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4 **Landscape-scale evaluation of habitat uses by sympatric mammals foraging for bark and buds in a**  
5 **heavy snowfall area of northern Japan**

6

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16

17 **Abstract**

18 This study focused on influences of 3 different growing populations of mammals foraging for bark and

19 buds—Japanese serows (*Capricornis crispus*), Tohoku hares (*Lepus brachyurus angustidens*) and  
20 Japanese macaques (*Macaca fuscata*)—on a cool-temperate forest in northern Japan. To acquire the initial  
21 knowledge to facilitate ecological monitoring of the influences, we evaluated habitat uses by each species  
22 on a landscape scale by using ecological-niche factor analysis (ENFA), and identified commonalities and  
23 differences among the uses by using discriminant analysis (DA). Within a 50-km<sup>2</sup> area, we selected five  
24 5-km transects and recorded tracks of each mammal on the snow surface along transects during the month  
25 of March in 2008 and 2009. The track data were used as the proof of species presence for entry into  
26 ENFA and DA. Marginality and specialization of species habitat use, computed by ENFA, indicated that  
27 the macaque habitat represented the most heterogeneous distribution and the lowest environmental  
28 tolerance, which was strictly limited by altitude and terrain conditions to prevent exposure to severe cold  
29 climate conditions. This refuge selection by macaques resulted in habitat segregation from serows,  
30 although it appears that both mammals prefer the same young broadleaf forests. Meanwhile, the serow  
31 was observed to be distinctly inclined to use mountainous forests and to avoid artificial environments. As  
32 a result, its habitat could be differentiated from that of the hare, as confirmed by coefficients of a  
33 discriminant factor. These findings indicate that the impact of 3 different mammals foraging on the native  
34 vegetation could be quite restrictive.

35

36 **Key-words:** cool-temperate forest; habitat use; landscape; mammal; snow

37

38 **Introduction**

39 Analyses of mammal–habitat relationships are critical to not only biogeographers but also  
40 mammalogists for understanding the abundance and distribution of subject species (Morrison et al. 2006).  
41 Recent developments in ecological modeling techniques allow users to evaluate the relationships at  
42 different landscape scales by using various environmental factors of interest (Guisan and Thuiller 2005).  
43 To date, these techniques have been applied to practical issues in conservation and management planning,  
44 such as the design of biological reserves (Loiselle et al. 2003), identification of suitable recolonization  
45 areas for threatened species (Cianfrani et al. 2010), and risk assessment of human–wildlife interactions  
46 (Enari and Suzuki 2010).

47 In this study, we applied these emerging techniques to evaluate impacts of mammals on native forests.  
48 Concerns regarding the effects of bark stripping and buds foraging by mammals, especially ungulate  
49 species, on the succession and productivity of native woody plants have been growing over the past few  
50 decades (Gill 1992; Côté et al. 2004; Takatsuki 2009). In mainland Japan, the native ungulate species,  
51 sika deer (*Cervus nippon*) and Japanese serows (*Capricornis crispus*), forage bark and buds in winter. The  
52 effects of foraging by deer on the forest ecosystem are well known (Takatsuki 2009). In addition, there is  
53 a gradual increase in evidence that browsing by serows on bark and buds of certain woody plants during  
54 winter affects the growth and development of these plants, thereby damaging them (Suzuki et al. 1978;  
55 Tsubuku 1991). Ochiai (1999) reported that browsing of serows does not always have a drastic impact on

56 overall vegetation structure and composition because they have low population densities that are related  
57 to their strict territoriality. However, other mammals affecting woody plants in real forest ecosystems do  
58 not share these characteristics. In order to evaluate the influences of mammalian herbivory on regional  
59 forests, we should focus not only on a particular mammal species but also comprehensively on existing  
60 assemblages of local mammals and their interspecies relationships. Although serow and deer occur  
61 allopatrically in most cases (Koganezawa 1999; Nowicki and Koganezawa 2001), the distribution of the  
62 Tohoku hare (*Lepus brachyurus angustidens*; a subspecies of the Japanese hare *Lepus brachyurus*) and  
63 the Japanese macaque (*Macaca fuscata*) coincide with serows on a biogeographical scale in  
64 cool-temperate forests (Biodiversity Center of Japan 2010); as with serows, these 2 species forage for  
65 bark and buds and have remarkable influences on the growth and development of some tree species (e.g.,  
66 Yamada 1991 for hares; Enari and Sakamaki 2010 for macaques).

67 This study focuses on the integrated influence of foraging for bark and buds by multiple existing  
68 mammals (serows, hares, and macaques) on cool-temperate forests in the Shirakami Mountains, a heavy  
69 snowfall area in northern Japan. To acquire the initial knowledge to facilitate ecological monitoring of the  
70 influence, we analyzed the habitat use of each species within its range in a landscape scale (i.e.,  
71 third-order habitat selection process, defined by Johnson 1980), by using ecological-niche factor analysis  
72 (ENFA; Hirzel et al. 2002). Because ENFA requires only data reflecting the presence of a subject species,  
73 we recorded tracks of 3 mammals on the surface of the snow during the month of March in 2008 and

74 2009. The records of the tracks were considered proof of the presence of the species. In addition, to  
75 identify a specific commonality or differentiation among respective species habitats, we conducted  
76 discriminant analysis (DA) using the same track data.

77

## 78 **Study area and species**

79 We recorded tracks of the 3 mammals within an area of 5 km × 10 km at altitudes between 80 m and  
80 600 m above sea level in the northeastern adjacent region of the Shirakami Mountains World Natural  
81 Heritage site, which is located in western Aomori Prefecture (40.5°N, 140.2°E) (Fig. 1). This area was  
82 selected to include almost every landscape found in the Shirakami Mountains, which comprised of highly  
83 diverse ecotones that range from natural woodlands in the mountainous areas to the lowland fuelwood  
84 forests bordering farming villages. This type of landscape structure is traditionally observed in rural Japan,  
85 which is often referred to as Satoyama (Takeuchi 2003).

86 Settlements are concentrated in river terraces at an altitude below 200 m. Primary forests of *Fagus*  
87 *crenata* are mainly distributed in the inner mountainous area. Secondary forests consisting of deciduous  
88 broad-leaved trees and coniferous plantations of *Cryptomeria japonica* are located near the settlements.  
89 The proportion of each type of land cover over the entire area was 43.5% broadleaf forest, 35.9% conifer  
90 plantations, 15.1% settlements, and 5.5% grasslands.

91 The area is in a cool-temperate climatic zone. The mean air temperatures in March 2008 and March

92 2009 were  $3.4 \pm 3.7$  (SD) °C and  $2.5 \pm 2.3$  (SD) °C, respectively ( $n = 31$ , for both). The temperature data  
93 were obtained from the public database of the Shirakami Mountains World Heritage Conservation Center.  
94 The period of snowfall usually lasts from December to March. The maximum snow depth is 2 m in  
95 lowland areas and 3–5 m in mountainous areas.

96 Apart from Tohoku hares, Japanese serows, and Japanese macaques, there have been 11 medium- to  
97 large-sized mammal species in the Shirakami Mountains. Because gray wolves (*Canis lupus*) were  
98 eradicated by the beginning of the 20th century, there have been no large-sized mammal carnivores in the  
99 study area, which means that serows and macaques do not have predators here. Meanwhile, Japanese  
100 marten (*Martes melampus melampus*), Japanese red fox (*Vulpes vulpes japonica*), and golden eagle  
101 (*Aquila chrysaetos*) are the main predators of hares.

102 Although several populations of serows and macaques were threatened by extinction during the early  
103 20th century due to excessive hunting by local residents, these populations have recovered across the  
104 Shirakami Mountains in recent years (Biodiversity Center of Japan 2004, 2011). Because large-scale  
105 population control measures against these mammals have not been implemented in and around the subject  
106 area for more than 50 years, it is reasonable to assume that these 3 mammals have had sufficient time to  
107 become fully distributed in areas with suitable habitat conditions.

108 Hares and serows generally range individually, whereas macaques move in troops, with the exception  
109 of adult males. Hares are nocturnal and macaques are diurnal. Serows alternate between resting and active

110 behaviors every few hours at any time of the day or night. The home range sizes of these mammals vary  
111 widely with environmental conditions and usually range between 10–30 ha for hares and 10–100 ha for  
112 serows and macaques in deciduous broadleaf forests (for a review, see Ohdachi et al. 2009). The habitat  
113 occupation of the macaques is influenced by human activities between summer and fall because a part of  
114 macaque troops feed on the agricultural crops during those seasons. Such influences, however, were  
115 almost negligible for macaques as with the other 2 mammals during the study period, when there was no  
116 available artificial food resource in and round settlements.

117       Although the diets of these mammals vary greatly in different seasons, in snowy regions, they  
118 commonly feed on bark and buds of woody plants during winter. More specifically, serows prefer twigs,  
119 bark, and buds of bushy broadleaved trees and seedlings of conifer plantations in winter. Occasionally,  
120 they consume almost all twigs and shoots of a specific tree (Suzuki et al. 1978; Takatsuki et al. 1988;  
121 Tsubuku 1991; Takatsuki et al. 1995; Koganezawa 1999; Ochiai 1999). Hares have feeding habits similar  
122 to those of serows and can inflict fatal damage to seedlings and bushy trees of both broadleaved trees and  
123 conifers (Horino and Kuwahata 1984; Yamada 1991; Shimizu and Shimano 2010). On the other hand,  
124 macaques tend to feed more frequently on the bark and buds of various broadleaf trees, including  
125 upper-story trees during winter, as a result of their ability to climb trees (Nakayama et al. 1999; Sakamaki  
126 et al. 2011). Because the dietary habits of the 3 mammals during snowfall are commonly euryphagous and  
127 opportunistic, distinctions of bark and buds selections among those mammals are not always obvious.

128 **Methods**

129 Data collection

130 *Environmental variables*

131 First, in order to sort out the environmental variables used in ENFA and DA, we assembled previous  
132 studies associated with habitat use by the 3 mammals (Step 1 in Fig. 2). Although limited studies have  
133 been conducted involving landscape-scale multivariate evaluation of relationships between mammal  
134 habitats and environmental conditions (for serows, Natori and Porter 2007; for macaques, Enari and  
135 Sakamaki 2011), there is some information on the subject of important environmental features that are  
136 expected to influence habitat use by the 3 mammals examined in this investigation. A common  
137 environmental factor potentially influencing the habitation of these mammals is the type of forest cover  
138 (including forest age). Hares often prefer young conifer plantations with an open canopy (Shimano et al.  
139 2006). Such areas are usually located at the edge of a forest (Yatake et al. 2003). Serows and macaques  
140 commonly prefer broadleaf forests (for serows, Ishida et al. 1993; for macaques, Enari and Sakamaki  
141 2011). Moreover, serows and macaques are sensitive to geographic features. Serows tend to occupy steep  
142 sloping land (Ishida et al. 1993; Nowicki and Koganezawa 2001; Ishida et al. 2003), but generally avoid  
143 north-facing slopes (Ishida et al. 1993). Macaques prefer lowland forests close to rivers (Enari and  
144 Sakamaki 2011).

145 In accordance with these descriptions on habitat use by each mammal, we prepared 15 environmental



146 variables (Table 1), which include forest cover classifications (6 variables), geographic features (6  
147 variables), and distributions of human land-use (3 variables). With regard to forest cover, because the  
148 biomass of understory plants drastically changes with the openness of the canopy (as determined by the  
149 incremental growth of overstory trees) (Agetsuma 2007; Sakamaki et al. 2011), we selected a conifer  
150 forest age of 40 years as a cutoff value (the time taken for a forest canopy to become completely closed in  
151 the cool-temperate zone; Sakamaki et al. 2011) and a broadleaf forest age of 100 years as a cutoff value  
152 (the age at which a broadleaf forest can be roughly regarded as a primary forest).

153 We arranged raster maps with 50-m grid resolution for each variable as defined by the Universal  
154 Transverse Mercator (UTM) coordinate system (Table 1). The size of the grid resolution was in  
155 accordance with Enari and Sakamaki (2011), which corresponded to the lowest geographic resolution that  
156 was available in the dataset for each variable. Because only a variable with a quantitative dataset is usable  
157 in ENFA, we provided a continuous-valued attribute to variables with a Boolean data type (i.e., true or  
158 false) by calculating the mean value for each variable within a circular moving window with a 250-m  
159 radius, using block statistics in ArcGIS 9.3 (ESRI, Redlands, CA, USA) (Step 2 in Fig. 2).

160

#### 161 *Species presence data*

162 To collect species presence data with respect to the 3 mammals, we prepared parallel 5-km transects at  
163 2-km intervals within the study area (Step 3 in Fig. 2). While recording mammal tracks on the surface of

164 the snow, transect set  $x$  (Fig. 1) was concurrently followed by 5 investigators 3 times on foot or skis  
165 during the month of March, 2008 (Step 4 in Fig. 2). To avoid pseudo-replication of data sampling, each  
166 track recording was conducted on the day following snowfall, which was enough to obscure the previous  
167 tracks. Moreover, to expand the tracking area, we prepared new transect sets  $y$  and  $z$  based on a  
168 systematic sampling technique involving random selection of  $r$  points on the baseline and then  
169 assembling transects at each of the selected  $r$  positions. Tracks were recorded after exploring all transect  
170 sets once during the month of March, 2009. To reduce sampling biases caused by weather conditions, we  
171 recorded tracks on each day except for snowfall days. Spatial distributions of tracks (i.e., species presence  
172 data) may be sensitive to temporal fluctuations of available food resources. However, for the  
173 simplification of the present analysis, we presumed that annual fluctuations of resource biomass of bark  
174 and buds in the study area were negligible because most woody plant species in the study area are found  
175 in abundance and the succession and productivity of those trees are commonly restricted due to cold  
176 climate.

177 We then prepared respective mammal presence maps with raster-based grid cells ( $50 \times 50$  m) using all  
178 of the data described above. These maps contained 823, 346, and 140 grid cells representing tracks of  
179 hares, serows, and macaques.

180

181

182 Habitat evaluation by ENFA

183 On the basis of the above environmental variables and track data, we evaluated the habitat use of the 3  
184 mammals by using multiple algorithms inherent in ENFA. To select a final model with the maximum  
185 predictive performance for each species, we then validated respective constructed models by using a  
186 cross-validation technique. The details of the theoretical account and actual procedures of the present  
187 ENFA are as follows.

188

189 *Features of ENFA*

190 Similar to principle component analysis (PCA), ENFA summarizes multiple environmental variables  
191 into a few uncorrelated factors that explain potential habitat use of subject species. However, unlike that  
192 in PCA, these summarized factors directly provide 2 ecological interpretations. One is “marginality,”  
193 which indicates the deviation from the mean environmental conditions of the ecological optimum for the  
194 species. Another is “specialization,” which is defined as the narrowness of the species variance (or  
195 ecological optimum for the species) relative to the global variance (Hirzel et al. 2002; Basille et al. 2008).  
196 The first summarized factor (i.e., Factor 1) expresses all of the marginality and part of the specialization;  
197 therefore, “Factor 1” is often simply referred to as “marginality axis” or “marginality factor”. The  
198 remaining factors (i.e., Factor 2 and subsequent factors) express the residual specialization. In addition,  
199 ENFA provides generic indices with regard to the habitat use of a subject species. These indices are global

200 marginality ( $M$ ) and global specialization ( $S$ ), and allow comparison of marginalities and specializations  
201 of different species within a subject area.  $M$  usually ranges from 0 to 1; as the  $M$  value increases, the  
202 species distribution becomes more biased relative to the mean available environmental conditions of a  
203 study area.  $S$  ranges from 1 to infinity. As the value of  $S$  increases, the species' ecological adaptability  
204 decreases. The inverse of  $S$  (i.e., ranging from 0 to 1) indicates the tolerance of the species, which is  
205 referred to as global tolerance ( $T$ ).

206

#### 207 *Practical procedure*

208 Before conducting ENFA, we first normalized the distributions of respective environmental variable  
209 maps using the Box-Cox algorithm (Sokal and Rohlf 1981) because multivariate normality is a  
210 prerequisite for conducting ENFA (Step 5 in Fig. 2). In most cases, multi-collinearity and redundancy  
211 among input variables negatively affect the predictive performance of the constructed model; hence, we  
212 removed variables that were found to be strongly correlated ( $r > 0.8$ ) or variables with remarkably low  
213 eigen values (Step 6 in Fig. 2). Consequently, we discarded 3 out of the 15 variable maps, and 12  
214 variables were assigned as inputs for the model (Table 1). After summarizing the 13 variables using  
215 ENFA, we selected several significant factors to retain for further analysis using broken-stick heuristics  
216 (Hirzel et al. 2002).

217 By using multiple algorithms, we calculated the habitat suitability for the habitat of each mammal. The

218 algorithm selected generally highly influences the predictive performance of the constructed model  
219 according to spatial pattern of the species presence that is input into ENFA (Step 7 in Fig. 2). This study  
220 adopted 3 algorithms; the median algorithm modified by Braunisch et al. (2008), the geometric mean  
221 algorithm (Hirzel and Arlettaz 2003), and the harmonic mean algorithm (Hirzel et al. 2002). Habitat  
222 suitability values in each grid cell vary from 0 (unsuitable habitat) to 100 (optimum habitat) to indicate  
223 how the combination of variables in a cell suits the requirements of a subject species.

224 We evaluated the predictive performance of each habitat model using a 10-fold area-adjusted  
225 frequency cross-validation procedure (Fielding and Bell 1997; Boyce et al. 2002), which consists of the  
226 steps of partitioning the species dataset into 10 sets, constructing a model on the basis of 9 sets, and  
227 validating the model with the remaining data set (Step 8 in Fig. 2). This procedure is repeated 10 times  
228 and provides a mean and a variance for the validation measure. In the present evaluation, we set the  
229 number of bins to 3. The habitat suitability value was reclassified into 3 classes of equal size: unsuitable  
230 (0–33), suitable (34–66), and optimal (67–100). We then computed the Boyce index on the basis of the  
231 Spearman correlation coefficient (Boyce et al. 2002) as a measure of the accuracy of the model. The  
232 Boyce index varies from  $-1$  for an inverse model to 0 for a random model to 1 for a perfect model (Hirzel  
233 et al. 2006). Finally, after generating multiple species-habitat models by using different habitat suitability  
234 algorithms, the model with the highest Boyce index was selected for each species (Step 9 in Fig. 2).

235 We performed all of these procedures using Biomapper 4.0 (Hirzel et al. 2008).

236 Commonalities and differentiation of habitat uses

237 *Application of ENFA*

238 To identify commonalities of habitat use by the 3 mammals, we extracted overlapping areas among the  
239 optimal habitats for all the species that were calculated by ENFA (Step 10 in Fig. 2). We then evaluated  
240 the environmental characteristics of the overlapping areas by comparing the mean of each variable within  
241 the overlap area to the global mean. We also calculated Hurlbert's niche breadth index ( $B'$ ) (Hurlbert  
242 1978) for the overlapping optimal habitat in the study area (Step 11 in Fig. 2).

243 To evaluate habitat overlap among the 3 mammals, we calculated correlation coefficients by  
244 performing pairwise comparisons of habitat suitability values assigned in each grid cell as computed by  
245 ENFA (Step 12 in Fig. 2).

246

247 *DA procedure and its application*

248 To obtain a more explicit comparison of the habitat uses explained by the marginalities and  
249 specializations of the 3 mammals, we also performed DA using Biomapper 4.0 (Sattler et al. 2007; Hirzel  
250 et al. 2008) (Step 13 in Fig. 2). This multivariate analysis computes the first discriminant factor that  
251 maximizes the interspecific variance while minimizing the intraspecific variance. We used the  
252 discriminant factor as an integrative variable with which to compare the habitat uses (Step 14 in Fig. 2).

253

254 **Results**

255 Habitat evaluations by ENFA

256 First, we conducted algorithm selection to calculate a habitat suitability value for each grid cell for the  
257 3 mammal species. The model performance was quite sensitive to selected algorithms, and was found to  
258 be the highest for the habitats of hares and macaques when using the harmonic mean algorithm (Table 2).  
259 The serow habitat model constructed by the geometric mean algorithm was found to be the most robust.  
260 We then used these algorithms with the highest Boyce index for further analysis.

261 In accordance with broken-stick heuristics, 4 summarized factors were commonly retained for each  
262 habitat model (Table 3). The summarized factors accounted for more than 75% of the total variance and  
263 for more than 50% of the total specialization of the species habitat use of all models. The value of  $M$  for  
264 macaque habitat was found to be the highest, followed by the serow habitat and then by the hare habitat.  
265 According to the values of  $S$  and  $T$ , the hare habitat had the highest environmental tolerance.

266 Marginality axes (i.e., factor 1) computed by ENFA clearly showed specific ecological features of  
267 habitat use by the mammals (Table 4). As indicated by the coefficients of the axes associated with forest  
268 cover, serow and macaque habitats were found to include young broadleaf forests, whereas the hare  
269 habitat was dominated by young evergreen conifers (Table 4). Variables related to geographical features  
270 (i.e., mean altitude, slope, and SD of altitude) on the marginality axes indicated that the hare and serow  
271 habitats were located in areas of higher elevation than the macaque habitat. The serows and macaques

272 were found to prefer more rugged mountainous areas. Moreover, hares and serows were more likely to  
273 occupy areas close to rivers or lakes, while most macaque habitats were located next to roads. The largest  
274 variance of the specialization was commonly attributed to factor 1 for each mammal habitat, indicating  
275 that these species are quite sensitive to shifts in their optimal conditions.

276 We then created habitat suitability maps for each mammal by allocating computed suitability values to  
277 a geographic space (Fig. 3). The preferred habitat for serows in the study area was largest in size,  
278 followed by the hare habitat, and then the macaque habitat. The optimal, suitable, and unsuitable habitats  
279 were 9.0 km<sup>2</sup>, 12.5 km<sup>2</sup>, and 28.5 km<sup>2</sup> for hares, 10.5 km<sup>2</sup>, 16.1 km<sup>2</sup>, and 23.4 km<sup>2</sup> for serows, and 2.9  
280 km<sup>2</sup>, 8.6 km<sup>2</sup>, and 38.5 km<sup>2</sup> for macaques, respectively.

281

## 282 Commonality and differentiation of habitat uses

283 We identified areas of overlap among the optimal habitats of the 3 mammals. The size of this  
284 overlapping area was 0.56 km<sup>2</sup>, representing 0.67% of the entire study area. As for the 2 variable  
285 means—frequency of young deciduous broadleaf forests and distance to dwelling land—the differences  
286 from the global means were relatively high, while those from niche breadths ( $B'$ ) were relatively low  
287 (Table 5). As a whole, however, there were few differences for most variable means between the  
288 overlapping area and the study area. Half of the variables had  $B'$  values that were higher than 0.5. These  
289 results indicate that 3 mammals share only a very limited area with fairly-specialized environments, i.e.,



290 young broadleaf forests bordering on settlements.

291 The correlation matrix among habitat suitability values of the 3 mammals also indicates that the  
292 commonality of habitat uses is quite narrow, although the correlation coefficient between the hare and  
293 serow habitats was relatively high, compared to the other pairwise comparisons (Table 6). Meanwhile,  
294 differentiation of habitat uses was distinctly detected by DA (Table 7). Each of the discriminant factors  
295 indicated that (1) the differentiation of hare and macaque habitats was characterized by the observation  
296 that hares favor gradual southern-slopes with young evergreen conifers, while macaques prefer young  
297 broadleaf forests; (2) serow and hare habitats were distinguished by the observation that serows more  
298 frequently occupy mountainous areas, with the exception of northern slopes in young broadleaf forests;  
299 and (3) macaque and serow habitats were distinguished by the observation that macaques are found more  
300 often in old evergreen conifer forests in lowland areas.

301

## 302 **Discussion**

303 While the tracks of hares, serows, and macaques were observed across the study area, species-specific  
304 trends emerged. As shown in terms of marginality and specialization of species habitat use, the macaque  
305 habitat represents the most heterogeneous distribution and the lowest environmental tolerance (Table 3).  
306 Considering that most primate species, including the genus *Macaca*, are geographically distributed in  
307 rain/humid forests between warm-temperate and tropical regions (Fooden 1982; Lehman and Fleagle

308 2006), Japanese macaques are a highly specific species that extended their distribution even into  
309 cool-temperate forests that receive heavy snowfall. This occurred after the last glacial period, i.e., ca.  
310 15,000 years ago (Kawamoto et al. 2007). There is evidence that Japanese macaques have become  
311 evolutionarily adapted to cold climate conditions (Ross 1992; Hamada and Yamamoto 2010; Hanya  
312 2010); however, it is unreasonable to assume that macaques have become more acclimatized to  
313 cool-temperate forests than have serows and hares, because the latter 2 mammals are eco-physiologically  
314 and morphologically adapted to snowy regions including subalpine areas, where macaques are no longer  
315 able to range. This is supported by the finding that the optimal macaque habitat is distinctly narrow (Fig.  
316 3) and strictly limited by altitude and terrain conditions to avoid cold and snowstorms wherever possible  
317 (Table 4; Enari and Sakamaki 2011). This specialized refuge selection by macaques has resulted in habitat  
318 segregation from serows (Table 7), despite the finding that both mammals have a preference for the same  
319 resources in young broadleaf forests (Table 4).

320 The serow has a distinct inclination to inhabit mountainous forests, and to rarely occupy conifer  
321 plantations (regardless of forest age) and areas close to dwelling land. This has resulted in differentiation  
322 of its habitat from the hare habitat (Tables 4 and 7). Unlike macaques, however, hares have habitat use  
323 that is partly correlated with the habitat use of serows (Table 6). This correlation may be rationalized by  
324 the existing Satoyama landscape in the study area (see “Study area and species”). It is reasonable to  
325 consider that such highly mosaic landscapes, or the diverse ecotones, restrict the optimal species-specific

326 habitat requirements of serows (i.e., less disturbed mountainous forests). These natural forests are patchly  
327 distributed in the study area, and therefore, the animals are forced to move in the alternative habitat within  
328 the Satoyama landscape, such as the disturbed fuelwood-forests, in search of their optimal habitat. The  
329 result is partial habitat overlap between serows and hares.

330

### 331 Conclusions and future challenges

332 Serows, hares, and macaques are recognized as sympatric mammal species as judged by their  
333 biogeographical and home-range scales (i.e., first- and second-order selections, respectively; Johnson  
334 1980). In addition, from the viewpoint of habitat selections within their ranges (i.e., third-order selection),  
335 overlapping optimal habitats among 3 mammals were confirmed to exist in young broadleaf forests  
336 around settlements, or a part of the Satoyama landscape (Table 5). This indicates that the existing  
337 landscapes with diverse ecotones may have some effects on the inhibition of obvious habitat segregation  
338 among the 3 mammals. There is still room for argument based on on-site monitoring of the physiological  
339 impact on plants caused by the mammal populations consuming native vegetation. In this regard, however,  
340 it seems quite probable that the impacts are quite restrictive, considering that habitat uses by mammals  
341 foraging for bark and buds are separated from each other by species-specific habitat selections as  
342 mentioned above.

343 On the other hand, it should be noted that the present conclusion with respect to impacts of growing

344 mammal populations on the vegetation may be drawn only at the current time. Given that the habitat  
345 occupation by all mammal species is sensitive to the age of overstory trees (or canopy openness), it is  
346 possible that the present habitat selectivity by mammals will be altered as forest growth progresses,  
347 especially in large-scale monotonous forests such as coniferous plantations (Agetsuma 2007). To acquire  
348 a more general conclusion, besides focusing on the patch size of respective habitat types and landscape  
349 structures, further research on time series variations of mammal-habitat relationships is required.

350

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492 **Figure captions**

493 **Fig. 1** Map of study area, located in the northeastern Shirakami Mountains of the northernmost mainland  
494 of Japan

495

496 **Fig. 2** Flow diagram of the evaluation of commonalities and differentiation among habitat uses by the 3  
497 mammal species

498

499 **Fig. 3** Habitat suitability maps for Tohoku hares, Japanese serows, and Japanese macaques in  
500 cool-temperate forests. White, gray, and black colored grid cell shows unsuitable (0–33), suitable (34–66),  
501 and optimum (67–100) species habitat, respectively

**Table 1** Environmental variables used in ecological-niche factor analysis for 3 mammalian species

Category Environmental variables	Global mean	Range	SD	Application for a final model	Source <sup>a</sup>
<b>Forest cover</b>					
Freq. <sup>b</sup> of old deciduous broadleaf forests	0.01	0.00–0.40	0.03	No	A, B
Freq. of young deciduous broadleaf forests	0.41	0.00–1.00	0.27	Yes	A, B
Freq. of old deciduous conifers	0.03	0.00–0.84	0.09	No	A, B
Freq. of young deciduous conifers	0.00	0.00–0.12	0.01	No	A, B
Freq. of old evergreen conifers	0.11	0.00–0.95	0.14	Yes	A, B
Freq. of young evergreen conifers	0.20	0.00–1.00	0.23	Yes	A, B
<b>Geographical features</b>					
Mean altitude (m)	258.72	76.98–578.26	92.59	Yes	C
Mean slope (°)	14.12	0.00–49.81	8.35	Yes	C
SD of altitude	26.25	0.00–82.90	12.28	Yes	C
Freq. of northern slope	0.42	0.00–1.00	0.20	Yes	C
Freq. of southern slope	0.29	0.00–1.00	0.20	Yes	C
Dist. to river or lake (m)	225.07	0.00–1,063.01	188.91	Yes	D, E
<b>Human land-use</b>					
Dist. to farmland (m)	520.63	0.00–2,531.80	528.87	Yes	D, E
Dist. to dwelling land (m)	1,124.98	0.00–4,123.11	796.91	Yes	D, E
Dist. to road (m)	321.74	0.00–1,500.83	304.65	Yes	D, E

<sup>a</sup> A: National forest planning map 2009 (1:5,000); Japan's Forest Agency

B: Private forest planning map 2009 (1:5,000); Aomori Prefectural Government

C: Digital elevation model (resolution = 10 m); Geographical Survey Institute, Japan

D: Digital national land information (vector data); Ministry of Land, Infrastructure, Transport and Tourism, Japan

E: High-resolution satellite images (optical resolution = 2.5 m) taken by the Advanced Land Observing Satellite (ALOS) in November 2009

<sup>b</sup> “Frequency” means “the average value for each variable within a circular moving window with a 250-m radius.”

**Table 2** Mean and standard deviation (SD) of Boyce index for each habitat model of Japanese hares, Japanese serows, and Japanese macaques, calculated by area-adjusted frequencies of cross-validation technique (bin # = 3) using different algorithms for computing habitat suitability

Algorithms	Hares		Serows		Macaques	
	Mean	SD	Mean	SD	Mean	SD
Median	0.40	0.73	0.55	0.32	0.70	0.34
Geometric mean	0.50	0.55	0.60	0.28	0.55	0.57
Harmonic mean	0.70	0.26	0.55	0.32	0.85	0.32

**Table 3** Global marginality, specialization, and tolerance values for predicted habitat models for Japanese hares, Japanese serows, and Japanese macaques in the Shirakami Mountains of northern Japan

	Hares	Serows	Macaques
Marginality ( $M$ )	0.23	0.49	0.57
Specialization ( $S$ )	1.14	1.23	1.43
Tolerance ( $T$ )	0.88	0.81	0.70
Number of summarized factors used in final model	4	4	4
Variance explained (%)	75.7	79.8	81.8
Specialization explained (%)	51.4	59.5	63.5



**Table 4** Variance explained by the first two summarized factors and coefficient values for each variable for Tohoku hares, Japanese serows, and Japanese macaques. The amount of specialization in each factor is given between parentheses<sup>a</sup>

Variables	Hares		Serows		Macaques	
	Factor 1 <sup>b</sup>	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
	(17.6)	(14.9)	(22.6)	(19.0)	(20.8)	(17.0)
Freq. of young deciduous broadleaf forests	0.07	-0.08	0.55	0.06	0.29	0.22
Freq. of old evergreen conifers	0.01	-0.21	-0.01	-0.10	0.05	0.11
Freq. of young evergreen conifers	0.67	0.10	-0.02	0.23	0.03	0.12
Mean altitude	0.37	0.39	0.39	0.38	-0.23	-0.40
Mean slope	0.03	0.07	0.33	0.22	0.39	-0.02
SD of altitude	0.02	-0.57	0.26	-0.26	0.47	0.37
Freq. of northern slope	0.21	0.02	-0.13	0.07	0.01	0.17
Freq. of southern slope	-0.11	0.00	0.05	0.11	-0.06	0.07
Dist. to river/lake	0.51	-0.02	0.34	0.23	-0.03	-0.03
Dist. to farmland	-0.01	-0.25	0.30	-0.73	-0.15	0.10
Dist. to dwelling land	0.31	-0.62	0.26	-0.26	-0.40	0.76
Dist. to road	-0.06	0.03	0.27	0.11	-0.54	0.02

<sup>a</sup>Specialization coefficients range from -1 to +1: the higher the absolute value, the more restricted the range of macaques on the corresponding variable.

<sup>b</sup>Coefficients of the marginality factor (= factor 1) range from -1 to +1 for each variable: positive coefficient values indicate positive selection, whereas negative values indicate negative selection relative to the mean conditions in the reference area.

**Table 5** Environmental characteristics of the overlapping area among optimal habitats of Japanese hares, Japanese serows, and Japanese macaques in the Shirakami Mountains of northern Japan

Variables	Mean (SD)	Difference from the global mean	Hurlbert's niche breadth index: $B'$
Freq. of young deciduous broadleaf forests	0.67 (0.14)	0.25	0.29
Freq. of old evergreen conifers	0.08 (0.08)	-0.03	0.79
Freq. of young evergreen conifers	0.19 (0.09)	-0.01	0.41
Mean altitude	282.29 (37.89)	23.57	0.37
Mean slope	15.80 (5.46)	1.68	0.71
SD of altitude	27.88 (6.52)	1.64	0.54
Freq. of northern slope	0.45 (0.16)	0.03	0.68
Freq. of southern slope	0.21 (0.16)	-0.08	0.03
Dist. to river/lake	272.16 (124.69)	47.09	0.64
Dist. to farmland	494.55 (181.99)	-26.08	0.36
Dist. to dwelling land	799.26 (234.57)	-325.74	0.39
Dist. to road	165.33 (121.87)	-156.41	0.58

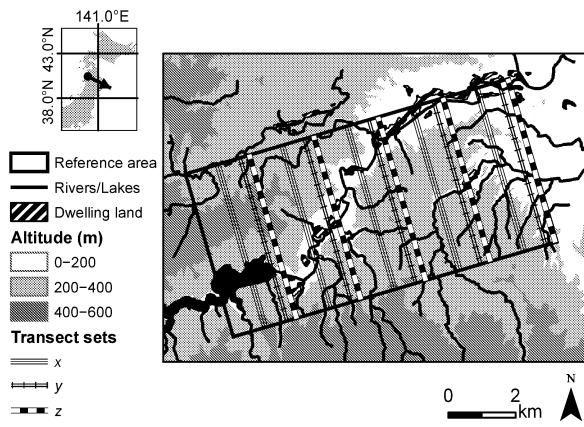
**Table 6** Correlation matrix among habitat suitability values of Japanese hares, Japanese macaques, and Japanese serows, computed by ENFA

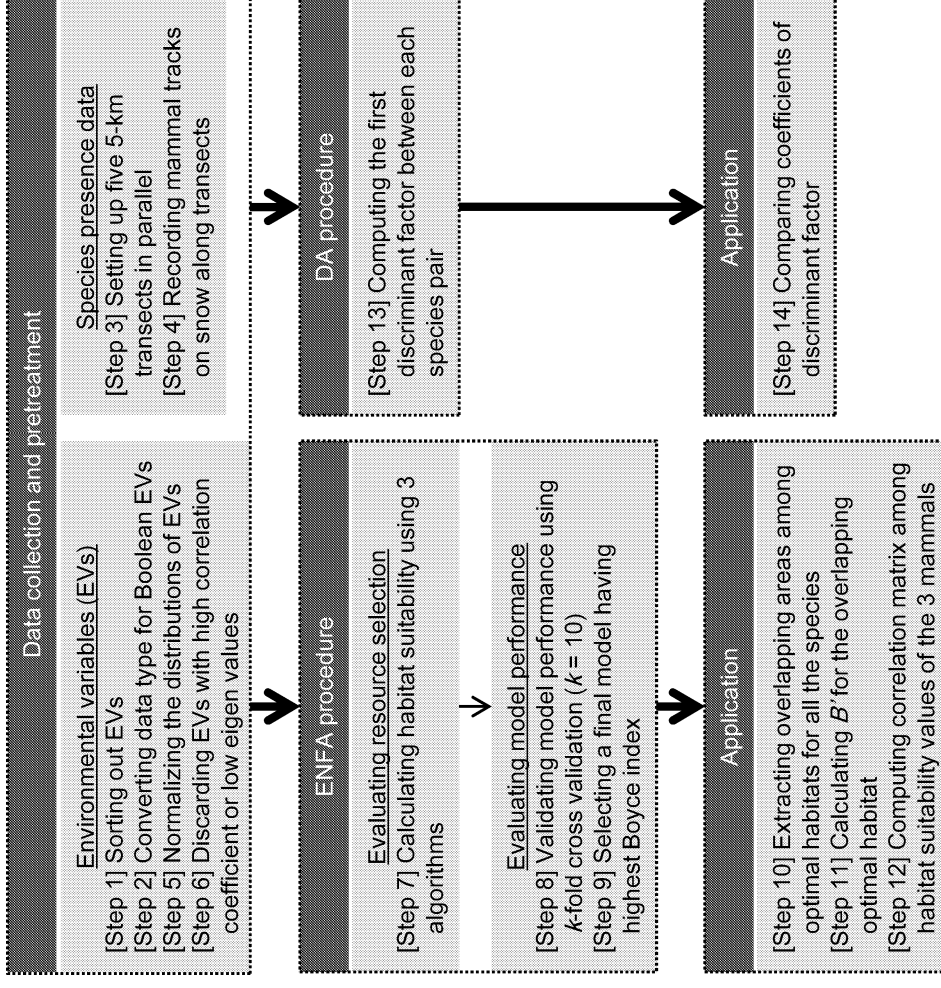
	Hares	Serows	Macaques
Hares	1	0.28	0.17
Serows	0.28	1	0.18
Macaques	0.17	0.18	1

**Table 7** Coefficients of the first discriminant factor<sup>a</sup> between the habitat characteristics of each mammalian species and their niche overlaps

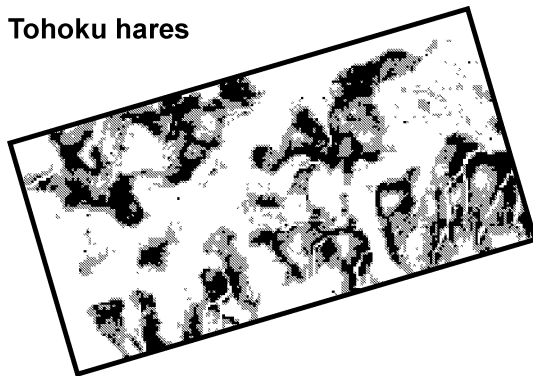
Variables	Species 1	Hares	Serows	Macaques
	Species 2	vs. Macaques	vs. Hares	vs. Serows
Freq. of young deciduous broadleaf forests		-0.40	0.37	-0.24
Freq. of old evergreen conifers		-0.23	0.22	0.50
Freq. of young evergreen conifers		0.25	-0.26	0.17
Mean altitude		0.11	0.24	-0.35
Mean slope		-0.05	0.43	-0.27
SD of altitude		-0.01	0.11	-0.21
Freq. of northern slope		0.02	-0.43	0.10
Freq. of southern slope		0.51	-0.22	-0.26
Dist. to river/lake		0.29	0.13	-0.31
Dist. to farmland		0.52	0.36	-0.31
Dist. to dwelling land		0.29	0.18	-0.28
Dist. to road		0.13	0.30	-0.27

<sup>a</sup> Positive coefficients indicate variables that favor species 1, while negative coefficients favor species 2.

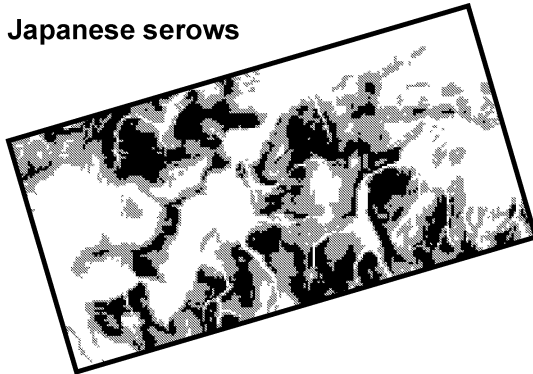




**Tohoku hares**



**Japanese serows**



**Japanese macaques**

