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

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29

30 **Abstract**

31 Very few attempts have been made at ecological investigations of the distribution and  
32 composition of dung beetle species utilizing feces of wild mammals, especially in  
33 cool-temperate forests. This paper recorded and evaluated the community structure of dung  
34 beetle species utilizing feces of Japanese monkeys (*Macaca fuscata*) by conducting a  
35 macro-scale inventory survey in the northeastern Shirakami Mountains, located in the  
36 northernmost part of mainland Japan. Moreover, to assess the influence of human-induced forest  
37 disturbance on species assemblages in this cool-temperate area, in this study we carried out field  
38 sampling using pitfall traps baited with monkey feces in primary forests, secondary forests, and  
39 coniferous plantations, during every season except winter. Our findings were as follows: (1) 14  
40 dung beetle species comprising eight dwellers and six tunnellers utilized monkey feces; (2)  
41 *Aphodius eccoptus* was the core species in dung beetle assemblages attracted to the feces during  
42 spring and summer; (3) the frequency of occurrence of every species was prominently high in  
43 spring; and (4) human-induced forest disturbance did not increase species richness or biomass in  
44 cool-temperate forests.

45

46 **Key-words:** cool-temperate forest; dung beetle; *Macaca fuscata*; pitfall trap; Shirakami  
47 Mountains.

48 **Introduction**

49 Coprophagous dung beetles have the highest species richness and biomass among insect  
50 fauna utilizing animal feces in natural ecosystems (Yasuda 1996). Apart from being recognized  
51 as important decomposer organisms (involved with nutrient recycling) (Hanski and Krikken,  
52 1991), they have recently received increasing attention to their ecological role as a secondary  
53 seed disperser (Estrada and Coates-Estrada 1991; Vullnec 2002). It has been reported worldwide  
54 that the species diversity of dung beetles has been rapidly decreasing with fragmentation and  
55 isolation of their habitats arising directly or indirectly due to increasing human activities (Klein  
56 1989; Davis et al. 2001; Halfpeter and Arellano 2002; Feer and Hingrat 2004). There are 152  
57 species and 9 subspecies of indigenous dung beetles on the Japanese archipelago (Kawai et al.  
58 2005). Forty-five percent of these have been recognized as a vulnerable or endangered species  
59 (Imura 2007) and appropriate conservation initiatives are required for their protection  
60 (Tsukamoto 2003).

61 In Japan, most ecological-studies on dung beetle species have been performed in open  
62 pastures for investigating their functions as biological pest control such as controlling livestock  
63 parasites by removing of sources of infection (Sasayama et al. 1984; Yasuda 1984; Kuramochi  
64 et al. 2000; Yamada et al. 2007; Imura 2007). Hence, little attention has been given to the  
65 distribution and composition of forest dung beetle species, especially in the cool-temperate zone.  
66 The diversity of forest dung beetle assemblages in the area concerned is generally influenced by  
67 the distribution and composition of existing wild mammals that provide the essential resource  
68 (i.e., feces) on which the dung beetles feed or oviposit (Fincher et al. 1970; Hanski and  
69 Cambefort 1991a; Yasuda 1996; Feer and Hingrat 2004). There have been, however, only  
70 several studies, including unpublished reports, that focus on interspecies relationships between  
71 temperate dung beetles and wild mammals (e.g., for sika deer [*Cervus nippon*]: Ikeda et al.

72 2002; Kanda et al. 2005; Koike et al. 2006a, for Asiatic black bears [*Ursus thibetanus*]: Koike et  
73 al. 2006b). The same holds true for Japanese monkeys (*Macaca fuscata*), although this animal is  
74 one of the most widespread forest mammals in Japan inhabiting climatic zones ranging from  
75 subtropical to cool-temperate (Biodiversity Center of Japan 2004).

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

89 The diversity of dung beetle species is highly sensitive not only to the availability of feces (as  
90 mentioned before) but also to environmental conditions such as vegetation cover type and soil  
91 conditions (Nealis 1977; Doube 1983). It has been recognized that human-induced habitat  
92 disturbance cannot be disregarded in evaluating the species diversity in the area concerned  
93 (Klein 1989; Davis et al. 2001; Halffter and Arellano 2002). We conducted field samplings,  
94 during every season except winter (i.e., the hibernation period), to quantitatively clarify the  
95 differences in dung beetle assemblages in primary forests, secondary forests, and coniferous

96 plantations in the mountains using pitfall traps baited with monkey feces. In this paper, we  
97 discuss the direct and indirect influence of human-induced forest disturbance on the distribution  
98 and composition of dung beetle species in cool-temperate forests, with reference to the changes  
99 in monkey distribution.

## 100 **Materials and Methods**

### 101 **Study area**

102 The Shirakami Mountains are one of the most extensive cool-temperate primary forests in  
103 East Asia, and has been designated as one of World Natural Heritage Sites by UNESCO since  
104 1993. We defined an area of approximately 12 × 16 km to record dung beetle species on the  
105 northeastern side of the mountains (Fig. 1). This area is the transition zone from human  
106 settlements to inner montane areas. The altitude of the area ranges from 50 m to 1,000 m above  
107 sea level. Human settlements are concentrated in the narrow flatlands along rivers at an altitude  
108 below 200 m and are located in the northeastern side of the area. Of the forested area, primary  
109 forests, mainly composed of Japanese beech (*Fagus crenata*) trees, are located in the inner  
110 montane area (the southwest side of the area). Secondary forests of beech and oak (*Quercus*  
111 *mongolica* var. *crispula*) trees and mature coniferous plantations of Japanese cedar  
112 (*Cryptomeria japonica*) are located near the settlements (mainly the northeast side of the area).  
113 The total areas of each forest cover type (primary, secondary, and plantation forests) were similar.  
114 Dwarf bamboo (*Sasa kurilensis*) commonly dominates the forest floors in mildly sloped  
115 broadleaf forests, while sparse forest floor plants grow in primary forests and mature coniferous  
116 plantations.

117 The area comes under the cool-temperate climatic zone. The mean air temperature ( $\pm$  SD)  
118 between May 2007 and June 2008 was  $11.6 \pm 8.8$  °C (Japan Meteorological Agency 2009). The  
119 annual precipitation amount in 2007 was 1,168 mm. The period of snowfall usually lasted from

120 early December to late March, with a maximum snow depth of 2 m in lowland areas and 3–5 m  
121 in mountainous areas. Fourteen species of middle- and large-sized mammals—such as Japanese  
122 monkeys, Asiatic black bears, Japanese serows (*Capricornis crispus*), martens (*Martes*  
123 *melampus*), raccoon dogs (*Nyctereutes procyonoides*), badgers (*Meles meles*), and hares (*Lepus*  
124 *brachyurus*), but not sika deer and wild boar—are confirmed in this area (Biodiversity Center of  
125 Japan 2004).

## 126 **Study animals**

127 Coprophagous dung beetles are classified as part of the superfamily Scarabaeoidea and  
128 utilize excrements and carcasses of animals as their food resource (Tsukamoto 1998). Dung  
129 beetles are commonly divided into three main functional groups according to their  
130 feces-processing behavior: (1) tunnellers, which make a burrow under the fecal pat and bring  
131 feces inside for feeding or breeding; (2) dwellers, which feed in the fecal pat and oviposit under  
132 or inside the pat; and (3) rollers, which make a fecal ball to transport feces away from the fecal  
133 pat and then bury it for feeding or breeding (Cambefort and Hanski 1991). Thus far, there has  
134 been no scientific report relating to the dung beetle fauna in and around the study area.

135 Japanese monkeys are gregarious forest mammals and naturally move in troops within a  
136 steady range. Monkeys inhabiting the Shirakami Mountains constitute the largest local  
137 population in the northern Tohoku district of Japan. The animals are continuously distributed in  
138 and around the study area (Enari et al. 2006). The mean size of the troops in the area is 23  
139 individuals (range 10–44,  $n = 8$ ). The mean population density of the animals in the study area is  
140 approximately 5 individuals/km<sup>2</sup>, or 0.2 troops/km<sup>2</sup>. Their distribution is heterogeneous in the  
141 area; it is high in secondary forests around human settlements and low in inner montane primary  
142 forests (Enari H, unpublished data). The monkeys in the mountains mainly feed on young leaves  
143 of broadleaf trees in spring, herbaceous plants and insects in summer, berries and nuts in autumn,

144 and bark and buds of broadleaf trees in winter (Enari et al. 2005).

### 145 **Inventory survey**

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

### 162 **Quantitative evaluation of dung beetle species by baited pitfall traps**

163 The technique using baited pitfall traps set on a transect can provide a fast, inexpensive, and  
164 relatively unbiased method in order to evaluate the diversity of dung beetle species in a site  
165 (Larsen and Forsyth 2005). The design of baited pitfall traps that we used was based on that of  
166 Hoga (1984). These traps were made from plastic containers (14 cm in diameter and 10 cm  
167 deep) and plastic cups (8 cm in diameter and 5 cm deep). First, each container holding 50%



168 ethylene glycol (used as a preserving fluid) was buried to its rim in the ground. Then, each cup  
169 was hung using wire in the container. Finally, fresh monkey feces (15 g) were put into each cup;  
170 the weight of feces under test was determined according to the mean weight of monkey feces ( $\pm$   
171 SD) in the area ( $12.0 \pm 9.8$  g,  $n = 489$ ). The freshness of animal feces generally influences its  
172 attractiveness to dung beetles (Masumoto 1973). Therefore, we collected fresh feces by  
173 following radio-tagged monkeys immediately before each study period, and stored them in  
174 airtight containers at  $-20$  °C. These feces were used in traps after they were completely thawed.  
175 The difference in the attractiveness between fresh and refrigerated feces to dung beetle species is  
176 generally small (Ikeda et al. 2002; Koike et al. 2006b).

177 Three traps were set at intervals of 10 m along a transect each in a primary beech forest with  
178 a closed canopy (located in inner mountains at 288 m elevation), a secondary beech-oak forest  
179 with an open canopy (located near human settlements at 275 m elevation), and a mature  
180 cedar-plantation with a closed canopy (located between the primary and secondary forests at 273  
181 m elevation) (Fig .1). Taking into account the diel and seasonal changes of the species-specific  
182 activity patterns, we conducted the samplings over three consecutive days in each season (22–24  
183 August, 2007 [summer], 23–25 October, 2007 [autumn], and 22–24 May, 2008 [spring]); at  
184 sunrise and sunset, and all trapped dung beetles were collected and spent feces were replaced  
185 with new. There was continuous sunny weather during every sampling period. The mean air  
186 temperature ( $\pm$  SD) during the study periods were; in summer,  $22.7 \pm 3.4$  °C during the daytime,  
187 and  $16.8 \pm 2.6$  °C during the nighttime; in autumn,  $12.2 \pm 3.3$  °C during the daytime, and  $8.3 \pm$   
188  $2.4$  °C during the nighttime; and in spring,  $19.5 \pm 3.5$  °C during the daytime,  $12.8 \pm 2.0$  °C  
189 during nighttime ( $n = 36$ , respectively) (Shirakami Mountains World Heritage Conservation  
190 Center, unpublished data).

191 In order to evaluate the completeness of our species collection in each trapping effort (=

192 sample), we estimated true species richness in each forest cover type, by using  
 193 species-by-sample data with abundance-based coverage estimator (ACE) (Chao and Lee 1992).  
 194 ACE is a nonparametric richness estimator, assuming that the observed number of species in a  
 195 sample comprises a number of abundant (common) and rare (infrequent) species, respectively.  
 196 We employed a cut-off value of 10 for the “rare” or “infrequent” boundary for our study as  
 197 recommended by Chazdon et al. (1997). We used the software EstimateS to generate the ACE  
 198 estimate (Colwell 2006) with 100 randomizations without replacement.

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

$$202 \quad H' = -\sum_{i=1}^s p_i \log_2 p_i \quad (1)$$

$$203 \quad J' = H' / \log_2 s \quad (2)$$

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

$$208 \quad E(S_n) = \sum_{i=1}^s \left[ 1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right] \quad (3)$$

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

## 212 **Results**

213 Fourteen species, composed of eight dwellers and six tunnellers, were confirmed by the

214 inventory survey and pitfall-trap samplings (Table 1). The dung beetle abundance observed in  
215 the inventory survey was much lower in number than in the pitfall-trap samplings; however, the  
216 inventory survey succeeded in recording a higher number of species. Two species (out of 14),  
217 *Onthophagus nitidus* and *O. atripennis*, have never been observed in monkey feces according to  
218 review works by Kawai et al. (2005) and Koike et al. (2006a, 2006b).

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

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

238 forest were calculated to be the lowest of the three forest cover types.

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

245 Quantitative evaluation of day-night differences in the number of dung beetles observed in  
246 pitfall traps showed that most species were collected during the daytime; while, only *A. eccoptus*  
247 swarmed over feces during the nighttime during spring and summer (Table 4).

## 248 **Discussion**

### 249 **Diversity of dung beetle species in cool-temperate forests**

250 Thus far, 29 species of temperate dung beetles, composed of 27 species of the family  
251 Scarabaeidae and 2 species of the family Geotrupidae, have been reported to utilize Japanese  
252 monkey feces, according to review works by Kawai et al. (2005) and Koike et al. (2006a,  
253 2006b). We did not observe the 17 species (out of the 29 species) in the present study. Seven of  
254 these (i.e., *Caccobius nikkoensis*, *A. yamato*, *A. ishidai*, *A. ritsukoae*, *A. tanakai*, *A. yasutakai*,  
255 and *Oxyomus ishidai*) are only distributed in much lower latitudes than the present study area,  
256 four (*A. rectus*, *A. atratus*, *A. nigrotessellatus*, and *O. lenzii*) mainly inhabit open pasture or  
257 grassland, and one (*A. morii*) is mainly distributed in alpine regions at an altitude above 1,000 m  
258 (Kawai et al. 2005); meanwhile, as for five of these (*Copris actidens*, *Caccobius jessoensis*, *A.*  
259 *mizo*, *A. quadrates*, and *A. hibernalis*), we cannot verify the reason for their absent in the present  
260 study due to the lack of information about ecological characteristics. Considering this, it seems  
261 probable that 14 dung beetle species (including two newly-observed species) that we confirmed

262 (Table 1) were most of the species utilizing monkey feces in cool-temperate forests.

263 The dung beetle species observed in the pitfall traps study during spring and summer were  
264 divided into two distinct types (Table 3): “core species,” which are abundant within sites and  
265 well spaced-out in niche space, and “satellite species,” which are sparse within sites and less  
266 spaced-out in niche space (Hanski 1982). The present data clearly indicated that *A. eccoptus* was  
267 the core species in dung beetle assemblages in this area. Apart from showing extremely high  
268 frequency of occurrence, they were acclimatized to the variety of forest types (Table 3) and  
269 altitudes (Fig. 2), and were less sensitive to the freshness of feces (Table 2), indicating that the  
270 species niche could be larger in width than that of the others. Interspecific competition among  
271 dweller species with a similar ecological niche often occurs (Cambefort and Hanski 1991).  
272 Given that the competition becomes more intense under limited resource conditions in  
273 cool-temperate forests, it is reasonable to consider that the abundance of most dweller species is  
274 stringently controlled by the core species.

### 275 **Temporal changes of dung beetle assemblages**

276 Based on diel activity changes, temperate dung beetle species are generally classified into  
277 two groups—diurnal and nocturnal types—except for some species (such as *O. lenzii*) that  
278 seasonally switch their activity pattern between diurnal and nocturnal types (Sasayama et al.  
279 1984; Koike et al. 2006a, 2006b). The diel activities of temperate dung beetles are naturally  
280 determined by their oviposition behavior (Sasayama et al. 1984). Sasayama et al. (1984)  
281 reported that most middle-sized species (body length > 5 mm) are diurnal, while most  
282 small-sized species (body length < 5 mm) are nocturnal. However, such ecological traits of the  
283 species diel rhythm do not necessarily support the present result, considering that the core  
284 species (i.e., *A. eccoptus*), which is classified as middle-sized species (Table 1), exhibited peak  
285 activity at night (Table 4).

286 In the northern Tohoku district, which with vulnerable resource providers for dung beetle  
287 communities (see Introduction), the monkey is one of the rare large mammals that provide stable  
288 resources (i.e., feces) for the communities. Based on our result (Table 4), all species showed an  
289 activity peak during daytime, except for *A. eccoptus*, which prefers monkeys' feces over that of  
290 other large mammals inhabiting the study area (i.e., black bears and Japanese serows) (Enari et  
291 al., unpublished data). Such nocturnal species seemingly have a disadvantage in accessing fresh  
292 monkey feces because monkeys are diurnal mammals. It is quite likely that *A. eccoptus* exhibits  
293 the species-specific trait of low sensitivity to the freshness of feces (Table 2) to compensate for  
294 this disadvantage. However, we do not have enough information on the life-history traits of the  
295 cool-temperate species to further discuss the eco-physiological aspects on this species-specific  
296 diel rhythm here.

297 Our data clearly showed that the prevalence of dung beetle species drastically changes during  
298 the year (Table 3). The seasonal prevalence of temperate dung beetle species is usually  
299 determined by each species-specific oviposition period (Yasuda 1984; Sasayama et al. 1984).  
300 Thus far, it has been reported that the species with peak activity in autumn are *O. ater*, *A.*  
301 *madara*, and *A. superatratus* (Yasuda 1984; Koike et al. 2006b) and that in summer is  
302 *Phelotrupes auratus* (Kawai et al. 2005; Koike et al. 2006a, 2006b); however, this is not  
303 supported by our results (Table 3). It is possible that locally specific climate conditions in this  
304 region influence the life-history traits of the species. Sasayama et al. (1984) empirically  
305 demonstrated that the air temperature that temperate dung beetle species can withstand generally  
306 ranges 10–28 °C and its optimal range is 19–24 °C. This most likely explains the finding that  
307 most dung beetle species were not to be observed during autumn in the present study (Table 3)  
308 because the diurnal and nocturnal air temperature in this study period ranged 3.7–16.4 °C and  
309 3.8–10.7 °C, respectively (Shirakami Mountains World Heritage Conservation Center,

310 unpublished data). Further eco-physiological studies focusing on the cool-temperate species  
311 could clarify this seasonal prevalence.

### 312 **Influence of human-induced forest disturbance on dung beetle assemblages**

313 Dung beetles have often been utilized as an environmental bioindicator species because they  
314 are highly sensitive to environmental disturbance such as vegetation changes and forest  
315 fragmentation (Davis et al. 2001; McGeoch et al. 2002; Halffter and Arellano 2002).

316 Intermediate human-induced forest disturbance (i.e., the formation of secondary forests) creates  
317 microsites without any vegetation cover (i.e., forest gaps) across the area. These microsites are  
318 generally avoided by forest dung beetle species (Sasayama et al. 1984; Halffter and Arellano  
319 2002). Shrubby or climbing plants that bear berries flourish at these microsites in temperate  
320 forests; therefore, most frugivorous mammalian fauna, including monkeys, are attracted to such  
321 secondary forests (Hanya et al. 2005). In fact, the density of the monkey population in secondary  
322 forests is the highest in the study area (see “Study animals”). This means that the amount of  
323 available feces for dung beetles is increased by a moderate forest disturbance. In brief, it may be  
324 considered that the formation of secondary forests concurrently has both positive (i.e., increasing  
325 feces) and negative effects (i.e., declining habitat quality for forest dung beetles) on species  
326 assemblages.

327 Although the present data showed that the Shannon index was higher for the secondary forest  
328 than the primary forest (Table 3), it does not imply that the secondary forest sustain more dung  
329 beetle species than the primary forest, as also shown in the value of ACE. This is because the  
330 core species (*A. eccoptus*) with its high frequency of occurrence drove down the value of  
331 Shannon index in the primary forest. Davis et al. (2001) demonstrated, in the tropical forests of  
332 Borneo, that the formation of secondary forests has potentially catastrophic impacts on species  
333 adapted to survive in primary forests. However, it creates opportunities for certain species

334 limited to forest gaps to expand their distribution; consequently, the total species richness  
335 increases (Davis et al. 2001). We did not observe any dung beetle species only specializing in  
336 open land (Table 1), indicating that the forest disturbance could not lead to increasing species  
337 richness in this cool-temperate forest, where the dung beetle fauna is originally poor. In  
338 conclusion, our findings regarding to the species diversity of dung beetle assemblages  
339 demonstrated that the negative effects of forest disturbance (declining habitat quality) on the  
340 distribution and composition of dung beetle species was stronger than its positive effects  
341 (increasing feces) in cool-temperate forests.

342 The diversity indices of coniferous plantations showed intermediate values between primary  
343 and secondary forests (Table 3). Mature cedar-plantation with a closed canopy is generally of  
344 small value in providing feeding sites for monkeys (Hanya et al. 2005; Agetsuma 2007),  
345 indicating that the supply of monkey feces could be small in this forest cover. The present data  
346 showed the biomass of the core species (i.e., *A. eccoptus*) in the primary forest was six times that  
347 of the mature cedar-plantation during spring (Table 3), although the difference in microhabitat  
348 conditions for dung beetle species between both forests cover types could be small (because  
349 both commonly have closed canopies and sparse undergrowth). Thus, these results may indicate  
350 that the amount of feces supplied has some effect in determining the biomass of core species  
351 under similar environmental conditions in cool-temperate forests.

352



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## Figure legends

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.

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.

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 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 <sup>a</sup>	General body length (mm) <sup>b</sup>	Functional group	Inventory survey <i>n</i> (%)	Baited pitfall traps <i>n</i> (%)	Previous <sup>c</sup> studies
<b>Scarabaeidae</b>					
<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	tunneller	82 (27.33)	192 (3.35)	yes
<i>O. nitidus</i>	5.0–8.2	tunneller	5 (1.67)		no
<i>O. fodiens</i>	7.0–11.3	tunneller	3 (1.00)		yes
<i>O. atripennis</i>	5.0–10.1	tunneller	1 (0.33)		no
<b>Geotrupidae</b>					
<i>Phelotrupes auratus</i>	12.4–22.0	tunneller	1 (0.33)	2 (0.03)	yes
<i>P. laevistriatus</i>	12.4–21.5	tunneller	1 (0.33)	6 (0.10)	yes
Abundance			300	5,737	
Number of species			13	10	

<sup>a</sup>Scientific names of the species were according to Kawai et al. (2005).

<sup>b</sup>Measured values in Japan that were derived from Kawai et al. (2005).

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



Table 2. Preference of dung beetles (observed at >10 individuals) for the freshness of 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 collected feces
	<i>n</i> (%)	<i>P</i> <sup>a</sup>	<i>n</i> (%)	<i>P</i> <sup>a</sup>	<i>n</i> (%)	<i>P</i> <sup>a</sup>	<i>n</i> (%)	<i>P</i> <sup>a</sup>	<i>n</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

<sup>a</sup>*P* means the species preference for the freshness of feces; plus (+) means significantly high preference and minus (–) means significantly low (*p* < 0.05).

Each confidential interval was calculated by Bonferroni *z*-statistics (Neu et al. 1974).

Table 3. Influences 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 to May 2008.

Species	Spring			Summer			Autumn		
	Primary broadleaf forests	Coniferous plantations	Secondary broadleaf forests	Primary broadleaf forests	Coniferous plantations	Secondary broadleaf forests	Primary broadleaf forests	Coniferous plantations	Secondary broadleaf forests
	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)
<i>Aphodius eccoptus</i>	<sup>c</sup> 4405 (98.83)	<sup>c</sup> 676 (92.86)	<sup>c</sup> 333 (72.39)	<sup>c</sup> 37 (94.87)	<sup>c</sup> 19 (55.88)	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. brevisusculus</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)	<sup>c</sup> 101 (21.96)	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	4457	728	460	39	34	16	1	0	2
Number of species	8	7	6	3	3	2	1	0	2
ACE <sup>a</sup>	8.58	8.52	6.00	4.00	3.00	2.00	1.00	—	3.00
Completeness (%) <sup>b</sup>	93.24	82.16	100.00	75.00	100.00	100.00	100.00	—	66.67
Shannon index ( <i>H'</i> )	0.12	0.47	1.15	0.34	1.31	0.95	0.00	—	1.00
Pielou <i>J'</i>	0.04	0.17	0.44	0.22	0.83	0.95	—	—	1.00

<sup>a</sup>Abundance-based coverage estimator (Chao and Lee 1992) with 100 randomizations without replacement.

<sup>b</sup>Percentage of ACE for number of species.

<sup>c</sup>The species that showed the significantly high frequency of occurrence within the forest cover type ( $P < 0.05$ ). Confidential intervals were calculated by Bonferroni  $z$ -statistics (Neu et al. 1974).

Table 4. Day-night differences of 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	4823	1	61	2	0	594	4884
<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.

Figure 1. / Enari et al.

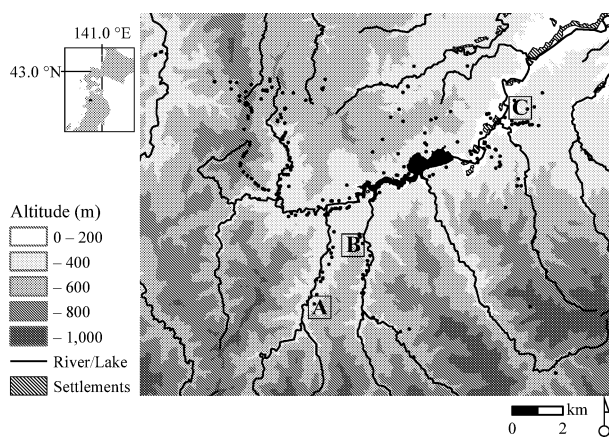


Figure 2. / Enari et al.

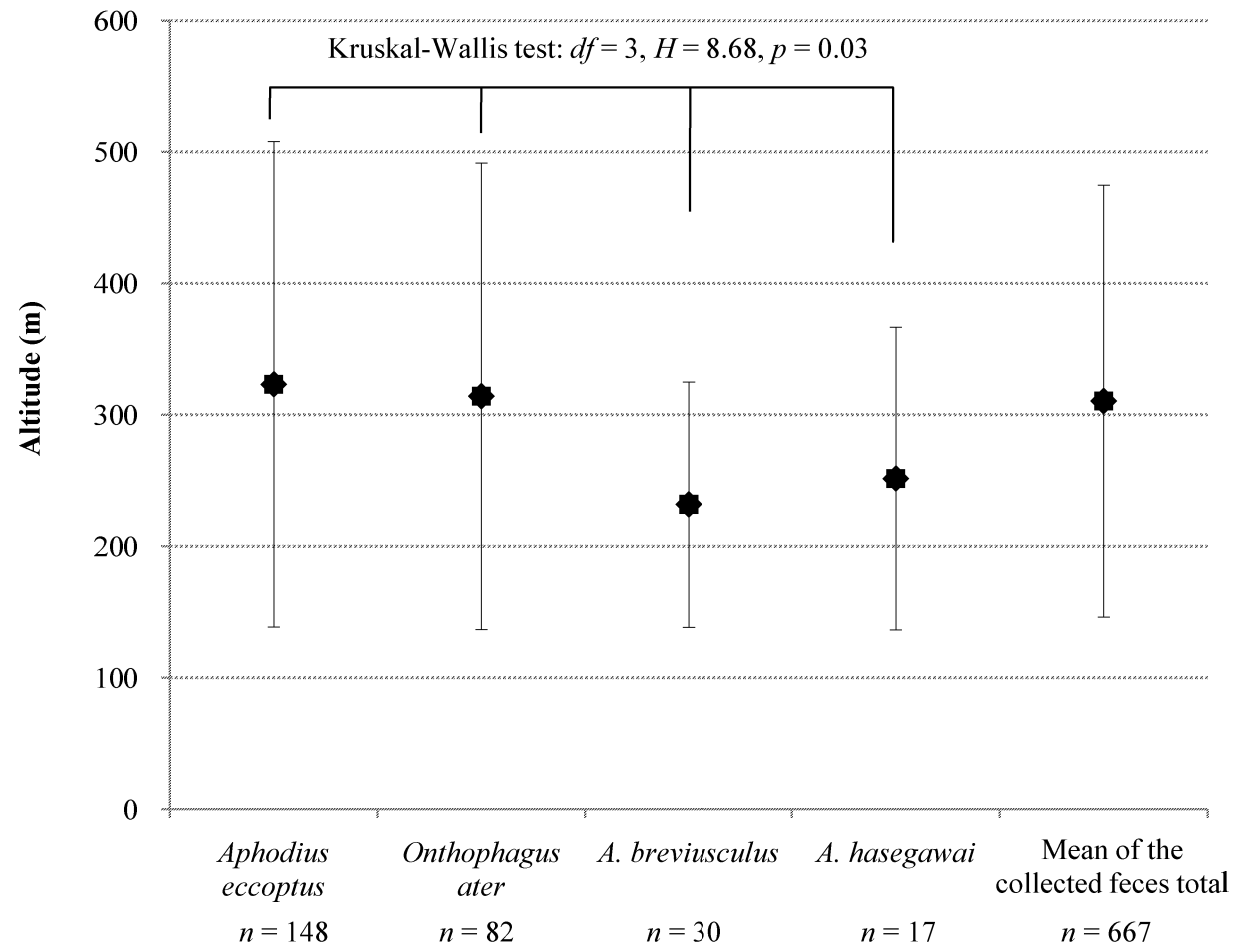


Figure 3. / Enari et al.

