

Assessing the diversity of dung beetle assemblages utilizing Japanese monkey feces in cool-temperate forests

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Abstract Ecological investigation of the distribution and composition of dung beetle species utilizing feces of wild mammals has rarely been attempted, especially in cool-temperate forests. In this study we recorded and evaluated the community structure of dung beetle species utilizing feces of Japanese monkeys (*Macaca fuscata*) by conducting a macro-scale inventory survey in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan. Moreover, to assess the effect of human-induced forest disturbance on species assemblages in this cool-temperate area, we also carried out field sampling using pitfall traps baited with monkey feces in primary forests, secondary forests, and coniferous plantations, during every season except winter. Our findings were: (1) 14 dung beetle species comprising eight dwellers and six tunnelers utilized monkey feces; (2) *Aphodius eccoptus*

was the core species in dung beetle assemblages attracted to the feces during spring and summer; (3) the frequency of occurrence of every species was extremely high in spring; and (4) human-induced forest disturbance did not increase species richness or biomass in cool-temperate forests.

Keywords Cool-temperate forest · Dung beetle · *Macaca fuscata* · Pitfall trap · Shirakami Mountains

Introduction

Coprophagous dung beetles have the highest species richness and biomass among insect fauna utilizing animal feces in natural ecosystems (Yasuda 1996). Apart from being recognized as important decomposer organisms (involved with nutrient recycling) (Hanski and Kriksen 1991), their ecological role as a secondary seed disperser has recently received increasing attention (Estrada and Coates-Estrada 1991; Vullnec 2002). It has been reported worldwide that the species diversity of dung beetles has been rapidly decreasing with fragmentation and isolation of their habitats arising directly or indirectly because of increasing human activity (Klein 1989; Davis et al. 2001; Halfpeter and Arellano 2002; Feer and Hingrat 2004). There are 152 species and 9 subspecies of indigenous dung beetles on the Japanese archipelago (Kawai et al. 2005). Forty-five percent of these have been recognized as vulnerable or endangered (Imura 2007) and appropriate conservation initiatives are required for their protection (Tsukamoto 2003).

In Japan, most ecological-studies on dung beetle species have been performed in open pastures to investigate their function in biological pest control, for example controlling livestock parasites by removing of sources of infection

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(Sasayama et al. 1984; Yasuda 1984; Kuramochi et al. 2000; Imura 2007; Yamada et al. 2007). Hence, little attention has been given to the distribution and composition of forest dung beetle species, especially in the cool-temperate zone. The diversity of forest dung beetle assemblages in this area is generally affected by the distribution and composition of existing wild mammals that provide the essential resource (i.e. feces) on which the dung beetles feed or oviposit (Fincher et al. 1970; Hanski and Cambefort 1991; Yasuda 1996; Feer and Hingrat 2004). There have, however, been few studies, including unpublished reports, focusing on interspecies relationships between temperate region dung beetles and wild mammals (e.g. for sika deer (*Cervus Nippon*): Ikeda et al. 2002; Kanda et al. 2005; Koike et al. 2006a, and for Asiatic black bears (*Ursus thibetanus*): Koike et al. 2006b). The same is true for Japanese monkeys (*Macaca fuscata*), although this animal is one of the most widespread forest mammals in Japan inhabiting climatic zones ranging from subtropical to cool-temperate (Biodiversity Center of Japan 2004).

The northern Tohoku district (located in the northernmost part of mainland Japan), with cool-temperate forests, is an area with heavy snowfall. During the nineteenth to early twentieth century, in this district, most large-mammals were overhunted by local residents for food and mammalian pest control (in order to prevent agricultural damage from the animals). Accordingly, the local populations of sika deer and wild boar (*Sus scrofa*) in this district became extinct and are still absent, except for deer inhabiting Goyozan and Kinkazan islands. In addition, the distribution of the monkey population has also become critically segmented and isolated (Biodiversity Center of Japan 2004). Thus, in terms of biodiversity conservation, it is important to record and evaluate the distribution and composition of dung beetle species in districts containing vulnerable mammalian fauna (i.e. resource provider) because of human disturbance in the past. In this context, we first conducted a macro-scale inventory survey for dung beetles utilizing monkey feces in the Shirakami Mountains, located in the northwestern side of Tohoku district.

The diversity of dung beetle species is highly sensitive not only to the availability of feces (as already mentioned) but also to environmental conditions such as vegetation cover type and soil conditions (Neails 1977; Doube 1983). It has been recognized that human-induced habitat disturbance cannot be disregarded in evaluating species diversity in the area concerned (Klein 1989; Davis et al. 2001; Halfpfer and Arellano 2002). We conducted field sampling, during every season except winter (i.e. the hibernation period), to quantitatively clarify differences between dung beetle assemblages in primary forests, secondary forests, and coniferous plantations in the mountains using pitfall traps baited with monkey feces. In this paper, we discuss

the direct and indirect effect of human-induced forest disturbance on the distribution and composition of dung beetle species in cool-temperate forests, with reference to changes in monkey distribution.

Materials and methods

Study area

The Shirakami Mountains are one of the most extensive cool-temperate primary forests in East Asia, and have been designated as a World Natural Heritage Site by UNESCO since 1993. We defined an area of approximately 12 × 16 km to record dung beetle species on the north-eastern side of the mountains (Fig. 1). This area is the transition zone from human settlements to inner montane areas. The altitude of the area ranges from 50 to 1,000 m above sea level. Human settlements are concentrated in the narrow flatlands along rivers at an altitude below 200 m and are located in the northeastern side of the area. Of the forested area, primary forests, mainly composed of Japanese beech (*Fagus crenata*) trees, are located in the inner montane area (the southwest side of the area). Secondary forests of beech and oak (*Quercus mongolica* var. *crispula*) trees and mature coniferous plantations of Japanese cedar (*Cryptomeria japonica*) are located near the settlements (mainly the northeast side of the area). The total areas of each type of forest cover (primary, secondary, and plantation forests) were similar. Dwarf bamboo (*Sasa*

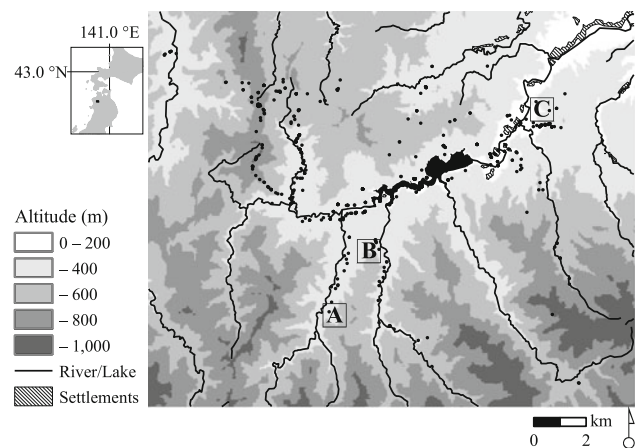


Fig. 1 Map of the study area in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan. The letters A, B, and C on the map indicate the sites where baited pitfall traps were set. These are located in primary forests mainly composed of *Fagus crenata* (A), artificial plantations of *Cryptomeria japonica* (B), and secondary broadleaved forests (C). Black spots inside the map show the collection sites of Japanese monkey feces

kurilensis) commonly dominates the forest floors in mildly sloping broadleaf forests, whereas sparse forest floor plants grow in primary forests and mature coniferous plantations.

The area is in the cool-temperate climatic zone. The mean air temperature (\pm SD) between May 2007 and June 2008 was $11.6 \pm 8.8^\circ\text{C}$ (Japan Meteorological Agency 2009). Annual precipitation in 2007 was 1,168 mm. The period of snowfall usually lasted from early December to late March, with a maximum snow depth of 2 m in lowland areas and 3–5 m in mountainous areas. Fourteen species of medium and large mammals—for example Japanese monkeys, Asiatic black bears, Japanese serows (*Capri-cornis crispus*), martens (*Martes melampus*), raccoon dogs (*Nyctereutes procyonoides*), badgers (*Meles meles*), and hares (*Lepus brachyurus*), but not sika deer and wild boar—are confirmed in this area (Biodiversity Center of Japan 2004).

Study animals

Coprophagous dung beetles are classified as part of the superfamily Scarabaeoidea and utilize excrements and carcasses of animals as their food resource (Tsukamoto 1998). Dung beetles are commonly divided into three main functional groups according to their feces-processing behavior:

1. tunnelers, which make a burrow under the fecal pat and bring feces inside for feeding or breeding;
2. dwellers, which feed in the fecal pat and oviposit under or inside the pat; and
3. rollers, which make a fecal ball to transport feces away from the fecal pat and then bury it for feeding or breeding (Cambefort and Hanski 1991).

There has been no previous scientific report relating to the dung beetle fauna in and around the study area.

Japanese monkeys are gregarious forest mammals and naturally move in troops within a steady range. Monkeys inhabiting the Shirakami Mountains constitute the largest local population in the northern Tohoku district of Japan. The animals are continuously distributed in and around the study area (Enari et al. 2006). The mean size of the troops in the area is 23 individuals (range 10–44, $n = 8$). The mean population density of the animals in the study area is approximately 5 individuals/km², or 0.2 troops/km². Their distribution is heterogeneous in the area; it is high in secondary forests around human settlements and low in inner montane primary forests (H. Enari, unpublished data). The monkeys in the mountains mainly feed on young leaves of broadleaf trees in spring, herbaceous plants and insects in summer, berries and nuts in autumn, and bark and buds of broadleaf trees in winter (Enari et al. 2005).

Inventory survey

We searched monkey feces throughout the study area and then recorded dung beetle species observed inside and outside the feces for the species inventory survey. To ensure we found fresh feces, we caught three adult female monkeys belonging to different troops in the study area by using box traps and attached radio collars (Advanced Telemetry Systems, Minnesota, USA) to each animal. They were then directly followed with the aid of their radio signals. The radio collar weighed 120 g, which was approximately 1% of the female's body mass and substantially less than the 5% of body mass recommended for maximum collar weight (American Society of Mammalogists 1998). For the purpose of maintaining the evenness of sampling intensity throughout the study area, we evenly collected feces from four sampling sections within the area; these were buffer zones 0–2, 2–4, 4–6, and 6–8-km distant from human settlements. We then collected >40 samples of feces in each section during July–August 2007, October–November 2007, and May–June 2008. A total of 667 samples of feces were collected (Fig. 1). When collecting feces, the geolocation (including altitude) and freshness (classified as fresh, completely wet; half-dry, wet inside and dry outside; and dry, completely dry) were recorded in order to evaluate the species preference for each environmental condition.

Quantitative evaluation of dung beetle species by use of baited pitfall traps

Use of baited pitfall traps set on a transect is a fast, inexpensive, and relatively unbiased means of evaluating the diversity of dung beetle species in a site (Larsen and Forsyth 2005). The design of baited pitfall traps that we used was based on that of Hoga (1984). These traps were made from plastic containers (14 cm in diameter and 10 cm deep) and plastic cups (8 cm in diameter and 5 cm deep). First, each container, containing 50% ethylene glycol (used as a preserving fluid), was buried to its rim in the ground. Then, each cup was hung in the container by use of wire. Finally, fresh monkey feces (15 g) were put into each cup; the weight of feces under test was determined according to the mean weight of monkey feces (\pm SD) in the area (12.0 ± 9.8 g, $n = 489$). The freshness of animal feces generally affects its attractiveness to dung beetles (Masumoto 1973). Therefore, we collected fresh feces by following radio-tagged monkeys immediately before each study period, and stored them in airtight containers at -20°C . These feces were used in traps after they were completely thawed. The difference in attractiveness between fresh and refrigerated feces to dung beetle species is generally small (Ikeda et al. 2002; Koike et al. 2006b).

Three traps were set at intervals of 10 m along a transect in each of a primary beech forest with a closed canopy (located in inner mountains at 288 m elevation), a secondary beech-oak forest with an open canopy (located near human settlements at 275 m elevation), and a mature cedar-plantation with a closed canopy (located between the primary and secondary forests at 273 m elevation) (Fig. 1). Taking into account the diel and seasonal changes of the species-specific activity patterns, we conducted the sampling over three consecutive days in each season (22–24 August 2007 (summer), 23–25 October 2007 (autumn), and 22–24 May 2008 (spring)); at sunrise and sunset, and all trapped dung beetles were collected and spent feces were replaced with new. There was continuous sunny weather during every sampling period. The mean air temperature (\pm SD) during the study periods were; in summer, $22.7 \pm 3.4^\circ\text{C}$ during the daytime and $16.8 \pm 2.6^\circ\text{C}$ during the nighttime; in autumn, $12.2 \pm 3.3^\circ\text{C}$ during the daytime and $8.3 \pm 2.4^\circ\text{C}$ during the nighttime; and in spring, $19.5 \pm 3.5^\circ\text{C}$ during the daytime and $12.8 \pm 2.0^\circ\text{C}$ during nighttime ($n = 36$, respectively) (Shirakami Mountains World Heritage Conservation Center, unpublished data).

In order to evaluate the completeness of our species collection in each trapping effort (=sample), we estimated true species richness in each forest cover type by using species-by-sample data with abundance-based coverage estimator (ACE) (Chao and Lee 1992). ACE is a non-parametric richness estimator, assuming that the observed number of species in a sample comprises a number of abundant (common) and rare (infrequent) species. We used a cut-off value of 10 for the “rare” or “infrequent” boundary for our study, as recommended by Chazdon et al. (1997). We used the software EstimateS to generate the ACE estimate (Colwell 2006) with 100 randomizations without replacement.

To measure the diversity of dung beetle assemblages in each forest cover type, we calculated species diversity by using the Shannon index H' (Shannon and Weaver 1949) and species evenness with Pielou J' (Pielou 1966):

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

$$J' = H' / \log_2 s \tag{2}$$

where s is the number of species and p_i is the proportion of the i th species in the sample. In addition, we estimated species richness by applying the rarefaction method (Sanders 1968; Hurlbert 1971), which compares species richness inherent in each subject area without being affected by dissimilar sample sizes:

$$E(S_n) = \sum_{i=1}^s \left[1 - \binom{N - N_i}{n} / \binom{N}{n} \right] \tag{3}$$

where $E(S_n)$ is the number of species in a sample of n individuals ($n \leq N$); N is the total number of individuals recorded; and N_i is the number of individuals in the i th species. We completed these operations by using the software R (R Development Core Team 2007).

Results

Fourteen species, composed of eight dwellers and six tunnellers, were confirmed by the inventory survey and pitfall-trap samplings (Table 1). The dung beetle abundance observed in the inventory survey was much lower in number than in the pitfall-trap sampling; however, the inventory survey succeeded in recording a higher number of species. Two species (out of 14), *Onthophagus nitidus* and *O. atripennis*, have not previously been observed in monkey feces according to review works by Kawai et al. (2005) and Koike et al. (2006a, b).

We confirmed the presence of dung beetles in 59 samples of feces (out of 667) in the inventory survey; only four species were observed at >10 individuals (Table 1). When evaluating the preference of these four species for fresh feces, all the species except *Aphodius hasegawai* avoided utilizing dry feces (Table 2). Only *A. eccoptus* selectively utilized fresh and half-dry feces. In terms of habitat utilization by these four species, *A. brevisculus* and *A. hasegawai* were mainly observed at an altitude below 300 m whereas *A. eccoptus* and *O. ater* were confirmed at almost every altitude where we collected feces (Fig. 2).

As a result of the trapping samplings, we confirmed the presence of eight species (5,645 individuals) in spring, four species (89) in summer, and two species (3) in autumn (Table 3). The expected true species richness, estimated using ACE, ranged from 1.00 to 8.58 species and, in primary broadleaf forests and coniferous plantations, ascended in the order: autumn $<$ summer $<$ spring. The completeness of the species collection from the three forest cover types in each season ranged from 66.67 to 100.00%; the mean value was 89.64%, which indicated that the sampling intensity of this study was adequate. It was remarkably low in autumn, indicating that a much greater sampling intensity was required to completely evaluate the species richness during this season when the absolute abundance of dung beetles was very small. During spring and summer, *A. eccoptus* was the common core-species in each forest cover type. The highest abundance and species richness of dung beetles were in primary forests in every season except autumn, and the indices of species diversity and evenness in this forest were calculated to be the lowest for the three forest cover types.

Table 1 Abundance of each dung beetle species utilizing Japanese monkey feces, observed by the inventory survey and baited pitfall trap experiments between July 2007 and June 2008 in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan

Family Species ^a	General body length (mm) ^b	Functional group	Inventory survey, <i>n</i> (%)	Baited pitfall traps, <i>n</i> (%)	Previous studies ^c
Scarabaeidae					
<i>Aphodius eccoptus</i>	7.5–9.4	Dweller	148 (49.33)	5,478 (95.49)	Yes
<i>A. superatratus</i>	6.0–9.6	Dweller	2 (0.67)	24 (0.42)	Yes
<i>A. hasegawai</i>	3.0–4.3	Dweller	17 (5.67)	14 (0.24)	Yes
<i>A. brevisculus</i>	4.0–6.0	Dweller	30 (10.00)	9 (0.16)	Yes
<i>A. igai</i>	5.5–9.0	Dweller	6 (2.00)	7 (0.12)	Yes
<i>A. unifasciatus</i>	4.5–6.8	Dweller	2 (0.67)	4 (0.07)	Yes
<i>A. madara</i>	3.5–4.1	Dweller		1 (0.02)	Yes
<i>A. isaburoi</i>	3.5–4.5	Dweller	2 (0.67)		Yes
<i>Onthophagus ater</i>	6.1–10.2	Tunneler	82 (27.33)	192 (3.35)	Yes
<i>O. nitidus</i>	5.0–8.2	Tunneler	5 (1.67)		No
<i>O. fodiens</i>	7.0–11.3	Tunneler	3 (1.00)		Yes
<i>O. aripennis</i>	5.0–10.1	Tunneler	1 (0.33)		No
Geotrupidae					
<i>Phelotrupes auratus</i>	12.4–22.0	Tunneler	1 (0.33)	2 (0.03)	Yes
<i>P. laevistriatus</i>	12.4–21.5	Tunneler	1 (0.33)	6 (0.10)	Yes
Abundance			300	5,737	
Number of species			13	10	

^a Scientific names of the species were according to Kawai et al. (2005)

^b Measured values in Japan, from Kawai et al. (2005)

^c Whether the species has been reported to utilize Japanese monkey feces in the previous studies (Kawai et al. 2005; Koike et al. 2006a, b)

Table 2 Preference of dung beetles (observed at >10 individuals) for fresh Japanese monkey feces, confirmed by the inventory survey between July 2007 and June 2008 in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan

Freshness of feces	<i>Aphodius eccoptus</i>		<i>Onthophagus ater</i>		<i>A. brevisculus</i>		<i>A. hasegawai</i>		Total number of feces samples collected <i>n</i> (%)
	<i>n</i> (%)	<i>P</i>	<i>n</i> (%)	<i>P</i>	<i>n</i> (%)	<i>P</i>	<i>n</i> (%)	<i>P</i>	
Fresh (completely wet)	73 (49.32)	+	71 (86.59)	+	23 (76.67)	+	5 (29.41)		231 (34.63)
Half-dry (wet inside and dry outside)	74 (50.00)	+	8 (9.76)	–	3 (10.00)	–	5 (29.41)		191 (28.64)
Dry (completely dry)	1 (0.68)	–	3 (3.66)	–	4 (13.33)	–	7 (41.18)		245 (36.73)
Total number of individuals	148		82		30		17		667

P means the species preference for fresh feces; plus (+) means significantly high preference and minus (–) means significantly low ($P < 0.05$). Each confidence interval was calculated by Bonferroni *z*-statistics (Neu et al. 1974)

We estimated rarefaction curves of dung beetle species only during spring when several species were observed in each forest cover type (Fig. 3). The expected species richness at *n* individuals, $E(S_n)$, was in the ascending order primary forests < coniferous plantations < secondary forests for $n < 400$ individuals; in actual figures, $E(S_{400})$ (\pm SD) was 3.65 ± 1.07 species in primary forests, 5.84 ± 0.84 species in coniferous plantations, and 5.98 ± 0.13 species in secondary forests.

Quantitative evaluation of day–night differences in the number of dung beetles observed in pitfall traps showed that most species were collected during the daytime; only

A. eccoptus swarmed over feces during the nighttime during spring and summer (Table 4).

Discussion

Diversity of dung beetle species in cool-temperate forests

Thus far, 29 species of temperate dung beetles, composed of 27 species of the family Scarabaeidae and 2 species of the family Geotrupidae, have been reported to utilize

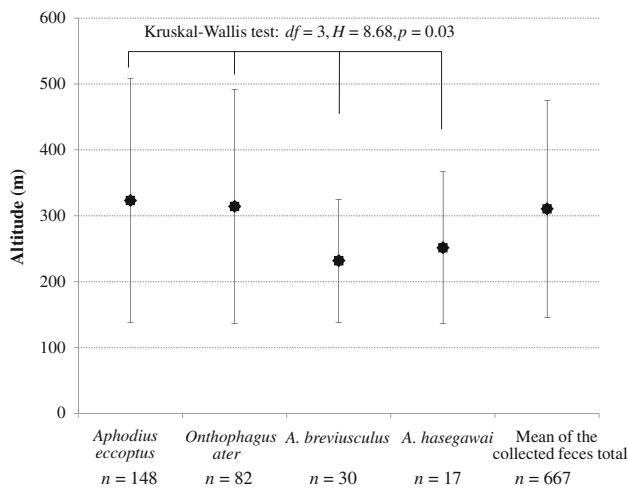


Fig. 2 Mean altitude occupied by four dung beetle species (of those with $n > 10$ individuals), observed by the inventory survey between July 2007 and June 2008 in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan. The bars inside the graph show SD

Japanese monkey feces, according to review works by Kawai et al. (2005) and Koike et al. (2006a, b). We did not observe 17 of the species (out of the 29 species) in this

study. Seven of these (*Caccobius nikkoensis*, *A. yamato*, *A. ishidai*, *A. ritsukoeae*, *A. tanakai*, *A. yasutakai*, and *Oxyomus ishidai*) are distributed only at much lower latitudes than this study area, four (*A. rectus*, *A. atratus*, *A. nigrotessellatus*, and *O. lenzii*) mainly inhabit open pasture or grassland, and one (*A. morii*) is mainly distributed in alpine regions at an altitude above 1,000 m (Kawai et al. 2005). For five of the species (*Copris actidens*, *Caccobius jessoensis*, *A. mizo*, *A. quadrates*, and *A. hibernalis*), we could not verify the reason for their absence in this study because of the lack of information about ecological characteristics. Considering this, it seems probable that 14 dung beetle species (including two newly-observed species) that we confirmed (Table 1) were most of the species utilizing monkey feces in cool-temperate forests.

The dung beetle species observed in the pitfall traps study during spring and summer were divided into two distinct types (Table 3): “core species”, which are abundant within sites and well spaced-out in niche space, and “satellite species”, which are sparse within sites and less spaced-out in niche space (Hanski 1982). The results obtained in this study clearly indicated that *A. eccoptus* was the core species in dung beetle assemblages in this area.

Table 3 Effects of seasonality and forest cover type on the composition of dung beetle species captured by pitfall traps baited with Japanese monkey feces in the northeastern Shirakami Mountains, located in northernmost part of mainland Japan, during August 2007–May 2008

Species	Spring			Summer			Autumn		
	Primary broadleaf forests n (%)	Coniferous plantations n (%)	Secondary broadleaf forests n (%)	Primary broadleaf forests n (%)	Coniferous plantations n (%)	Secondary broadleaf forests n (%)	Primary broadleaf forests n (%)	Coniferous plantations n (%)	Secondary broadleaf forests n (%)
<i>Aphodius eccoptus</i>	4,405 (98.83) ^c	676 (92.86) ^c	333 (72.39) ^c	37 (94.87) ^c	19 (55.88) ^c	6 (37.50)	1 (100.00)		1 (50.00)
<i>A. superatratus</i>	7 (0.16)	4 (0.55)	13 (2.83)						
<i>A. hasegawai</i>	7 (0.16)	5 (0.69)	2 (0.43)						
<i>A. brevisculus</i>	2 (0.04)	2 (0.27)	5 (1.09)						
<i>A. igai</i>		1 (0.14)	6 (1.30)						
<i>A. unifasciatus</i>	4 (0.09)								
<i>A. madara</i>				1 (2.56)					
<i>Onthophagus ater</i>	29 (0.65)	39 (5.36)	101 (21.96) ^c	1 (2.56)	12 (35.29)	10 (62.50)			
<i>Phelotrupes auratus</i>	2 (0.04)								
<i>P. laevistriatus</i>	1 (0.02)	1 (0.14)			3 (8.82)				1 (50.00)
Abundance	4,457	728	460	39	34	16	1	0	2
Number of species	8	7	6	3	3	2	1	0	2
ACE ^a	8.58	8.52	6.00	4.00	3.00	2.00	1.00	–	3.00
Completeness (%) ^b	93.24	82.16	100.00	75.00	100.00	100.00	100.00	–	66.67
Shannon index (H')	0.12	0.47	1.15	0.34	1.31	0.95	0.00	–	1.00
Pielou J'	0.04	0.17	0.44	0.22	0.83	0.95	–	–	1.00

^a Abundance-based coverage estimator (Chao and Lee 1992) with 100 randomizations without replacement

^b Percentage of ACE for number of species

^c The species with a significantly high frequency of occurrence within the forest cover type ($P < 0.05$). Confidence intervals were calculated by Bonferroni z -statistics (Neu et al. 1974)

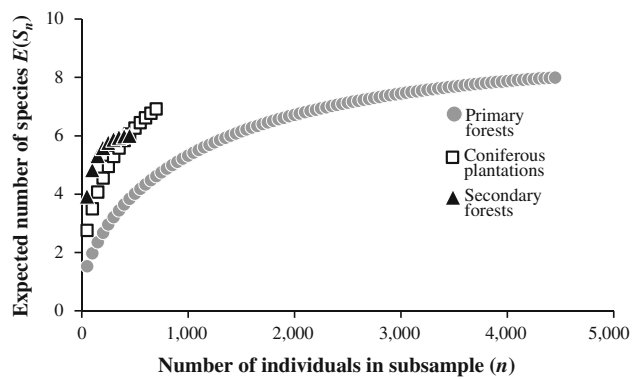


Fig. 3 Expected number of dung beetle species, $E(S_n)$, estimated by rarefaction method for each forest cover type in the northeastern Shirakami Mountains, located in northernmost part of mainland Japan, during May 2008

Table 4 Day–night differences between the number of dung beetles captured by pitfall traps baited with Japanese monkey feces in the northeastern Shirakami Mountains, located in the northernmost part of mainland Japan, during August 2007–May 2008

Species	Spring		Summer		Autumn		Total	
	n_d	n_n	n_d	n_n	n_d	n_n	n_d	n_n
<i>Aphodius eccoptus</i>	591	4,823	1	61	2	0	594	4,884
<i>A. superatratus</i>	21	3					21	3
<i>A. hasegawai</i>	8	6					8	6
<i>A. brevisculus</i>	9	0					9	0
<i>A. igai</i>	7	0					7	0
<i>A. unifasciatus</i>	4	0					4	0
<i>A. madara</i>			0	1			0	1
<i>Onthophagus ater</i>	165	4	21	2			186	6
<i>Phelotrupes auratus</i>	2	0					2	0
<i>P. laevistriatus</i>	2	0	3	0	1	0	6	0

n_d Number of species captured during the daytime, n_n number of species captured during the nighttime

Apart from an extremely high frequency of occurrence, they were acclimatized to the variety of forest types (Table 3) and altitudes (Fig. 2), and were less sensitive to the freshness of feces (Table 2), indicating that the species niche could be larger in width than that of the others. Interspecific competition among dweller species with a similar ecological niche often occurs (Cambefort and Hanski 1991). Given that the competition becomes more intense under limited resource conditions in cool-temperate forests, it is reasonable to assume that the abundance of most dweller species is highly affected by the core species.

Temporal changes of dung beetle assemblages

On the basis of diel activity changes, temperate dung beetle species are generally classified into two groups—diurnal and nocturnal types—except for some species (for example

O. lenzii) that seasonally switch their activity pattern between diurnal and nocturnal types (Sasayama et al. 1984; Koike et al. 2006a, b). The diel activities of temperate dung beetles are naturally determined by their oviposition behavior (Sasayama et al. 1984). Sasayama et al. (1984) reported that most middle-sized species (body length > 5 mm) are diurnal whereas most small-sized species (body length < 5 mm) are nocturnal. However, such ecological traits of the species diel rhythm are not necessarily supported by our results, considering that the core species (i.e. *A. eccoptus*), which is classified as middle-sized species (Table 1), was most active at night (Table 4).

In the northern Tohoku district, with vulnerable resource providers for dung beetle communities (see the “Introduction”), the monkey is one of the rare large mammals that provide stable resources (i.e. feces) for the communities. On the basis of our results (Table 4), all species were most active during daytime, except for *A. eccoptus*, which prefers monkeys’ feces to those of other large mammals inhabiting the study area (i.e. black bears and Japanese serows) (Enari et al., unpublished data). Such nocturnal species seemingly have a disadvantage in accessing fresh monkey feces because monkeys are diurnal mammals. It is quite likely that *A. eccoptus* has the species-specific trait of low sensitivity to the freshness of feces (Table 2) to compensate for this disadvantage. However, we do not have enough information on the life-history traits of the cool-temperate species to further discuss the eco-physiological aspects on this species-specific diel rhythm here.

Our results clearly showed that the prevalence of dung beetle species drastically changes during the year (Table 3). The seasonal prevalence of temperate dung beetle species is usually determined by each species-specific oviposition period (Sasayama et al. 1984; Yasuda 1984). Thus far, it has been reported that the species with peak activity in autumn are *O. ater*, *A. madara*, and *A. superatratus* (Yasuda 1984; Koike et al. 2006b) and that in summer is *Phelotrupes auratus* (Kawai et al. 2005; Koike et al. 2006a, b); however, this is not supported by our results (Table 3). It is possible that locally specific climate conditions in this region affect the life-history traits of the species. Sasayama et al. (1984) empirically demonstrated that the air temperature that temperate dung beetle species can withstand generally ranges from 10–28°C and the optimum range is 19–24°C. This probably explains the finding that most dung beetle species were not observed during autumn in this study (Table 3) because the diurnal and nocturnal air temperatures in this study period were in the ranges 3.7–16.4 and 3.8–10.7°C, respectively (Shirakami Mountains World Heritage Conservation Center, unpublished data). Further eco-physiological studies focusing on the cool-temperate species could clarify this seasonal prevalence.

Effect of human-induced forest disturbance on dung beetle assemblages

Dung beetles have often been utilized as an environmental bioindicator species because they are highly sensitive to environmental disturbance such as vegetation changes and forest fragmentation (Davis et al. 2001; Halffter and Arellano 2002; McGeoch et al. 2002). Intermediate human-induced forest disturbance (i.e. the formation of secondary forests) creates microsites without any vegetation cover (i.e. forest gaps) across the area. These microsites are generally avoided by forest dung beetle species (Sasayama et al. 1984; Halffter and Arellano 2002). Shrubby or climbing plants that bear berries flourish at these microsites in temperate forests; therefore, most frugivorous mammalian fauna, including monkeys, are attracted to such secondary forests (Hanya et al. 2005). In fact, the density of the monkey population in secondary forests was the highest in the study area (see the section “Study animals”). This means that the amount of feces available for dung beetles is increased by moderate forest disturbance. In brief, it may be considered that the formation of secondary forests concurrently has both positive (i.e. increasing feces) and negative effects (i.e. declining habitat quality for forest dung beetles) on species assemblages.

Although our results showed the Shannon index was higher for the secondary forest than the primary forest (Table 3), it does not imply that the secondary forest sustains more dung beetle species than the primary forest, as also shown in the value of ACE. This is because the core species (*A. eccoptus*) with its high frequency of occurrence drove down the value of the Shannon index in the primary forest. Davis et al. (2001) demonstrated, in the tropical forests of Borneo, that the formation of secondary forests has potentially catastrophic effects on species adapted to survive in primary forests. However, it creates opportunities for some species limited to forest gaps to expand their distribution; consequently, total species richness increases (Davis et al. 2001). We did not observe any dung beetle species specializing in open land only (Table 1), indicating that forest disturbance could not lead to increasing species richness in this cool-temperate forest, where the dung beetle fauna is originally poor. In conclusion, our findings regarding the species diversity of dung beetle assemblages revealed that the negative effects of forest disturbance (declining habitat quality) on the distribution and composition of dung beetle species was stronger than its positive effects (increasing feces) in cool-temperate forests.

The diversity indices of coniferous plantations were between those of primary and secondary forests (Table 3). Mature cedar-plantation with a closed canopy is generally of small value in providing feeding sites for monkeys (Hanya et al. 2005; Agetsuma 2007), indicating that the

supply of monkey feces could be small in this type of forest. Our results showed the biomass of the core species (i.e. *A. eccoptus*) in the primary forest was six times that in the mature cedar-plantation during spring (Table 3), although the differences between in microhabitat conditions for dung beetle species in these forests could be small (because both commonly have closed canopies and sparse undergrowth). Thus, these results may indicate that the amount of feces supplied has some effect in determining the biomass of core species under similar environmental conditions in cool-temperate forests.

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