEG + %WD + VDT]	135.70	1.95	0.09

Abbreviations: AICc, corrected Akaike information criterion; VDT, volume of downed trees; %VEG, percentage of ground vegetation; %WD, percentage of woody debris.

Table 3.
Variables selected by a model averaging procedure explaining the relationship between small-rodent populations (*Apodemus agrarius* and *A. peninsulae*) and habitat variables.

Species	Variables	Coefficient	SE	*Z*	*p*	95% CI	
						Lower	Upper
A. agrarius	Intercept	−3.3255	0.8358	3.979	<0.001	−4.9636	−1.6873
	%VEG	0.0228	0.0102	2.226	0.026	0.0027	0.0428
	%WD	−0.0183	0.0199	0.917	0.359	−0.0572	0.0207
A. peninsulae	Intercept	−3.2061	1.0706	2.995	0.003	−5.3043	−1.1078
	%VEG	0.0184	0.0131	1.403	0.164	−0.0073	0.0440
	%WD	0.0246	0.0262	0.940	0.347	−0.0267	0.0760
	VDT	−0.0205	0.0194	1.056	0.291	−0.0586	0.0176

Abbreviations: VDT, volume of downed trees; %VEG, percentage of ground vegetation; %WD, percentage of woody debris.

$Z = 7.082$, $p < 0.001$). In contrast, vegetation coverage in the overstory had a positive effect on percentage of ground vegetation (coefficient = 0.1007, $Z = 6.999$, $p < 0.001$).

The abundance of *A. agrarius* decreased with increasing slope gradient (coefficient = −0.0310, $Z = 2.099$, $p = 0.036$) (fig. 1). However, slope gradient did not affect abundance of *A. peninsulae* (coefficient = 0.026, $Z = 0.151$, $p = 0.880$). Trapping points where *A. agrarius* were captured had a lower slope gradient (75.78%) than non-capture trapping points (84.39%; $Z = -2.636$, $p = 0.008$) (table 6). There was no difference in slope gradient between capture (83.77%) and non-capture (83.19%; $Z = -0.028$, $p = 0.978$) trapping points.

Table 4.
Results of generalized linear mixed model (GLMM) procedure explaining the relationship between ground vegetation and slope gradient based on model selection (ΔAICc $<$ 2).

Dependent variable	Model	AICc	ΔAICc	Weight
%VEG	[Intercept + SP + UV + MV + OV + NST]	2635.10	0.00	0.66
	[Intercept + SP + UV + OV + NST]	2636.46	1.36	0.34

Abbreviations: AICc, corrected Akaike information criterion; MV, midstory vegetation coverage; NST, number of standing trees; OV, overstory vegetation coverage; SP, standardized slope gradient; UV, understory vegetation coverage; %VEG, percentage of ground vegetation.

Table 5.
Variables selected by the model averaging procedure explaining the relationship between ground vegetation and slope gradient.

Dependent variable	Variables	Coefficient	SE	*Z*	*p*	95% CI	
						Lower	Upper
%VEG	Intercept	5.0620	0.1759	28.779	<0.001	4.7175	5.4070
	SP	−0.0145	0.0009	15.911	<0.001	−0.0163	−0.0127
	UV	−0.1189	0.0168	7.082	<0.001	−0.1518	−0.0860
	MV	0.0288	0.0155	1.865	0.062	−0.0015	0.0592
	OV	0.1007	0.0144	6.999	<0.001	0.0725	0.1288
	NST	−0.0001	0.0000	1.954	0.051	−0.0001	0.0000

Abbreviations: MV, midstory vegetation coverage; NST, number of standing trees; OV, overstory vegetation coverage; SP, standardized slope gradient; UV, understory vegetation coverage; %VEG, percentage of ground vegetation

Table 6.
Comparison using a Mann-Whitney *U*-test of standardized slope gradient (mean ± SE) between traps in which small rodents (*Apodemus agrarius* and *A. peninsulae*) were captured and those with no captures (capture and non-capture traps, respectively).

Species	Traps	Standardized slope gradient (%)	*Z*	*p*
A. agrarius	Capture trap ($n = 26$)	75.78 ± 2.70	−2.636	0.008
	Non-capture trap ($n = 170$)	84.39 ± 1.10		
A. peninsulae	Capture trap ($n = 19$)	83.77 ± 3.37	−0.028	0.978
	Non-capture trap ($n = 177$)	83.19 ± 1.09		

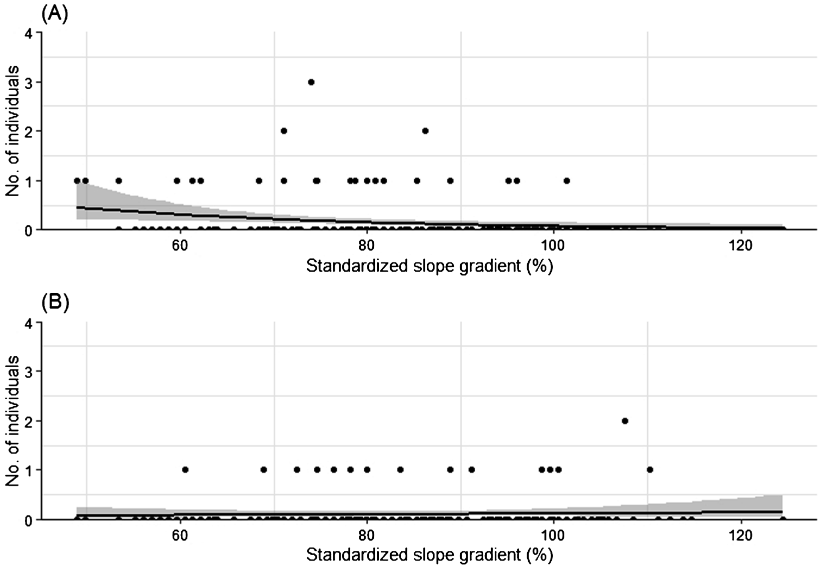

Figure 1. Relationship between small rodents and standardized slope gradient derived from a generalized linear mixed model (GLMM). (a) *Apodemus agrarius*, coefficient $= -0.0310$, $Z = 2.099$, $p = 0.036$; (b) *A. peninsulae*, coefficient $= 0.0026$, $Z = 0.151$, $p = 0.880$.

Discussion

In this study, we demonstrated cascade effects caused by the direct influence of slope gradient on ground vegetation, which in turn affects *A. agrarius* populations. Our analysis showed that, firstly, *A. agrarius* preferred microhabitats with dense ground vegetation; secondly, the negative effect of slope gradient on ground vegetation; and, finally, slope gradient had a negative effect on *A. agrarius* abundance.

Small-rodent species utilize microhabitats for survival and reproduction based on requirements such as food, water, den, shelter, and space; these habitat requirements are species-specific (Mallegowda et al., 2015; Coda et al., 2016). Microhabitat occupancies may therefore differ among sympatric species. In this study, we captured individuals of two small-rodent species, *A. agrarius* and *A. peninsulae*, which use different microhabitats in the same area. In this study, it was shown that *A. agrarius*, but not *A. peninsulae*, preferred microhabitats with dense ground vegetation. This agrees with findings that *A. agrarius* mainly inhabits areas of dense ground vegetation in order to access seeds and new growth vegetation as food, whereas *A. peninsulae* prefers to access tree seeds and acorns in dense forests and woodland (Jo, 2015; Lee et al., 2018). Hence, dense ground vegetation provides both food and shelter for *A. agrarius*, while this vegetation does not provide *A. peninsulae* with its preferred food resources.

The growth and survival of plants are influenced by abiotic factors, such as soil nutrients, water, and sunlight (Richards & Coley, 2007; Zhu, 2016). In our study, we found that the percentage cover of ground vegetation was affected by slope gradient, and the under- and overstory vegetation. As Pimentel (2006) points out, soil erosion can negatively modify soil nutrients and water. Increases in slope gradient can accelerate soil erosion. Therefore, we concluded that slope gradient has a negative effect on ground vegetation abundance.

Competition among plant species for sunlight affects the structure and function of vegetation in forest ecosystems (Clark & Bullock, 2007). In our study, we determined that under- and overstory vegetation cover negatively and positively affected ground vegetation, respectively. A dense understory inhibits the growth of ground vegetation. Similarly, a dense overstory will have a negative impact on understory vegetation; this yields indirect positive influences on ground vegetation cover.

Apodemus agrarius preferred a microhabitat with dense ground vegetation. However, ground vegetation decreased as slope gradient increased, and *A. agrarius* avoided high slope gradients (i.e., steep slopes). This species was therefore indirectly influenced by increasing slope gradient. This finding enabled us to confirm the cascade effect of slope gradient on *A. agrarius* populations through its negative effect on ground vegetation.

In conclusion, ground vegetation, given its function in providing food and cover resources, had a significant influence on *A. agrarius* abundance. However, the percentage of ground vegetation decreased with increasing slope gradient because of soil erosion. Therefore, slope gradient had an indirect and negative effect on the *A. agrarius* population. These results suggest that gradient can be a limiting factor in the occupation of microhabitats by small rodents. Slope gradient, therefore, should be considered in conservation policies that aim to promote both ground vegetation and small-rodent populations.

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