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4 **Ecological implications of mammal feces buried in snow through dung beetle activities**

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23 **Abstract**

24 In early spring, snow-buried mammal feces simultaneously emerge on the ground with the  
25 melting of the snow across heavy snowfall regions. Here we evaluated ecological implications  
26 of this phenomenon for the cool-temperate forest ecosystem in terms of the resource use of dung  
27 beetles (Coleoptera: Scarabaeidae), which have key roles of secondary seed dispersal and  
28 nutrient cycling. During May 2012 and 2013, we conducted cafeteria experiments in heavy  
29 snowfall regions with different forest covers in northern Japan by using pitfall traps baited with  
30 the snow-buried feces of Japanese macaques (*Macaca fuscata*), Japanese serows (*Capricornis*  
31 *crispus*), and Japanese hares (*Lepus brachyurus angustidens*). From the experiments, we  
32 identified 12 dung beetle species, indicating that the snow-buried feces could act as a valuable  
33 resource for vernal beetles. Most of the beetles had obvious fecal preferences. The snow-buried  
34 feces of serows were widely available resources for most vernal species, including dwellers and  
35 tunnelers, contributing to the biomass of those species. Although dung beetles using  
36 snow-buried feces in young broadleaf forests with rich feces supplies did not always exhibit the  
37 highest species richness, tunnelers frequently emerged in those forests and *Phelotrupes*  
38 preferred macaque feces. This finding could have important implications for plant regeneration  
39 as it relates to time-lagged mammal–beetles interactions. Endozoochorous seeds dispersed by  
40 macaques in the autumn have insufficient opportunities for secondary seed dispersal by beetles  
41 owing to their inactivity season, but those seeds are protected against predation by snow during  
42 winter and are safely preserved under soil by vernal tunnelers.

43 **Key words:** biological interaction; *Capricornis crispus*; dung beetle; *Lepus brachyurus*;  
44 *Macaca fuscata*

45

46 **Introduction**

47       The ecosystem functions provided by dung beetles (Coleoptera: Scarabaeidae), such as  
48 secondary seed dispersal and nutrient cycling, have attracted increasing attention from  
49 ecologists (Andresen and Feer 2005; Nichols et al. 2008). However, ecological knowledge  
50 regarding the seasonal distribution and prevalence of forest dung beetles has been accumulated  
51 only in limited landscapes across lower latitude regions (mostly the tropics). Based on recent  
52 evidence, it has been thought that the seasonal emergence of most dung beetles positively  
53 correlates with the rise of the ambient temperature and precipitation caused by the change in  
54 season (Doube et al. 1991; Morelli et al. 2002; Andresen 2005; Vernes et al. 2005; Nyeko 2009).  
55 In contrast, this correlation is not applicable to heavy snowfall regions, where the abundance  
56 and species richness of dung beetles are higher in spring, with a cooler and dryer climate, than  
57 in summer (Enari et al. 2011, 2013). The ecological rationale for this specific seasonal  
58 prevalence of dung beetles has remained unclear thus far.

59       The diversity and biomass of dung beetles have been shown to be sensitive to the  
60 availability of resources, i.e., dung (Hanski and Cambefort 1991b; Nichols et al. 2009). Here we  
61 focused on mammal feces buried in the snow during the winter. Snow-buried feces  
62 simultaneously emerge on the ground with the melting of the snow in early spring. In the  
63 northernmost mainland of Japan, which has some of the heaviest snowfall in the world, three  
64 mammals with similar winter food habits (see below for details)—Japanese macaques (*Macaca*  
65 *fuscata*), Japanese serows (*Capricornis crispus*), and Japanese hares (*Lepus brachyurus*  
66 *angustidens*)—are widely distributed. The estimated total amounts of their snow-buried feces  
67 are 56.6 kg/km<sup>2</sup> for macaques, 28.8 kg/km<sup>2</sup> for hares, and 76.8 kg/km<sup>2</sup> for serows—provided  
68 that the snowfall period lasts approximately 120 days from December to March; that the mean

69 population density is 5.9 individuals/km<sup>2</sup> for macaques (Enari and Sakamaki 2011), 60  
70 individuals/km<sup>2</sup> for hares (Yatake et al. 2003), and four individuals/km<sup>2</sup> for serows (Mizuno,  
71 Ueuma and Ibaraki, 1982); and that the fecal mass per day is 80 g for macaques (Enari H.,  
72 unpublished data), 40 g for hares (Hiraoka et al. 1977), and 160 g for serows (Takatsuki et al.  
73 1981).

74 In this context, this study tested whether the quality of mammalian feces that are  
75 cryogenically preserved in snow can be sufficiently maintained for dung beetles emerging in  
76 spring, and if so, whether differences in mammal feces and forest cover would influence the  
77 abundance and diversity of dung beetle assemblages. To test these hypotheses, we conducted  
78 cafeteria experiments using pitfall traps baited with the snow-buried feces of the three mammals.  
79 Based on this effort, we discuss the ecological roles of snow-buried feces by noting mammal–  
80 beetle interactions in the cool-temperate forest ecosystem.

81

## 82 **Materials and Methods**

### 83 Study area

84 The current study area constitutes the northeastern part of the Shirakami Mountains,  
85 located in northernmost mainland Japan (Fig. 1), where we have previously investigated the  
86 inventory of dung beetles using fresh mammal feces (Enari et al. 2011, 2013). In this area, cold  
87 winters with heavy snowfall are usually observed from December to March, and snow depths  
88 can reach 3 m. The snow cover in the area remains until the beginning of May. Typical  
89 cool-temperate forests—mainly composed of secondary broadleaf trees (e.g., *Fagus crenata* and  
90 *Quercus crispula*) and conifer plantations (*Cryptomeria japonica* and *Chamaecyparis*  
91 *obtusa*)—are observed.

92 Study species

93 In the study area, we have confirmed 14 species of dung beetles using fresh mammal feces  
94 (macaques, serows, and the Asiatic black bear *Ursus thibetanus*), composed of eight species of  
95 *Aphodius*, four species of *Onthophagus*, and two species of *Phelotrupes* (Enari et al. 2011,  
96 2013). While *Aphodius* spp. are typical dwellers (i.e., species which feed in the dung and  
97 oviposit under or inside it), *Onthophagus* spp. and *Phelotrupes* spp. are tunnelers (species which  
98 make a vertical chamber under the dung and bring dung inside for feeding and breeding)  
99 (Cambefort and Hanski 1991). No rollers (that make a dung ball to horizontally transport dung  
100 away from the dung before dung burial) have been confirmed thus far.

101 The three mammals listed above feed on similar diets during the winter; this diet is mostly  
102 composed of bamboo grasses (*Sasa kurilensis*), bark and buds of woody plants, and remaining  
103 autumnal fruits. As opposed to their common food habits, their forest uses are differentiated;  
104 during snowy seasons, while hares and serows frequently occupy young conifer and young  
105 broadleaf forests, respectively, macaques occupy young broadleaf forests as well as conifer  
106 forests regardless of forest age (Enari and Sakamaki 2012).

107

108 Collecting dung beetles

109 Aside from the geographical distance, different forest types greatly affect the composition of  
110 dung beetles (Hanski and Cambefort 1991b; Davis et al. 2001). Hence, we set pitfall traps in  
111 five experimental sites with different forest covers (Table 1). To avoid the differences in plant  
112 phenology and the timing of snow melting among sites, all traps were set at a similar elevation.  
113 The minimum and maximum distances between sites were 0.8 km and 5.0 km, respectively. In  
114 each site, we arranged five sampling points at 20-m intervals along a line transect for respective

115 cafeteria experiments using different mammal feces—each transect was placed in parallel rows  
116 at intervals of 50 m. In these sampling points, we caught dung beetles by traps baited with  
117 snow-buried macaque feces during the whole of May 2012 and traps with snow-buried hare and  
118 serow feces during the whole of May 2013. For the trap baits, we collected each mammal feces  
119 naturally buried in snow just before the experiments. The year difference of the experiments  
120 resulted from a failure of this feces collection. The ambient temperature and total precipitation,  
121 which potentially influence the emergence of vernal dung beetles, were similar,  $13.2 \pm 4.3$  °C  
122 and 70.0 mm in May 2012 and  $13.0 \pm 5.7$  °C and 49.5 mm in May 2013, according to a weather  
123 observation station set in the Shirakami-sanchi World Heritage Conservation Center  
124 ( $40^{\circ}34'41''\text{N}$ ,  $140^{\circ}17'54''\text{E}$ ).

125 The design of the pitfall traps was the same as that of Enari et al. (2011, 2013). Traps were  
126 made from plastic containers (14 cm in diameter and 10 cm deep) and plastic cups (8 cm in  
127 diameter and 5 cm deep), and each container holding 50% ethylene glycol (used as a preserving  
128 fluid) was buried to its rim in the ground, and the cup was hung by a wire in each container. The  
129 mass of baits was 100 g for macaques and serows and 30 g for hares according to the  
130 approximate weight of single fecal masses observed under snow cover.

131

## 132 Data analyses

133 We identified all dung beetles captured in pitfall traps and used generalized linear mixed  
134 models (GLMMs) to explain the abundance of dung beetles (the response variable) based on the  
135 types of forest cover and feces (the explanatory variables; categorical data). For this modeling,  
136 we used a Poisson distribution with a logarithmic link function, and the year when we set traps  
137 was allocated to the random factor. We selected the best-fitting model according to the Akaike

138 information criterion (AIC). For this modelling, we used R ver. 3.2.2 (R Core Development  
139 team) with the glmmML package.

140 We then compared the species richness of collected dung beetles among sites by using  
141 sample-based rarefaction and an extrapolation curve with 100 randomizations (Colwell et al.  
142 2012), which were predicted by EstimateS 9.1.0 (developed by Colwell, R. K., University of  
143 Connecticut, USA). For the comparison, we calculated the estimated number of species and  
144 two-sided 95% CIs from the reference sample or dung beetle assemblages captured in each trap.  
145 Moreover, to evaluate the similarity in the composition of beetle assemblages by the genus  
146 category among sites, we conducted a multiple correspondence analysis, assigning the genus of  
147 dung beetles, bait types, and forest cover types to variables, through the use of R ver. 3.2.2 and  
148 MASS package.

149

## 150 **Results**

151 We failed to collect dung beetles from one of the five traps baited with serow feces both in  
152 secondary shrubs and mature conifer-broadleaf mixed forests because the traps were trampled  
153 by unknown mammals. From the remaining traps, we confirmed 12 species (composed of six  
154 dwellers, five tunnelers, and one roller) from 715 dung beetles attracted to mammal feces  
155 preserved under snow (Electronic supplementary material, ESM, Table S1). According to the  
156 previous experiments using fresh mammal feces in the same area (Enari et al. 2011, 2013),  
157 seven out of 12 species that the current study observed have been known to use fresh feces;  
158 however, four *Aphodius* spp. and one *Phelotrupes* sp. using fresh feces were not attracted to  
159 snow-buried feces.

160 *Aphodius* spp. and *Onthophagus* sp. were observed most frequently (Table S1); therefore,

161 only those genera were used in the GLMM analyses. In the analyses, we chose the best fitting  
162 model using both explanatory variables (i.e., feces and forest cover) according to AIC (Table 2).  
163 The results indicated that both genera preferred snow-buried serow feces. Common habitat uses,  
164 including the preference for young broadleaf forests and avoidance of secondary shrubs, were  
165 observed for the two genera, while mature conifer-broadleaf mixed forests were only suitable  
166 habitats for *Aphodius* spp.

167 The rarefaction and extrapolation curves (Fig. 2) demonstrated that every curve was nearly  
168 saturated and narrow widths of 95% CIs were observed, except for traps baited with serow feces  
169 in mature conifer-broadleaf mixed forests and young conifer plantations because of insufficient  
170 sample sizes. This means that the current sampling efforts were sufficient for the evaluation of  
171 the species richness. Serow feces were most preferred by the majority of beetles regardless of  
172 forest cover types.

173 The multiple correspondence analysis succeeded in producing the two-dimensional maps  
174 explaining cross relationships of dung beetle compositions with bait types or forest cover types  
175 (cumulative variance explained = 0.69; Fig. 3). The map showed that (1) dwellers (i.e.,  
176 *Aphodius*) often used both serow and macaque feces in all types of forest covers excluding  
177 secondary shrubs, (2) while *Onthophagus* frequently occurred when using serow feces in young  
178 broadleaf forests, the remaining tunnelers (i.e., *Phelotrupes* and *Trox*) preferred macaque feces.

179

## 180 **Discussion**

181 The current findings indicate that snow-buried mammal feces could act as an available  
182 resource for dung beetles in terms of their qualitative aspects. Given the sudden increase of fecal  
183 biomass in spring, the snow-buried feces might also contribute to the spring outbreak of most



184 dung beetles uniquely observed in heavy snowfall regions. As a basis for sustaining this  
185 contribution, it should also be noted that this resource is continuously available for  
186 location-shifting vernal beetles for more than one month because of topographical features—as  
187 heavy snow regions are located in montane regions, the thawing rate of snow varies with  
188 elevation and/or slope direction. Some dung beetle species that are not attracted to fresh  
189 mammal feces used this resource (Table S1); however, a host of other species are widely  
190 observed in temperate forests (Kawai et al. 2005). Among the common species, most tunnelers  
191 (i.e., *Onthophagus* and *Phelotrupes*) exhibit a seasonal peak of emergence during summer in  
192 lower-latitude temperate forests (Koike et al. 2006a, 2006b). Given this, the seasonal prevalence  
193 of beetles specific to heavy snowfall regions could be caused by regional variations in their life  
194 history traits (i.e., phenotypic plasticity) to adapt to the seasonal changes in resource availability  
195 and external environment. In other words, such plasticity of beetles and broad environmental  
196 gradients might be factors driving the growth of intraspecific variations in life history traits  
197 within small geographical spaces, such as the Japanese archipelago, as has been noted in other  
198 studies conducted in warmer areas (Hanski 1980; Vessby 2001; Tomkins and Hazel 2011).

199 Most dung beetles had obvious fecal preferences (Table 2; Fig. 3). In particular, snow-buried  
200 serow feces were more widely available resources than the other mammal feces. This is similar  
201 to the results of a cafeteria experiment using fresh mammal feces (Enari et al. 2013). According  
202 to the studies accumulated in the tropics, the majority of dung beetles are considered generalists  
203 in their preferences, but some species are sensitive to the content and size of feces provided by  
204 mammals with different feeding habits—i.e., herbivore, carnivore, omnivore (Hanski and  
205 Cambefort 1991a; Martin-Piera and Lobo 1996). In this study, although the three mammals that  
206 we focused on potentially have different food habits—the macaque is a typical omnivore,

207 whereas the serow and hare are herbivores—there are few differences in their dietary selections  
208 during winter because of food resource scarcity. This means that the differences in the digestive  
209 processes (resulting in differences in fiber and nitrogenous contents) and/or in the mass and  
210 distribution of feces among mammals might explain the above fecal preference, as is true of the  
211 tropics (Davis 1989; Edwards 1991; Davis and Scholtz 2001). In fact, while the serow has a  
212 ruminant stomach and defecates in fixed sites, both the macaque and hare are monogastric  
213 mammals, but the former forms troops (meaning that feces occur in a clumped distribution) and  
214 the latter is herbivorous with a coprophagous habit. To explain the direct relationships between  
215 those differences and fecal preferences by beetles, more empirical studies would be needed.

216 Most mammals living in heavy snowfall environments are not uniformly distributed in their  
217 habitats. In fact, serows and macaques basically show high environmental requirements for their  
218 habitats during winters and frequently select young broadleaf forests (Enari and Sakamaki  
219 2012). In contrast to the rich feces supply in young broadleaf forests, dung beetles observed in  
220 the forests were not always the highest in species richness; however, it should be noted that  
221 tunnelers often emerged in those forests, and large-sized tunnelers (*P. laevistriatus*) selected  
222 only macaque feces. Those findings could be of essential importance in plant regeneration. In  
223 heavy snowfall regions, most dung beetles, including *P. laevistriatus* with its superior ability for  
224 seed burial (Koike et al. 2012a; Enari and Sakamaki-Enari 2014), can be active only between  
225 May and September (Enari et al. 2011). This logically means that endozoochorous seeds  
226 produced in autumn have insufficient opportunities for secondary seed dispersal by dung beetles  
227 within the current season. Most seeds just dispersed by mammals or birds are frequently  
228 removed and consumed by rodents without seed burial by dung beetles; e.g., >90% seeds  
229 dispersed by Asiatic black bears are removed by rodents in temperate forests (Koike et al.

230 2012b). In heavy snowfall regions, however, such risk of rodent predation for autumnal seeds is  
231 expected to be low due to the presence of snowfall from late autumn. In consequence, the  
232 autumnal seeds dispersed by macaques are likely to be safely preserved under soil by the burial  
233 activities of tunnelers emerging in spring. Thus, it is reasonable to consider that sufficient  
234 snowfall establishes the time-lagged mammal–beetle interaction via snow-buried feces and links  
235 their individual ecological roles more functionally.

236

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242

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**Table 1.** Environmental conditions of study sites in the Shirakami Mountains, northern Japan

	Forest covers				
	Mature conifer-broadleaf mixed forests	Young conifer plantations	Young broadleaf forests	Secondary shrubs	Mature broadleaf forests
Above sea level (m)	299	305	296	291	224
Mean canopy openness (%) <sup>a</sup>	47.5	40.8	58.2	42.5	47.2
Mean slope (°)	25.5	20.5	14.0	16.3	16.3
Dominant trees	<i>Quercus crispula</i> <i>Cryptomeria</i> <i>japonica</i>	<i>C. japonica</i>	<i>Fagus</i> <i>crenata</i> <i>Q. crispula</i>	<i>Viburnum</i> <i>furcatum</i> <i>Aralia elata</i>	<i>F. crenata</i>

<sup>a</sup>The percentage was calculated by using CanopOn 2.03 (Takenaka, 2009) with hemispherical photographs



**Table 2.** Mean  $\pm$  SE of coefficients of explanatory variables in the best fitting model, constructed by the generalized-linear mixed model, to estimate the abundance of dung beetles (by genus) frequently observed in the Shirakami Mountains, Japan

Response variables	Feces				Forest cover <sup>a</sup>					AIC	AIC (null)
	Intercept	Macaque	Serow	Hare	MCB	SS	YB	YC	MB		
<i>Aphodius</i> <i>N</i> = 73 traps	1.55 $\pm$ 0.13*	0.04 $\pm$ 0.12	0.49 $\pm$ 0.10*	0	0.57 $\pm$ 0.14*	-0.78 $\pm$ 0.20*	0.45 $\pm$ 0.14*	0.12 $\pm$ 0.14	0	337.4	430.0
<i>Onthophagus</i> <i>N</i> = 73 traps	1.38 $\pm$ 0.17*	-1.16 $\pm$ 0.25*	0.32 $\pm$ 0.16*	0	-0.69 $\pm$ 0.25*	-0.83 $\pm$ 0.26*	0.46 $\pm$ 0.18*	-12.40 $\pm$ 69.06	0	183.3	311.6

<sup>a</sup> MCB, mature conifer-broadleaf mixed forests; SS, Secondary shrubs; YB, Young broadleaf forests; YC, Young conifer plantations; MB, Mature broadleaf forests

Asterisks indicate  $Pr(z) < 0.05$

1 **Figure legends**

2

3 **Fig. 1.** Shaded-relief map of the study area, located in the northeastern Shirakami Mountains,  
4 the northernmost mainland area of Japan. The study sites where pitfall traps were set are shown  
5 in the box: A, mature conifer-broadleaf mixed forests; B, young conifer plantations; C, young  
6 broadleaf forests; D, secondary shrubs; E. mature broadleaf forests.

7

8 **Fig.2** Expected number of dung beetle species using different mammal feces in each forest  
9 cover, estimated by rarefaction and extrapolation curves. Black bars show 95% CIs.

10

11 **Fig. 3.** Similarity in the composition of dung beetle assemblages using different mammal feces  
12 in each forest cover (MCB, mature conifer-broadleaf mixed forests; SS, Secondary shrubs; YB,  
13 Young broadleaf forests; YC, Young conifer plantations; MB, Mature broadleaf forests),  
14 represented by a multiple correspondence analysis.

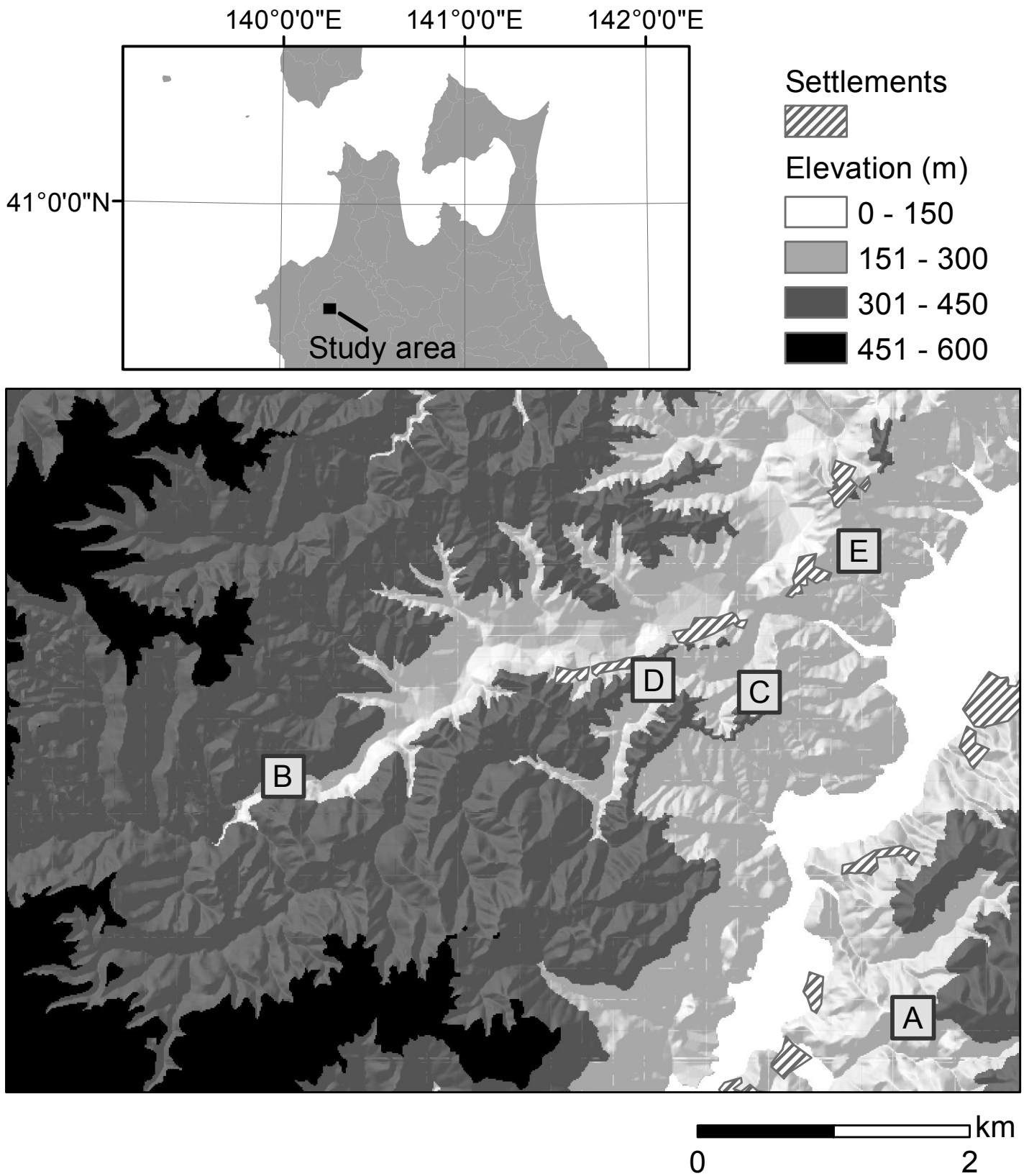
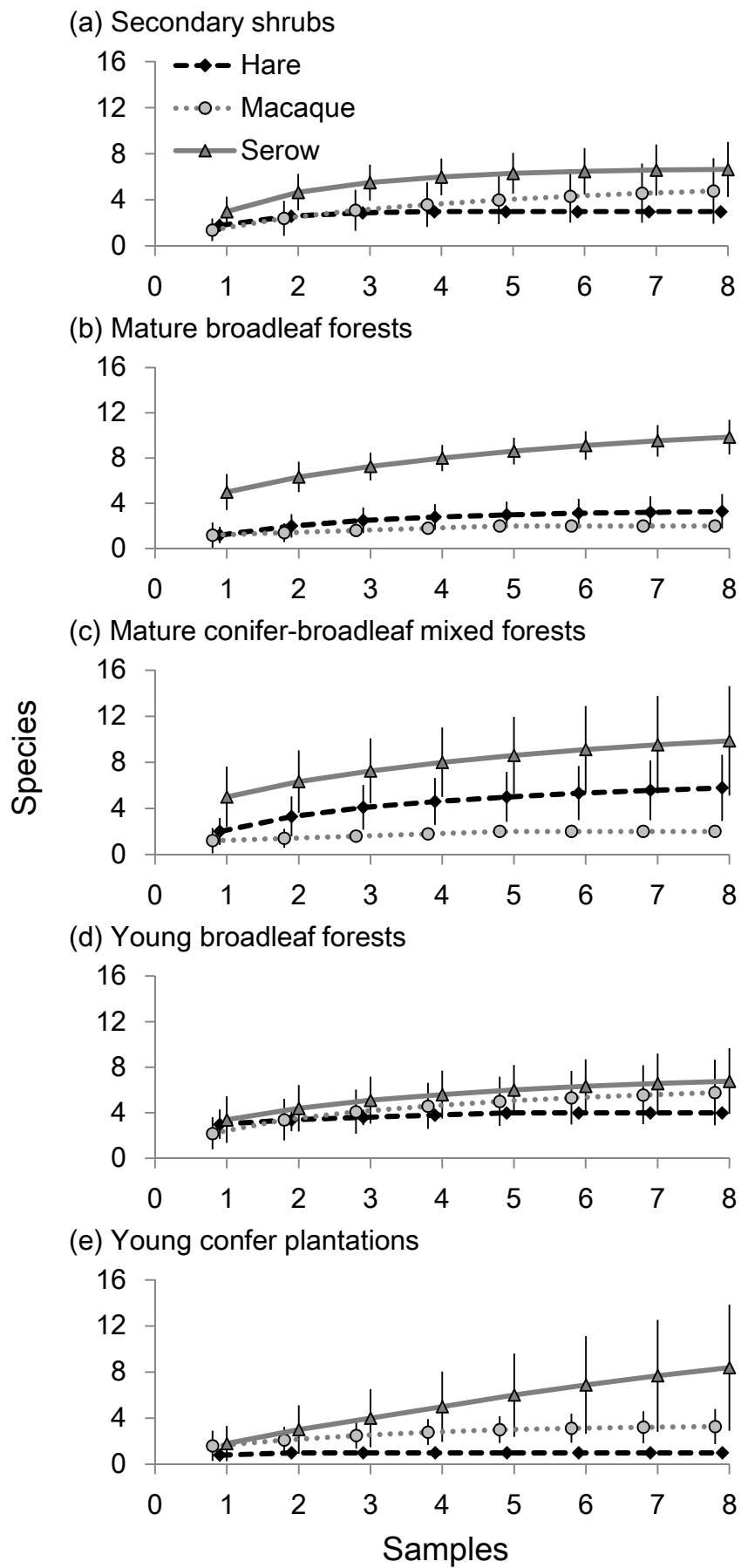


Fig. 2. Enari et al.



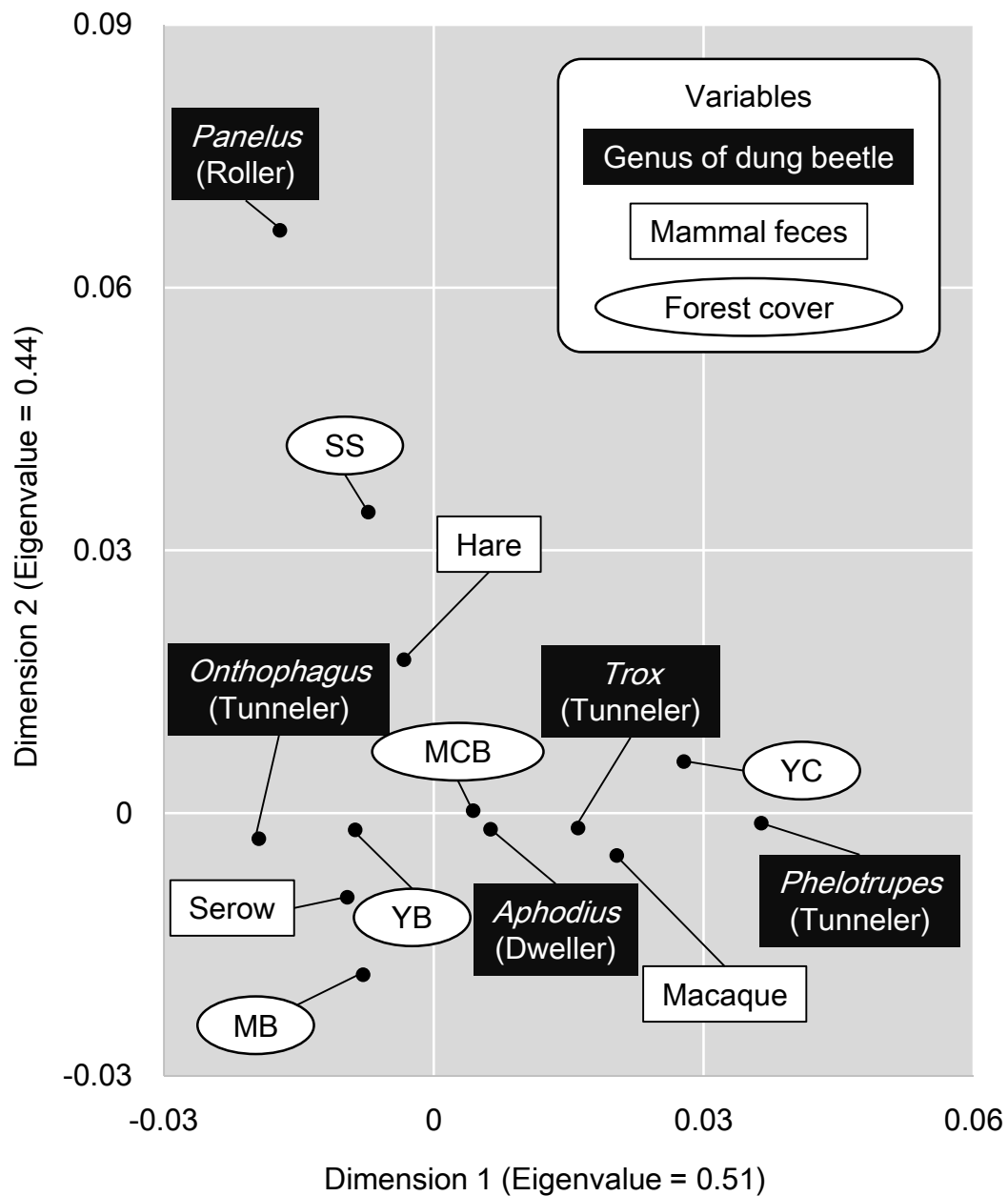


Table S1. Compositions of dung beetles captured by pitfall traps baited with the snow-buried feces of Japanese macaque, Japanese serow, and Japanese hare in the Shirakami Mountains, Japan.

Name	Forest cover															Previously confirmed <sup>b</sup>
	MCB <sup>a</sup>			YC			YB			SS			MB			
	Macaque (N=5)	Serow (N=4)	Hare (N=5)	Macaque (N=5)	Serow (N=5)	Hare (N=5)	Macaque (N=5)	Serow (N=5)	Hare (N=5)	Macaque (N=5)	Serow (N=4)	Hare (N=5)	Macaque (N=5)	Serow (N=5)	Hare (N=5)	
<b>SCARABAEIDAE</b>																
<i>Aphodius</i> (Dweller)																
<i>A. hasegawai</i>	46	4	21	45	7	42	16	1	32	2	4	20	34	1	5	Yes
<i>A. rectus</i>							1									No
<i>A. hibernalis</i>				1	1											No
<i>A. brevisculus</i>		26	10		1			74			2			40	1	Yes
<i>A. superatratus</i>		31						5			7			4		Yes
<i>A. unifasciatus</i>		1	1		1			1	6		1				2	Yes
<i>Onthophagus</i> (Tunneler)																
<i>O. ater</i>	2	12	9				9	34	38	9	7	4	1	34	16	Yes
<i>Panelus</i> (Roller)																
<i>P. parvulus</i>		3	5					4	1		1	8				No

**GEOTRUPIDAE**

***Phelotrupes* (Tunneler)**

*P. laevistriatus* 3 10 2 Yes

**TROGIDAE**

***Trox* (Tunneler<sup>c</sup>)**

*T. mandli* 1 1 1 No

*T. opacotuberculatus* 1 No

*T. mutsuensis* 1 1 Yes

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Abundance	48	79	46	49	12	42	37	119	77	14	22	32	35	79	24
Number of species	2	8	5	3	6	1	5	6	4	4	6	3	2	4	4

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<sup>a</sup> MCB, mature conifer-broadleaf mixed forests; YC, Young conifer plantations; YB, Young broadleaf forests; SS, Secondary shrubs; MB, Mature broadleaf forests

<sup>b</sup> Whether the species has been reported to use fresh mammal feces in the current study area (Enari et al., 2011, 2013)

<sup>c</sup> Those species carry foods underground for consumption during the young stage (Palestrini et al., 2009); accordingly, we tentatively classified the genus as tunnelers