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6 **Influence of heavy snow on the feeding behavior of Japanese macaques (*Macaca***
7 ***fuscata*) in northern Japan**

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9 Hiroto ENARI ^a, Haruka SAKAMAKI-ENARI ^{a, b}

10

11 ^aSatoyama Science Research Center, Faculty of Agriculture, Utsunomiya University

12 ^bThe United Graduate School of Agricultural Sciences, Iwate University

13

14 **Short title:** Influence of snow on Japanese macaques

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16 **Corresponding author:**

17 Hiroto ENARI

18 Satoyama Science Research Center, Faculty of Agriculture, Utsunomiya University,

19 350 Minemachi, Utsunomiya, Tochigi 321-8505, Japan

20 E-mail: h_enari@hotmail.com

21 Tel: +81 28 649 8164

22 Fax: +81 28 649 8165

23 **ABSTRACT**

24 Natural disasters can degrade primate habitat and alter feeding behavior. Here, we
25 examined the influence of unusually heavy snow on diet and feeding-site use by
26 Japanese macaques (*Macaca fuscata*) in northern Japan. To compare the
27 winter-feeding behavior under different snow conditions, we recorded the plant species
28 foraged on by macaques in multiple transects of the Shirakami Mountains from 2008
29 to 2012 (excluding 2011). We used cluster analysis to describe foraged plant
30 assemblages, and applied multiple dimensional scaling and decision tree modeling to
31 evaluate annual variation in feeding-site use by macaques. Our cluster analysis
32 revealed five types of foraged plant assemblages. The proportion of each type present
33 in transects varied considerably across the years, indicating that the diet of macaques in
34 heavy snow conditions was influenced more by resource accessibility than by
35 preference. Multiple dimensional scaling and decision tree modeling demonstrated that
36 heavy snow conditions restricted feeding-site use. Moreover, the distribution of refuges
37 relative to severe external ambient environments was a stronger limiting factor for
38 feeding-site use than was the availability of food resources. While most primate
39 species facing unexpected starvation employ risk-prone foraging tactics (i.e., choosing
40 the option with higher pay-off by accepting risk), Japanese macaques have a tendency
41 to adopt risk-averse foraging behavior (i.e., minimizing energy loss when searching for
42 preferred diet items under long-lasting heavy snow conditions), because winters with
43 temperatures below freezing have higher thermoregulatory costs.

44

45 **KEYWORDS:** cool-temperate forest; feeding trace; *Macaca fuscata*; resource use;
46 Shirakami Mountains

47

48 INTRODUCTION

49 Natural disasters are known to have negative influences on wild primate populations,
50 including reductions in population size. For example, black howler (*Alouatta pigra*)
51 populations were reduced by Hurricane Iris [Pavelka et al., 2007]; wild populations of
52 chacma baboons (*Papio ursinus* [Hamilton, 1985]) and ring-tailed lemurs (*Lemur catta*
53 [Gould et al., 1999]) suffered losses in response to severe drought; and endangered
54 populations of snub-nosed monkeys (*Rhinopithecus roxellana*) were affected by a
55 heavy snowstorm [Li et al., 2009]. However, in the face of natural disaster, such
56 primate species often employ defensive tactics to minimize any negative impacts on
57 the population by varying their foods, activity budgets, or intragroup diet patterns. For
58 instance, black howlers affected by Hurricane Iris coped with the depletion of their
59 usual food resources (especially figs with high calcium content) by foraging on mature
60 leaves (with similar mineral contents as that in figs) as alternative foods [Behie &
61 Pavelka, 2012a, b]. To compensate for reduced food availability following a typhoon,
62 Japanese macaques (*Macaca fuscata*) altered their activity budgets, mainly by reducing
63 their time spent traveling and accelerating their feeding speed [Tsuji & Takatsuki,
64 2008]. Furthermore, spider monkeys (*Ateles geoffroyi yucatanensis*) responded to a
65 dramatic decrease in fruit availability caused by Hurricanes Emily and Wilma, by
66 increasing the level of fission–fusion dynamics to reduce intragroup feeding
67 competition [Schaffner et al., 2012]. To date, evaluation of changes in the behavioral
68 patterns of other primates after a disaster has resulted in similar findings (*Macaca*
69 *sinica* [Dittus, 1988]; *M. fascicularis* [Berenstain, 1986]; *Colobus badius rufomitratu*
70 [Decker, 1994]; *Gorilla gorilla gorilla*, *Pan troglodytes*, *Mandrillus sphinx*, *Colobus*
71 *satanas*, *Cercocebus albigena*, *Cercopithecus nictitans*, *C. pogonias*, and *C. cephus*
72 [Tutin et al., 1997]).

73 By the late Pleistocene, Japanese macaques had expanded their distribution into the
74 northernmost habitat of any nonhuman primate species, namely, a cool-temperate
75 forest where snowfall can reach >2 m in depth [Iwamoto & Hasegawa, 1972].
76 Alongside the recent climate destabilization associated with global climate change,
77 northern Japan has experienced increases in the frequency of very heavy snow and
78 winter warming [Kawamura, 2008]. Historical meteorological data collated by the
79 Aomori Meteorological Observatory, which is located geographically close to the
80 northernmost habitat of Japanese macaques, show that the coefficient of variation (CV)
81 of the annual maximum snow depth during the last 15 years (1998–2012) is 0.36,
82 which is 1.5 times the CV of the previous 15 years (0.24 for 1983–1997). This
83 indicates a greater difference between the highest and lowest maximum snowfalls
84 during the second period. Heavy snowfall, such as that expected during years with
85 maximum snowfall, often leads to the increased mortality of infant Japanese macaques
86 [Koganezawa & Imaki, 1999]; when combined with cold temperatures and failure of
87 the autumnal fruit harvest, the lengthy heavy snowfall is resulted in a 30% reduction of
88 the macaque population on Kinkazan Island in northern Japan [Izawa, 2009].

89 Snow also restricts macaques from traveling on the ground [Watanuki & Nakayama,
90 1993; Izumiya, 1999], leading to a reduction in their winter range, which is less
91 than half the size of their range during other seasons [Wada & Ichiki, 1980;
92 Koganezawa & Imaki, 1999; Imaki et al., 2000; Enari et al., 2006]. In addition,
93 macaques aggregate on southern slopes at low altitudes (e.g., less than 300 m above
94 sea level in the Shirakami Mountains) to prevent exposure to severe cold [Enari &
95 Sakamaki, 2011, 2012; Sakamaki & Enari, 2012]. Besides these behavioral constraints,
96 snow cover affects diet. When snow covers all plant species on the ground [Suzuki,
97 1965; Taroda, 2002], the number of available food sources is reduced. As a result,

98 macaques depend on dwarf bamboo (*Sasa* spp.) and sedge (*Carex* spp.) in
99 light-snowfall areas (maximum depth <100 cm), and on the bark and buds of woody
100 plants in heavy-snowfall areas (maximum depth >100 cm), rather than on the leaves,
101 seeds, and fruit consumed in the absence of snow. Thus, in areas with heavy-snowfall,
102 the winter diet of macaques is limited to foods with a low feeding-rate (i.e., slow speed
103 of nutrient intake), and the distribution of feeding sites is more restricted than that of
104 resting or traveling sites [Sakamaki & Enari, 2012]. Consequently, the energy intake of
105 macaques in winter accounts for only 60% of their energy expenditure in cool
106 temperate forests, even under normal climate conditions [Nakagawa, 1989a; Nakagawa
107 et al., 1996; Nakayama et al., 1999; Tsuji et al., 2008]. Apart from these basic findings
108 on the winter ecology of Japanese macaques inhabiting cold areas, little is known
109 about how macaques cope with the long-lasting, very heavy snow caused by recent
110 climate destabilization.

111 An extraordinarily heavy snowfall occurred in northern Japan from January–March
112 2012. The number of days in which the snow depth was at least one meter in a lowland
113 human settlement (40°34'40.97"N, 140°17'56.55"E), in which almost all plant species
114 except tall trees were buried in snow, was 77 in 2012, 19 in 2008, 0 in 2009 and 17 in
115 2010 (data provided by the Shirakami-Sanchi World Heritage Conservation Center).
116 This paper aims to investigate the influence of long-lasting heavy snow on the
117 winter-feeding behavior of Japanese macaques, based on comparisons with light
118 snowfall years. For this purpose, we evaluated interannual variation in food
119 consumption and feeding-site use in the Shirakami Mountains, one of the northernmost
120 habitats in the species range, between 2008 and 2012 (excluding 2011).

121 **METHODS**

122 **Study area and subject species**

123 We studied the feeding behavior of Japanese macaques in the northeastern part of
124 the Shirakami Mountains (center coordinates 40°32'9"N, 140°14'43"E). The area is a
125 cool-temperate climatic zone, which includes deciduous broadleaf forests of Japanese
126 beech (*Fagus crenata*) and oak (*Quercus crispula*), and evergreen coniferous forests of
127 Japanese cedar (*Cryptomeria japonica*). According to the public database of the
128 Shirakami-Sanchi World Heritage Conservation Center, the mean air temperature
129 during winter (January–March) was -0.6°C in 2008, -0.3°C in 2009, -0.6°C in 2010,
130 and -2.2°C in 2012.

131 The Japanese macaques inhabiting the Shirakami Mountains constitute the largest
132 population in northern Japan [Enari & Suzuki, 2010; Biodiversity Center of Japan,
133 2011]. In March 2008, the individual and troop densities in and around the study area
134 were determined to be 5.19 individuals/km² (including non-troop males) and 0.15
135 troops/km², respectively [Enari & Sakamaki, 2011]. Meanwhile, the mean troop size
136 (which we constantly monitored in the study area) was approximately 35 individuals
137 ($N = 4$). In recent decades, there has been no large-scale population culling; therefore,
138 the population statistics and home ranges were free from artificial impacts during the
139 study period. The dominant foods of these macaques during snowfall seasons are the
140 bark and buds of deciduous broadleaf trees [Enari & Sakamaki, 2010; Sakamaki et al.,
141 2011], and, particularly, the bark and buds of shade-intolerant shrub and vine species
142 (i.e., heliophytes [Sakamaki et al., 2011]).

143 **Data collection**

144 We evaluated the feeding behavior of macaques not by observing individual animals,
145 but by recording external signs within transects. We used bite marks and stripped bark
146 as the external signs [Li et al., 2002; Enari & Sakamaki, 2010; Sakamaki et al., 2011].
147 Macaques feed on only the cambium layer of bark or a part of buds, and therefore,

148 these signs are unequivocally left on every woody plant foraged on by macaques. We
149 readily distinguished fresh feeding traces from old ones by an obvious difference in
150 color and while Japanese hares (*Lepus brachyurus*) and Japanese serows (*Capricornis*
151 *crispus*) feed on the bark and buds of woody plants, their foraging traces were
152 distinguishable from those of macaques by an obvious difference in appearance of the
153 feeding traces [Enari & Sakamaki, 2010]. Direct field observations previously
154 indicated that, Japanese macaques inhabiting the study area fed on the bark and buds of
155 woody plant species during snowy seasons (i.e., January–March), and that this
156 accounted for >80% of their total feeding time [Enari et al., 2005]. Hence, it is
157 reasonable to assume that such feeding traces accurately reflect the macaques' diet.

158 To assess winter feeding behavior, we set up five 40-m wide transects along forest
159 roads within the area, away from human settlements (Fig. 1; Table I). The forest roads
160 were located in relatively low areas along rivers or streams, which macaques
161 preferentially use for winter-feeding sites [Sakamaki & Enari, 2012]. Recent artificial
162 disturbance to the five transects (such as deforestation or afforestation) was negligible,
163 because forestry management had been conducted at a low frequency since 1990.
164 Moreover, the sika deer (*Cervus nippon*)—a well-known ecosystem engineer—is not
165 present in the study area. Thus, we assumed that the abundance and distribution of
166 food plants did not change significantly during the study period.

167 We explored the transects at the end of March in 2008, 2009, 2010, and 2012, to
168 record fresh feeding traces that remained on the bark or buds of all woody plant
169 species marked by macaques during the current year. We selected the end of March as
170 the best period for counting all of the feeding traces marked by macaques during the
171 current snowy season. Moreover, because this was the snowmelt month, we were able
172 to record almost all of the feeding traces, even if macaques burrowed beneath the snow

173 to feed on shrub species or seedlings. We explored 7.25 km (29.0 ha) of transects in
174 2008, 12.15 km (48.6 ha) in 2009, 6.40 km (25.6 ha) in 2010, and 12.35 km (49.4 ha)
175 in 2012. The variations in total lengths were caused by sudden snowstorms or
176 avalanches. For the same reason, we were unable to explore transects D and E in 2008
177 and 2010. To reduce sampling bias related to overlooked feeding traces, the two
178 authors performed the investigation simultaneously, using binoculars and walking at a
179 speed of <0.5 km/h, on calm sunny or cloudy days.

180 Our data collection procedure adhered to the American Society of Primatologists
181 principles for the ethical treatment of primates, and complied with the laws governing
182 wildlife research in Japan.

183 **Data analysis**

184 As the amount of bark and buds foraged by macaques varies, even among individual
185 plants of the same species [Nakayama et al., 1999; Enari & Sakamaki, 2010], we could
186 not assume that the number of woody plants with bite marks accurately reflected
187 macaque diet preferences. Hence, we evaluated the annual winter diet in terms of
188 biotic assemblages consisting of woody plant species foraged by macaques in different
189 transect segments. We divided each of the five transects into 50-m segments. We
190 evaluated each segment as a macaque feeding site, and segments were thus the units in
191 our analyses. We investigated 145 segments in 2008, 243 segments in 2009, 128
192 segments in 2010, and 247 segments in 2012. We determined the segment length based
193 on the spatial distribution of macaque individuals within a troop during snowy seasons
194 in the study area [Enari & Sakamaki, 2011]. To reduce complexity, we classified all
195 foraged plant species according to plant type (vine, shrub, and tree) and shade
196 tolerance (shade-tolerant, intermediary, and shade-intolerant), as outlined by the Forest
197 Development Technological Institute [1985]. The shade tolerance of plant species is

198 known to influence the winter diet of macaques [Sakamaki et al., 2011]. We excluded
199 any species that were rarely eaten by macaques, according to the statistical selectivity
200 index calculated by Sakamaki et al. [2011], who previously compared macaque feeding
201 frequency and local availability of each woody plant species in the same study area
202 during the winters of 2008 and 2009.

203 After the pretreatment procedures, we conducted nonhierarchical cluster analysis to
204 define assemblages of plants foraged by macaques, and classified each segment by
205 assembly type. We used the expectation maximization (EM) algorithm [Dempster et al.,
206 1977], which is a model-based clustering technique. We adopted a final model with an
207 optimum number of clusters (i.e., assemblage types) by using a 10-fold
208 cross-validation technique based on the Bayesian information criteria. We used the
209 ArcGIS 9.3 (ESRI, Redlands, CA) and WEKA 3.7 [Hall et al., 2009] software for all
210 analytical procedures.

211 We used a two-step process to evaluate the influence of snow accumulation on
212 macaque feeding-site use. Firstly, to evaluate the particularity of feeding-site use under
213 long-lasting heavy snow, we compared feeding-site use in different years using
214 multiple dimensional scaling (MDS [Ludwig & Reynolds, 1988]), based on the pattern
215 similarity index of the sequence of assemblage types in each transect during each year.
216 MDS is a multivariate statistical technique that visually represents similarities among
217 sample sets (i.e., annual patterns of feeding-site use in our study). Secondly, to identify
218 differentiators of feeding-site uses under different snowfall conditions, we examined
219 the ecological correlates of the assemblage types in each transect segment, in 2009
220 (light-snowfall year) and 2012 (heavy-snowfall year), using decision tree modeling
221 [Quinlan, 1986]. We excluded the records for 2008 and 2010 (normal snowfall years),
222 because of insufficient sampling effort. The decision tree modeling is a type of

223 nonlinear discriminant analysis, which unbiasedly estimates the value of a discrete
224 dependent variable with a finite set of values (i.e., class), from the values of a set of
225 independent variables (i.e., attributes). We assigned assemblage type as the class, and
226 10 environmental variables (Table I) as the attributes. For this modeling, we added
227 foraged plant assemblage type F, which was a segment without any observed feeding
228 traces. We selected environmental variables that potentially influence
229 winter-feeding-site use by Japanese macaques, based on previous landscape-scale
230 studies [Enari & Sakamaki, 2012; Sakamaki & Enari, 2012]. We standardized the
231 distributions of all environmental variables contained in each segment (i.e., instance)
232 using a z transformation (i.e., mean = 0, SD = 1). We used the J48 algorithm [Quinlan,
233 1986] with the machine-learning package WEKA 3.7 [Hall et al., 2009] to determine
234 the decision tree. This algorithm, which is based on the concept of information entropy,
235 draws explicit classification rules from a hierarchical tree structure. The generation of a
236 classification rule, or tree construction, proceeds recursively as a top-down induction
237 of decision trees [Witten & Frank, 2005]. For each hierarchy, we selected the most
238 informative attribute as a branching node of the tree, and determined a threshold for
239 the classification rules according to gain ratio. All of the attributes were continuous
240 values, and therefore we created two branches at each node based on this threshold.

241 After initial construction, we pruned the model to reduce the number of
242 classification rules, and enhance the classification performance by eliminating noise
243 [Witten & Frank, 2005]. We constructed multiple decision tree models with different
244 pruning intensities, and selected the model with the highest performance in terms of
245 the percentage of correctly classified instances, or true positive rate of all the input
246 data.

247 In addition to decision tree modeling, we evaluated the relationship between

248 existing feeding-site use and actual food abundance. To simplify the analysis, we only
249 evaluated beech trees, because they are the most typical upper story plant-forms that
250 are consistently foraged by macaques in the study area every year [Enari et al., 2005;
251 Sakamaki et al., 2011]. We compared feeding-site use of beech trees by macaques with
252 the proportion of segments containing beech trees at different altitudes, based on the
253 National and Private Forest Planning Maps.

254 **RESULTS**

255 **Annual variation in foraged plant assemblages**

256 We observed 28 woody plant species with signs of macaque foraging during the
257 study period (Table II). The abundance and species richness of these plants per 1 km
258 transect were highest in 2009 (light-snowfall year) and lowest in 2012 (heavy-snowfall
259 year). With the exception of a single species (*Lindera umbellata*), macaques did not
260 feed on shade-tolerant vines or shrub species; therefore, we excluded shade-tolerant
261 vine and shrub species from the cluster analysis. We also omitted eight species for
262 which macaques showed low selectivity, based on Sakamaki et al. [2011] (i.e., species
263 with a minus sign in Table II).

264 The results of cross validation in the EM algorithm revealed that the optimal
265 number of foraged plant assemblages was five (Table III). Type A included a relatively
266 high frequency of a shade-intolerant tree species. Types B, C, and E were mainly
267 composed of shade-tolerant tree species—namely, beech trees (see Table II)—, vine
268 species, and shrub species, respectively. Type D included the highest frequencies of
269 shrub species and tree species (excluding beech trees).

270 The proportions of the types of foraged plant assemblages in each transect varied
271 during the study period (Fig. 2). In 2012 (heavy-snowfall year), the proportion of types
272 D and E decreased, while the proportion of type A increased. The proportions of types

273 B and C posted constant values between 2009 and 2012, but increased and decreased,
274 respectively, in 2008.

275 **Feeding-site use**

276 Our MDS analysis showed that the patterns of feeding-site use in 2008 and 2010
277 closely resembled each other, but differed substantially from those in 2009
278 (light-snowfall year) and 2012 (heavy-snowfall year) (Fig. 3). To investigate
279 differences in feeding-site use during conditions of light and heavy snow, we excluded
280 type D, which mainly consisted of shrub and tree species without beech trees, and for
281 which we had few records for 2009 and 2012 (Fig. 2). The total classification accuracy
282 of our decision tree model for 2009 (light-snowfall year) was not always high; the
283 percentage of correctly classified instances, or true positive data, within all of the input
284 data for 2009 was 50.9% (Table IV), indicating that the environmental variables used
285 in the analysis were not strongly related to the assemblage type in each segment.
286 However, the individual classification accuracies of types A, E, and F were higher,
287 with accuracy rates of >50%, followed by type B with an accuracy rate of 31%. The
288 model for 2009 mainly proposed four interpretations. (1) Type E, which predominantly
289 consists of shrub species, occurs in segments with old broadleaf forests (leaf 1 in Fig.
290 4[a]), or flatlands at higher altitudes (leaf 10). (2) Type A, which mainly includes
291 shade-intolerant tree species, tends to appear in segments at lower altitudes and close
292 to rivers (leaf 2). (3) Type F, which comprises unused plants, is found in segments at
293 higher altitudes without old conifer forests—used by macaques as a refuge from
294 blizzards (leaf 8). (4) Type B, which consists of beech trees, occurs in high-altitude
295 segments (leaf 9).

296 The decision tree model for 2012 (heavy-snowfall year) generated a higher total
297 classification accuracy, with correctly classified instances of 61.2% (Table IV). This

298 indicates that the assemblage type in each segment was more sensitive to
299 environmental conditions. The individual classification accuracy was particularly high
300 for type F, followed by types A and B. The model was unable to predict types C and E,
301 because of an insufficient number of the appropriate segments (i.e., instances). The
302 model for heavy-snowfall conditions mainly indicated three interpretations. (1) Type F,
303 which comprises unused plants, tends to occur in segments at higher altitudes (leaf 1 in
304 Fig. 4[b]), far from rivers (leaf 4), in young conifer forests (leaf 5), or on north-facing
305 slopes at lower altitudes (leaf 8). (2) Type A, which mainly includes shade-intolerant
306 tree species, is likely to appear on sloping land (leaf 3), or in segments with old conifer
307 forests that are close to rivers (leaf 6). (3) Type B, which consists of beech trees, is
308 found in segments at the lowest altitudes (leaf 2), or in areas close to rivers where the
309 slope is not north-facing (leaf 9).

310 Type B occurred at a relatively high frequency in transects, regardless of snow
311 conditions (Fig. 2). Nevertheless, the environmental conditions in which this type
312 appeared varied considerably between 2009 and 2012. Thus, when we focused on
313 annual location changes of the segment with foraged beech trees, we observed a
314 declining tendency of feeding site altitude with increasing snow accumulation,
315 regardless of species abundance and distribution (Fig. 5).

316 **DISCUSSION**

317 Our present findings suggest that Japanese macaques inhabiting cold areas respond
318 flexibly to unusually long-lasting heavy snow by changing their feeding behavior
319 responding to the accessibility, or acquisition cost, of foods. This behavioral flexibility
320 may be a result from the high phenotypic plasticity of Japanese macaques to
321 acclimatize to diverse environments—from warm-temperate rainforests to subalpine
322 forests [Hanya, 2010]. Such plasticity is not limited to Japanese macaques, but has

323 frequently been observed for other macaque species inhabiting forests with high
324 environmental gradients similar to that of the Japanese archipelago (e.g., *M. sylvanus*
325 [Ménard, 2002], *M. mulatta* [Fooden, 2000], *M. radiata* [Sinha, 2005]).

326 The current population of Japanese macaques used a wider range of woody plant
327 species and their selection was less affected by environmental features in the
328 light-snowfall year than in the heavy-snowfall year (Table IV). This may be because
329 the energy content and crude protein content per unit of bark and buds do not differ
330 substantially among different species of food plants [Nakagawa et al., 1996; Nakayama
331 et al., 1999]. Moreover, the ambient temperature in the light-snowfall year was higher
332 than that in the heavy-snowfall year. This may have further contributed to euryphagous
333 feeding behavior, because the time spent feeding per day is positively correlated with
334 the ambient temperature during cold winters [Wada & Tokida, 1981; Watanuki &
335 Nakayama, 1993; Agetsuma & Nakagawa, 1998]. Thus, when macaques have
336 increased feeding time, they have the potential to search for food plants that have
337 additional edible parts (such as trees with more buds, or younger trees with tender
338 bark), in wider areas of their habitat.

339 The feeding behavior in the heavy-snowfall year differed markedly from that in the
340 light-snowfall year. In particular, macaques fed on few shrub species, which are the
341 preferred food items [Sakamaki et al., 2011]. Some shrub species (e.g., mulberry,
342 *Morus bombycis*) are low in condensed tannin content, and may therefore be
343 preferentially selected by macaques [Enari & Sakamaki, 2010]. Japanese macaques
344 have previously been found to cope with a reduction in preferred food sources by
345 digging beneath the snow to find alternative food sources. This type of extractive
346 foraging has frequently been observed in rural macaque populations, which burrow
347 beneath the snow to feed on waste agricultural crops [Enari et al., 2005; Enari 2007].

348 In our present study, we did not find evidence of this behavior, even when the preferred
349 food resources (i.e., shrub species) were buried under extraordinarily heavy snow.

350 There are two possible explanations for this behavioral choice, namely, bioenergetic
351 cost-effectiveness (i.e., optimal foraging theory) and discovery rate. Besides the
352 nutrient balance between energy content and secondary compounds of a diet [Freeland
353 & Janzen, 1974], the speed of nutrient intake (i.e., feeding rate) and accessibility of
354 each food type are critical factors determining food selection by Japanese macaques,
355 especially during periods of limited food resources [Nakagawa, 1989a, b; Nakagawa et
356 al., 1996; Nakayama et al., 1999]. Unlike agricultural crops with a high feeding rate,
357 wild food resources buried under snow are unlikely to become favorable enough food
358 items to offset the additional energy expenditure required for extractive foraging. With
359 regard to the discovery rate, waste crops occur at a specific location on agricultural
360 land, whereas wild diets buried under snow are generally distributed in a random
361 manner, making it difficult for macaques to find them.

362 Under long-lasting heavy snow conditions, macaques depended more heavily on
363 tree species. In light-snowfall years, they also fed on tree species; however, the use of
364 arboreal feeding sites was sensitive to snow accumulation. Typically, we observed a
365 declining tendency of feeding-site altitude with increasing snow accumulation,
366 regardless of species abundance and distribution (Fig. 5). This observation is in
367 accordance with those of previous studies conducted in the same study area [Enari &
368 Sakamaki, 2011, 2012; Sakamaki & Enari, 2012]. Taken together, these findings
369 indicate that winter-feeding-site use by Japanese macaques in heavy snow conditions
370 becomes more restricted by the distribution of refuges within their range than by the
371 abundance and distribution of food resources. With regard to refuges, closed-canopy
372 evergreen conifers on low-elevation steep land are less subject to severe external

373 ambient environmental factors, such as snowstorms.

374 A limited number of primate species inhabit areas with a cold climate. Apart from *M.*
375 *fuscata*, only four species—*M. sylvanus*, *Rhinopithecus roxellana*, *R. bieti*, and
376 *Trachypithecus geei*—range outside the Tropics of Cancer and Capricorn. Similar to
377 Japanese macaques, the behavioral pattern of *R. bieti* is strongly influenced by ambient
378 temperature, particularly with respect to daily path length [Baoping et al., 2009]. By
379 contrast, *R. roxellana* individuals spend more time feeding per day during the cold
380 season than during warmer seasons [Guo et al., 2007], which is in contrast with the
381 behavior of Japanese macaques in heavy-snow regions [Wada & Tokida, 1981].
382 Moreover, in winter, *R. bieti* occupies a high elevation range (4100–4400 m ASL),
383 where increased solar radiation and longer sunshine duration cause the snow to melt
384 faster and food to be exposed earlier [Quan et al., 2011]. By contrast, our present
385 observations suggest that Japanese macaques adopt a risk-averse foraging behavior, i.e.,
386 minimizing energy loss during extended periods of heavy snowfall, by foregoing their
387 preferred diet in favor of alternative, more readily available food. This tactic is
388 incongruous with the traditional risk-sensitivity foraging model, which predicts that
389 animals facing starvation because of stochastic environmental fluctuations tend to
390 adopt risk-prone foraging (i.e., choosing the option with higher pay-off by accepting
391 risk), by decreasing their diet quality [Kacelnik & Bateson, 1996; Bateson, 2002]. This
392 incongruity may be explained in terms of the cold-resistant ability inherent in Japanese
393 macaques. Unlike *R. roxellana* and *R. bieti*, the Japanese macaque is not specialized
394 solely for cold areas. Consequently, it has a relatively high thermoregulatory cost in
395 winter. Indeed, with a decrease in ambient temperature macaques need to spend more
396 time resting or sunbathing to maintain body temperature [Watanuki & Nakayama,
397 1993; Agetsuma & Nakagawa, 1998]. It is reasonable to conclude that this additional

398 cost compels macaques to adopt a risk-averse foraging behavior, even under conditions
399 of food scarcity caused by long-lasting heavy snow conditions.

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1 **Figure Captions**

2 **Fig. 1** Map of the study area, which was located in the Northeastern Shirakami Mountains,
3 Northern Japan. The total transect lengths were 3.4 km, 1.5 km, 2.2 km, 2.0 km, and 3.3 km
4 for transects A–E, respectively.

5 **Fig. 2** Interannual variation in the types of foraged plant assemblages (A–E, clustered by
6 the expectation maximization algorithm) occurring in transects. For details of each
7 assemblage, see Table III.

8 **Fig. 3** Similarity of winter feeding-site use by Japanese macaques in the Shirakami
9 Mountains across four years, as revealed by a multiple dimensional scaling analysis. This
10 analysis was based on the similarity index of the emerging pattern of assemblage type in
11 transects during the study period.

12 **Fig. 4** Decision tree models using the J48 algorithm, which presents the classification rules
13 for predicting feeding-site use by Japanese macaques in the Shirakami Mountains during [a] a
14 light-snowfall year and [b] an extraordinarily heavy snowfall year. Black-colored nodes, or
15 leaves, show the type of foraged plant assemblage, A–E (see Table III). Type F is a segment
16 without any observed feeding traces. The numbers within the square brackets represent leaf
17 numbers. Gray-colored nodes, or internal nodes, show environmental variables. To develop a
18 hierarchical tree structure that presents explicit classification rules, the J48 recursively selects
19 the most informative environmental variables as internal nodes for each hierarchy. Two
20 branches with signed values extending from each internal node show the threshold for the
21 classification rule. We standardized the distributions of all of the environmental variables
22 contained in this analysis; hence, “threshold value = 0” indicates the overall mean of its
23 variable within the whole study area. The values in parentheses indicate classification
24 precision by following its corresponding classification rule. The precision was calculated by
25 means of the following formula: $TP/(TP + FP)$, where TP = true positive (i.e., correctly

26 classified instances) and FP = false positive (i.e., incorrectly classified instances).

27 **Fig. 5** Altitudinal variation in the sites used by Japanese macaques to feed on the bark and
28 buds of Japanese beech trees (graph [a]; black dots = mean, bars = standard deviations, the
29 values in parentheses = N of segments), and the proportion of the number of segments with
30 beech trees at different altitudes, according to the National and Private Forest Planning Maps
31 (graph [b]). The labels on the horizontal axis in graph [b] only present the lower bounds of
32 each 50-m altitude level.

Table I. Environmental conditions of transects located in the Shirakami Mountains, Japan. These environmental variables were also included in the decision tree models for predicting feeding site use by Japanese macaques.

Environmental variables	Overall mean	Range	SD	Data source ^c	Influence on feeding site use in winter ^d
Mean altitude (m)	269.6	136.6–396.9	56.8	A	Negative
Mean slope (°)	18.0	3.0–52.5	8.5	A	Negative
Standard deviation of altitude (i.e., undulation of land surface)	9.0	2.9–26.0	3.8	A	Positive*
Proportion of northern slope	0.4	0.0–1.0	0.4	A	Negative
Proportion of southern slope	0.2	0.0–1.0	0.3	A	Positive
Distance to river (m)	153.2	8.3–618.9	119.5	B	Negative*
Proportion of old broadleaf forests ^a	0.0	0.0–1.0	0.2	C	Negative
Proportion of young broadleaf forests ^a	0.5	0.0–1.0	0.5	C	Positive
Proportion of old conifer forests ^b	0.2	0.0–1.0	0.3	C	Negative
Proportion of young conifer forests ^b	0.2	0.0–1.0	0.4	C	Positive

^a We decided on a threshold value of 100 years for broadleaf forests for when they can be roughly regarded as primary forests in the absence of artificial disturbances.

^b The threshold value was 40 years for conifer forests for when the canopy becomes completely closed [Sakamaki et al., 2011].

^c A: Digital elevation model (DEM) according to an open source from the Geospatial Information Authority of Japan; B: Advanced Land Observing Satellite (optical resolution = 2.5 m) according to a commercial database service by the Remote Sensing Technology Center of Japan; C: National and Private Forest Planning Maps (scale, 1:5,000) from 2009 that were publicly provided by the Tohoku Regional Forest Office and the Aomori Prefecture, respectively.

^d These were judged by the preceding studies: no sign = Sakamaki & Enari [2012]; * = Enari & Sakamaki [2012].

Table II. Density of woody plants (N) foraged by Japanese macaques in the Shirakami Mountains, northern Japan. The unit used for N is “trees/km.”

Morphology (Shade tolerance)	Plant parts		2008 ^b	2009 ^b	2010	2012
Species	foraged	Selectivity ^a	N (%)	N (%)	N (%)	N (%)
Vine species (Intolerance)						
<i>Actinidia</i> spp.	Bark/buds	+	4.69 (11.33)	7.90 (12.29)	8.44 (21.26)	7.77 (35.82)
<i>Hydrangea petiolaris</i>	Bark/buds	Untested				0.16 (0.75)
<i>Schizophragma hydrangeoides</i>	Buds	Untested		0.33 (0.51)		
Shrub species (Tolerance)						
<i>Lindera umbellata</i>	Bark	—		0.08 (0.13)		
Shrub species (Intolerance)						
<i>Salix</i> spp.	Bark	n.s.	0.14 (0.33)	0.41 (0.64)		
<i>Morus bombycis</i>	Bark/buds	+	25.52 (61.67)	28.48 (44.30)	14.06 (35.43)	3.48 (16.04)
<i>Aralia elata</i>	Bark/buds	n.s.	1.10 (2.67)	1.15 (1.79)	1.09 (2.76)	
<i>Euonymus oxyphyllus</i>	Bark/buds	n.s.	1.38 (3.33)	1.32 (2.05)	2.34 (5.91)	
Tree species (Tolerance)						
<i>Fagus crenata</i>	Bark/buds	n.s.	1.66 (4.00)	1.23 (1.92)	1.25 (3.15)	2.83 (13.06)
<i>Hamamelis japonica</i>	Bark	—		0.41 (0.64)	0.63 (1.57)	0.24 (1.12)
<i>Acer</i> spp.	Bark/buds	—		0.16 (0.26)	0.16 (0.39)	
Tree species (Intermediate)						
<i>Aesculus turbinata</i>	Buds	+	2.76 (6.67)	12.35 (19.21)	5.94 (14.96)	3.72 (17.16)
<i>Pterocarya rhoifolia</i>	Bark/buds	n.s.		0.58 (0.90)	0.16 (0.39)	0.08 (0.37)
<i>Magnolia obovata</i>	Bark/buds	n.s.	1.79 (4.33)	5.19 (8.07)	2.50 (6.30)	1.86 (8.58)
<i>Juglans mandshurica</i>	Bark/buds	n.s.		0.99 (1.54)		0.08 (0.37)
<i>Acanthopanax sciadophylloides</i>	Bark/buds	n.s.	0.55 (1.33)	1.23 (1.92)	0.94 (2.36)	0.65 (2.99)
<i>Magnolia praecocissima</i>	Buds	n.s.	0.14 (0.33)			
<i>Kalopanax pictum</i>	Bark/buds	n.s.	0.14 (0.33)	0.16 (0.26)	0.31 (0.79)	
Tree species (Intolerance)						
<i>Cornus controversa</i>	Buds	n.s.	0.69 (1.67)	0.82 (1.28)	1.25 (3.15)	0.49 (2.24)
<i>Alnus hirsuta</i>	Bark	n.s.	0.14 (0.33)	0.16 (0.26)		
<i>Styrax obassia</i>	Bark/buds	—	0.41 (1.00)	1.07 (1.66)		0.08 (0.37)
<i>Rubus</i> spp.	Buds	—	0.14 (0.33)			
<i>Rhus trichocarpa</i>	Buds	—		0.16 (0.26)	0.16 (0.39)	
<i>Viburnum dilatatum</i>	Buds	—	0.14 (0.33)			
<i>Castanea crenata</i>	Bark	—		0.08 (0.13)		
<i>Fraxinus sieboldiana</i>	Bark/buds	Untested			0.47 (1.18)	0.08 (0.37)
<i>Prunus</i> spp.	Bark	Untested				0.08 (0.37)
<i>Quercus crispula</i>	Buds	Untested				0.08 (0.37)
Sum			41.38 (100.00)	64.28 (100.00)	39.69 (100.00)	21.70 (100.00)
Number of species			16	21	15	15

^a Dietary selections by macaques for woody plant species, as reported previously [Sakamaki et al., 2011]; plus and minus signs mean significantly high and low selectivity, respectively ($\alpha = 0.05$).

^b Original data were partly reported in the previous studies [Enari & Sakamaki, 2010; Sakamaki et al., 2011].

Table III. Constituents of the respective foraged plant assemblages that were clustered by the expectation maximization algorithm.

		Type of foraged plant assemblage				
		A	B	C	D	E
Category	Shade tolerance	Mean ^a (SD)	Mean ^a (SD)	Mean ^a (SD)	Mean ^a (SD)	Mean ^a (SD)
Vine species	Intolerance	0.19 (0.39)	0.34 (0.57)	2.09 (1.73)	0.13 (0.34)	0.82 (0.95)
Shrub species	Intolerance	0.19 (0.39)	0.62 (1.04)	1.15 (1.65)	3.98 (5.64)	3.62 (5.22)
Tree species	Tolerance	0.00 (0.56)	0.64 (1.05)	0.05 (0.22)	0.09 (0.30)	0.00 (0.56)
Tree species	Middle	0.25 (0.43)	0.41 (0.57)	1.19 (1.05)	1.41 (1.65)	0.00 (0.76)
Tree species	Intolerance	0.75 (0.76)	0.13 (0.33)	0.58 (0.79)	2.89 (1.79)	0.34 (0.69)
Sum		1.38	2.14	5.06	8.50	4.78
Number of clustered instances		201	108	57	26	76

^a These values are also regarded as the expected value of "the frequency of occurrence of each tree species within a segment."

Table IV. Confusion matrix for predicting the type of foraged plant assemblages in the light snow year (i.e., 2009) and in the extraordinarily heavy snow year (i.e. 2012), based on the decision tree model. For the details of the abbreviations of the type of assemblage (i.e., A–E), see Table III. *N* shows the actual total number classified as each type. The bold numbers indicate the correctly classified instances, or true positives.

Actual type of assemblage	Predicted type of assemblage						Classification accuracy (%) ^c
	A	B	C	D ^a	E	F ^b	
<u>Light snow year</u>							
A (<i>N</i> = 75)	54	0	2	—	4	15	(72.0)
B (<i>N</i> = 35)	10	11	1	—	1	12	(31.4)
C (<i>N</i> = 28)	7	3	4	—	10	4	(14.3)
D ^a	—	—	—	—	—	—	—
E (<i>N</i> = 33)	8	4	0	—	18	3	(54.6)
F ^b (<i>N</i> = 55)	20	3	1	—	3	28	(50.9)
<i>Total classification accuracy (%)^d</i>							<i>(50.9)</i>
<u>Heavy snow year</u>							
A (<i>N</i> = 72)	36	4	0	—	0	32	(50.0)
B (<i>N</i> = 26)	8	10	0	—	0	8	(38.5)
C (<i>N</i> = 14)	2	0	0	—	0	12	(0.0)
D ^a	—	—	—	—	—	—	—
E (<i>N</i> = 11)	1	2	0	—	0	8	(0.0)
F ^b (<i>N</i> = 122)	16	2	0	—	0	104	(85.3)
<i>Total classification accuracy (%)^d</i>							<i>(61.2)</i>

^a Type D was preliminarily omitted in order to construct the model because of its insufficient instances.

^b Type F shows the segment without any feeding traces of macaques.

^c This was calculated as the percentage of "the value of true positive divided by *N* in each type."

^d The total classification accuracy was calculated as the percentage of "the sum of the true positive values divided by the sum of *N* in each year."

Fig. 1

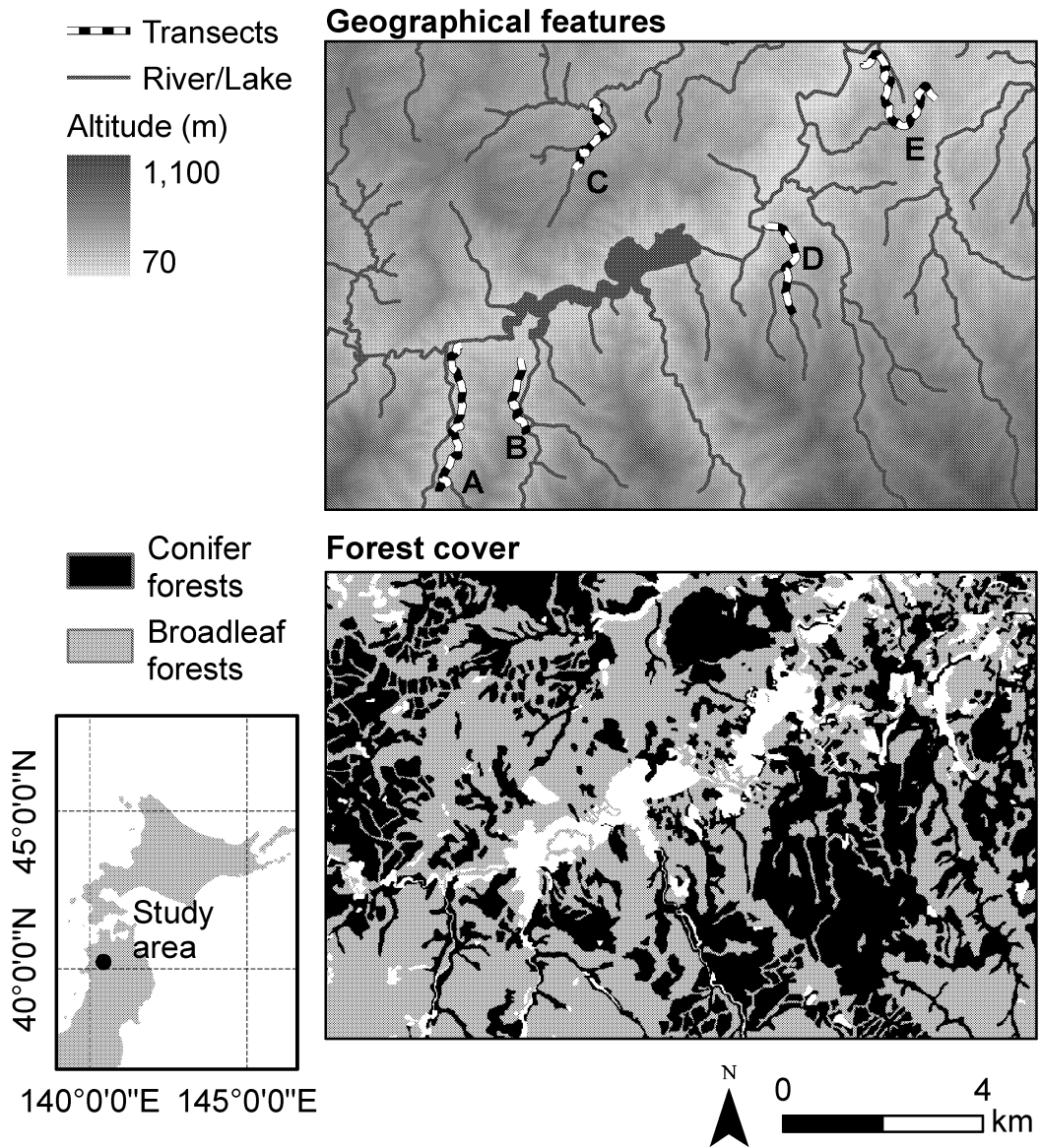


Fig. 2

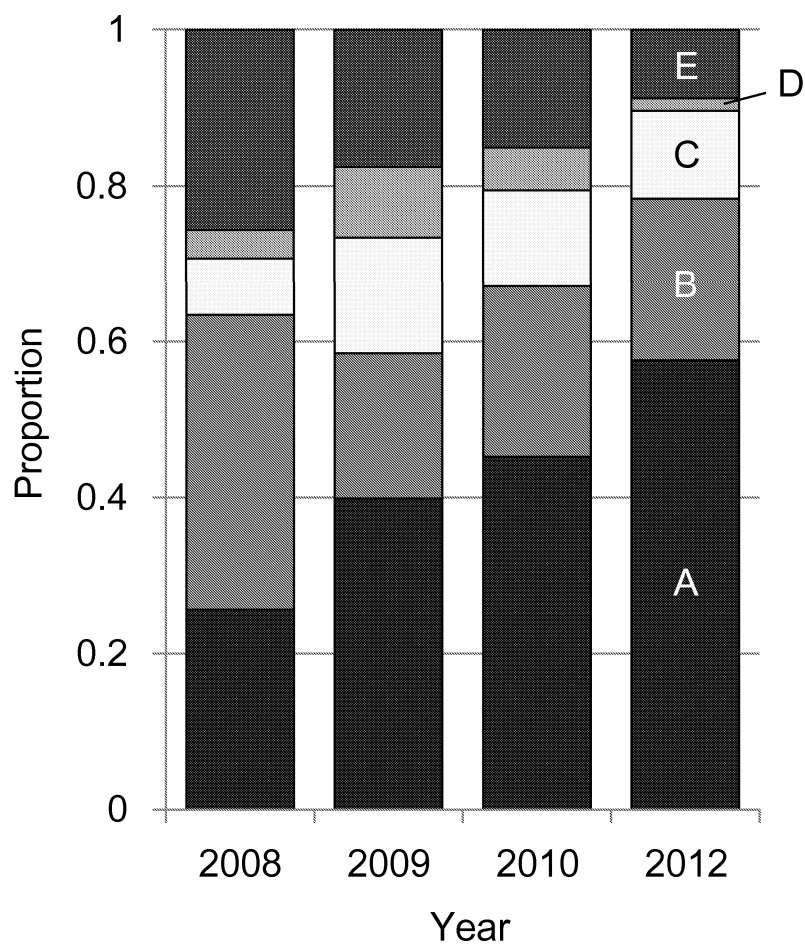


Fig. 3

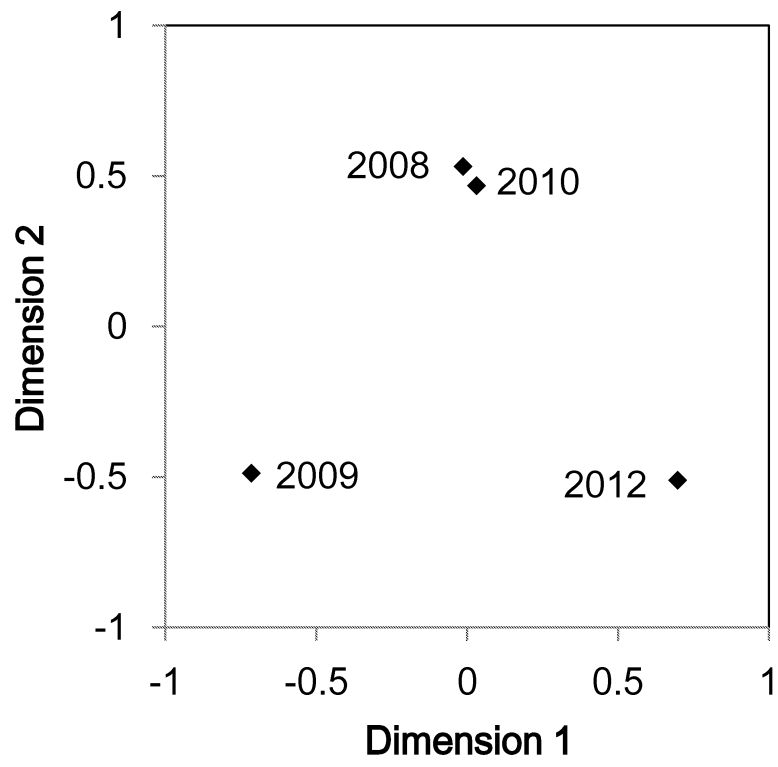


Fig. 4

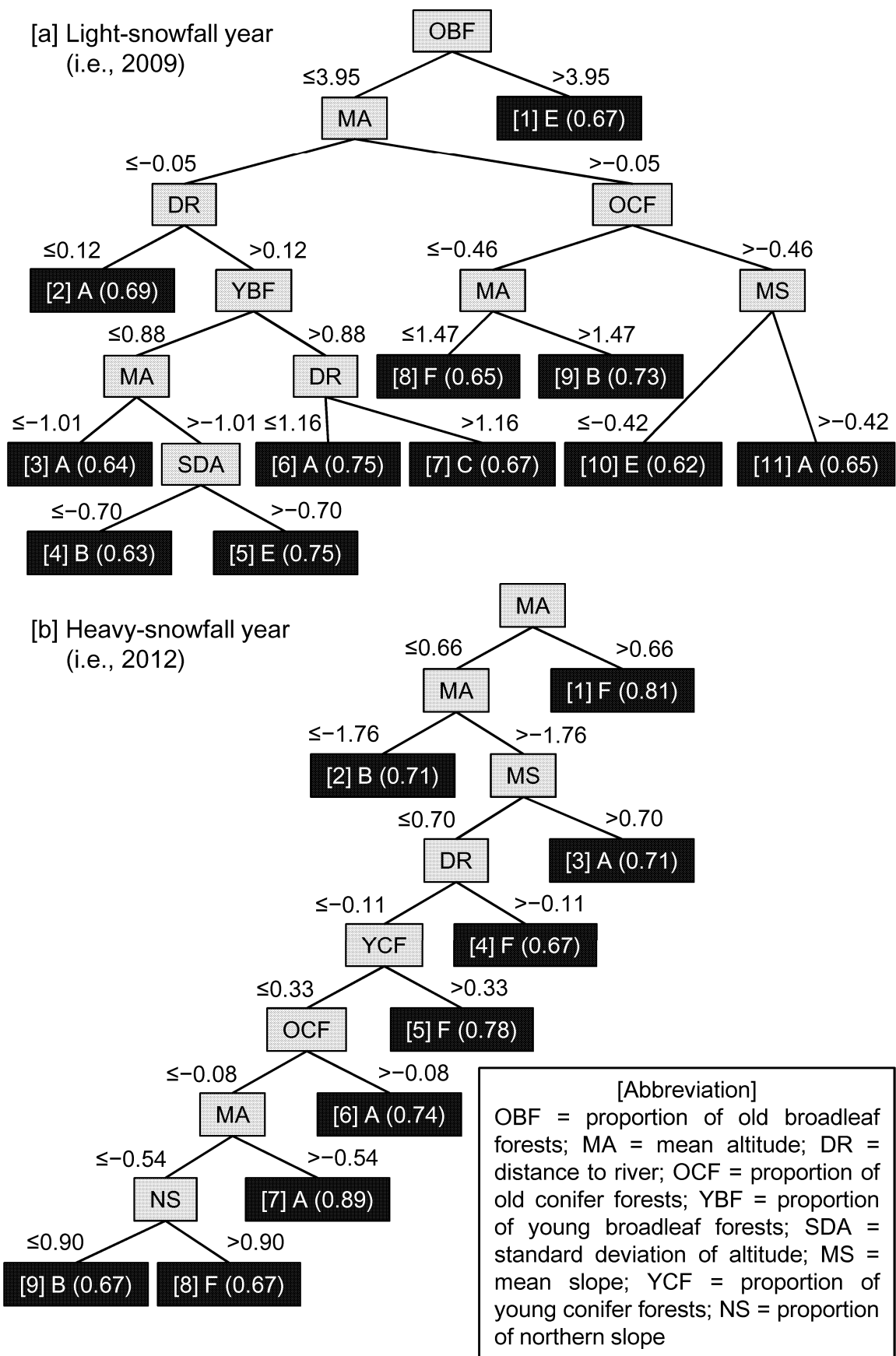


Fig. 5

