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5 **Early-stage ecological influences of population recovery of large mammals on dung beetle**

6 **assemblages in heavy snow areas**

7

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18

19 **Abstract:**

20 Past conservation initiatives and rapidly decreasing human populations in modern Japan have

21 contributed to population recoveries of Sika deer (*Cervus nippon*), wild boar (*Sus scrofa*), and Japanese

22 macaque (*Macaca fuscata*) throughout the country. Ironically, however, these recoveries have not

23 always received a favorable reception, because these mammals can also be agricultural pests. To open

24 public debate on the recoveries, based on a thorough understanding of their multifaceted roles in
25 sustaining the local ecosystem, we evaluated the initial stage ripple effects caused by the mammalian
26 population recovery on the community assembly of dung beetles, which are keystone decomposer
27 organisms in terrestrial ecosystems. For the evaluation, we conducted manipulative snapshot
28 experiments, using camera and pitfall traps, for mammal and dung beetle assemblages, respectively, in
29 four different mountain ranges within the heavy snow areas of northern Japan, where the recovery of
30 three mammal populations was at an early stage. The current findings implied that, although the feces of
31 every recovering mammal species could provide valuable resources for most beetles, the ripple effects
32 from the mammal population recoveries were subject to hysteresis of the local ecosystem, i.e.,
33 catastrophic shifts in ecosystems originating from the historical background of regional mammal
34 defaunation. In particular, the abundance of tunnelers that could benefit from positive ripple effects
35 decreased with an increase in past disturbances, which resulted in *emptier forests*, i.e., an ecosystem
36 with fewer large mammals. The findings suggested that recovering populations of large mammals do not
37 always contribute to the restoration of the original dung beetle communities, at least initially.

38

39 **Keywords:**

40 *Cervus nippon*, defaunation, empty forest, hysteresis, *Macaca fuscata*, *Sus scrofa*

41 **1. Introduction**

42 As part of the recently growing trend for biodiversity conservation, there are several cases where the
43 recovery of vulnerable or extinct mammal populations in their native ranges has been a success of
44 ecological conservation or restoration initiatives (Morrison, 2009; Steinmetz *et al.*, 2010). However, the
45 recovery of populations could also lead to discord among various stakeholders, if the species also
46 functions as an agricultural pest, or ecosystem engineer, that creates irreversible environmental changes
47 inconsistent with our modern way of life (Augustine & Frelich, 1998; Morzillo *et al.*, 2007; Olson *et al.*
48 2015). Japan is a typical country facing such a dilemma. In addition to past conservation initiatives, the
49 rapidly declining human population throughout the country has become a strong driving force for
50 recovering various native large mammals that were once threatened with extinction owing to massive
51 human disturbances (i.e., excessive hunting and forest exploitation); as a result of those recoveries,
52 unprecedented human-wildlife conflicts have begun to occur in recent years (Enari & Suzuki, 2010;
53 Sakurai *et al.*, 2013; Ohashi *et al.*, 2016). In particular, in cool-temperate forests with heavy snow in
54 northern mainland Japan, the recent population recovery of Sika deer (*Cervus nippon*), wild boar (*Sus*
55 *scrofa*), and Japanese macaque (*Macaca fuscata*) (Fig. 1) represents a prime example of this; the
56 agricultural damage by these recovering populations has continued to spread. As a result, many local
57 governments have now adopted an official policy to prevent these populations from further recovery.

58 It is possible that these three mammals also fulfill some positive roles within the original ecosystem
59 functions, but these have not previously been carefully validated, with very few exceptions (for boars,
60 Barrios-Garcia & Ballari, 2012; for macaques, Enari & Sakamaki-Enari, 2014). In this context, the
61 present study focused on interspecies relationships between recovering mammal populations, and dung
62 beetle assemblages; we treated beetles belonging to the families Scarabaeidae, Geotrupidae, and
63 Trogidae as dung beetles in a broad sense owing to their shared role, i.e., dung decomposition. Dung

64 beetles are organisms that draw widespread attention because of their multiple key roles in sustaining
65 regional ecology, with functions ranging from secondary seed dispersal and nutrient cycling, to parasite
66 suppression (Nichols *et al.*, 2008). Moreover, dung beetles are often considered as ecological indicators
67 because of their short life cycle, broad distribution, high abundance, and rapid response to
68 environmental fluctuations (Davis *et al.*, 2001; McGeoch *et al.*, 2002; Nichols *et al.*, 2007; Viegas *et al.*,
69 2014). In fact, the abundance and richness of dung beetles is highly sensitive to the distribution of
70 mammals, which leave excrement on which the beetles feed or oviposit (Fincher *et al.*, 1970; Hanski &
71 Cambefort, 1991b; Nichols *et al.*, 2007; Culot *et al.*, 2013; Bogoni *et al.*, 2016). Therefore, when
72 environmental disturbances lead to the defaunation of native mammals—i.e., the nonrandom loss of
73 medium- to large-bodied vertebrates (Redford, 1992)—the abundance and richness of dung beetles are
74 often severely disrupted; this is widely described as an ecological cascade of downstream extinctions
75 (Nichols *et al.*, 2009; Culot *et al.*, 2013). However, less attention has been paid to the opposite effects of
76 the ecological cascade, i.e., whether mammal population recovery has some positive ripple effects to
77 benefit the abundance and richness of dung beetles. Here, we aimed to validate our hypothesis
78 concerning the existence of such ripple effects caused by mammal population recovery, by establishing a
79 study area within cool-temperate forests with heavy snowfall. Such high-latitude forests can potentially
80 support a limited biomass of mammals, resulting in a corresponding limited abundance and diversity of
81 dung beetles, when compared to those in warmer forests (Hanski & Cambefort, 1991b; Davis *et al.*,
82 2002; Enari *et al.*, 2011, 2013). Thus, the recovery from defaunation might be more strongly expected to
83 restore the self-sustaining ecosystem, owing to lower initial functional redundancy in the forests.

84 As with the above three mammal species, it is possible that most other mammals have also been
85 affected by the overexploitation of natural resources and, therefore, their abundance and distribution
86 varies greatly among different mountain ranges. Allowing for the possibility that native species pools of

87 beetle fauna were already missing because of past mammal defaunation, we designed verification
88 experiments for the hypothesis, concerning positive ripple effects in four different mountain ranges with
89 similar physical environments (Fig. 1) based on the following three steps: (1) evaluating the influences
90 of the different mammal community compositions observed in each mountain range on the composition
91 of dung beetles; (2) predicting ecological outcomes caused by the new resource supply produced by
92 recovering populations of deer, boar, and macaques, by quantifying the feces preference of existing
93 beetles; and (3) discussing regional differences between potential ripple effects, in terms of hysteresis
94 (i.e., catastrophic shifts in ecosystems; Scheffer *et al.*, 2001; Mayer & Rietkerk, 2004) originating from
95 the historical background of regional mammal defaunation, which potentially determines the
96 differentiation of the native species pool of the dung beetle community.

97 **2. Materials and Methods**

98 **2.1. Study area and subject species**

99 We set four study sites—S (40° 30' N, 140° 12' E; 250 m above sea level, ASL), H (40° 30' N, 140° 46';
100 450 m ASL), A (38° 30' N, 139° 49' E; 670 m ASL), and T (38° 45' N, 139° 44' E; 270 m ASL)—within
101 different mountain ranges of Shirakami, Hakkoda, Asahi, and Takadate, respectively, located in
102 northeastern Japan (Fig. 1). Each mountain range is a designated nature reserve—UNESCO World
103 Nature Heritage site (Shirakami), National parks (Hakkoda and Asahi), prefectural natural park
104 (Takadate)—with undisturbed natural broad-leaved forests, mainly composed of beech (*Fagus crenata*)
105 and oak (*Quercus crispula*). Annual mean air temperature and total precipitation in 2015 ranged from
106 9.0 °C (Site A) to 13.6 °C (Site T), and from 1,519.5 mm (Site H) to 2,282.0 mm (Site A). Snowfall was
107 observed from December to March in each mountain range. Although the deer and boar populations
108 became extinct throughout these mountain ranges by the late 19th century, macaques narrowly avoided
109 being eradicated in two sites, S and A (Tsujino *et al.*, 2010). Except for the macaques in these two sites,

110 the recovery of the three mammal populations was at an early stage in every site. Details of the historical
111 distribution changes for other mammals are unknown.

112 In the Japanese archipelago, 152 species and 9 subspecies of indigenous dung beetles have been
113 observed to date (Kawai *et al.*, 2005). Among them, only 21 species of dung beetles—including 11
114 dwellers (species that feed in the dung and oviposit under or inside it), 9 tunnelers (species that make a
115 vertical chamber under the dung and bring the dung inside for feeding and breeding), and 1 roller (species
116 that make a dung ball to horizontally transport away from the dung before dung burial)—have been
117 confirmed in heavy snow areas (Enari *et al.*, 2011, 2013, 2016). While all the dwellers and roller are
118 classified as small-sized species (<1 cm in body length), the size of the tunnelers is relatively large
119 (mostly >1 cm in length) (Kawai *et al.*, 2005). Although most dung beetles have generalist feeding
120 behavior (Hanski & Cambefort, 1991a), the preference for feces excreted by common mammals by dung
121 beetles in cool-temperate forests is quite obvious; besides the composition of feces having been affected
122 solely by the type of food intake, the digestive process specific to each mammal—which potentially
123 influences the fiber, nitrogen, moisture, and volatile contents of feces—is considered a prime determinant
124 of this preference (Enari *et al.*, 2013), which was also confirmed in various ecosystems (Davis, 1989;
125 Edwards, 1991; Carpaneto *et al.*, 2010). The prevalence of dung beetles in forests drastically changes by
126 season; the active period of every dung beetle, strictly regulated by ambient temperature—the threshold
127 temperature is 10–28 °C (Sasayama *et al.*, 1984)—, is observed only during spring and summer (Enari *et*
128 *al.*, 2011).

129 **2.2. Assessing mammal assemblages**

130 As preparation to validate the hypothesis, we evaluated the current mammal assemblages in every study
131 site, by measuring the relative abundance index (RAI) using camera trap surveys (O'Brien *et al.*, 2003).
132 We defined RAI as the number of photos of each mammal per survey effort (camera night, CN). We set

133 four cameras in Sites S, H, and A, and two cameras in Site T, at greater than 100 m intervals along
134 different suspected-trails of animals, from May to November 2013 (Sites S and T) and 2015 (Sites H and
135 A). We used low-glow infrared cameras (Model HC500, Reconyx, Wisconsin, U.S.A.), with
136 standardized camera settings: three burst shots per capture, with a 1 h capture delay. H. E. and H. S. E.
137 identified each captured image and repositied all the data in Yamagata University.

138 The composition of dung beetle assemblages is influenced both by abundance and type of available
139 feces (Barlow *et al.*, 2010; Culot *et al.*, 2013; Bogoni *et al.*, 2016). For a rough comparison of the total
140 amount of feces supplied per site, we estimated the relative mammalian biomass, using the sum of the
141 product of RAI and mean body weight (Ohdachi *et al.*, 2015) for each mammal species. For
142 group-living mammals (i.e., macaques), we then multiplied the sum of products by the mean group
143 size—i.e., 35 individuals for general macaque troops living in cool-temperate forests (Enari &
144 Sakamaki-Enari, 2013). To statistically compare the mammalian fauna among sites and visualize the
145 differences and similarities in their compositions, we performed a permutational multivariate analysis of
146 variance, PERMANOVA (Anderson, 2001) and a correspondence analysis (CA), respectively, based on
147 the RAI in each site. These two analyses were conducted using the packages VEGAN and MASS of R
148 3.4.0 (R Development Core Team, 2017), respectively. When conducting PERMANOVA, we used the
149 number of replicate permutations as 10,000, and assigned the Chao dissimilarity index (Chao *et al.*,
150 2005).

151 **2.3. Collecting dung beetles**

152 Besides being affected by the existing mammal species composition, dung beetles are highly
153 sensitive to changes in habitat structure (Halffter & Arellano, 2002; Nichols *et al.*, 2007; Gardner *et al.*,
154 2008; Bogoni *et al.*, 2016). To remove the confounding effect of habitat, we assessed dung beetle
155 assemblages in four study sites with similar environmental conditions: canopy-closed beech and oak

156 trees, with the understory composed of sparse shrubs and bamboo grasses (*Sasa kurilensis*), a typical
157 landscape specific to the cool-temperate zone. In each site, we placed three line transects in parallel rows
158 at intervals of 50 m, and set five pitfall traps at 20 m intervals along each transect (this design was
159 compliant with that of Enari *et al.*, 2013, 2016), using one of three different mammal feces (deer, boar,
160 or macaque), as trap bait. We collected fresh feces for trap baits in and around the study area,
161 immediately before the experiments. It was difficult to find fresh wild boar feces in the field, so we used
162 feces directly from the rectum of deceased boars.

163 The design of the pitfall traps was similar to what we used previously (Enari *et al.*, 2011, 2013,
164 2016): traps were made from plastic containers (14 cm in diameter and 10 cm deep), and plastic cups (8
165 cm in diameter and 5 cm deep). Each container held a soapy water solution used as a preserving fluid,
166 and was buried to its rim in the ground. The cup was hung in each container by a wire. The mass of bait
167 was 30 g for each mammal feces. Allowing for the limited active period of beetles in the forest as
168 described above, we conducted the experiments using the above sampling procedure during one week in
169 spring (the beginning of June) and summer (the middle of August) 2015, at every site. The ambient
170 temperature in each site during the study period was 14.6–19.0 °C in spring and 21.7–24.7 °C in summer.
171 Voucher specimens were deposited at Yamagata University and the species identification was conducted
172 under the responsibility of S. K.

173 **2.4. Data analysis for hypothesis testing**

174 We confirmed differences in the existing genera of dung beetles among sites, by conducting CA and
175 PERMANOVA (replicate permutations = 10,000, dissimilarity index = Chao), with the composition of
176 beetle assemblages pooled from all the experiments in each site. We then evaluated seasonal changes in
177 beetle abundance (using χ^2 goodness-of-fit test) and diversity (inverse Simpson index, $1/\lambda$) for each site.

178 To compare the species richness among beetle assemblages attracted to the different mammal feces,

179 we statistically drew sample-based rarefaction and extrapolation curves with 100 randomizations
180 (Colwell *et al.*, 2012), using all the sets of beetles collected in each trap as the reference samples. When
181 drawing extrapolation curves, we predicted the expected species richness and two-sided 95% confidence
182 intervals (CIs) for up to 10 samples. This comparison was conducted for every site using EstimateS 9.1.0
183 software (developed by R. K. Colwell, University of Connecticut, USA).

184 Finally, we examined the effects of type of mammal feces and regionality (i.e., hysteresis
185 determining the differentiation of the native species pool) on the abundance of each dung beetle species
186 captured in each season. For this examination, we developed generalized linear mixed models (GLMMs),
187 using the abundance of dung beetles classified into three functional groups (tunneler, dweller, and roller)
188 as the response variable, and either the types of feces or the study site as the single categorical
189 explanatory variable. For the model development, we used a Poisson distribution with a logarithmic link
190 function, and either the study site or feces type—the one which had not been used as the explanatory
191 variable—was considered a random factor. To perform this modeling, we used R version 3.4.0. with the
192 glmmML package (R Development Core Team, 2017). Model performance was validated using the
193 Akaike information criterion (AIC), and the percentage of deviance explained was used to quantify each
194 model's goodness-of-fit, i.e., %DE = $(1 - \text{Deviance}/\text{Null deviance}) \times 100$.

195 **3. Results**

196 **3.1. Site variations in existing mammal fauna**

197 Total values of RAI (individuals/100 CN) and species diversity ($1/\lambda$) for medium- to large-sized
198 mammals, confirmed by the camera trap surveys at each site, were 16.92 and 4.03 in Site S, 16.45 and
199 4.07 in Site H, and 11.69 and 4.63 in Site A, respectively (for details, see Table A.1). No mammals were
200 captured in Site T. Mammals from recovering populations were rarely observed, except for macaques,
201 which were thoroughly distributed in Sites S and A (Table 1). Relative mammalian biomass observed in

202 Sites H (259.1 kg/100 CN) and T (0.0) was very low, compared with Sites S (1579.5) and A (1313.3).

203 PERMANOVA was conducted after excluding Site T, where no mammals were observed. The
204 results clearly showed that the composition of mammal assemblages varied significantly among sites
205 (d.f. = 2, pseudo-F = 8.93, P = 0.003). The CA succeeded in creating a two-dimensional map explaining
206 the differences in mammal fauna among sites (map I of Fig. 2). Axis 1 with a larger contribution ratio
207 (0.73) showed that large-sized mammals, such as macaque, black bears (*Ursus thibetanus*), and Japanese
208 serow (*Capricornis crispus*), became major components of mammal fauna in Sites S and A, whereas
209 middle-sized carnivores were frequently recorded in Site H. Axis 2 discerned between Sites S and A, and
210 indicated that the newly expanding populations of deer and masked palm civet (*Paguma larvata*,
211 introduced species) were observed only in Site A.

212 3.2. Site and seasonal variations in dung beetle fauna

213 We captured 15 dung beetle species, a total of 2,558 specimens, from the current experiments (see Table
214 A.2 for the entire list of trapped beetles). Their diversity index ($1/\lambda$) was 5.50 in Site S, 2.13 in Site H,
215 2.25 in Site A, and 2.10 in Site T. As with the mammal fauna, the result of PERMANOVA demonstrated
216 that the composition of the dung beetle fauna also differed significantly between sites (d.f. = 3, pseudo-F
217 = 39.07, P < 0.001), indicating the composition of existing mammals in a site could highly influence the
218 beetle composition. However, the influence of the type of mammal feces (i.e., trap baits) on the beetle
219 compositions was limited (PERMANOVA, d.f. = 2, pseudo-F = 1.77, P = 0.13). The two-dimensional
220 map created by CA provided specific reasons for the differences in beetle compositions (map II of Fig.
221 2), showing a high abundance of dwellers (*Aphodius* spp.) and large tunnelers (*Phelotrupes* spp.), in
222 Sites H and A, whereas middle-sized tunnelers (*Onthophagus* spp. and *Copris* spp.), and *Trox* spp. (the
223 species also functioning as scavengers), were common beetle fauna from Sites S and T, respectively.

224 Seasonal prevalence of dung beetles was obvious in every site, excluding Site T where very few

225 beetles appeared (Fig. 3). From spring to summer, the abundance of tunnelers and dwellers largely
226 exhibited a downward trend in Sites S, H, and A (χ^2 goodness-of-fit test: $P < 0.001$ for each), except for
227 the tunnelers in Site H, which showed an upward trend. Similarly, the species diversity ($1/\lambda$) was on a
228 downward trend between the seasons in every site.

229 **3.3. Factors influencing the composition of beetle assemblages**

230 We drew rarefaction and extrapolation curves for dung beetle assemblages in spring only, not in summer,
231 because of the insufficient appearance frequency of estival beetles for extrapolation (Fig. 4). The
232 obtained curves showed that the proportion of species richness at 5 samples (i.e., observed value) to one
233 at 10 samples (i.e., expected value) was >0.8 , meaning that the sampling intensity we adopted was fairly
234 sufficient to assess the species richness. These curves demonstrated that there were obvious differences
235 among sites (in summary: Site S $>$ Sites H and A $>$ Site T) rather than among the types of mammal
236 feces.

237 Rollers and estival dwellers were rarely observed in the current experiments (Table A.2) and,
238 therefore, we conducted GLMMs to explore the reasons for the differences in observed beetle abundance,
239 by omitting these functional groups. The key outcomes from GLMMs were as follows: (1) in spring,
240 both dwellers and tunnelers were frequently attracted to macaque feces (models #1 and #3; Table 2); (2)
241 deer feces, which dries quickly owing to its particle shape, were poorly frequented by estival tunnelers
242 (model #5); (3) judging from AIC and %DE, the models using “study sites” as an explanatory variable
243 showed a higher predictive performance than those using “feces types,” suggesting that regional
244 difference in hysteresis relating to the native species pool had a greater influence on determining the
245 amount of newly available feces; (4) whereas the amount of newly available feces for tunnelers became
246 higher in Site S—where the expected feces supply was the richest—during both seasons (models #2 and
247 #6), those for vernal dwellers were enriched in Site A—where the diversity of mammal fauna was

248 highest (model #4).

249 **4. Discussion**

250 **4.1. Dung beetle fauna established in different mountain ranges**

251 In heavy snow areas, various mammal feces excreted between late fall and early spring accumulate
252 under deep snow, and simultaneously emerge on the ground as the snow melts. A recent study conducted
253 around Site S demonstrated the possibility that this phenomenon, which leads to a great increase in
254 mammal feces within the specified period, contributes to the spring outbreak of cool-temperate beetles
255 (Enari *et al.*, 2016). The current research further supported the possibility that this phenomenon is
256 widespread in snowy areas, explaining the seasonal prevalence of beetles uncorrelated with ambient
257 temperature (Fig. 3), but also showed that the composition of such beetle assemblages varied greatly
258 among different mountain ranges (Fig. 2). In particular, a dramatic regional variation was shown in Site
259 T, which was a typical *empty forest*—i.e., an ecosystem without large mammals (Redford, 1992).
260 Although the apparent forest landscape in this site is the same as the other study sites, at least for now,
261 this region has already lost the ability to sustain most dung beetles (Fig. 3), possibly resulting in the loss
262 of ecological functions provided by them, such as soil seed accumulation to increase the resilience of
263 forests to natural catastrophes (Enari & Sakamaki-Enari, 2014).

264 The recent study conducted in subtropical forests showed that 40% of the total variation in the dung
265 beetle assemblages could be explained in terms of two environmental factors: mammal species
266 composition, and habitat structure (Bogoni *et al.*, 2016). Therefore, it is possible that the main cause of
267 the current regional variations in beetle assemblages was the difference in mammal fauna, as we
268 standardized the latter factor among study sites. It should be noted, however, that the abundance and
269 diversity of dung beetles were unlikely to be simply explained by the biomass and diversity of mammals
270 (see values of $1/\lambda$ for each community of mammals and beetles; models #2, #4, and #6 in Table 2),

271 contrary to observations from other ecoregions (Nichols *et al.*, 2009; Bogoni *et al.*, 2016). The rationale
272 for this discrepancy might be provided by the fact that the influence of the presence/absence of each
273 mammal species on beetle assemblages could differ, largely dependent on the dietary habits of mammals.
274 In fact, herbivores and omnivores have been considered more influential mammals for sustaining most
275 dung beetles than carnivores (Carpaneto *et al.*, 2005; Bogoni *et al.*, 2016) and, among omnivores,
276 primates could have the greatest impact on regional dung beetle diversity (Estrada *et al.*, 1999; Vulinec
277 *et al.*, 2006). Given the considerations according to research conducted in warmer forests with richer
278 mammal fauna (i.e., higher functional redundancy), it is reasonable to consider that beetles in
279 cool-temperate forests with vulnerable mammal fauna (i.e., low functional redundancy), respond more
280 sensitively to the loss of mammal populations. This justification could be reinforced by the current
281 consequences: namely, the crash of dung beetle communities in Site T with the empty forests, and a
282 sharp increase in both vernal dwellers and tunnelers in Sites S and A (Fig. 3), which were the sites where
283 the primate populations have constantly survived.

284 **4.2. Ripple effects caused by recovering mammal populations**

285 Carefully following the chronosequence of mammal population recovery in the long term offers a better
286 understanding of its ripple effects on the community assembly of dung beetles. However, allowing for
287 urgent situations created by social dilemmas over the recovery of mammal populations (i.e., agricultural
288 damage), in the present study we have tried to predict the expected ripple effects through manipulative
289 snapshot experiments. The current findings clearly demonstrated that recovering populations of the three
290 mammal species appeared to provide valuable resources for most dung beetles, and among them,
291 macaque feces was the most favorably received by beetles. However, the ripple effects caused by the
292 new feces supplies from the recovering populations were restricted by hysteresis of the local ecosystem
293 (Table 2; Fig. 4). In fact, the dung beetle guilds that could benefit from the newly available resources

294 (i.e., large-size feces) largely differed owing to the surviving mammal species in each forest. It has
295 become known that the native species pool of larger-sized dung beetles—represented by tunnelers in the
296 case of cool-temperate forests—is vulnerable to the loss of large-sized mammals (Culot *et al.*, 2013);
297 hence, the abundance of tunnelers that could reap the benefits decreased with an increase in past
298 disturbances, which has led to *emptier forests* with fewer large mammals (model #2 in Table 2). Thus,
299 the findings suggested that recovering populations of large mammals do not always contribute to the
300 restoration of the original dung beetle communities, at least initially.

301 A related lesson has come from research focusing on a tropical forest restoration attempt (Audino
302 *et al.*, 2014)—the research did not include the assessment of the community assembly of mammals
303 along a restoration chronosequence, but highlighted the difficulties in recovering species and functional
304 richness of forest-restricted dung beetles, at least for a limited period of time (i.e., 18 years). Even
305 though the cool-temperate ecosystem is sustained by a simpler biological network than that observed in
306 such tropical forests, there can be little doubt that the comprehensive restoration of the underlying
307 species pool, let alone the local community composition which has already been transforming into the
308 alternative stable state, will require a substantial amount of time. Developing an understanding of the
309 assembly rules of dung beetles, affected by habitat connectivity, landscape matrix, regional species pool,
310 and various other biotic/abiotic factors (Grimbacher & Catterall, 2007; Majer, 2009; Brudvig, 2011), is
311 necessary to draw conclusions on the ripple effects from mammal population recovery. Unfortunately,
312 minimal information about the dispersal process and capacity of most dung beetles is known (Roslin &
313 Viljanen, 2011), and cool-temperate species are no exception in this regard.

314 To explore the ripple effects along the chronosequence of mammalian population recoveries, their
315 direct/indirect influences on the transformation of local ecosystem processes need to be studied further.
316 A first example of this is the ecosystem change caused by a rapidly increasing deer population.

317 Extensive debarking by deer often results in a shift from natural forest to a monotone landscape
318 composed of bamboo grassland, resulting in the loss of dung beetle diversity (Kanda *et al.*, 2005). More
319 precisely, although the guild of dwellers is prone to suffer adverse effects owing to feces drying out
320 because of a reduction in understory vegetation, only larger-sized beetles (mainly tunnelers excelling in
321 open habitats) could receive much benefit from the rapidly growing feces supply (Koike *et al.*, 2014).
322 Aside from the influences of deer, the predation of dung beetles by macaques (Tsuji *et al.*, 2012), and
323 habitat manipulation by boars—especially the overturning of extensive areas of soil vegetation, which
324 affects organisms both above and below ground by physically changing habitat characteristics
325 (Barrios-Garcia & Ballari, 2012)—should also be considered. Post initial-stage ecological influences of
326 mammalian population recovery will not be fully understandable without trying to uncover such
327 multi-layered ecological processes.

328

329 **Conflicts of interest**

330 The authors state that they have no conflict of interest.

331

332 **Author contributions**

333 HE and HSE conceived and designed the research; HE, HSE, YS, KO and YK performed field
334 experiments; SK played a main role to identify dung beetle species; HE and HSE analyzed the data; HE
335 made a draft of this manuscript.

336

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Table 1. Relative abundance index (RAI = individuals/100 camera nights) of recovering mammal species, estimated by camera-trap surveys^a from four study sites in heavy snow areas in northern Japan.

Species	Study sites			
	Site S	Site H	Site A	Site T
Sika deer (<i>Cervus nippon</i>)	0.00	0.00	0.13	0.00
Japanese macaque (<i>Macaca fuscata</i>)	5.26	0.16	5.24	0.00
Wild boar (<i>Sus scrofa</i>)	0.00	0.00	0.00	0.00
Camera nights, CN	532	620	744	306

^a For the summary of RAI for all mammal species recorded in the surveys, see Table A.1.

Table 2. Mean \pm SE of explanatory variables in each generalized linear mixed model^a, to estimate the abundance of dung beetles in heavy snow areas in northern Japan.

Models	Response variables ^b	Intercept	Types of feces (Categorical)			Study sites (Categorical)				AIC	%DE ^d
			Macaque	Deer	Boar ^c	Site S	Site H	Site A	Site T		
#1	#Tunneler	1.64	0.99	-0.15						400.6	37.6
	in spring	$\pm 0.57^e$	$\pm 0.09^e$	± 0.11	0						
#2	#Tunneler	2.49				0.65	-0.54		-2.39	393.6	55.0
	in spring	$\pm 0.30^e$				$\pm 0.09^e$	$\pm 0.11^e$	0	$\pm 0.24^e$		
#3	#Dweller in	0.14	1.50	1.05						867.9	25.8
	spring	± 1.69	$\pm 0.10^e$	$\pm 0.11^e$	0						
#4	#Dweller in	3.44				-0.79	-1.13		-14.23	857.2	48.8
	spring	$\pm 0.36^e$				$\pm 0.08^e$	$\pm 0.09^e$	0	± 52.48		
#5	#Tunneler	2.18	-0.02	-1.11						409.6	31.1
	in summer	$\pm 0.75^e$	± 0.08	$\pm 0.11^e$	0						
#6	#Tunneler	1.71				1.21	1.47		-2.34	401.4	61.3
	in summer	$\pm 0.31^e$				$\pm 0.12^e$	$\pm 0.12^e$	0	$\pm 0.35^e$		

^a We could not build GLMMs for dwellers in summer owing to an insufficient abundance of beetles

^b $N = 60$ for every model

^c Reference for the categorical variable

^d DE indicates deviance explained

^e $Pr(z) < 0.05$

1 **Figure captions**

2

3 Fig. 1. Map of the study area (I) and current distribution of recovering populations of Japanese
4 macaques, wild boar, and Sika deer (II) according to the Ministry of the Environment (unpublished data).
5 Green-colored areas show the distribution of forests. Blue and red grids (5 km resolution) in (II) indicate
6 each mammal's distribution as of 2003, and their recovery areas by 2015, respectively.

7

8 Fig. 2. Similarity in the species compositions of mammals (I) and dung beetles (II), identified by surveys
9 using camera traps and bait traps, respectively, in each study site for the entire study period, as shown by
10 a corresponding analysis. Site T was absent from (I) because no target mammals were confirmed. The
11 values in parentheses on each axis were contribution ratios. Abbreviations between brackets in (II)
12 showed the functional groups of each beetle, i.e., t = tunneler, d = dweller, and r = roller.

13

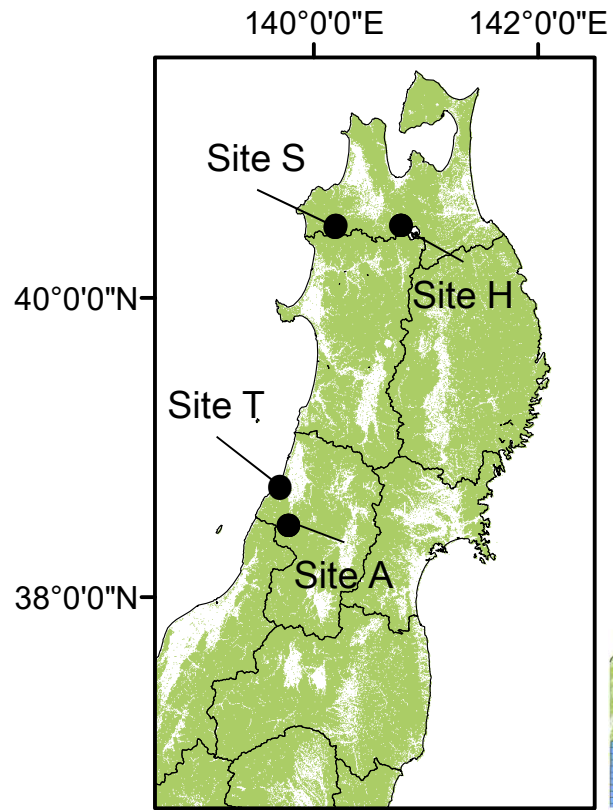
14 Fig. 3. Abundance (bars) and species diversity (lines) of dung beetle assemblages observed in four study
15 sites, Japan. Description of the abundance of rollers was omitted because only a single individual was
16 found in Takadate.

17

18 Fig. 4. Expected species richness of dung beetles, using different mammal feces in each area during
19 spring, estimated by rarefaction and extrapolation curves. Solid and dashed lines show expected values
20 and 95% confidence intervals, respectively.

Fig. 1

(I) Placement of 4 study sites



(II) Status of recovering distributions of 3 mammals

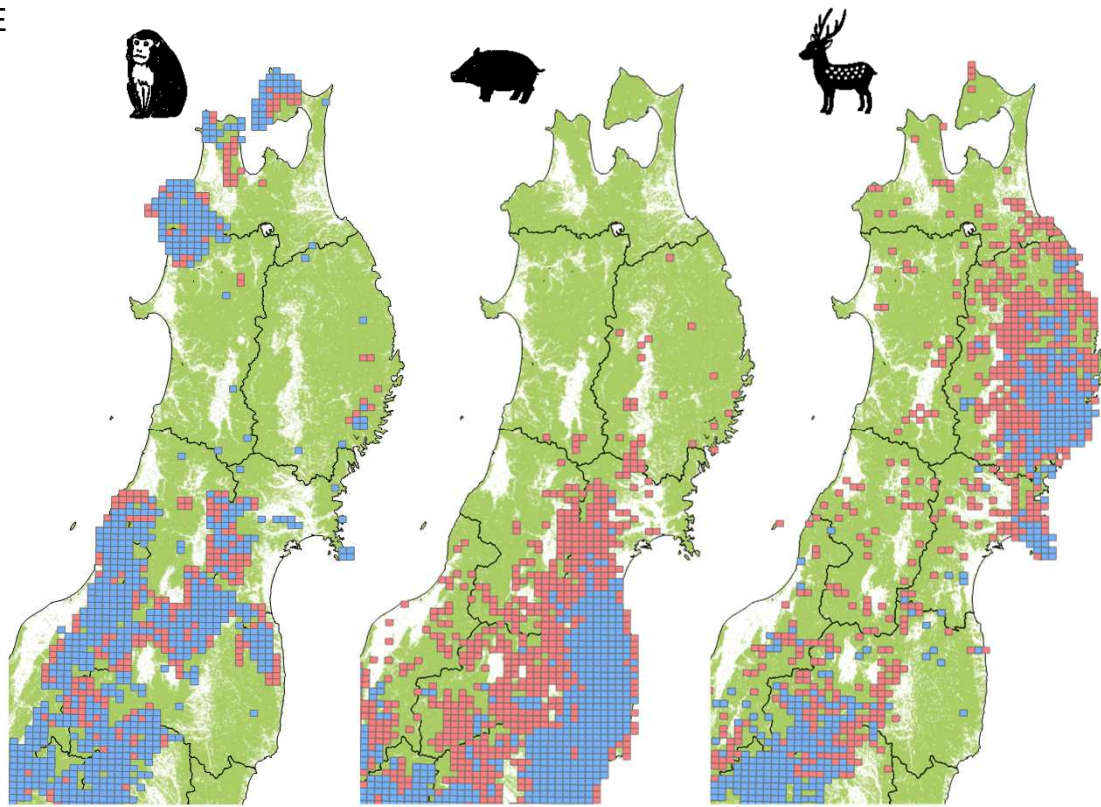
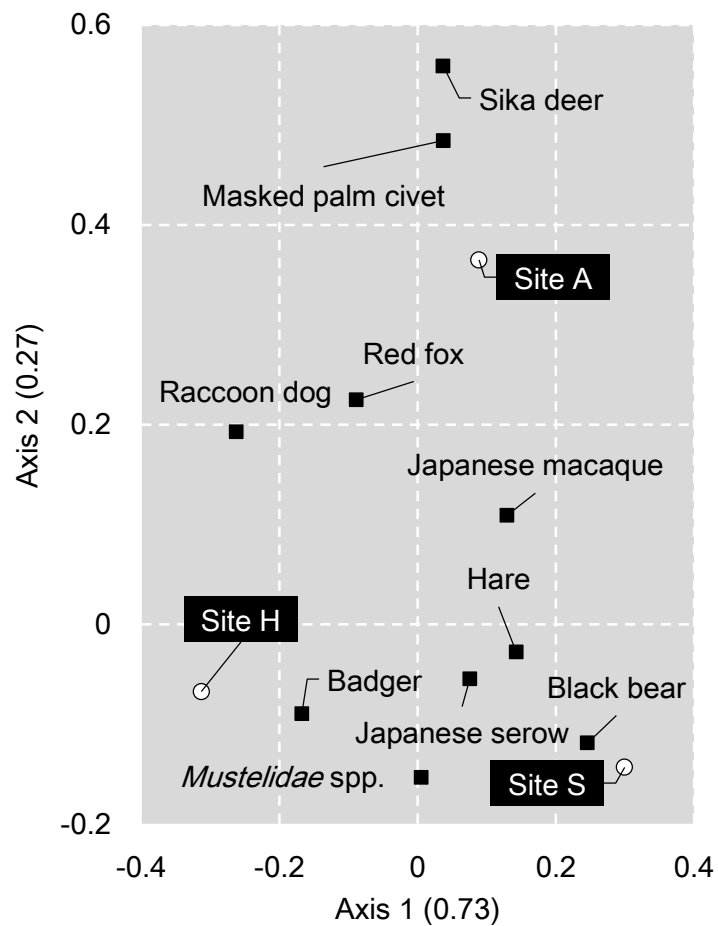


Fig. 2

(I)



(II)

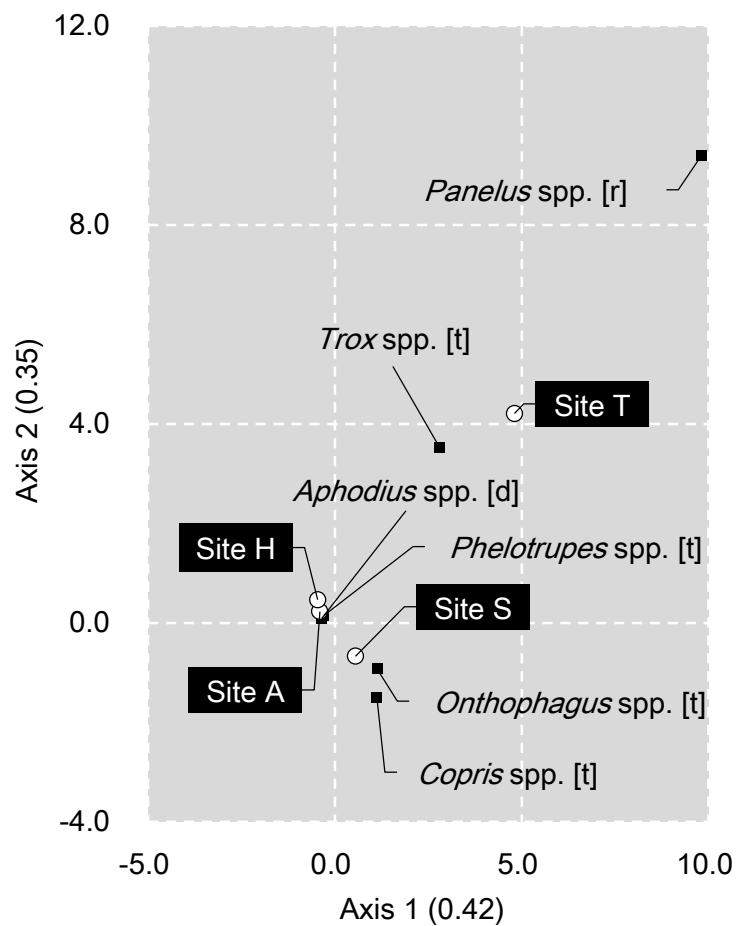


Fig. 3

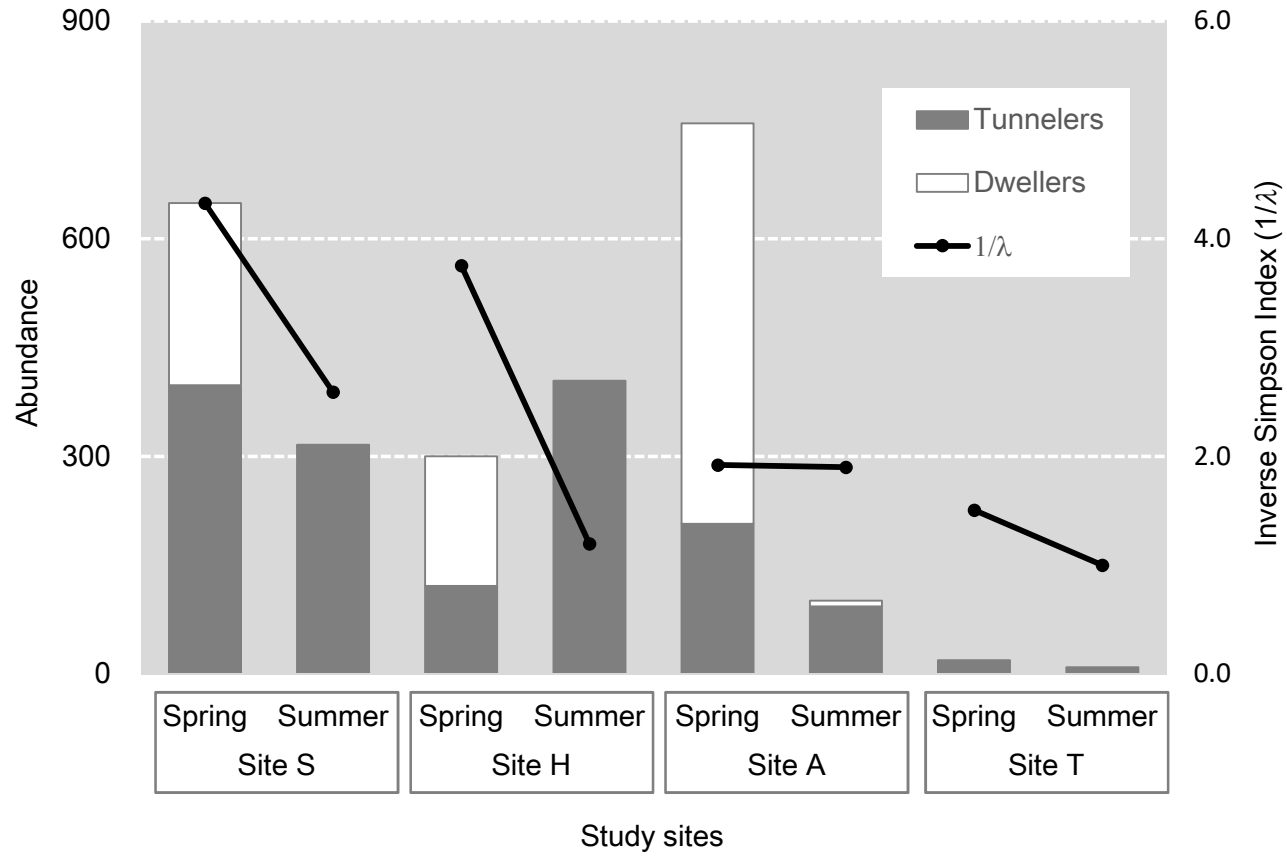


Fig. 4

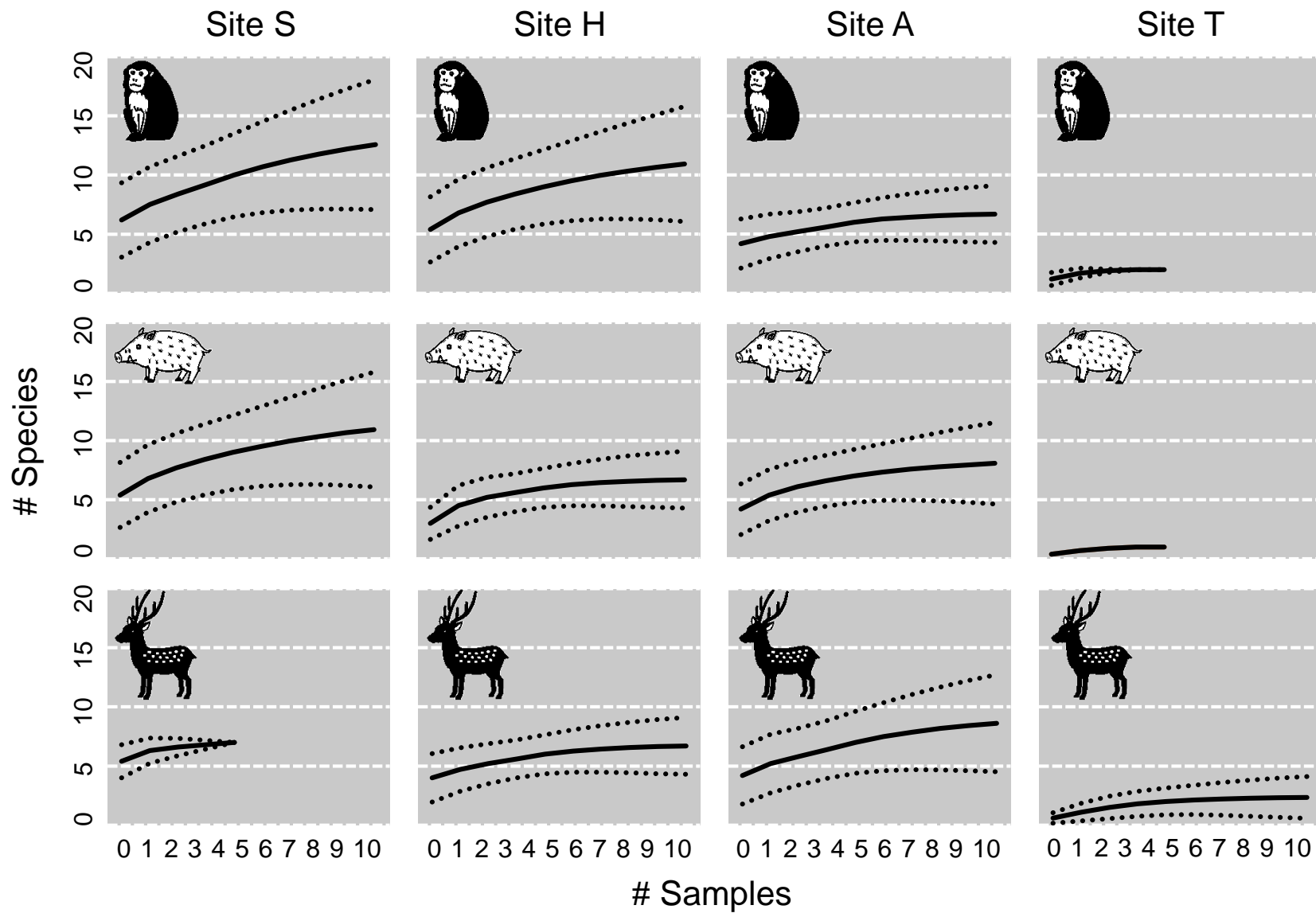


Table A.1. Relative abundance index (RAI = individuals/100 CN) of medium and large mammals, estimated by camera-trap surveys from four study sites in heavy snow areas in northern Japan.

	Species	Study sites			
		Site S	Site H	Site A	Site T
Large mammals					
Black bear	<i>Ursus thibetanus</i>	2.26	0.48	0.67	
Sika deer	<i>Cervus nippon</i>			0.13	
Japanese serow	<i>Capricornis crispus</i>	6.77	2.74	3.36	
Japanese macaque	<i>Macaca fuscata</i>	5.26	0.16	5.24	
Medium mammals					
Marten or weasel	Mustelidae spp.	1.13	0.97	0.13	
Japanese badger	<i>Meles anakuma</i>		9.19	0.27	
Japanese hare	<i>Lepus brachyurus angustidens</i>	1.50	0.81	0.67	
Raccoon dog	<i>Nyctereutes procyonoides</i>		1.77	0.81	
Red fox	<i>Vulpes vulpes</i>		0.32		
Masked palm civet	<i>Paguma larvata</i>			0.40	
Total value of RAI for large mammals		14.29	3.39	9.41	0.00
Total value of RAI for medium mammals		2.63	13.06	2.28	0.00
Species richness		5	8	9	0
Camera nights, CN		532	620	744	306

Table A.2. Abundance of each dung beetle species attracted to feces from three different mammals per study site in northern Japan.

(I) Spring

Scientific name	Site S			Site H			Site A			Site T		
	Boar	Deer	Macaque	Boar	Deer	Macaque	Boar	Deer	Macaque	Boar	Deer	Macaque
<i>Phelotrupes auratus</i>	10	16	57		2	6	6	12	39			
<i>P. laevistriatus</i>	14	14	50	19	39	39	32	13	46			
<i>Copris acutidens</i>	5	11	7									
<i>C. pecuarius</i>			1									
<i>Onthophagus ater</i>	36	30	131			2	10	1	35			
<i>O. atripennis</i>	1		13									3
<i>Aphodius eccoptus</i>	39	115	54	3	13	86	54	149	332			
<i>A. brevisculus</i>	1		1	1	1							
<i>A. ishidai</i>								1				
<i>A. hasegawai</i>				1	5	1	1	1	1			
<i>A. superatratus</i>	13	19	8	3	22	37	2	10	1			
<i>A. unifasciatus</i>			1			6						
<i>Trox opacotuberculatus</i>	1	1		12		1	13			4	2	10
<i>T. mutsuensis</i>						1						
<i>Panelus parvulus</i>											1	
Total	120	206	323	39	82	179	118	187	454	4	3	13
Species richness	9	7	10	6	6	9	7	7	6	1	2	2

(II) Summer

Scientific name	Site S			Site H			Site A			Site T		
	Boar	Deer	Macaque	Boar	Deer	Macaque	Boar	Deer	Macaque	Boar	Deer	Macaque
<i>Phelotrupes auratus</i>	9	1	15	10	8	15	5	3	12			
<i>P. laevistriatus</i>	58	8	73	125	78	165	27	19	24			
<i>Onthophagus ater</i>	1		6						2			
<i>O. atripennis</i>	109		27			1			1	3		6
<i>Aphodius eccoptus</i>			2				1		7			
<i>A. hasegawai</i>		1										
<i>Copris acutidens</i>	4		1									
<i>Trox mutsuensis</i>	1			2								
Total	173	9	109	127	78	166	28	19	34	3	0	6
Species richness	6	3	6	3	2	3	3	2	5	1	0	1