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Impact assessment of dam construction and forest management for Japanese macaque habitats in snowy areas

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Abstract

Japanese macaques (*Macaca fuscata*) in their northernmost habitats represent a keystone species and play a central role in heavy snowfall ecosystems. However, distributions have been restricted by pre-war hunting, and populations are facing issues of natural forest losses caused by new dam constructions and massive conifer plantations. In the present study, we predicted the influences of these environmental conditions on macaque habitats during each season, and evaluated the effect of natural forest restoration as a mitigation measure. We constructed multiple habitat suitability models on the basis of different forest change scenarios, by using maximum entropy modeling (Maxent). We predicted the influence of each scenario by calculating the habitat unit (habitat quality × habitat quantity). We made the following predictions: (1) the influences of environmental conditions on habitat models vary seasonally, but dam construction destroys the optimum macaque habitats in every season; (2) restoration of conifer plantations to semi-natural forests does not always contribute to the improvement of total habitat unit, except in snowy seasons; and (3) in comparison with encouraging natural forest restoration in plantation areas and maintaining the standard-rotation plantation management, the implementation of long-rotation plantation in existing plantation areas provides more suitable alternative habitats for macaques in non-snowy seasons.

Keywords: conifer plantation; habitat suitability; maximum entropy modeling; mitigation; scenario analysis

Introduction

Population losses of keystone species, which undergo strong interactions with the ecological community, can trigger a cascade of secondary extinctions and have destructive effects on the stability of native ecosystem processes [Koh et al., 2004]. In tropical forests, primates represent a typical keystone species [Chapman & Onderdonk, 1998], because they comprise a large proportion of folivorous or frugivorous mammal biomass and function as ecosystem engineers with an important role in structuring the ecosystem through their feeding activities [Chapman et al., 2013].

Only five primate species (*Macaca sylvanus*, *M. fuscata*, *Rhinopithecus roxellana*, *R. bieti*, and *Trachypithecus geei*) have expanded their distributions from the torrid zone to the temperate zone. By the late Pleistocene, Japanese macaques (*M. fuscata*) had reached the northernmost habitat of any nonhuman primate [Iwamoto & Hasegawa, 1972]. In these habitats, other large mammal fauna (such as ungulate species) are strongly limited by heavy snow (up to 2 m in depth), indicating that the existing forest ecosystem has a restricted functional redundancy. Thus, macaques represent a keystone species with the following central roles: (1) seed dispersers for zoochores [Otani, 2003; Tsuji et al., 2011]; (2) skillful pruners that stimulate compensatory plant growth by foraging on bark and buds [Enari & Sakamaki, 2010]; and (3) resource (i.e., feces) providers that sustain a unique community of dung beetles [Enari et al., 2011, 2013], which are recognized as important decomposers and secondary seed dispersers [Koike et al., 2012].

During the early twentieth century, macaques in their northernmost habitats were excessively hunted, resulting in their notably limited distributions [Enari & Suzuki, 2010]. Since 1991, the Japanese Government has designated the remnant populations as endangered. Among the northernmost habitats, the Shirakami Mountains contain the largest remnant populations (Fig. 1) and provide the broadest sanctuary—approximately 170 km^2, composed mainly of primary forests of beech, *Fagus crenata*—which has been registered as a World Nature Heritage site since 1993. Nevertheless, a new dam construction (estimated flooded area of 5.1 km^2) was initiated in the northeastern region of the mountains (i.e., adjacent to the heritage site) in 2008, and is scheduled for completion in 2016. Moreover, since the 1960s, approximately 70% of native broadleaf forests adjacent to the heritage site have been replaced by monotonous conifer plantations to sustain domestic timber production [Sakamaki & Enari, 2012]. As a mitigation measure, the regional forest office and some non-governmental organizations have recently embarked on the restoration of native natural forests, by cutting down conifer plantations and replanting beech trees.

Ecosystem manipulations should only be implemented with careful planning and scientific monitoring [Morrison, 2009]. However, the above human-induced environmental changes, including forest restoration, have progressed without sufficient evaluation of the potential influences on habitats of terrestrial mammal fauna, including macaques. In the present study, we predicted the influences of dam construction, plantation management, and natural forest restoration on macaque habitats. In a previous study, Enari & Sakamaki-Enari [2013a] constructed static models to estimate seasonal resource use by macaque troops in the northeastern part of the Shirakami Mountains. Here, we extended the previous findings by using scenario analysis. We constructed multiple habitat suitability models on the basis of different forest change scenarios, by assigning the dataset regarding habitat uses by multiple troops in the same study site from 2007 to 2009 (partly using the same dataset of the previous study). We calculated the habitat unit (i.e., habitat quality × habitat quantity), which is commonly used in habitat evaluation procedures [Nevo & Garcia, 1996; Urich & Graham, 1983], as a measure of the amount of suitable habitat, and predicted the extent of the impacts caused by forest changes.

Methods

Study area and species

The Shirakami Mountains are located in the northern end of mainland Japan (Fig. 1). The climate is cool temperate, with a mean annual ambient temperature of approximately 10°C. The mean snow depth between January and March at a lowland area was 59.2 ± SD 34.5 cm (maximum, 107.8 cm) in 2008 and 45.4 ± SD 22.1 cm (maximum, 101.7 cm) in 2009. During the study periods, the snow depth in the mountainous areas reached 3–5 m.

The present study focused on four separate troops of Japanese macaques (troops S, O, F, and T), which were continuously distributed in the northeastern part of the mountains. The mean troop size was 30–40 individuals. We used a 100% minimum convex polygon of the presence sites (defined below) of the four troops as a reference area for evaluating macaque habitats because of the statistical technicality of Maxent.

Japanese macaque troops move in search of foods within fixed ranges, the size of which varies seasonally [Hanya et al., 2006]. During the study period, the mean seasonal range size for the above troops was 21.8 ± SD 6.3 km^2 in spring, 15.9 ± SD 4.8 km^2 in summer, 13.8 ± SD 4.8 km^2 in autumn, and 14.6 ± SD 1.3 km^2 in winter [Enari

& Sakamaki-Enari, 2013a]. The staple diets of macaques in snowy areas comprise young leaves of broadleaf trees in spring, herbaceous plants and bramble fruits in summer, berries and nuts in autumn, and the bark and buds of broadleaf trees in winter [Enari et al., 2005; Sakamaki et al., 2011].

Tracking of macaque troops

Adult female macaques generally remain in their natal groups for their entire lifetime. We therefore captured two, four, two, and two adult females from troops S, O, F, and T, respectively, and attached a radio collar (Advanced Telemetry Systems Inc. Isanti, Minnesota, USA) to each individual. To record the presence sites for each troop twice daily (i.e., around 0900 and 1500), we directly followed each troop from a distance of approximately 30 m, with the help of radio signals. We continued our recording during each season—spring (April–June), summer (July–September), autumn (October–December), and winter (January–March)—until more than 30 presence sites of each troop were obtained. The attachment of radio collars was completed at different times, and therefore the total number of presence sites varied among the troops (Table I). For each troop, we used the mid-point of the location of the macaques fitted with radio collars as the presence site of that troop.

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

Habitat evaluation

We predicted macaque seasonal habitats by using maximum entropy modeling, or Maxent [Phillips et al., 2006], with the program Maxent ver. 3.3.3k (downloaded via http://www.cs.princeton.edu/~schapire/maxent/ [accessed on October 1, 2013]). Maxent is an ecological niche model for predicting the relative habitat suitability that provides the potential geographic distribution of a species. The modeling relates the presence data of a species to the environmental data, to provide a correlative model of the environmental conditions that meet a species' ecological requirements. A key feature of Maxent is the construction of a model that minimizes the relative entropy between two probability densities—the first estimated from the presence data and the second estimated from the landscape—defined in covariate space [Elith et al., 2011]. Maxent maintains high standards of performance when predicting species habitats in various situations. It not only outperforms other recently developed niche modeling techniques [Elith et al., 2006], but is also a useful tool for estimating changes in habitat suitability over time, given a specific scenario for environmental change [Elith et al., 2011].

We integrated the presence sites of the four study troops with respect to each season (Table I) and created raster maps with a 50-m grid resolution, according to Enari & Sakamaki-Enari [2013a]. Next, we prepared raster maps with the same resolution, showing 13 environmental predictors that potentially explained the distribution of the presence sites (Table II). We selected those predictors on the basis of the following assumptions on habitat use by macaques in snowy regions: (1) their habitat use is fundamentally sensitive to food resources, which are related to forest cover type, maturation stage of forests [Sakamaki et al. 2011; Sakamaki & Enari, 2012], and land use (such as distribution of forest edges) [Imaki et al., 2006]; (2) the distribution of refuges against snowstorms, which is determined by topography (such as elevation and terrain conditions) and the distribution of evergreen conifers, strongly limits macaque occurrence during winter [Enari & Sakamaki, 2011, 2012]. Of the 13 predictors, the five describing forest cover types were calculated from National and Private Forest Planning Maps (analog maps, reduction scale = 1/5,000), provided by the Japanese Forest Agency and the Aomori Prefectural Government. For the maturation stage of forests, we decided on a threshold value of 40 years for conifer forests (when the canopy becomes completely closed [Sakamaki et al., 2011]) and a threshold value of 100 years for broadleaf forests (when the forests can be roughly regarded as primary forests in the absence of artificial disturbances). Predictors regarding topography were obtained from a digital elevation model (native cell resolution = 10 m) provided by the Geospatial Information Authority of Japan. For land use, we assigned two predictors, “distance to river or lake” and “distance to roads” (showing the index of forest edge effects), which were obtained from the Advanced Land Observing Satellite (sensor name = AVNIR-2; ground resolution = 2.5 m), taken in November 2009, and from field surveys conducted by the authors in 2009. For predictors with Boolean values (i.e., presence or absence), we calculated the proportion for each predictor within a circular moving window with a 500-m radius; in other words, the values of each grid cell were updated by storing the mean value assigned to the nearest grid cells within the circular coverage. The size of the moving window was based on the minimum distance that macaque troops can travel in six hours during daytime, taken from the time interval between respective presence sites that we had collected previously [Enari & Sakamaki, 2011].

When building each seasonal model, we removed highly correlated predictors (i.e., correlation coefficient of >0.7 [Dormann et al., 2012]) to prevent model overfitting, as well as to minimize the interrelating effects of multiple predictors on macaque habitats.

Moreover, we conducted a Jackknife test to remove environmental predictors that decreased the predictive performance of the habitat models; this allowed us to estimate the significance of individual environmental predictors.

When constructing our model by using Maxent, we assigned the regularization multiplier—which influences the degree of generality in the resulting models [Phillips et al., 2006]—with the default multiplier (i.e., 1). Moreover, when constructing habitat models, we used the default values of the Maxent interface for the remaining setting—background points 10,000; maximum iterations 500; convergence threshold 0.00001—according to Phillips & Dudik [2008]. We obtained the model output in logistic format, which gives the value of habitat suitability index in each grid cell within the range from 0 (unsuitable habitat) to 1 (optimum habitat). To visualize and interpret the output in raster, we used the software ArcGIS 9.3 (ESRI, Redlands, California).

We evaluated the model fitness by using the following 10-fold cross-validation technique [Fielding & Bell, 1997]: (1) random partitioning of the species presence data into 10 sets; (2) construction of a model based on nine sets; (3) validation of the model by using the remaining presence data; and (4) 10 repetitions of steps 1–3, to provide the mean and variance of the validation measure. To validate the model, we conducted receiver operating characteristics (ROC) analysis, which evaluates the usefulness of the constructed habitat model compared to random prediction [Fielding & Bell, 1997]. We used the area under the ROC function (termed AUC), which measures the ability of a model to discriminate between species' presence and absence sites [Hanley & McNeil, 1983]. The AUC generally ranges from 0.5 to 1, where a score of 1 indicates perfect discrimination, and a score of 0.5 implies predictive discrimination that is no better than a random guess [Liu et al., 2005].

Impact assessment of human-induced environmental alterations

To predict the impact of dam construction on each seasonal habitat, we compared the total habitat unit (THU) within the reference area, before and after dam construction. Based on traditional habitat evaluation procedures [Nevo & Garcia, 1996; Rittenhouse et al., 2011], we defined THU as the product of the habitat suitability value and the size of the corresponding habitat areas (km2) estimated using Maxent, i.e., THU was calculated as the whole sum of habitat suitability values owned by each grid cell within the reference area.

Next, we predicted the variations in THU two decades from now (i.e., after dam construction) under three possible forest change scenarios.

- Scenario 1: encouraging natural forest restoration in plantation areas—namely, recovery of secondary broadleaf forests by clear-cutting the existing old-conifer plantations.
- Scenario 2: maintaining the standard-rotation plantation management—a conventional measure that places value on wood production efficiency and is actually observed in the reference areas, according to the National Forest Planning Maps, i.e., planting conifer saplings after harvesting the existing old conifers; then, harvesting the planted conifers before turning the old ones (i.e., >40 years old).
- Scenario 3: implementing long-rotation plantation management, i.e., planting conifer saplings after harvesting the existing old conifers; then, harvesting the planted conifers after turning the old ones (i.e., approximately 80 years old).

Long-rotation plantation management is believed to mitigate the reducing effects of regional biodiversity caused by the creation of monocultural plantations, and has therefore gradually been embraced by forest managers during recent years [Nagaike et al., 2006]. In the present study, we explored the most suitable scenario that would contribute to macaque habitat conservation after dam construction, by calculating the THUs in the reference area for the three scenarios during each season.

Results

Habitat suitability

The seasonal habitat suitability models constructed by using Maxent showed that the mean AUC values for spring, summer, autumn, and winter were 0.73 ± SD 0.05, 0.86 ± SD 0.01, 0.87 ± SD 0.02, and 0.91 ± SD 0.02, respectively. The spring model provided a relatively low predictive performance, because of the diffusion of presence sites. By contrast, the summer, autumn, and winter models maintained a relatively high performance.

The influence of each environmental predictor on habitat models varied seasonally (Fig. 2). The predictor “mean elevation” strongly influenced the models in every season; however, the extent of the influence varied markedly according to season: (1) in spring, while the peak of habitat suitability was observed in relatively lowland areas, macaques notably avoided the bottom of the mountains; (2) in summer, the suitability value constantly decreased with increasing elevation; (3) in autumn, the suitability value maintained a constant level at every elevation; and (4) in winter, macaques preferred only lowland areas. We further observed the following distinctive features of the respective predictor influences: (1) while old broadleaf forests hardly provided any suitable habitats in autumn and winter, the presence of young broadleaf forests became a key component of spring and winter habitats; (2) in summer and autumn, relatively high suitability values were observed in areas close to roads (i.e., forest edges); (3) a high proportion of grassland (i.e., few forest covers) depressed the suitability of summer and winter habitats; (4) whereas macaques preferred areas with a high "standard deviation of elevation" (i.e., rugged mountain ranges) in spring, they exceled on sloping land in summer.

Habitat maps, obtained by visualizing the results of habitat evaluations within the reference area, demonstrated that, in spring, the suitable habitats became diffuse in geographic space, whereas, in winter, they appeared in a locally concentrated manner (Fig. 3).

Impact assessment

Prior to dam construction, the THU value was highest in spring (three-fold higher than that in winter) (Table III). The percentage loss rate of THU caused by dam construction was highest in winter, followed by summer. The loss rate of THU in every season exceeded that of the expectation value calculated according to the size of the estimated flooded area, which accounted for 5.5% of the reference area. Thus, the flooded area possessed a high potential value for macaque habitats in every season.

The THU for scenario 3 (long-rotation plantation management) was highest in spring, followed by summer and autumn (Table IV). Meanwhile, scenario 1 (natural forest restoration) was selected as the most effective way of mitigating the influence of dam construction on winter macaque habitats.

Discussion

Impact of dam construction

Among primate species, some macaque species have undergone a unique evolutionary process, which has increased their breadth of distribution from the tropics to cool temperate zones, including snowy areas. This expansion of their natural distributions may have been attained by their adaptive phenotypic plasticity in terms of diet, grouping patterns, and time budget, to cope with diverse environments [Fooden, 2000; Hanya, 2010; Ménard, 2002; Richard et al., 1989; Sinha, 2005]. Such plasticity represents a marked capacity to optimize the use of limited resources, which are generally distributed in a spatially inhomogeneous manner. Our present findings regarding the seasonal habitat features of macaques (Figs. 2 and 3) exemplified such a capacity, i.e., Japanese macaques responded flexibly to seasonally restricted abundance and distribution of food resources in cool-temperate forests [Maruhashi et al., 1998; Tsuji, 2010] by altering their seasonal habitat uses—except in spring, when resources (i.e., fresh leaves) were superabundant. For example, during the fruit-eating season (summer–autumn), macaques selectively occupied forest edge sites, where a mantle community (comprising bushes and bines) with high berry yield often flourishes (Fig. 2; see also Imaki et al. [2006]).

Heavy snow and blizzards—physical limiting factors of daily animal movements [Watanuki & Nakayama, 1993]—are considered as new natural threats for primates from the perspective of their evolutionary process. To cope with these threats, Japanese macaques often adopt a risk-averse foraging tactic, i.e., minimizing energy loss when searching for dietary items [Enari & Sakamaki-Enari, 2013b]. In the present study, such a tactic resulted in extremely limited habitat use in winter (Fig. 3). This may be explained by the fact that macaques are prone to occupy sunny sites located in depression contours, which can reduce the influence of blizzards [Enari & Sakamaki-Enari, 2013a; Sakamaki & Enari, 2012]—the winter habitat use of macaques is more sensitive to thermoregulatory cost than the cost of searching for dietary items, i.e., bark and buds of broadleaf trees [Agetsuma & Nakagawa, 1998; Watanuki & Nakayama, 1993].

These findings likely expose a distinctive ecological feature of macaques living in heavy snow regions, i.e., heterogeneous habitat uses biased to marginal environments. Consequently, this feature may lead to the current result that, to a large extent, the optimum habitats of macaques overlapped the estimated flooded area of the new dam (i.e., the intermontane trough), resulting in a marked reduction of the THU value, especially in summer and winter (Table III), when macaque diets in cool temperate forests are notably constrained [Nakagawa, 1997; Tsuji et al., 2008]. In particular, given that the highest habitat unit loss rate occurred in winter (which showed the lowest THU value among seasons), we propose that the impact of human-induced loss of suitable winter habitats on the population dynamics of macaques should be carefully monitored.

Impact of forest management

As demonstrated by the “field of dreams paradigm,” we cannot expect that restoration of a modified habitat structure to its original state will lead to the return of native organisms, and the recovery of the original ecosystem processes [Palmer et al., 1997]. This paradigm holds true for our present findings. The restoration of conifer plantations to semi-natural forests has attracted considerable public attention in terms of recovery of the original ecosystem function [Masaki et al., 2004; Yamagawa et al., 2010]. Nevertheless, our present results indicate that such restoration practices will hardly contribute to the improvement of the THU; by contrast, the implementation of long-rotation plantation will provide more suitable alternative habitats for macaques in every season, except winter (Table IV). This unexpected result may be derived from with two resource-related aspects—food and cover. With respect to food, snow damage to conifer plantations—generating canopy gaps—occurs frequently in heavy snow areas, especially those located on east-facing slopes [Masaki et al., 2004]. This promotes the maintenance of shrubby broadleaf trees (staple dietary items of macaques in winter; Sakamaki et al. [2011]), even within the conifer plantations. With respect to cover, conifer plantations provide the only evergreen trees in snowy areas, and mature conifers can offer macaques protection from snowstorms [Enari & Sakamaki-Enari, 2013a; Imaki et al., 2006]. In this way, the plasticity inherent in macaques may enable them to generate higher resource values from the artificially modified environment than from native forests.

On the other hand, in the present study, the implementation of long-rotation plantation did not necessarily create suitable macaque habitats in winter. The rationale for this result may be explained by the thermoregulatory cost; as discussed above, in cold environments, macaques need to maintain their body temperature by allocating sufficient time for sunbathing [Hanya et al., 2007]. Therefore, the limited amount of insolation available under or on trees with closed canopies, the crowns of which also possess a heavy covering of snow in most situations, may lead macaques to avoid mature conifer plantations [Sakamaki & Enari, 2012].

Our present prediction models indicated that the standard-rotation plantation provided an insubstantial amount of preferred landscape for macaques every season.

This finding contradicts those of previous studies conducted in winter [Sakamaki et al., 2011; Sakamaki & Enari, 2012], which indicated that, in comparison with native broadleaf forests, young plantations create a higher resource value in terms of winter resources for food and cover. The reason for this contradiction may be landscape structure (e.g., size and distribution of each forest patch). Under standard-rotation plantation management, the upper-story trees comprise only young conifers, often resulting in a large-scale homogeneous landscape structure compared with long-rotation plantations or semi-natural forests. Such a monotone landscape often leads to losses of ecological function and, hence, possibly decreases in the habitat quality of wild mammals, including macaques [Agetsuma, 2007]. Thus, it is reasonable to consider that such a homogeneous landscape structure potentially degrades the THU for the macaques, regardless of whether the constituent resource is preferred. To verify this rationale, further studies regarding resource selection functions focusing on the spatial structure of respective resources are required.

Implications for practice

The current model predictions provide the following new insights into the conservation initiatives for the northernmost macaque habitats, which can contribute to biodiversity conservation in heavy snowfall ecosystems:

1. It is highly likely that dam construction markedly decreases the THU of existing macaque troops.
2. The marked loss of THU in winter—a bottleneck season in terms of food availability [Hanya et al., 2006]—is of particular concern for maintaining vulnerable macaque distributions.

3. Restoring semi-natural broadleaf forests by cutting down the existing conifer plantations does not always improve the THU of macaques, and is unlikely to represent the best option for mitigating the adverse impacts of dam construction.
4. To combat a decline in the THU during snowy seasons, replacement of conifer plantations in lowland areas with semi-natural forests may be effective.
5. Implementation of long-rotation management for existing plantation areas in higher elevations contributes to an increase in the THU during non-snowy seasons, thereby leading to enhanced compatibility between timber production and primate conservation.

Fundamentally, ecological niche modeling (including Maxent) that uses the locations where a species is present can only estimate the realized niche as a subset of the fundamental niche, which results in limited applications in changing environmental situations that cannot be directly incorporated into the habitat models [Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005]. Considering the macaque society—the behavioral patterns of its troops are determined by not only resource distributions but also some social relationships, such as inter-group competitions [Maruhashi et al., 1998]—realized habitat use of a troop is likely sensitive to the spatial distributions of neighboring troops. This means that the above implications might be effective only under similar population conditions (i.e., troops were fully distributed in the reference areas [Enari & Sakamaki, 2011]). To further enhance the generality of the above implications, we would require information on the influence of exclusive range use by existing macaque troops on their realized niche, which might be ultimately determined by troop density.

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Figure legends

Fig. 1 Location of the study area in the Shirakami Mountains, northern Japan. (A) Distribution of Japanese macaques in 2009; (B) and (C) forest cover and ground form, respectively, of a reference area (109.6 km^2); (D) flooded area caused by construction of a new dam.

Fig. 2 Marginal response curves for the four most important predictors of each seasonal macaque habitat. Black solid lines indicate mean values; gray-colored areas indicate SD; x-axes and y-axes show the values of each predictor and the suitability values, respectively; percentage figures in parentheses represent the estimates of the relative contributions of each predictor to the model. ME = mean elevation; YDB = proportion of deciduous broadleaf forests; ODC = proportion of old deciduous conifer plantations; SDE = SD of elevation; DR = distance to road; GR = proportion of grassland; MS = mean slope; ODB = proportion of old deciduous broadleaf forests.

Fig. 3 Seasonal habitat suitability maps for Japanese macaques in the Shirakami Mountains. HSI = habitat suitability index.

Table I Number of presence sites of the four macaque troops recorded in the Shirakami Mountains

Troop	Winter (Jan–Mar)	Spring (Apr–Jun)	Summer (Jul–Sep)	Autumn (Oct–Dec)	Tracking period
F	81	75	110	135	Summer 2007–Autumn 2009
O	87	73	85	85	Winter 2008–Autumn 2009
S	86	72	108	136	Summer 2007–Autumn 2009
T	30	30	31	32	Winter 2009–Autumn 2009
Total	284	250	334	388	

Table II Environmental predictors used to build macaque habitat suitability models by using Maxent

Category Environmental predictors	Mean ± SD in the study area	Application for model construction			
		Spring	Summer	Autumn	Winter
Forest cover					
Proportion of old deciduous broadleaf forests	0.2 ± 0.3	Yes	Yes	Yes	Yes
Proportion of young deciduous broadleaf forests	0.4 ± 0.3	Yes	Yes	Yes	Yes
Proportion of old deciduous conifer plantations[a]	0.0 ± 0.1	Yes	Yes	Yes	Yes
Proportion of old evergreen conifer plantations	0.1 ± 0.1	Yes	Yes	Yes	Yes
Proportion of young evergreen conifer plantations	0.2 ± 0.2	Yes	Yes	Yes	Yes
Proportion of grassland	0.0 ± 0.0	Yes	Yes	Yes	Yes
Topography					
Mean elevation (m)	356.8 ± 148.4	Yes	Yes	Yes	Yes
Mean slope (°)	21.6 ± 9.6	Yes	Yes	Yes	Yes
SD of elevation (= topographic relief)	54.0 ± 22.9	Yes	Yes	Yes	Yes
Proportion of northern slope	0.3 ± 0.1	No	Yes	Yes	Yes
Proportion of southern slope	0.2 ± 0.1	No	Yes	Yes	Yes
Land use					
Distance to river or lake (m)	285.4 ± 232.1	Yes	Yes	Yes	Yes
Distance to road (m)	718.6 ± 661.3	Yes	Yes	Yes	Yes

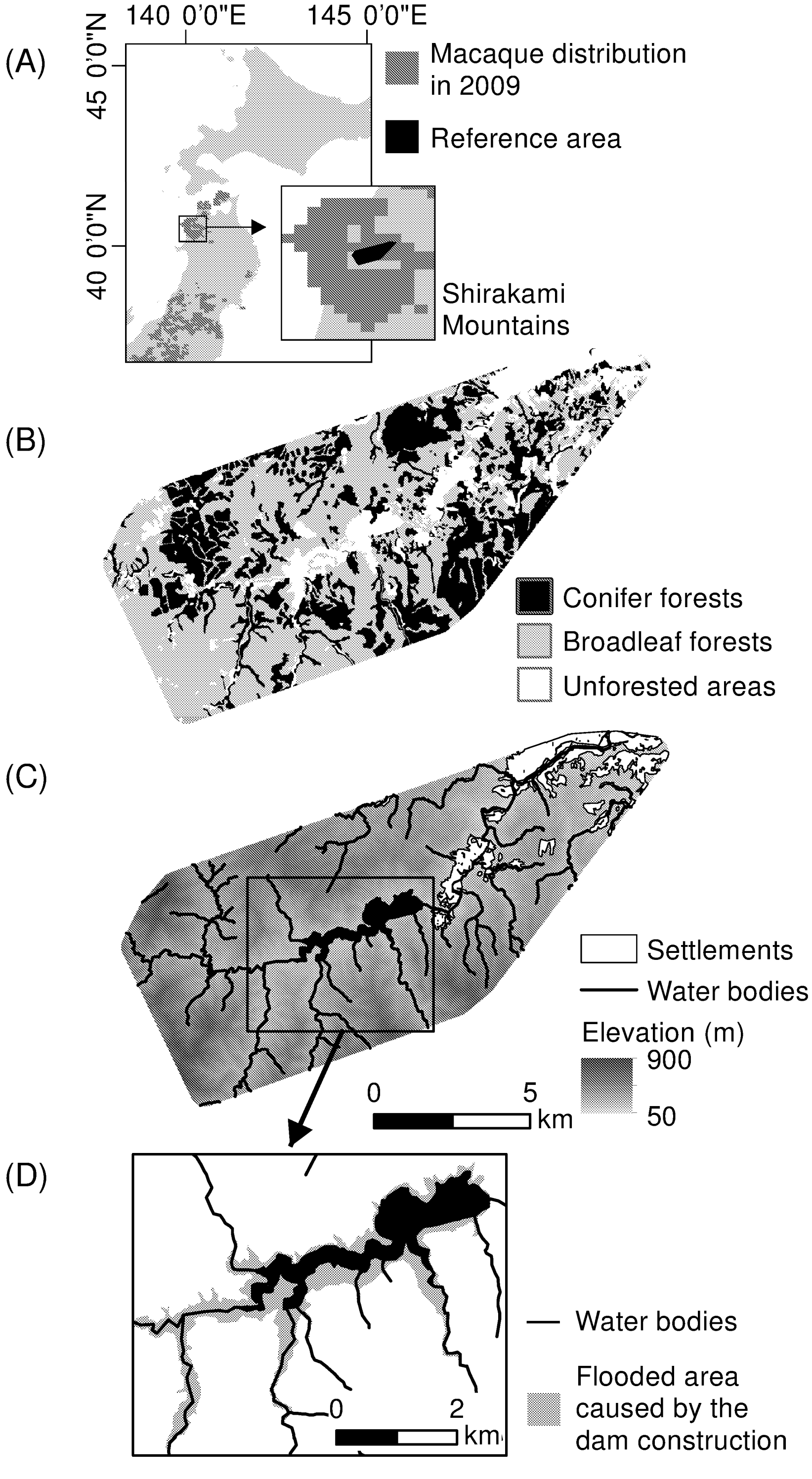
[a] We omitted the predictor “young deciduous conifer plantations” because of highly limited distribution.

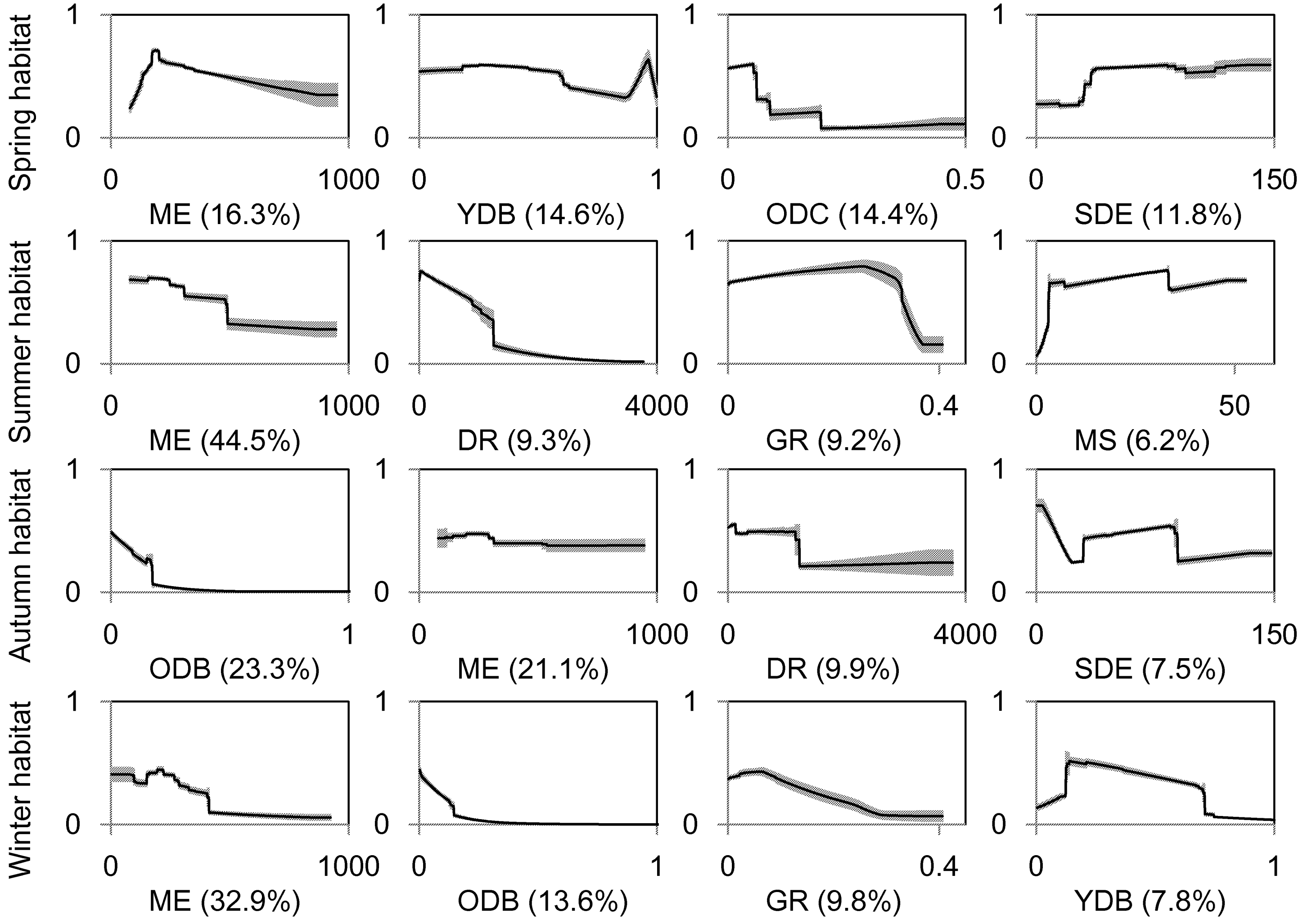
Table III Impact of dam construction on the total habitat unit (THU) of macaques in the Shirakami Mountains

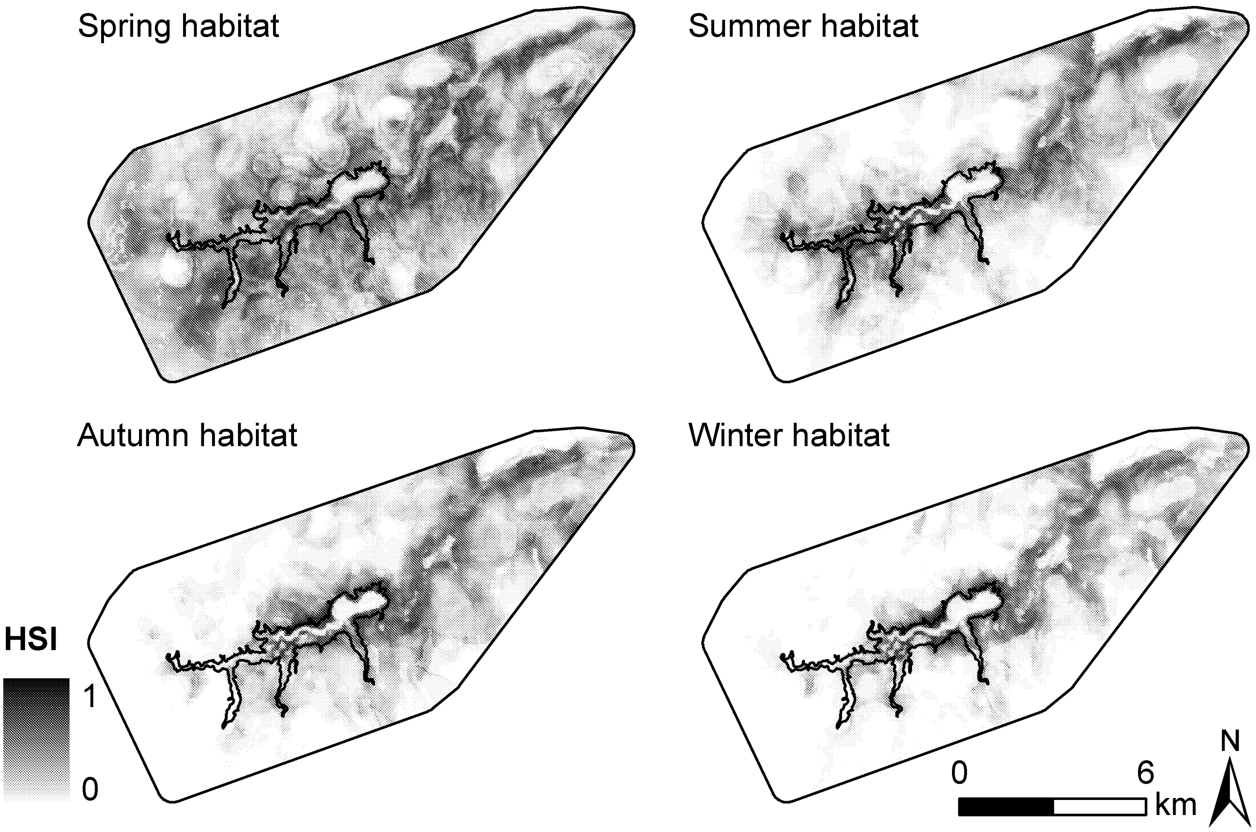
	Spring habitat	Summer habitat	Autumn habitat	Winter habitat
THU before dam construction (**A**)	12,367.5	6,180.6	5,708.1	4,113.9
Habitat unit within an estimated flooded area caused by dam construction (**B**)	974.9	961.7	728.9	671.3
Percentage of loss rate of THU (**B**/**A** × **100**)	7.9	15.6	12.8	16.3
THU after dam construction (**A–B**)	11,392.6	5,218.9	4,979.2	3,442.6

Table IV Total habitat units of Japanese macaques after dam construction based on three different forest change scenarios

	Spring	Summer	Autumn	Winter
Scenario 1: Recovery of secondary broadleaf forests by clear-cutting the existing old-conifer plantations	9,226.5	2,865.4	2,985.3	2,407.4
Scenario 2: Maintaining the standard-rotation plantation management in the existing plantation areas	8,442.4	2,951.7	2,580.6	1,891.1
Scenario 3: Implementing long-rotation plantation management in the existing plantation areas	11,045.0	4,656.1	3,373.2	2,129.7


(A)
140 0'0"E
145 0'0"E
45 0'0"N
40 0'0"N
Macaque distribution in 2009
Reference area
Shirakami Mountains
(B)
Conifer forests
Broadleaf forests
Unforested areas
(C)
Settlements
Water bodies
Elevation (m)
900
50
0
5
km
(D)
Water bodies
Flooded area caused by the dam construction
0
2
km


Spring habitat
Summer habitat
Autumn habitat
Winter habitat
1
0
0
1000
ME (16.3%)
0
1
YDB (14.6%)
0
0.5
ODC (14.4%)
0
150
SDE (11.8%)
0
1000
ME (44.5%)
0
4000
DR (9.3%)
0
0.4
GR (9.2%)
0
50
MS (6.2%)
0
1
ODB (23.3%)
0
1000
ME (21.1%)
0
4000
DR (9.9%)
0
150
SDE (7.5%)
0
1000
ME (32.9%)
0
1
ODB (13.6%)
0
0.4
GR (9.8%)
0
1
YDB (7.8%)


Spring habitat
Summer habitat
Autumn habitat
Winter habitat
HSI
1
0
0
6
km
N