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Diversity of dung-beetle community in declining Japanese subalpine forest caused by an increasing sika deer population

Abstract The Ohdaigahara subalpine plateau in Japan has recently suffered a reduction in primary forest land caused by an increasing population of sika deer (*Cervus nippon*). Deer have debarked many trees, causing dieback, gradually changing the primary forest first to light forest with a floor that is densely covered with sasa grass (*Sasa nipponica*) and then to *S. nipponica* grassland. To examine the effects of vegetative transformation on the dung-beetle community, we compared the diversity and abundance of dung-beetle assemblages in the primary forest, transition forest, and *S. nipponica* grassland using dung-baited pitfall traps. The species richness and species diversity (Shannon-Wiener index) were significantly highest in the primary forest and lowest in the *S. nipponica* grassland. The evenness (Smith-Wilson index) was highest in the primary forest and nearly equal in the transition forest and *S. nipponica* grassland. The abundance was apparently greater in the transition forest than in the primary forest and *S. nipponica* grassland. These results suggest that loss of primary forest resulting from an increasing deer population decreases the diversity of the dung-beetle community while increasing the abundance of dung beetles in the transition forest. Sika deer use transition forests and grasslands more frequently than primary forests as habitat, but an increase in dung supply there does not necessarily increase the diversity or abundance of dung-beetle assemblages.

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Introduction

The diversity of local dung-beetle communities is primarily influenced by vegetation cover, soil type and moisture, and resource (dung) availability (Doube 1987; Davis 2002). Hence dung-beetle communities might be expected to be impacted seriously by deforestation, which increases solar radiation at the soil surface and decreases ground moisture (Hanski 1989; Gill 1991; Estrada et al. 1998). High solar radiation accelerates the loss of moisture from dung mass, making dung unavailable for beetles. Furthermore, deforestation changes the species composition and abundance of dung-producing mammals, affecting the availability of dung for beetles (Cambefort and Walter 1991; Estrada et al. 1993, 1999). Since dung beetles have different preferences for dung of different mammals based on texture, the structure of dung-beetle communities is influenced by the local mammalian fauna. Many studies in tropical South America and Southeast Asia have demonstrated that deforestation caused by human activities (e.g. logging, pasture clearing, and plantation cutting) reduces the diversity of dung-beetle communities (Klein 1989; Estrada et al. 1998; Davis 2000; Davis et al. 2001; Estrada and Coates-Estrada 2002; Halffter and Arellano 2002; Horgan 2002; Medina et al. 2002). Deforestation has sometimes decreased the numbers of mammals producing dung for beetles (Estrada et al. 1993, 1998, 1999; Estrada and Coates-Estrada 2002). This suggests that although vegetation cover may be most important for determining the structure of dung-beetle communities (Halffter and Arellano 2002), mammalian fauna may substantially influence the diversity of dung-beetle communities.

The Ohdaigahara subalpine plateau on the Kii Peninsula in Japan has the southernmost spruce forest [*Picea jezoensis* (Sieb. et Zucc.) Carrière var. *hondoensis* (Mayr) Rehder] and the largest beech forest (*Fagus crenata* Blume) in western Japan (Ide and Kameyama 1972). However, the plateau has recently suffered deforestation caused by an increasing population of sika deer (*Cervus nippon* Temminck), which strip the bark of many coniferous trees, causing dieback (Akashi and Nakashizuka 1999; Yokoyama et al. 2001). Canopy loss increases light inside the forest, allowing the forest floor to become densely covered with sasa grass (*Sasa nipponica* Makino et Shibata), which grows well with more light (Kawahara and Tadaki 1978). *S. nipponica* is a major forage of sika deer because it is richer in protein than other forage plants (Yokoyama et al. 1996; Yokoyama and Shibata 1998a). Moreover, *S. nipponica* can tolerate heavy browsing by sika deer (Yokoyama and Shibata 1998b). The dense covering of *S. nipponica* inhibits conifer seedlings from growing and surviving on the forest floor (Yamamoto 1993). Seedlings are browsed by the sika deer (Takeda 1994). As a result, the plateau has been partly changed from coniferous forest to *S. nipponica* grassland (Yokota and Nakamura 2002). Accordingly, the sika deer have come to use the grassland as habitat more intensively than the coniferous forest (Maeji et al. 1999; Yajima et al. 2002).

The change from dense forest into *S. nipponica* grassland may affect the community structure of organisms inhabiting the Ohdaigahara subalpine plateau. For example, Hino (2000) has shown that a dense population of sika deer decreases the diversity and abundance of bird communities because the deer heavily graze undergrowth foliage that forms nesting sites for birds and cause loss of canopy trees through trunk barking. However, despite the widely held view that the structure of dung-beetle communities is strongly affected by changes in vegetation and the composition and abundance of mammals, no study on dung-beetle community has been made in Ohdaigahara.

This paper examines how the diversity of the dung-beetle community has been affected by the reduction in primary forest caused by an increasing population of sika deer on the Ohdaigahara subalpine plateau. We compared the diversity of dung-beetle assemblages in primary forest, transition forest with floor dominated by *S. nipponica*, and *S. nipponica* grassland using dung-baited pitfall traps. We referred to data on sika deer habitat use and the distribution of deer fecal pellets, and evaluated the relative importance of vegetation and dung supply as factors that determine the diversity of the dung-beetle community.

Methods

Study site

This study was carried out on the Ohdaigahara subalpine plateau (34°12′N, 136°06′E) at an altitude of 1,400–1,695 m on the Kii Peninsula, Japan. The climate

is characterized by cool temperatures (annual mean 6.4°C) and high precipitation (annual average > 4,500 mm) (Japan Forest Technology Association 2001). The plateau is covered with snow from mid-December to late March. The primary vegetation of the plateau is evergreen coniferous forest dominated by spruce (*P. jezoensis* var. *hondoensis*) in the eastern area and a mixed forest dominated by beech (*F. crenata*) and fir (*Abies homolepis* Sieb. et Zucc.) in the western area (Ide and Kameyama 1972). More than half the coniferous trees, such as spruce, fir, hemlock (*Tsuga diversifolia* Masters) and cypress (*Chamaecyparis obtusa* Endl.), have been debarked by sika deer. In particular, 75.9% of spruce trees suffer debarking with a resultant mortality ranging from 17.8–25.9% (Yokoyama et al. 2001). The population density of sika deer on the plateau in 1996 and 1997 was estimated at 17.5–30.9 individuals km^{-2} (Maeji et al. 1999).

The Ohdaigahara subalpine plateau harbors several species of large or medium-sized mammals that produce dung for dung beetles, including sika deer, Japanese serow [*Capricornis crispus* (Temminck)], Japanese monkey [*Macaca fuscata* (Blyth)], red fox [*Vulpes vulpes* (L.)], raccoon dog [*Nyctereutes procyonoides* (Gray)], badger [*Meles meles* (L.)], black bear [*Selenarctos thibetanus* (Cuvier)], wild boar (*Sus scrofa* L.), and marten [*Martes melampus* (Wagner)]. Sika deer are the most abundant (E. Shibata, unpublished data).

Three sampling sites comprising different types of vegetation were selected (Fig. 1). Site A is primary or dense mixed forest (1,560 m a.s.l.) dominated by beech and fir with the forest floor covered mainly with sasa grass (*S. nipponica*) and perennial herbs (*Skimmia japonica* Thunberg). The crown coverage at 1 m is 77%
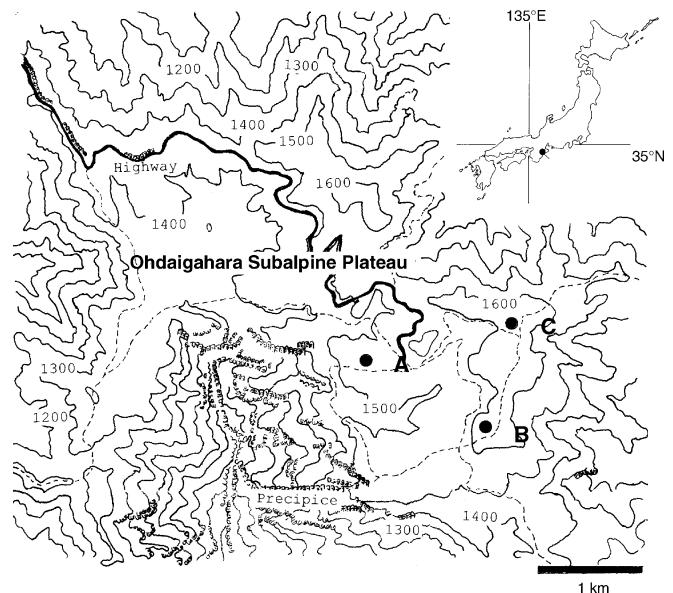

Fig. 1 Map of Ohdaigahara subalpine plateau showing location of three trapping sites. *A* Dense mixed forest or primary forest, *B* *S. nipponica* grassland, *C* transition forest with forest floor densely covered with *S. nipponica* grass. *Dashed lines* indicate trails and *solid lines* indicate contour lines (in 100-m intervals)

according to image analysis of hemispheric photographs (LIA for Win32; Yamamoto 2003). Site B is grassland (1,680 m a.s.l.) where azalea shrubs (*Rhododendron quinquefolium* Bisset et Moor) are distributed sparsely and *S. nipponica* covers the floor densely. The crown coverage is 20%. Until the 1980s, this area was forest dominated by spruce, but it has suffered deforestation resulting from an increasing population of sika deer (Yokota and Nakamura 2002). Site C is transition forest between mixed forest and grassland (1,650 m a.s.l.) dominated by spruce and beech with a forest floor covered densely with *S. nipponica*. The crown coverage is 77%, which is similar to the primary or dense mixed forest.

Sampling methods

Dung beetles were sampled using dung-baited pitfall traps designed by Hoga (1982). Plastic containers (130 mm diameter, 95 mm deep) containing 150 ml of 50% ethylene glycol as a preserving fluid were buried to the rim in the ground. A plastic cup (85 mm diameter, 45 mm deep) containing 35 g of fresh deer dung was suspended with wire at the mouth of the container. Sampling was conducted at the three sites at the end of each month from May 2001 to November 2001. Three traps were buried in the soil at 20-m intervals on a transect line at each site for 7 days with no rebaiting. A voucher collection of dung beetles was deposited at Department of Biological Sciences, Nara Women's University.

Dung-beetle diversity

Species diversity in a community takes two components into account: species richness (number of species in sample) and evenness (degree to which species are equally abundant) (Magurran 1988). The Shannon-Wiener index H' was used in the present study to measure species diversity

$$H' = - \sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where s is the number of species, p_i is the proportion of total sample belonging to species i. Species richness was estimated by the rarefaction method (Krebs 1999). This method estimates the number of species expected in a random sample $\left(E(\hat{S}_n)\right)$ of n individuals taken from a collection

$$E(\hat{S}_n) = \sum_{i=1}^{S} \left(1 - \frac{\left[\begin{array}{c} N - N_i \\ n \end{array} \right]}{\left[\begin{array}{c} N \\ n \end{array} \right]} \right)$$

where S is the number of species in the sample, N_i is the number of individuals of species i, N is the total number of individuals in the collection, and n is the value of the sample size chosen for standardization ($n \leq N$). The Smith-Wilson index E_{var} was used to measure evenness (Smith and Wilson 1996):

$$E_{var} = 1 - \frac{2 \arctan \left[\sum_{i=1}^{S} \left\{ \ln(n_i) - \sum_{j=1}^{S} \ln(n_j/S) \right\}^2 \middle/ S \right]}{\pi}$$

where n_i and n_j are the numbers of individuals in species i and j, respectively, in the sample, and S is the number of species in the entire sample. This index is nearly independent of species richness and is sensitive to both rare and common species in the community (Krebs 1999; note that his equation should be altered to the above).

Calculation and statistics

We calculated the species richness and its standard deviation predicted by the rarefaction method, the Shannon-Wiener measure H', bootstrap mean H' based on 5,000 iterations and its 99% confidence limit, and the Smith-Wilson measure E_{var} using the software EcoMeth (Kenney and Krebs 2003). Bootstrap procedure for E_{var} was not conducted because appropriate software was not available. Differences in the abundance of dung beetles among the primary forest, transition forest and *S. nipponica* grassland were tested by two-way factorial ANOVA, after the original data were transformed by Box-Cox method (Sokal and Rohlf 1995). Statistical tests were performed with the software BIOMstat (Rohlf and Slice 1999) or SPSS (SPSS 2002).

Results

Species composition

A total of 2,299 dung beetles belonging to two species of Geotrupidae and ten species of Scarabaeidae were captured (Table 1). Several traps, including three traps in the transition forest in July, were lost owing to natural disturbances. Hence, the abundance of each species is expressed not as the actual number of captures, but instead as the sum of mean numbers of captures per trap in a sampling episode. As a whole, the dominant species was *Aphodius superatratus* Nomura and Nakane, followed by *A. igai* Nakane. These two species comprised 73.4% of all captures.

The composition of abundant species differed among the three habitats. In the primary forest, *A. igai* comprised 50% of the captures, and three species, *A. unifasciatus* Waterhouse, *A. superatratus,* and *A. isaburoi* Nakane, made up 35% of the captures. In the transition forest, *A. superatratus* was most abundant followed by *A. igai* and *A. unifasciatus*; these species accounted for 85% of the captures. In the *S. nipponica* grassland, *A. superatratus* was dominant followed by *A. igai*; these two species comprised 89% of the captures.

Table 1 The sum of mean numbers (and percentages) of individuals per trap in one trapping episode

Family/subfamily/species	Site			Total
	Primary forest	Transition forest	*S. nipponica* grassland	
Geotrupidae				
Phelotrupes auratus[a] (Motschulsky)	0.67 (2.4)	2.88 (3.5)	0.62 (3.2)	4.16 (3.2)
Phelotrupes laevistriatus[b] (Motschulsky)	0.05 (0.2)	0.25 (0.3)		0.30 (0.2)
Scarabaeidae				
Scarabaeinae				
Caccobius jessoensis Harold	0.33 (1.2)	0.56 (0.7)	0.10 (0.5)	0.99 (0.8)
Onthophagus ater Waterhouse		0.06 (0.1)		0.06 (0.1)
Aphodiinae				
Aphodius igai Nakane	13.95 (49.9)	25.06 (30.6)	5.43 (28.4)	44.40 (34.5)
Aphodius superatratus Momura and Nakane	3.14 (11.2)	35.44 (43.3)	11.57 (60.4)	50.15 (38.9)
Aphodius unifasciatus Nomura and Nakane	3.95 (14.1)	8.63 (10.5)	0.14 (0.7)	12.72 (9.9)
Aphodius eccoptus Bates	0.67 (2.4)	0.63 (0.8)	0.10 (0.5)	1.39 (1.1)
Aphodius isaburoi Nakane	2.86 (10.2)	6.31 (7.7)	0.05 (0.2)	9.22 (7.1)
Aphodius madara Nakane	0.86 (3.1)	2.00 (2.4)	1.14 (6.0)	4.00 (3.1)
Aphodius uniformis Waterhouse	0.19 (0.7)			0.19 (0.2)
Oxyomus ishidai Nakane	1.29 (4.6)			1.29 (1.0)
Total number of individuals	27.96 (100.0)	81.81 (100.0)	19.14 (100.0)	128.91 (100.0)
Species richness				
Observed number of species	11	10	8	12
Expected number of species estimated at 400 individuals ($\pm$SD)	10.7 ± 0.48	9.0 ± 0.67	8.0 ± 0.07	10.3 ± 0.82
Observed E_{var}	0.268	0.165	0.175	0.154
Species diversity				
Observed H'	2.348	2.110	1.511	2.207
Mean H' estimated by bootstrapping	2.345	2.109	1.506	2.206
99% lower confidence limit	2.295	2.084	1.455	2.186
99% upper confidence limit	2.394	2.135	1.559	2.226

The expected numbers of species at 400 individuals were estimated by rarefaction method. The bootstrap estimates of mean H' and its 99% confidence limits were based on 5,000 iterations. Scientific names are in accordance with Fujioka (2001)

[a] Previously treated as *Geotrupes auratus*
[b] Previously treated as *Geotrupes laevistriatus*

Diversity of dung-beetle assemblages

The primary forest had the highest species richness followed by the transition forest, and the *S. nipponica* grassland (Table 1). The differences between the habitats were significant based on the expected species richness at 400 individuals estimated using the rarefaction method (Scheffé test, $P < 0.01$; Sokal and Rohlf 1995). Figure 2 shows rarefaction curves for the three habitats. Expected species richness was highest in the primary forest and lowest in the *S. nipponica* grassland for all sample sizes.

Figure 3 shows species rank–abundance curves for the three habitats; the slope of rank–abundance curves reflects diversity (Magurran 1988). The transition forest and *S. nipponica* grassland show similar species rank–
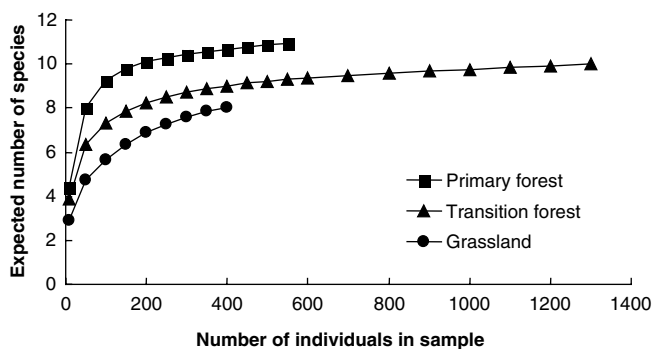

Fig. 2 Rarefaction curves for dung-beetle assemblages in primary forest, transition forest and *S. nipponica* grassland
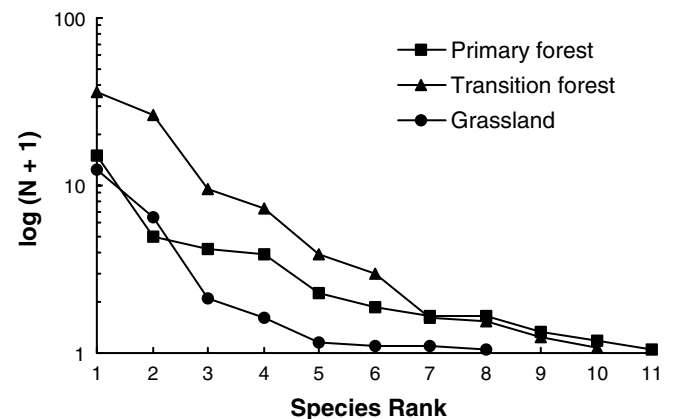

Fig. 3 Rank–abundance curves for samples of dung beetles caught by dung-baited pitfall traps in primary forest, transition forest and *S. nipponica* grassland. The abundance of each species is expressed as the actual number of individuals (*N*)

abundance slopes, and accordingly, similar evenness (Smith-Wilson index, E_{var}). On the other hand, the primary forest has a shallower slope than the other habitats, demonstrating the highest evenness (Table 1).

Shannon-Wiener index (H') was highest in the primary forest, intermediate in the transition forest, and lowest in the *S. nipponica* grassland (Table 1). The differences were statistically significant because the 99% confidence limits of bootstrap mean H' in one habitat always exclude bootstrap mean H' in the other habitats.

Monthly species richness and abundance of dung beetles

The species richness of dung beetles decreased at each site as the season progressed (Fig. 4a). The grassland had the poorest species richness in all months, while the primary forest had the highest species richness in all months except September. More dung beetles were caught in May and June at all sites (Fig. 4b). After July, the number remained very low in the primary forest and *S. nipponica* grassland. In the latter, especially, no more than one dung beetle was trapped after August. In the transition forest, however, the abundance increased slightly in August through September. A two-way ANOVA (with the July data excluded because there were none for the transition forest) revealed that the pattern of monthly abundance significantly differed
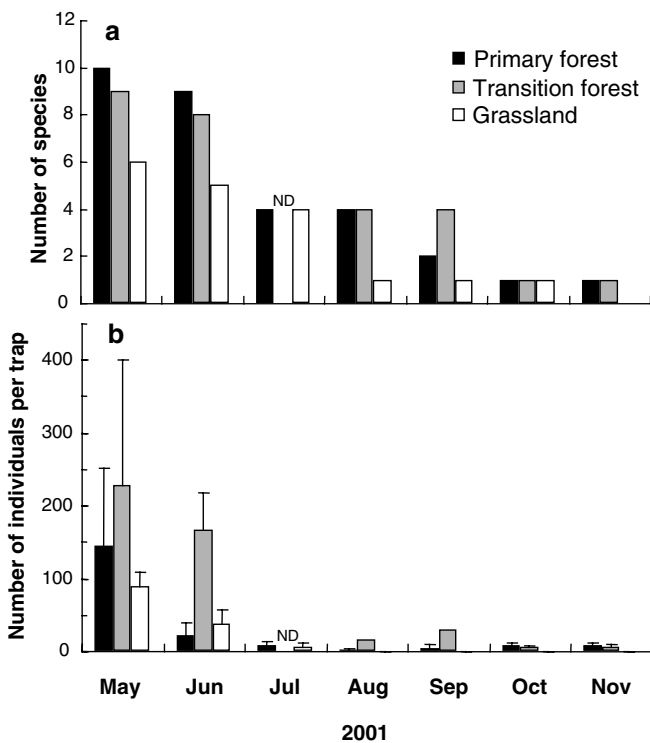

Fig. 4 Seasonal changes in species richness (**a**) and number of dung beetles caught in traps (**b**) in primary forest, transition forest and *S. nipponica* grassland. *Vertical bars* indicate SD. *ND* no data

among the sites ($P < 0.001$ for site × month interaction; Table 2). The transition forest exceeded the other sites in abundance until September and was nearly equal to the primary forests in October and November. The *S. nipponica* grassland showed lower abundance through the season except in June.

Discussion

Twelve species were recorded in the present study. The collection includes almost all the subalpine species recorded for western Japan (Masumoto and Ochi 1985). Only two species, *A. gotoi* Nomura and Nakane and *A. hasegawai* Nomura and Nakane, were not captured. Since there has been no record of these species from the Ohdaigahara subalpine plateau, it is probable that neither of them inhabits the area.

The diversity of dung-beetle assemblages measured as species richness, E_{var}, and H' was significantly or substantially higher in the primary forest than the *S. nipponica* grassland and transition forest. Data were lost for the transition forest in July, so the species richness might be underestimated there. However, the possibility seems unlikely because the species that were trapped in the primary forest and the *S. nipponica* grassland in July were caught in the transition forest in other months. The grassland had the lowest species richness in all months, while the primary forest had the highest richness except in September. Thus, the diversity of dung beetle assemblages can be regarded as highest in the primary forest and lowest in the *S. nipponica* grassland.

The transition forest did not show an edge effect, i.e. species richness was not greater at the boundary between two adjacent habitats (Odum 1971). No species were collected only from the *S. nipponica* grassland, which suggests that species specializing in open lands were not present. Any possible edge effect was minimized by the absence of species specific to open habitats; there is no mixture of species that inhabit the grassland and species that inhabit the forest to increase species richness at the boundary (i.e. transition forest) between the two adjacent habitats. There are two reasons for the absence of species specializing in open lands. One is a topological reason—the Ohdaigahara subalpine plateau is sur-

Table 2 Two-way ANOVA table for monthly abundance of dung beetles in three sites: primary forest, transition forest and *S. nipponica* grassland

Source	SS	df	MS	F	P
Site	13.56	2	6.780	66.724	< 0.001
Month	29.14	5	5.829	57.359	< 0.001
Site×month	6.67	10	0.667	6.563	< 0.001
Error	3.46	34	0.102		

The data were transformed by Box-Cox method before analysis. The July data were excluded from the analysis because data for the transition forest of the month had been lost

rounded by dense forests, and thus hardly receives immigrations of dung beetles from open lands. The other is a historical reason—since the primary vegetation of the plateau is dense coniferous and dense mixed forest (Ide and Kameyama 1972), no dung beetle specializing in open lands is likely to maintain its population.

Although the pattern of monthly abundance of dung beetles significantly differed among the habitats, the abundance tended to be greatest in the transition forest, intermediate in the primary forest, and lowest in the S. nipponica grassland. Transition forests and grasslands are used more intensively by sika deer from spring to autumn than primary forests (Maeji et al. 1999; Yajima et al. 2002). Furthermore, the mean number of fecal pellets during May 2001 and June 2001 was higher in the S. nipponica grassland (666.4/10 m^2; min = 98, max = 1,825, n = 10) (M. Matsumura, unpublished data) than the primary forest (24.5/10 m^2, min = 0, max = 125, n = 15) (T. Hino, unpublished data). This suggests a higher deer population density in the grassland than the primary forest. Additionally, during the censuses of sika-deer fecal pellets, no dung of other mammals was found. Thus, an increase in dung supply by sika deer does not necessarily increase the abundance of dung beetles.

So far, we have proceeded under the assumption that the number of dung beetles caught in dung-baited traps reflects the abundance of dung beetles in a habitat. One might question this assumption, raising the possibility that, if a large number of dung pellets are deposited, pellets would hinder dung-baited traps from attracting dung beetles, or if there are few pellets around the traps, more dung beetles would be attracted to the traps than expected. However, Lobo et al. (1998) have demonstrated that the number of trapped beetles was in accordance with estimated population sizes of beetles in three pastures with different-sized flocks of sheep. Hence, our assumption may be acceptable.

Halffter and Arellano (2002) have noted that vegetation cover rather than dung supply is important for determining the structure and diversity of a dung-beetle community in a tropical region of Mexico. In the Ohdaigahara subalpine plateau, the abundance of dung beetles seems to be influenced by ground moisture, which is determined by solar radiation and transpiration (Horgan 2002). The dense coniferous and mixed forests should have very moist ground because of high annual precipitation (> 4,500 mm) and low solar radiation. This ground condition is unlikely to favor dung beetles because it decreases the survivorship of the offspring in brood chambers in the soil (Vessby and Wiktelius 2003). On the other hand, the transition forest should have moderately moist ground because Sasa grasses have high transpiration rates (Takagi et al. 1999; Kitamura et al. 2000). In fact, Furusawa et al. (2001) have demonstrated experimentally that soil moisture measured by matrix potential at a depth of 6 cm was significantly lower in the forest floor covered with S. nipponica grass than in the forest floor without grass in the Ohdaigahara subalpine plateau. The low abundance of dung beetles in the

S. nipponica grassland is probably due to high solar radiation, which dries dung mass at a faster rate. Furthermore, the low abundance in the grassland may be attributable to the inability of forest dung beetles, such as A. igai, A. unifasciatus, A. eccoptus Bates, A. isaburoi and Oxyomus ishidai Nakane in the present study (Masumoto and Ochi 1985), to extend their activity into open land (Howden and Nealis 1975; Peck and Forsyth 1982; Doube 1983; Nummelin and Hanski 1989; Estrada et al. 1998; Halffter and Arellano 2002).

The reduction in primary forest caused by debarking by sika deer and the resultant dieback of coniferous trees has resulted in loss of diversity in the dung-beetle community as a result of an increase in S. nipponica grassland on the Ohdaigahara subalpine plateau. Although dung beetles are most abundant in transition forests with a floor densely covered with S. nipponica grass, the community structure is simpler, showing reduced evenness. The increasing population of sika deer supplies more dung for beetles, but the increased dung supply does not necessarily increase the abundance or diversity of dung beetles. Instead, sika deer reduce the primary forest by debarking, which in turn decreases the diversity of the subalpine dung-beetle community.

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