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Research Article

Effects of Deer Grazing on Vegetation and Ground-Dwelling Insects in a Larch Forest in Okutama, Western Tokyo

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Sika deer (*Cervus nippon*) have experienced a rapid increase in the Japanese archipelago. Although the effects of deer grazing have been widely studied, the indirect effects have received little attention. Using an eight-year-old deer exclosure in western Tokyo (Japan), we studied the direct effects on plants and the indirect effects on insects and microenvironments. Plant biomass was 14 times higher inside the exclosure than outside. Shrubs (e.g., *Aralia elata* and *Hydrangea paniculata*) and trees (e.g., *Symplocos sawafutagi* and *Clethra barbinervis*) were more abundant inside, whereas only unpalatable trees in poor condition grew outside (e.g., *Pterostyrax hispida* and *Cynanchum caudatum*). In the summer months, the maximum temperature was 8–10°C higher outside the exclosure and humidity was lower. Soil movement was 80 times more pronounced outside than inside. These results suggest that the abiotic environment became less stable for ground-dwelling insects. Carabid beetles were less abundant outside than inside, suggesting that deer grazing reduced plants and subsequently lowered habitat quality for these beetles. In contrast, carrion beetles, dung beetles, and camel crickets were more abundant outside. The increase in these insects is attributed to the availability of deer feces and carcasses and is a direct effect of deer presence.

1. Introduction

Grazing by deer (Cervidae) affects vegetation in various ways, for example, by reducing undergrowth in forests [1–3], increasing the number of unpalatable plants [4, 5], blocking forest regeneration [3–8], and affecting seed dispersal [9]. Populations of sika deer (*Cervus nippon*) have increased in Japan: from 1978 to 2003 and their range expanded 74% [10, 11]. As a result, vegetation has been affected [1, 7, 12].

The effects of deer grazing on vegetation have been widely studied [1, 2, 4, 6, 7, 13–15], but the indirect effects have received little attention. One typical indirect effect is a decrease in herbivorous insects due to a reduction in plant leaves caused by deer grazing. McShea [16] found that consumption of acorns by white-tailed deer decreased the populations of some rodents in the eastern USA. Miller et al. [14] reported a phenomenon of white-tailed deer (*Odocoileus virginianus*) reducing populations of a forb, *Lupinus perennis*, which led to a decrease in the population of endangered butterfly *Lycaeides melissa samuelis* in New England, USA. Wheatall et al. [17] demonstrated a marked decrease in phytophagous insect larvae caused by white-tailed deer grazing in the eastern USA, and Baines et al. [18] showed that grazing by red deer (*Cervus elaphus*) reduced Lepidopterous larvae in Scotland. These indirect effects occur through food webs or as a result of food resource changes.

Structural changes in plant communities caused by ungulate grazing can lead to abiotic environment alteration and have indirect effects on other animals. Studies have shown the decline in the number of small mammals through habitat alteration by deer grazing, for example, Rocky Mountain elk (*Cervus elaphus*) in Arizona, USA [19], and several cervids in Britain [20]. Population reduction due to habitat alteration by deer grazing is also known to affect birds [21–23]. Similar effects have been observed on insects. Long-term grazing by the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) lowered the numbers and species richness of insects of various taxa on islands in British Columbia, Canada [24]. Studies in boreal forests showed that ungulate grazing can affect carabid beetle populations, but the results are not

consistent. Some studies reported an increase in carabid beetles as a result of ungulate grazing [25–28], whereas others reported no effect [29, 30]. In Japan, sika deer grazing decreased *Sasa nipponica*, a dwarf bamboo, but did not affect carabid beetle populations [31].

Plant reduction caused by sika deer grazing also leads to the loss of surface soil [32–35]. In and around the area of the present study, the leaves of *Sasamorpha borealis*, a dwarf bamboo that covers the forest floor, were heavily grazed by the deer and plants were dying. As the rhizomes of this bamboo are soil binding, mortality of this plant is likely to accelerate soil erosion.

We investigated the direct effects of sika deer grazing on plant populations and the indirect effects on insects and abiotic environments in western Tokyo, Japan, using an eight-year-old deer exclosure. We hypothesized that deer grazing would reduce plants and this direct effect would have indirect effects on the microclimate and soil movements. These changes would then indirectly affect ground-dwelling insects. At the same time, it is expected that the availability of deer feces and carcasses would favor decomposer insects such as dung beetles and carrion beetles (direct rather than indirect effects). We tested these hypotheses by making comparisons inside and outside the exclosure.

2. Study Area

We selected a study area in Okutama, western Tokyo. The topography of Okutama is generally steep: above 500 m, the gradient is 30° or more. Beech (*Fagus crenata*) forest is predominant in the area at 1000–1700 m. Japanese hemlock (*Tsuga sieboldii*) and Nikko fir (*Abies homolepis*) are predominant in the subalpine forest above 1700 m. The study area is in the climate zone of the Pacific side of Japan, where precipitation is concentrated in summer and the climate is dryer in winter [36]. Annual mean temperature and precipitation are 11.8°C and 1586 mm, respectively (Meteorological Information Center of Japan, http://www.data.jma.go.jp/obd/stats/etrn/index.php).

Sika deer were virtually extinct in this area in the 1940s and hunting was prohibited in 1976. After this, the deer population gradually recovered and agricultural and forestry damage began in the 2000s [10]. Although deer density is only 3.8/km^2 [10], 60% of the area is covered by a coniferous plantation [37] with a poor forest floor, resulting in very intensive deer grazing and browsing [1]. Using a deer exclosure built in 2003, we were able to compare plants, insects, and microenvironments inside and outside the construction.

3. Methods

Densities of fecal pellet groups were determined on 20 plots (5 m × 5 m) as an index for deer density.

The deer exclosure was built in 2003 in a larch (*Larix kaempferi*) forest on a gentle slope at 1360 m (Figure 1). It covers about 1 ha and is built of plastic wire mesh hung from 2 m high poles. Surveys were conducted in 2011, eight years after construction.



Figure 1: View of the eight-year-old deer exclosure in a larch forest in Okutama, western Tokyo, Japan. Photo taken in May, 2011.

Tree composition was determined by obtaining the diameter at breast height (DBH) of trees taller than 1.2 m on a 10 m × 10 m plot inside the exclosure and a 20 m × 20 m plot outside. The inside plot was set in the center of the exclosure and the outside plot was established about 20 m away from it on the same slope. Recordings were taken on July 4, 2011.

The cover (%) and the height (cm) to the nearest 1 cm of all plants present on five 2 m × 2 m quadrants both inside and outside the exclosure were recorded on June 25, 2011. Plots approximately 10 m apart were randomly defined inside and outside the exclosure. The biomass index for each plant species was calculated by multiplying height (cm) by cover (cm^2/m^2) [38]. A total biomass index of each growth form was determined, following a partly modified version of Gimingham [39]: e: erect form; fe: fern form; g: graminoids (tufted form); l: liane form; r: rosette form; sh: shrub form; and t: tree form. Palatability for sika deer was also recorded. The number of plant species and the biomass indices inside and outside the exclosure were compared using a Mann-Whitney U test. Diversity of species composition was expressed by the Shannon-Wiener diversity index ($H' = -\Sigma p_i \times \log_2 p_i$, where p_i is the proportion of individuals belonging to species i).

Microclimate (temperature and humidity) on the ground was measured using data loggers (TR-74Ui, T and D Corp., Japan) from June 25 to October 19, 2011. The sensor was inserted into a polyvinyl chloride pipe (200 mm long; 80 mm diameter) and the pipe was laid on the ground. The mean, maximum and minimum temperature, and humidity values were calculated. Microclimate values inside and outside the exclosure were compared using the Mann-Whitney U test.

Four wooden boxes (150 mm high × 250 mm wide × 200 mm deep) were used to determine soil movements at the ground surface. Two boxes were placed inside and two outside the exclosure. The rear of each box was covered with mesh net to allow water to pass through. On June 25, 2011, the boxes were placed on the surface of the ground in a location with a 32° gradient. We collected soil from the boxes from July 4 to October 2, 2011, approximately every 10 days, except for some stormy days when typhoons hit. After collection, the soil was dried at 60°C for 48 h in an oven dryer and dry weights were recorded. The weights inside and outside the exclosure were compared using a Mann-Whitney U test.

Insects were collected in pitfall traps [40]. Twenty plastic cups (67 mm diameter at top) were buried in the ground so that the top edge of the cup was at the same level as the surface of the soil. Cups were placed about 1 m apart. Outside the exclosure, the cups were placed about 20 m away from the construction. Surfactant liquid was put in the bottom of the cups to stop insects from escaping. The traps were set for 88 trap nights from June 9 to October 2, 2011. The sampling interval was ca. 10 days except for some stormy days. Insects found in the traps were brought to the laboratory, identified, and counted. Although grouping was not consistent in terms of taxonomical hierarchy, groups containing numerous individuals were divided to the lower level and less numerous groups were "rounded." Beetles were sorted into carrion beetles, carabid (or ground) beetles (Carabidae and Harpalinae), dung beetles, rove beetles or staphylinids (Staphylinidae), and others. Other insects were grouped to the order level. After checking for normality, differences between the major insect groups inside and outside the exclosure were tested by either Student's t-test or the Mann-Whitney U test. Diversity was determined by the Shannon-Wiener index of diversity (H').

4. Results

The mean value of the density of fecal pellet groups of the sika deer in the study area was 3.90 ± 1.96 group/10 m^2.

The total basal area of trees inside and outside the exclosure (1743 cm^2/m^2 and 1909 cm^2/m^2, resp.) showed no significant differences (Mann-Whitney U test, $P > 0.05$, Table 1). This is because of the dominance of larch (*Larix kaempferi*) trees on both sides of the exclosure. However, the results for smaller trees were different: 12 tree species were present inside the exclosure but only four occurred outside (Table 1), and five shrub species with a density as high as 89.0/100 m^2 grew inside but no shrubs grew outside.

The plant species documented in the understory on the five plots inside and outside the exclosure totaled 41 and 26, respectively. The mean number of plant species found inside (14.4 species) was significantly higher than outside (9.7 species, Mann-Whitney U test, $P < 0.01$, Table 2). Biomass indices were higher inside (14.4 times, Mann-Whitney U test, $P < 0.01$), and diversity indices (H') were also significantly higher inside ($H' = 2.86$) than outside ($H' = 1.77$, Table 2).

The dominant plants (plant form type) inside the exclosure were *Aralia elata* (sh: shrub form), *Hydrangea paniculata* (sh), *Callicarpa japonica* (sh), *Symplocos sawafutagi* (t: tree form), and *Clethra barbinervis* (t, Table 3). These woody plants accounted for more than 80% of the biomass index inside. Outside the exclosure, *Cynanchum caudatum* (l: liane form, u: unpalatable), *Pterostyrax hispida* (t, u), and *Festuca rubra* (g: graminoid) accounted for more than 90% of the total biomass index outside (Table 3). These results show that heavy deer grazing not only reduced biomass, but also decreased species and growth form diversities. Species-area curves clearly showed no difference in species numbers between the inside and the outside at smaller plot size, but, as plot size increased, differences appeared and became more pronounced (Figure 2).

The temperature was recorded inside and outside the exclosure from late June to October. From June to August, the maximum temperature was often higher outside than inside but was similar on both sides in September and October (Figure 3(a)). The minimum temperatures on each side were similar from late June to September (Figure 3(b)). In October, however, the minimum temperature was lower outside than inside.

The highest humidity values in July were almost 100% both inside and outside, but in late July and early August they decreased and were slightly lower outside. From mid-September, humidity values increased again to almost 100% inside but were around 40–60% outside (Figure 4(a)). The lowest humidity values were more variable than the maximum values. Outside values were lower in late July and August and early September and October (Figure 4(b)).

Daily fluctuations in temperature and humidity from July 5 to July 12, 2011, are shown in Figure 5 as an example. The nocturnal temperature showed no difference between the inside and outside, but diurnal values followed a different pattern. During the day, the highest temperature outside showed sharp "peaks" on sunny days that were not observed inside (Figure 5(a)). Similarly, the humidity outside showed sharp "valleys," dropping to about 50% on sunny days, whereas the values inside rarely fell below 80% (Figure 5(b)).

The diurnal temperature and humidity ranges were higher outside than inside (Figure 6). The monthly means were significantly higher outside in July, August, and October (Mann-Whitney U test, $P < 0.05$) but not in September ($P > 0.05$). These results suggest that the microclimate was less stable outside than inside because of plant reduction.

The mean amount of soil captured in the boxes outside the exclosure (8.04 g/day) was 80 times higher than the amount in the boxes inside (0.11 g/day, Mann-Whitney U test, $P < 0.01$). The amount of soil captured outside increased in June and then dropped before increasing again in the middle of August and September (Figure 7), when typhoons hit the area.

During the study period, the insects collected inside and outside the exclosure totaled 950 and 1,682, respectively. Table 4 shows the insect groups that included more than 100 individuals. The number of carabid beetles collected inside (10.9/100 TN) was significantly higher than outside (3.8/100 TN, Mann-Whitney U test, $P < 0.01$). In contrast, carrion beetles (Silphidae, 5.8/100 TN inside, 8.5/100 TN outside), dung beetles (8.0/100 TN inside, 35.5/100 TN outside), and camel crickets (6.3/100 TN inside, 12.4/100 TN outside) were significantly more abundant outside (Mann-Whitney U test, $P < 0.01$). Densities of ground beetles and rove beetles, or staphylinids (Staphylinidae), were not significantly different between the two sides (Mann-Whitney U test, $P > 0.05$). Diversity indices were 3.02 inside and 2.79 outside.

5. Discussion

As the exclosure was located in a single larch forest, the canopy trees were the same inside and outside.

Table 1: Densities and basal area of trees and shrubs appearing in 10 m × 10 m plot inside and 20 m × 20 m plot outside the exclosure at Okutama, western Tokyo, Japan.

	Tree/shrub	Inside		Outside	
		n/plot	Basal area (m^2/ha)	*n*/100 m^2	Basal area (m^2/ha)
Larix kaempferi	t	2	11.64	2.75	17.86
Pterostyrax hispida	t	15	1.63	—	—
Toxicodendron trichocarpum	t	2	1.09	—	—
Euonymus hamiltonianus	t	2	0.94	—	—
Carpinus cordata	t	5	0.09	0.25	0.50
Salix bakko	t	3	0.08	—	—
Clethra barbinervis	t	6	0.05	—	—
Betula ermanii	t	1	0.04	—	—
Fraxinus lanuginosa	t	3	0.03	—	—
Swida controversa	t	1	0.02	—	—
Castanea crenata	t	1	0.01	—	—
Acer diabolicum	t	—	—	0.25	0.36
Acer pictum	t	—	—	0.25	0.36
Hydrangea paniculata	s	37	1.26	—	—
Aralia elata	s	6	0.38	—	—
Callicarpa japonica	s	36	0.14	—	—
Stephanandra incisa	s	9	0.03	—	—
Lindera praecox	s	1	0.00	—	—
Subtotal trees		41	15.61	4	19.09
Subtotal shrubs		89	1.82	0	0.00
Total		**130**	**17.43**	**4**	**19.09**

Table 2: Mean values of numbers, biomass indices*, and Shannon-Wiener's diversity indices H' of plant species appearing in 2 m × 2 m plots inside ($n = 5$) and outside ($n = 5$) the deer exclosure at Okutama, western Tokyo, Japan.

	Inside	Outside
Species number	14.4	9.7
Biomass index*	564,710	39,290
Diversity index H'	2.86	1.77

*Biomass index = cover (cm^2) × height (cm).

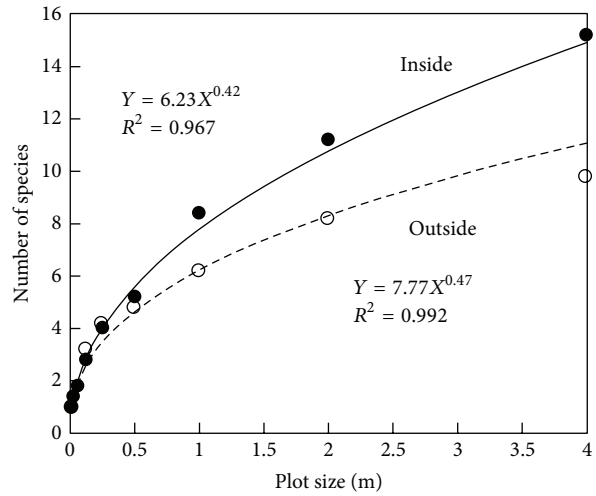


Figure 2: Relations of plot size and mean number of species present on each of the five 2 m × 2 m plots inside and outside the deer exclosure in Okutama, western Tokyo, Japan.

The mean value of the density of deer fecal pellet groups was 3.9 group/10 m^2. This was lower than the result of a count made on Kinkazan Island, where deer density was as high as 50 deer/km^2, but higher than the result obtained among deciduous broadleaved forests in the mountains of central Japan (around 1/10 m^2). This suggests that the deer density in the study area is very high. In addition, we did not find any feces of other mammals, such as hare (*Lepus brachyurus*) or Japanese macaque (*Macaca fuscata*). These findings support our hypothesis that the differences in habitat inside and outside the deer exclosure can be attributed to deer grazing.

A limitation of this study is that it is restricted to one deer exclosure and therefore the conclusions must be taken with caution. However, we carefully selected locations for the plots where the topography and canopy trees were as similar as possible (see Figure 1). Despite this limitation, the data for inside and outside the exclosure showed marked differences.

The results of the undergrowth vegetation clearly showed that the values for plant species numbers, biomass, composition, and diversity were lower outside the exclosure. These differences suggest the strong direct effects of deer grazing. It is known that in many areas of central Japan, including

Table 3: Mean values of biomass indices* of undergrowth plants appearing in five 2 m × 2 m plots inside and outside the deer exclosure at Okutama, western Tokyo.

	Growth from**	Palatability	Inside	Presentage		Outside	Presentage	Abundant on
Pterostyrax hispida	l	U	400	0.07	<	18400	46.83	Outside
Cynanchum caudatum	t	U	40	0.01	<	13860	35.28	Outside
Viola sieboldii	r		0	—	<	40	0.10	Outside
Athyrium yokoscense	fe		0	—	<	40	0.10	Outside
Betula ermanii	t		0	—	<	20	0.05	Outside
Viola eizanensis	r		0	—	<	10	0.03	Outside
Swida macrophylla	t		0	—	<	10	0.03	Outside
Carex conica	g		0	—	<	10	0.03	Outside
Festuca rubra	g		47500	8.41		4200	10.69	Both sides
Carex leucochlora	g		1000	0.71		2000	5.09	Both sides
Agrostis clavata	g		200	0.04		420	1.07	Both sides
Viola grypoceras	r		30	0.01		50	0.13	Both sides
Schizophragma hydrangeoides	l		20	0.00		20	0.05	Both sides
Aralia elata	sh	U	160000	28.33	>	0	—	Inside
Hydrangea paniculata	l		112000	19.83	>	0	—	Inside
Callicarpa japonica	sh		94000	16.65	>	10	+	Inside
Symplocos sawafutagi	t		60000	10.62	>	0	—	Inside
Clethra barbinervis	t		50420	8.93	>	200	0.51	Inside
Cerasus jamasakura	t		12000	2.12	>	0	—	Inside
Rubus crataegifolius	sh		6000	1.06	>	0	—	Inside
Carpinus cordata	t		6000	1.06	>	0	—	Inside
Aralia cordata	sh		5000	0.89	>	0	—	Inside
Actinidia polygama	l		2440	0.43	>	0	—	Inside
Vitis coignetiae	l		1000	0.18	>	0	—	Inside
Celastrus orbiculatus	l		800	0.14	>	0	—	Inside
Carex curvivicollis	g		800	0.14	>	0	—	Inside
Chamaecyparis obtusa	t		800	0.14	>	0	—	Inside
Fraxinus lanuginosa	t		400	0.07	>	0	—	Inside
Rubus palmatus	sh		400	0.07	>	0	—	Inside
Tilia japonica	t		200	0.04	>	0	—	Inside
Clematis apiifolia	l		200	0.04	>	0	—	Inside
Carex alopecuroides	g		20	+	>	0	—	Inside
Quercus crispula	t		20	+	>	0	—	Inside
Clinopodium multicaule	e		20	+	>	0	—	Inside
Total			**564.710**	**100**		**39.290**	**100**	

Biomass index* = cover (cm^2) × height (cm). Growth form**: e: erect, fe: fern, g: graminoid, l: liane, r: rosette, sh: shrub, and t: tree. Palatability: U: unpalatable. +: < 0.1%.

the area of this study, quantitative compositions of plants have been affected by deer grazing [1]. It is expected that such strong effects on plant communities would also alter habitat structure and indirectly affect insect communities [25–28, 30, 41].

The microclimate was quite different inside and outside the exclosure, suggesting that the reduction in plants caused by deer grazing increased the amount of direct sunlight, resulting in increased daytime temperatures and dryness outside the exclosure. The air temperature near the ground surface was up to 40°C, indicating that the ground temperature must have been hotter. Humidity was always lower outside than inside, although it was 100% on many days (presumably rainy days) during the study period. These differences in microclimate would affect ground-dwelling insects. Carabid beetles were more abundant inside the exclosure, probably because of the gentle, stable microclimate inside. The habitat preferences of Japanese carabid beetles are not well known, but because forest vegetation predominates and the summer climate is humid in the Japanese archipelago, it is likely that most carabid beetles would prefer a habitat where litter is abundant and the microclimate is more humid and stable. A study on the indirect effects of sika deer on ground-dwelling insects in western Japan showed that a species of large carabid beetle, *Carabus kumagai* (23–36 mm in length), was more abundant in a habitat containing more *Sasa nipponica*,

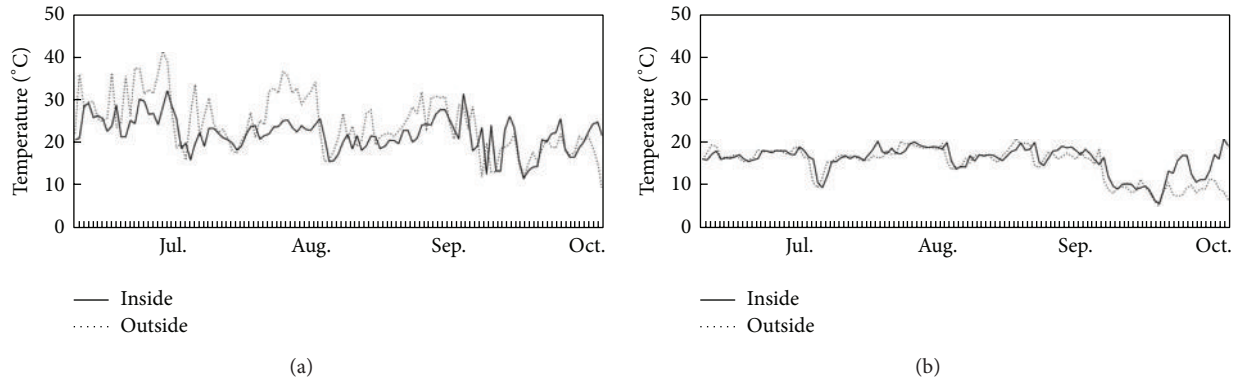


Figure 3: Daily maximum (a) and minimum (b) air temperature near the ground from late June to October, 2011, inside and outside the deer exclosure in Okutama, western Tokyo, Japan.

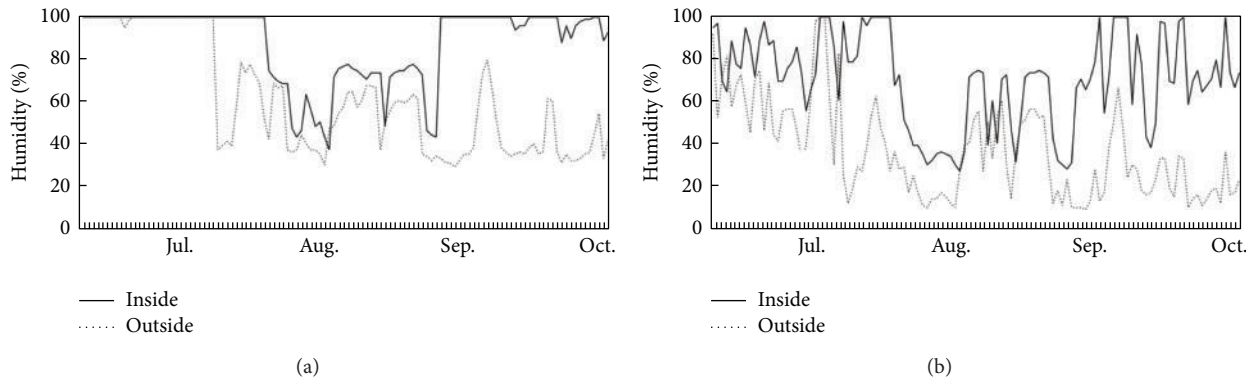


Figure 4: Daily maximum (a) and minimum (b) humidity near the ground from late June to October, 2011, inside and outside the deer exclosure in Okutama, western Tokyo, Japan.

Table 4: Numbers of insects (/100 TN; trap night) collected by pitfall traps inside and outside the deer exclosure at Okutama, western Tokyo, Japan.

	Inside			Outside	
	Mean	SD		Mean	SD
Carabid beetle (Carabinae)	10.9	5.9	>	3.8	2.3
Carrion beetle (Silphidae)	5.8	5.1	<	8.5	5.8
Dung beetle	8.0	6.2	<	35.5	5.0
Camel cricket	6.3	3.7	<	12.4	13.8
Ground beetle (Harpalinae)	10.8	5.2		11.1	6.1
Rove beetle (Staphylinidae)	2.0	1.6		4.8	10.2

a dwarf bamboo [31]. As many carabid beetles are flightless and prefer more stable habitats [42–44], they would provide a good reflection of differences in microenvironments. The results of our study and of a study conducted in western Japan [31] suggest that deer grazing indirectly decreases carabid beetles, in contrast to results obtained in boreal forests [25–28].

It is noteworthy that more carrion beetles, dung beetles, and camel crickets were collected outside the exclosure than inside (Table 4). This indicates that some insects were favored by the presence of deer. Carrion beetles prey on carcasses, particularly of vertebrates [42]. Deer carcasses would therefore be important resources for them, as shown in Scandinavia [45]. It was not surprising that deer grazing would increase the number of dung beetles, because deer provide food resources. Similar relationships have been shown in other deer habitats in Japan, such as Kinkazan Island, Nara Park, and Miyajima Island [46]. In terms of the category of the effects of ungulates, the increase in dung beetles is not caused by an indirect effect of deer grazing but by the direct effect of providing a food resource. Effects of deer grazing are usually categorized as negative effects on herbivorous animals through plant reduction [16, 17] and as structural alteration of habitats [19, 20, 23, 47, 48]. However, increases in dung beetles and carrion beetles outside the exclosure suggest that the presence of deer is positive for these decomposers.

The higher number of camel crickets outside the exclosure is difficult to explain, as they are omnivorous and eat a wide variety of foods and are often found in dark, humid habitats. The reason for their increased presence outside the exclosure is unknown.

Soil movement on the ground was much more extensive outside the exclosure. Live plants and leaf litter help to prevent soil movement by rainfall [34, 49]. Removal of plants and leaf litter by deer would allow raindrops to hit the soil

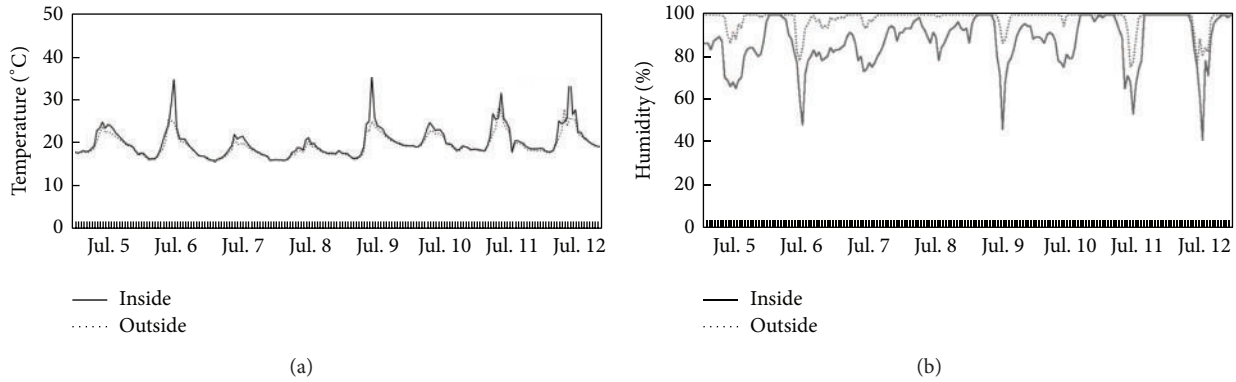


Figure 5: Temperature (a) and humidity (b) near the ground during representative weeks in July, 2011, inside and outside the deer exclosure in Okutama, western Tokyo, Japan.

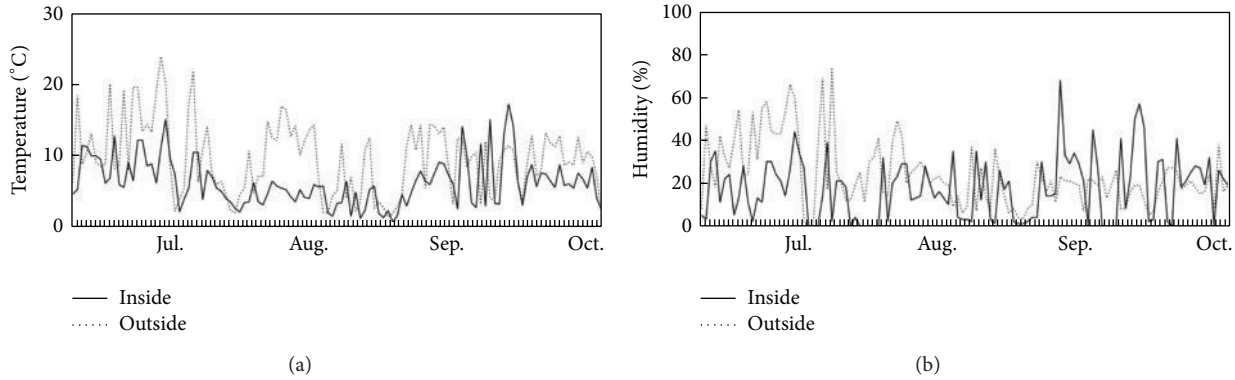


Figure 6: Diurnal temperature (a) and humidity (b) near the ground from late June to October, 2011 inside and outside the deer exclosure in Okutama, western Tokyo, Japan.

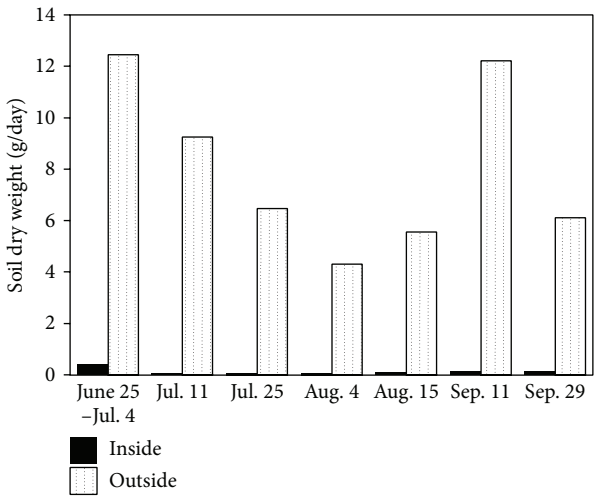


Figure 7: Weight of soil captured in box traps inside and outside the deer exclosure in Okutama, western Tokyo, Japan, from late June to mid-September, 2011.

directly, accelerating soil movement. This was observed at Mount Tanzawa [34] and on the Boso Peninsula [35], in eastern Japan. *Sasamorpha borealis*, a dwarf bamboo, once densely covered much of the study area, but its leaves have been extensively grazed by deer since approximately 2000. This bamboo is vulnerable to grazing [50] and is rapidly decreasing in and around the study area. As the rhizomes of *S. borealis* are soil binding [51] and the topography of the study area is quite steep, it is quite plausible that, after decomposition of the rhizomes, soil movement would be more intensive in this area than in other locations.

6. Conclusions

The effects of grazing and browsing by sika deer have intensified in many parts of Japan in the last decade. Using an eight-year-old deer exclosure in western Tokyo (Japan), this study shows not only the direct effects on vegetation, but also the indirect effects on soil movements, the microclimate, and ground-dwelling insects. Plants outside the exclosure were reduced and only a few unpalatable plants survived. Because of the steep topography and high rainfall in summer, soil movement was indirectly accelerated by deer grazing outside the exclosure (Figure 8). The maximum temperature outside increased and the humidity indirectly decreased, resulting in a higher diurnal temperature and humidity range. Carabid beetles were less abundant outside, constituting an indirect

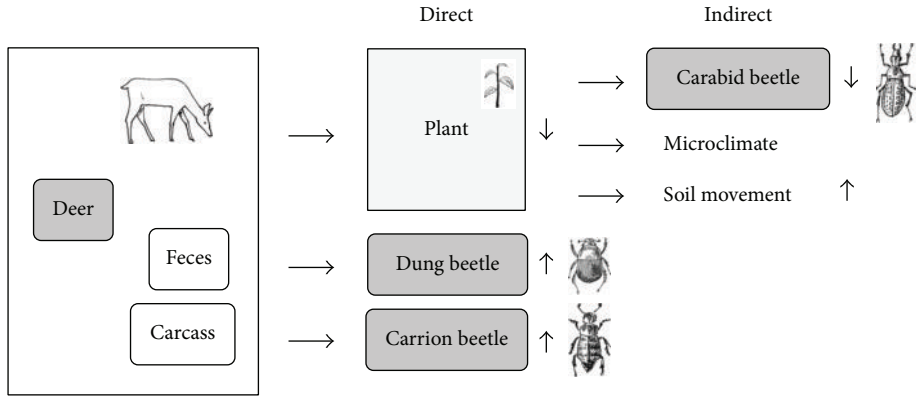


Figure 8: Summary of indirect effects of sika deer grazing on plants and decomposer insects and indirect effects on microenvironment, soil movements, and carabid beetles at Okutama, western Tokyo, Japan.

effect of deer grazing through abiotic environment alteration. In contrast, carrion beetles and dung beetles were more abundant outside, revealing a direct effect of deer presence (Figure 8). This study shows several patterns of the direct and indirect effects of deer grazing.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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