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**Ecological consequences of herbivory by Japanese macaques (*Macaca fuscata*) on
succession patterns of tree assemblages: a case of snowy regions in Japan**

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Abstract

Apart from frugivory, we have limited knowledge of the ecological consequences of primate herbivory. We aimed to ascertain the effects of spring folivory and winter bark/bud herbivory by Japanese macaques (*Macaca fuscata*) on tree species and succession patterns of cool-temperate forests with heavy snow. To evaluate the impact of herbivory on individual trees, we assessed the growth and mortality of trees consumed by simulating herbivory on nine tree species over four years. Additionally, we assessed the cumulative impacts of bark/bud herbivory observed at the tree community level by monitoring the patterns of natural herbivory for almost a decade and evaluating the structure of tree assemblages in places with different cumulative impacts of herbivory. The results of simulated herbivory showed that the mortality caused by both spring and winter herbivory was limited (<20%) for almost all tree species monitored; however, the simulated folivory led to delayed tree growth and/or weakening of tree architecture. In contrast, the simulated bark/bud herbivory sometimes resulted in overcompensation of the tree consumed. The multi-year monitoring of natural herbivory demonstrated that, while bark/bud herbivory did not reduced the diversity and biomass of tree assemblages, the cumulative impacts of natural herbivory could have affected the tree succession pattern, resulting in increasing the availability of bark/buds preferably fed by macaques. The key cause for this feedback effect of herbivory on available foods of macaques might be heavy snow conditions, which could physically and physiologically restrain the excessive bark/buds herbivory by macaques.

Keywords: bark, bud, compensation, folivory, tolerance

1 Introduction

To date, there have been broad and in-depth efforts to elucidate the influences of quantity, quality, and distribution of food resources on primates in terms of population dynamics (Chapman et al., 2018; Hanya & Chapman, 2013), intra- and inter-specific competition (Ganzhorn, 1988; Koenig, 2002; Schreier et al., 2009), activity budgets (El Alami et al., 2012; Ruppert et al., 2018; Vasey, 2005), and habitat selection (Barton et al., 1992; Enari & Sakamaki-Enari, 2013a; Gabriel, 2013). In contrast, little is known about the ecological consequences of primate herbivory, including changes in plant fitness and succession patterns and the feedback effects of such plant responses on primates themselves. Frugivory is an exception to this. A great deal of research on endozoochory by primates has been conducted, especially in tropical forests, arguing that primate-mediated seed dispersal plays a core role in sustaining the succession and species diversity of plant assemblages in forests highly dependent on frugivores (Andresen et al., 2018; Chapman, 1995; Chapman & Dunham, 2018; Corlett, 2017; Dew & Wright, 1998; Lambert & Garber, 1998; McConkey, 2018). Thus far, most studies on post-dispersal processes have identified positive fitness effects on plants (e.g., directed dispersal, which allows plants to reach habitats with advantageous conditions for survival; Brodie et al., 2009; Haurez et al., 2015; Rogers et al., 1998; Tsujino & Yumoto, 2009), as well as positive feedback effects caused by endozoochory, enhancing primate fitness through habitat regeneration (Chapman & Onderdonk, 1998; Di Fiore & Suarez, 2007; Howe & Miriti, 2004).

Apart from frugivory, primate herbivory, which includes folivory, florivory, and nectarivory, is also expected to influence plant fitness and succession patterns (Chapman et al., 2013). Though the evidence is quite limited, the influence of folivory might be situation-dependent. In the case of Japanese macaques (*Macaca fuscata*) living

on Yakushima Island in southern Japan, where the proportion of leaf consumption to leaf production by macaques was minimal (0.21%–0.90%), the impact of folivory on plant fitness was negligible both in the immediate term and long term (Hanya et al., 2014). In contrast, research in Kibale National Park, Uganda, where colobines (Colobinae) are present as typical folivores with large biomass, demonstrated the growth inhibition of preferred food plant species (Chapman et al., 2010), sometimes resulting in a decrease in those populations (Chapman et al., 2013). Studies on bark herbivory by primates are less common than those on folivory, but the destructive impact on commercial trees, such as plantations of *Eucalyptus* spp. and *Pinus* spp., are relatively well known (Di Bitetti, 2019). However, there is some contrasting evidence suggesting that compensatory regrowth occurs following primate herbivory by increasing the production of leaves, shoots, and flowers (e.g., folivory by *Celtis durandii* and *Funtumia latifolia* in Kibale, Chapman et al., 2013; bark/buds-feeding by Japanese macaques in northern Japan, Enari & Sakamaki, 2010; branch-feeding by *Cebus capucinus* in the middle of the Panama Canal, Oppenheimer & Lang, 1969; herbivory by *Gorilla gorilla* in East Africa, Watts, 1987). Hence, it would be premature to conclude that the herbivory of leaves and bark always negatively impacts plant fitness, i.e., undercompensation (Strauss & Agrawal, 1999).

Thus, we currently have limited knowledge of plant responses to primate herbivory, excluding frugivory, such as changes in longevity, growth, and reproduction of plant individuals, especially on the plant assemblages eventually established. To address this issue, we aimed to reveal the impacts of herbivory by Japanese macaques. For the following three reasons, we focused on changes in the succession patterns of tree assemblages observed after herbivory in the Shirakami Mountains, northern Japan (Fig. S1), which is one of the heaviest snowfall districts globally and one of the northernmost

habitats for wild primate populations (Enari, 2014). First, there is a severe deficiency of related research on cool-temperate forests. In fact, traditional fieldwork to reveal ecosystem processes via primate species has been conducted mostly in tropical or warm-temperate forests (Andresen et al., 2018; Chapman et al., 2013; McConkey, 2018). Second, cervids (Cervidae), recognized as typical ecosystem engineers that alter plant assemblages on a massive scale, were absent during the study period (Enari et al., 2019). This implies that the influence of macaque herbivory can be more readily uncovered. Third, the short growing season observed in high-latitude cool-temperate forests, compared to that in lower-latitude regions, likely deprives plant species of a chance to recover from the phenological delay, such as foliation, flowering, and fruit and seed production, caused by herbivory (Tiffin, 2000).

All Japanese macaques are omnivorous. Their staple diets vary seasonally: fresh leaves during spring, fruits and nuts during summer and fall, and bark and buds during winter in deciduous forests with sufficient snow (Suzuki, 1965; Tsuji et al., 2015). The same holds for the current study area; folivory and bark/bud herbivory by macaques account for approximately 80% of the time spent feeding during spring and winter, respectively (Enari, 2007).

Given the intensive herbivory by macaques in snow regions, we hypothesized that the impacts of spring folivory and winter bark/bud herbivory could exceed the tolerance of their preferred food trees; therefore, the cumulative impact of herbivory could alter the succession patterns of tree assemblages. To address this hypothesis, we assessed the growth and mortality of the individual food trees by conducting multi-year experiments of simulated herbivory, i.e., artificial removal of plant parts to systematically regulate the impact of herbivory (Tiffin & Inouye, 2000). To evaluate the cumulative impact of herbivory on tree assemblages, we monitored the natural herbivory patterns of

macaques for nearly a decade. Moreover, to assess the feedback effects of herbivory on macaque food resources, we noted variations in the availability of food trees preferred by macaques in forest patches with different frequencies of their usage.

2 Methods

Our data collection procedure adhered to the legal requirements of the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and complied with the laws governing wildlife research in Japan.

2.1 Study area

We conducted field research in the northeastern part of the Shirakami Mountains, the district bordering a UNESCO World Natural Heritage site, located in northernmost mainland Japan (40°29'–40°34' N, 140°11'–140°19' E; Fig. S1). The study area is a low-montane zone (170–420 m above sea level) and covered with cool-temperate deciduous broadleaved forests—mainly composed of undisturbed beech (*Fagus crenata*) and oak (*Quercus crispula*) trees—and conifer plantations, such as cedar (*Cryptomeria japonica*) and larch (*Larix kaempferi*) (Biodiversity Center of Japan, 2020). Freezing winters with heavy snowfall are observed from December to April, and the snow depth can reach 2 m. The mean ambient temperature in the coldest month (January) and warmest month (August) for the past 30 years were –3 and 25 °C, respectively (MLIT, 2020).

The population density of Japanese macaques in and around the study area is approximately 5 individuals/km² (including solitary males) or 0.2 troops/km² (Enari & Sakamaki, 2011), representing 1/6–1/20 of the population densities observed in southern habitats with warm-temperate evergreen forests (Hanya et al., 2006). Japanese serows

(*Capricornis crispus*) and Japanese hares (*Lepus brachyurus*) are distributed as herbivores similar to macaques, whereas sika deer (*Cervus nippon*), a typical ecosystem engineer in Japan, became extinct over a century ago (Enari et al., 2019).

2.2 Influences of herbivory at the individual tree level

2.2.1 Research design for simulated herbivory

To assess the effects of macaque herbivory on each tree species, we selected eight preferred tree species for spring folivory and five for winter bark/bud herbivory (Table 1) based on previous research in the same study area (Enari et al., 2005; Enari & Sakamaki-Enari, 2013a; Enari & Sakamaki, 2010; Sakamaki et al., 2011). Although all the species monitored are tall trees, we selected 7–11 saplings (approximately 5–10 years old) of species from each treatment, in view of terrestrial accessibility by macaques (Enari & Sakamaki-Enari, 2013a). These trees were sparsely scattered in the study area, with a low frequency of use by existing macaque troops (Enari & Sakamaki-Enari, 2013b).

To validate the impacts of spring folivory on the growth and mortality of tree species, we performed a simulated herbivory experiment by annually defoliating 80% evenly from the sun and shade crown of the sample trees in 2014, 2015, and 2016. We decided to use this defoliation percentage based on the maximum folivory intensity on saplings (Enari, 2007). We conducted the defoliating treatment in June, when the foliation of most species is completed and macaques intensively feed on fresh leaves in deciduous forests (Tsuji, 2010). We then compared the diameter at breast height (DBH), tree height, and shoot number of each sample tree before (2014) and after (2017) defoliation. Furthermore, we defined trees without any shooting buds as dead and calculated the mortality for each species' treatment. In this evaluation, we prepared

controls (i.e., trees without any treatments) for each tree species (the sample size is shown in Table 1) and measured their growth and mortality in the same manner.

To assess the impact of winter bark/bud herbivory, we removed all the bark and buds of each sample tree above the snow surface (a ground height of approximately 1.5 m) once in January 2015 because macaques rarely excavate snow cover for feeding (Enari & Sakamaki-Enari, 2013a). Incidentally, macaques in the study areas feed on both the bark and buds for every species monitored, except for *Magnolia obovata* and *Aesculus turbinata* (Table 1), whose bark is not consumed very often (Enari & Sakamaki-Enari, 2013a). For these two species, we did not strip the bark. As was the case with the folivory experiment, we compared the growth and mortality of each tree sample, including the controls, in 2014 and 2017. Four out of five tree species monitored were also included in the folivory experiment (Table 1); the control samples for these species were included in the bark/bud herbivory experiment.

It is supposed that the tolerance of the trees consumed is sensitive to the stand density of the site, which determines resource competition and the photoenvironment (Strauss & Agrawal, 1999). We then measured the mean canopy openness at the site of every sample tree using the CanopOn 2.03 software (Takenaka, 2009) with hemispherical photos. We took the hemispherical photos at a ground height of 1 m using an EX-FR200 camera (Casio, Tokyo, Japan) during the summer (i.e., leafy season).

2.2.2 Statistical processing

We used *R* ver. 4.0.2 (R Core Team, 2020) for all data processing as follows.

To clarify the differences in mortality between defoliation or bark/bud removal and the controls during the study period, we conducted hypothesis testing for equality of population proportions ($\alpha = 0.05$) and calculated the effect size (Cohen's *h*) using the *R*

187 package *pwr*.

188 To determine the differences in tree growth among the different treatments, we
 189 conducted an analysis of covariance (ANCOVA) with canopy openness as a covariate.
 190 For this, we used the *anova* function, included in the *R* package *car*, and calculated the
 191 effect size (Cohen's *f*). As for the tree species with significant differences shown by the
 192 ANCOVA, we built three generalized linear models (GLMs) by assigning the increment
 193 in DBH, tree height, and shoot number for each tree species as response variables. Here,
 194 we used the treatments (categorical data) and mean canopy openness (continuous data)
 195 as explanatory variables. We adopted a gamma distribution (link function = log) for
 196 DBH and tree height models and a Gaussian distribution (link function = identity) for
 197 the shoot number model. Considering that tree growth is sensitive to the original size of
 198 each tree sample, we assigned tree height as an offset term. When building these
 199 models, we omitted the tree samples that died during the study period. We developed
 200 GLMs without an intercept to calculate the coefficients and 95% confidence intervals
 201 (CIs) for all three treatments. We judged the effect size of each explanatory variable and
 202 the performance of models built using the change in Akaike information criterion
 203 [ΔAIC ; i.e., $AIC_{(\text{model built with all variables})} - AIC_{(\text{model built with all variables excluding the variable concerned})}$]
 204 and the percentage of deviance explained [i.e., $\%DE = (1 - \text{Deviance}/\text{Null deviance}) \times$
 205 100], respectively.

206

207 **2.3 Long-term influence of herbivory at the community level**

208 To investigate the cumulative impact of herbivory on the succession patterns of tree
 209 assemblages, this study focused solely on winter bark/bud herbivory for the following
 210 reasons. Unlike folivory, bark/bud herbivory often occurs intensively on a specific
 211 individual tree in particular forest patches (Enari & Sakamaki-Enari, 2013a) because of

the behavioral suppression of macaques leading to narrowing geographical range and niche breadth of their habitat use, which is caused by increasing the thermoregulatory and moving costs against the cold and snow, respectively (Enari & Sakamaki-Enari, 2013b; Sakamaki & Enari, 2012). In addition, bark herbivory may result in widespread impacts on trees not only by stripping the cambium and phloem from the xylem, indicating the disruption of carbon and organic nutrient transport between roots and leaves (Salisbury & Ross, 2002), but also by causing fungal damage in wounded stems (Arhipova et al., 2015). Therefore, we supposed that winter herbivory could have stronger influence on tree assemblage than macaque herbivory observed in other seasons.

We arranged five 40-m wide belt-transects within the study area (total extension of 12.4 km; Fig. S1) as a sampling frame for evaluating the cumulative impacts of bark/bud herbivory on tree assemblages. The transects were composed of five forest types: old evergreen conifers (forest age > 40 years) with an area of 7.6 ha, young evergreen conifers (<40 years old) with 12.2 ha, old deciduous broadleaf forests (>100 years old) with 2.2 ha, young deciduous broadleaf forests (<100 years old) with 23.9 ha, and old deciduous conifers (>40 years old) with 3.7 ha. For more details on these transects, see Enari and Sakamaki-Enari (2013a).

2.3.1 Selectivity of winter feeding sites

For the synthetic assessment of the impacts of bark/bud herbivory on tree assemblage, we first identified the environmental conditions of forest patches that could increase the frequency of macaque herbivory (i.e., herbivory pressure) during winter by conducting a multivariable analysis. For this, we set up 52 sampling plots (10 m × 10 m) along the belt-transects. We measured the following conditions for each plot, and these were

considered explanatory variables: (i) geographical features, measuring the elevation and slope inclination using a digital elevation model with a 10-m grid resolution (according to an open-source data from the Geospatial Information Authority of Japan); (ii) forest types, using the above five categories; (iii) photoenvironment (i.e., elements influencing the thermoregulatory costs of macaques; Hanya et al., 2007), calculating the mean canopy openness using the same procedure as that in section 2.2.1; and (iv) availability of preferred food trees, as described below.

We first evaluated the selectivity of macaques for each food tree. For this, we conducted an inventory survey and counted trees with a height of >2 m, which macaques could access even under snow conditions, in every sampling plot during the summer of 2016–2020. Next, we calculated Manly’s standardized selection ratio (α_i) (Manly et al., 2007) for each tree species:

$$\alpha_i = \widehat{w}_i / \sum_{j=1}^m \widehat{w}_j$$

$$\widehat{w}_i = o_i / \pi_i$$

where o_i is the proportion of the frequency in tree species i consumed to that in all the tree species consumed (i.e., 1, 2, ..., m), and π_i is the proportion of the availability of tree species i to that of all the tree species. To measure o_i , we recorded all the trees with fresh macaque bite marks on the bark/buds (for details on mark identification, see Enari & Sakamaki-Enari, 2013a) by exploring all the belt-transects during the late winter (end of March). We continuously conducted these recordings between 2012 and 2020, and the total count of trees consumed reached 4,447. To obtain π_i , we used the summation of “the expectation of abundance of species i in each of the five different forest types” and “the proportion of each forest type in the belt-transects.” To calculate the former, we used the inventory survey results at five representative sampling plots, with each forest

type selected from the 52 sampling plots. Finally, we calculated Manly's α for each species following the above equations and assigned the summation of Manly's α , that is, $\sum_i^m (\alpha_i \times \text{abundance of species } i)$, to "(iv) availability of preferred food trees" for each sampling plot.

To assess the cumulative herbivory pressure by macaques at each sampling plot (i.e., objective variable), we utilized geolocations of the trees with fresh bite marks given above. Given the tree succession, the value of "(iv) availability of preferred food trees" could be affected by the year the inventory survey was conducted. Therefore, we defined herbivory pressure for five years after the inventory survey was conducted. We calculated herbivory pressure as the abundance of trees consumed in each geolocation or spatial density. We calculated the spatial density of the trees consumed for each survey plot within a circular focal area 120 m in diameter, equivalent to the mean spatial extent of a troop in the study area (Enari & Sakamaki, 2011), using the Focal Statistics tool in ArcGIS 10.7 (ESRI, Redlands, CA).

Based on these variables, we built a generalized linear mixed model (GLMM) to predict herbivory pressure. We assigned a gamma distribution (link function = log) for the model construction and used the *glmer* function included in the *R* package *lme4*. We assigned the ID of belt-transects to a random intercept to account for differences in food selection by different macaque troops occupying each belt-transect. We judged the effect size of each variable and model performance using ΔAIC and %DE, respectively.

2.3.2 Cumulative impact of herbivory on tree assemblages

We built three GLMMs to compare the structures of tree assemblages in areas with different levels of cumulative impact due to bark/bud herbivory (species richness, tree abundance, and the summation of Manly's α) in sampling plots as objective variables.

When preparing these variables, we used the inventory survey results and counted all trees above breast height in this case. We assigned explanatory variables with cumulative herbivory pressure, mean canopy openness, elevation, slope inclination, and forest types in each sampling plot, which was the same dataset described in section 2.3.1. We used the ID of belt-transects as a random intercept and adopted Poisson and gamma distributions (link function = log) for the models with species richness and tree abundance and the model with the summation of Manly's α , respectively. We judged the variable importance and model performance using the same methods as described in section 2.3.1.

3 Results

3.1 Impacts of herbivory on the growth and mortality of individual trees

The results of the simulated herbivory demonstrated that the mortality caused by spring defoliation and winter bark/bud removals was <20% and showed no significant difference from the controls for every species, except for a pioneer species (i.e., *Aralia elata*) in defoliation with a large effect size (Cohen's $h > 1.0$) (Table 2). In contrast, we confirmed a significant variations of tree growth among the treatments, specifically five, three, and two tree species with the increments in DBH, tree height, and shoot number, respectively, which commonly posed large effect sizes (Cohen's $f > 0.7$) (Table S1).

The performance of the GLMs built to identify factors explaining these revealed influences was fairly good in most models (%DE > 30; Table 3), meaning that the factors we assigned could largely determine the increment in tree growth. All the GLMs with particularly high performance (%DE > 50) commonly showed that "Treatments" was a more influential variable than "Canopy openness" (see ΔAIC in Table 3). As for the GLMs explaining DBH increments, the coefficients of both defoliation and bark/bud

removal were mostly lower than those of the control, showing the negative impacts of herbivory. The results of GLMs regarding the increments in tree height indicated that, whereas defoliation exerted negative impacts, bark/bud removal generated positive impacts. The model explaining the increment in shoot number showed a negative impact of defoliation.

3.2 Long-term influence of bark/bud herbivory on tree assemblages

Environmental factors, including geographical features and food availability, did not sufficiently explain the frequency of macaque herbivory, or herbivory pressure (%DE = 5.91; Table 4). Among the explanatory variables, “Forest types” was the most influential variable ($\Delta AIC = -26.71$), and among forest types, young evergreen coniferous forests were strongly selected. Subsequently, “Elevation” affected herbivory pressure ($\Delta AIC = -10.11$), but the availability of preferred food trees (i.e., the summation of Manly’s α) contributed little to it ($\Delta AIC = -1.61$).

Among the GLMMs explaining factors determining the structures of tree assemblages, “Forest Types” were commonly influential (see ΔAIC s in Table 5). Herbivory pressure contributed little to species richness (Model 1 in Table 5), whereas the tree abundance (Model 2) and the summation of Manly’s α (Model 3) significantly increased with mounting herbivory pressure.

4 Discussion

4.1 Tree tolerance to macaque herbivory

The findings in the simulated herbivory experiment did not support the current hypothesis, i.e., bark/bud herbivory, let alone folivory (as with the case of Hanya et al., 2014), had a limited effect on the mortality of trees (Table 2). However, the simulated

herbivory undoubtedly led to a delay in tree growth and/or the weakening of tree architecture through defoliation (i.e., a decrease in photosynthesis rate) or bark/bud removal (i.e., the loss of apical and lateral meristems) (Table 3). The low mortality and the difference in regrowth rate of trees consumed may be explained in terms of the degree of tolerance exhibited by each tree species against herbivory (i.e., compensatory), which is highly dependent on the number and distribution of meristems remaining in the plants (Stowe et al., 2000).

From the simulated herbivory, the spring folivory may frequently result in undercompensation of the tree consumed (decreasing tree fitness), at least in terms of the increment in tree height and shoot number (Table 3). Besides, although in some limited cases, the phenological delay caused by folivory could result in the death of tree species, let alone pioneer species (Table 2), vulnerable to resource competition, especially over the photoenvironment at an early stage (Turner, 2001). In addition, in the simulated bark/bud herbivory, we confirmed undercompensation, especially DBH increment. It should be noted, however, that overcompensation (increasing plant fitness) was occasionally observed in the simulated bark/bud herbivory (Table 3), and the mortality was still lower than that in the simulated folivory (Table 2). These intriguing results may be explained by two rationales. First, recovery from phenological delay could be relatively easily attained because bark/bud herbivory occurs in plant-dormant seasons; sufficient supporting evidence for this claim based on plant physiology is available, especially for various horticultural crops, such as dormant pruning (Kozłowski et al., 2012). Second, the lateral meristem in the cambium near the tree's trunk base remains unbruised because of sufficient snow protection against natural herbivory, possibly facilitating the reallocation of stored resources, similar to the well-known example of *Morus bombycis* (Enari & Sakamaki, 2010).

4.2 Exploring tree assemblage consequences caused by herbivory

Along with the spatiotemporal pattern and intensity of herbivory (Hulme, 1996), plant tolerance following herbivory influences succession patterns and plant–herbivore mutualism, resulting in the establishment of plant community structures (Edwards, 2009; Kohyani et al., 2009; Mariotte et al., 2013; Stowe et al., 2000). Similar to predator–prey interactions, the tolerance of food trees (prey) can be fed back to the population dynamics of consumers (predators) (Fornoni, 2011). This means that maintaining the state of dynamic equilibrium observed in tree–herbivore interactions is important for retaining the fitness of herbivores as well as trees. This importance might be increasing in ecosystems with strictly restricted alternative food resources for herbivores, such as in cool-temperate forests, which frequently witness severe energy deficits for macaques during winter (Enari, 2014; Nakagawa et al., 1996).

The current multi-year monitoring of natural herbivory demonstrated that, whereas bark/bud herbivory rarely reduced the diversity and biomass of tree assemblages, the succession pattern of tree assemblages was altered, resulting in increasing the availability of food trees preferred by macaques (Table 5). These important findings could be attributed to the following three justifications stemming from the behavioral plasticity of macaques. The first is the food habits inherent in macaques. Our nearly decade-long observations clearly demonstrated that macaques are typical euryphagous during winter (see also Enari & Sakamaki-Enari, 2013a; Sakamaki et al., 2011), also consuming a sufficient amount of pioneer species with competitive advantage (Table S2). These facts could outweigh the destructive effects of herbivory on tree species diversity.

The second justification is the ecological role of macaques. Despite the physical

protection provided by accumulated snow against herbivory (see section 4.1), herbivory created forest gaps through the small-scale killing and wide-scale weakening of tree architecture, resulting in increased tree abundance (Table 5). In high-latitude forests, originally with limited tree species diversity, the increase in tree abundance resulted in shifting the tree species composition by increasing pioneer species, rather than just enhancing tree species richness (Table 5). The shift in such succession patterns could also be due to the fact that most of the pioneer species bear fleshy fruits, of which macaques serve as efficient seed dispersers. In fact, macaques potentially contribute to seed dispersal for half of all the tree species consumed during winter (Table S2; Enari & Sakamaki-Enari, 2014; Tsuji et al., 2011).

The third justification is the spatiotemporally non-uniform pressure of macaque herbivory. In snowy seasons, the optimal food patches where macaques were selected were not necessarily abundant in preferred food trees (Table 4). During seasons with colder ambient temperatures, macaques require more time resting to offset thermoregulatory costs (Hanya et al., 2007). Consequently, the time spent feeding by macaques is considerably constrained, accounting for approximately 25% of the total activity budget during snowy days (Wada & Tokida, 1981), far below the winter average of the species at 40% (Tsuji, 2010). Under such severe winter environments, the accessibility of food trees is often prioritized over their potential preferences. This theory has been confirmed by observations, i.e., the risk-averse foraging behaviors by switching food selections, including habitat use, to minimize the influence of yearly fluctuating snow conditions (Enari & Sakamaki-Enari, 2013a). This could benefit the trees consumed by decreasing the likelihood of repeated annual herbivory, which leads to unfavorable consequences, such as ring-barking or girdling, which altogether stop nutrient cycling in plants (Salisbury & Ross, 2002).

The above three justifications for the positive feedback effects of macaque herbivory on their food abundance are consistent with the well-known mechanism that promotes the coexistence of plant species introduced by Hulme (1996). However, it is clear that macaques in cool-temperate forests are unable to instigate disturbance effects that are large enough to alter the existing succession pattern within a short period, as with cervids. Thus, we will only be able to confirm the ecological role of macaques as an allogenic ecosystem engineer if the macaque–tree interactions characterized by risk-averse macaque behaviors to thrive under heavy snow conditions are retained for long periods.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Availability of data and material

The dataset used during the current study is available from the corresponding author upon reasonable request.

Authors' contributions

HE and HSE contributed equally to all aspects of this research, from designing the study to analyzing the results. HE wrote the manuscript, and HSE checked and revised the

436 manuscript.

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Table 1 Tree species used to assess the impacts of herbivory by Japanese macaques in cool-temperate forests, northern Japan

Family	Species	Succession property	Shade-tolerance	<i>n</i> for each treatment			Tree height (m) ^a	DBH (cm) ^{a,b}
				Defoliation	Bark/bud removal	Control		
Fagaceae	<i>Fagus crenata</i>	climax	tolerant	8	—	8	1.8±0.1	0.7±0.1
Magnoliaceae	<i>Magnolia obovata</i>	climax	tolerant	—	11 ^c	10	2.8±0.3	2.3±0.3
Rosaceae	<i>Prunus grayana</i>	intermediate	tolerant	7	—	8	2.0±0.1	0.8±0.1
Cornaceae	<i>Cornus controversa</i>	intermediate	tolerant	8	—	8	1.6±0.1	0.5±0.1
Oleaceae	<i>Fraxinus sieboldiana</i>	intermediate	intermediate	8	10	8	1.8±0.1	1.2±0.2
Moraceae	<i>Morus bombycis</i>	pioneer	tolerant	8	10	10	2.2±0.1	1.7±0.4
Araliaceae	<i>Chengiopanax sciadophylloides</i>	pioneer	intolerant	8	10	8	2.1±0.2	1.9±0.4
Araliaceae	<i>Kalopanax pictus</i>	pioneer	intolerant	10	—	9	1.6±0.1	0.9±0.1
Araliaceae	<i>Aralia elata</i>	pioneer	intolerant	9	11	9	2.3±0.2	2.8±0.5

^a The values show the mean and standard error for the trees monitored at the beginning of the experiment

^b Diameter at breast height

^c We picked only buds

Table 2 Mortality (%) of tree species preferred by Japanese macaques under three different treatments. Values in parentheses show effect size (Cohen's *h*) against the control

Species	Treatments ^a		
	Defoliation	Bark/bud removal	Control
<i>Fagus crenata</i>	12.5 (0.7)	–	0.0
<i>Magnolia obovata</i>	–	18.2 (0.0)	20.0
<i>Prunus grayana</i>	16.7 (0.8)	–	0.0
<i>Cornus controversa</i>	12.5 (0.7)	–	0.0
<i>Fraxinus sieboldiana</i>	0.0 (0.0)	0.0 (0.0)	0.0
<i>Morus bombycis</i>	12.5 (0.7)	0.0 (0.0)	0.0
<i>Chengiopanax sciadophylloides</i>	0.0 (0.0)	10.0 (0.6)	0.0
<i>Kalopanax pictus</i>	10.0 (0.6)	–	0.0
<i>Aralia elata</i>	88.9 ^b (1.2)	27.3 (0.1)	33.3

^a Sample size of each treatment is shown in Table 1

^b $p < 0.05$ based on significant tests for the population proportion against the control

Table 3 Coefficients and 95% confidence intervals of explanatory variables in generalized linear models to estimate the increment in DBH (Model_(DBH)), tree height (Model_(height)), and shoot number (Model_(shoot)) of tree species preferred by Japanese macaques under three different treatments

Explanatory variables	Model _(DBH) : <i>Magnolia obovata</i>		Model _(DBH) : <i>Fraxinus sieboldiana</i>		Model _(DBH) : <i>Morus bombycis</i>		Model _(DBH) : <i>Chengiopanax sciadophylloides</i>		Model _(DBH) : <i>Kalopanax pictus</i>	
	Coefficients	Δ AIC ^a	Coefficients	Δ AIC	Coefficients	Δ AIC	Coefficients	Δ AIC	Coefficients	Δ AIC
Treatments		0.14		−11.04		−9.50		−2.55		1.87
Defoliation	NA		0.10 (0.04–0.27)		0.01 (0.00–0.18)		0.12 (0.03–0.43)		0.13 (0.03–0.55)	
Bark/bud removals	0.37 (0.10–1.48)		0.22 (0.05–1.07)		0.01 (0.00–0.29)		0.08 (0.01–0.53)		NA	
Control	1.38 (0.61–3.11)		0.15 (0.06–0.39)		0.03 (0.00–0.52)		0.13 (0.03–0.48)		0.21 (0.04–1.19)	
Canopy openness	0.96 (0.91–1.02)	1.27	1.00 (0.93–1.07)	2.00	1.22 (0.99–1.50)	−2.84	1.04 (0.95–1.15)	1.44	1.02 (0.92–1.15)	1.97
AIC	35.52		0.34		30.28		13.08		−0.12	
%DE ^b	41.79		67.02		73.42		50.21		30.81	

Explanatory variables	Model _(height) : <i>Prunus grayana</i>		Model _(height) : <i>Fraxinus sieboldiana</i>		Model _(height) : <i>Aralia elata</i>		Model _(shoot) : <i>Prunus grayana</i>		Model _(shoot) : <i>Kalopanax pictus</i>	
	Coefficients	Δ AIC	Coefficients	Δ AIC	Coefficients	Δ AIC	Coefficients	Δ AIC	Coefficients	Δ AIC
Treatment		−4.67		−25.41		−13.95		−4.02		−14.46
Defoliation	0.34 (0.16–0.75)		0.12 (0.05–0.27)		0.18 (0.08–0.43)		−206.54 (−391.44–21.64)		−3.62 (−18.63–11.40)	
Bark/bud removal	NA		0.22 (0.06–0.90)		0.60 (0.27–1.38)		NA		NA	
Control	0.47 (0.22–1.07)		0.17 (0.07–0.38)		0.41 (0.25–0.67)		−119.73 (−313.26–73.79)		9.50 (−6.86–25.85)	
Canopy openness	0.95 (0.90–1.01)	−0.82	1.00 (0.94–1.07)	1.99	0.98 (0.95–1.01)	−0.52	7.69 (−6.75–22.13)	0.65	−0.80 (−1.89–0.28)	−0.37
AIC	−8.79		−7.80		9.42		151.94		115.67	
%DE	95.49		86.08		91.66		59.88		82.62	

^a AIC_(model built with all variables) − AIC_(model built with all variables excluding the variable concerned)

^b Percentage of deviance explained

Table 4 Factors influencing the frequency of bark/bud herbivory by Japanese macaques in cool-temperate forests, northern Japan, estimated by a generalized linear mixed model

Explanatory variables (data type) ^a	Coefficients (95% CI) ^b		Δ AIC ^c
Summation of Manly's α (continuous) ^d	1.16	(0.99–1.35)	–1.61
Elevation (continuous)	0.68	(0.55–0.85)	–10.11
Canopy openness (continuous)	0.92	(0.77–1.10)	1.15
Slope (continuous)	1.09	(0.92–1.27)	1.00
Forest types (categorical) ^e			–26.71
Old deciduous broadleaf forests	648.85	(327.01–1286.91)	
Old deciduous coniferous forests	1077.28	(639.06–1826.21)	
Old evergreen coniferous forests	758.27	(502.70–1152.86)	
Young deciduous broadleaf forests	1156.53	(720.54–1863.11)	
Young evergreen coniferous forests	1387.31	(880.07–2186.37)	
AIC		807.91	
Percentage of deviance explained		5.91	

^a We standardized the value in variables with continuous data type

^b CI = confidence interval

^c $AIC_{(\text{model built with all variables})} - AIC_{(\text{model built with all variables excluding the variable concerned})}$

^d This is an index showing the availability of preferred food trees with a height of 2 m, which are accessible resources for macaques even under deep snow cover conditions

^e To calculate the coefficients and 95% CI of all forest types, the current model was developed without an intercept

Table 5 Coefficients of explanatory variables in generalized linear mixed models describing the long-term influence of bark/bud herbivory by Japanese macaques on tree assemblages in cool-temperate forests, northern Japan

Explanatory variables (data type) ^a	<u>Model 1: Species richness</u>			<u>Model 2: Tree abundance</u>			<u>Model 3: Summation of Manly's α</u>		
	Coefficients (95% CI ^b)		Δ AIC ^c	Coefficients (95% CI)		Δ AIC	Coefficients (95% CI)		Δ AIC
Herbivory pressure (continuous)	1.07	(0.95–1.21)	0.63	1.37	(1.29–1.45)	–111.79	1.47	(1.08–2.00)	–4.03
Canopy openness (continuous)	0.84	(0.77–0.91)	–14.7	0.95	(0.91–1.00)	–2.59	0.89	(0.69–1.16)	1.31
Elevation (continuous)	1.17	(1.04–1.32)	–5.71	1.59	(1.47–1.72)	–137.85	1.17	(0.85–1.60)	1.14
Slope (continuous)	0.97	(0.89–1.05)	1.38	1.04	(0.99–1.09)	–0.88	0.72	(0.55–0.94)	–3.11
Forest types (categorical) ^d			–47.65			–328.14			–2.49
Old deciduous broadleaf forests	14.40	(11.30–18.30)		55.70	(36.97–83.93)		1.98	(0.98–4.00)	
Old deciduous coniferous forests	11.50	(9.11–14.60)		63.43	(43.82–92.76)		0.93	(0.47–1.81)	
Old evergreen coniferous forests	16.70	(14.30–19.50)		93.69	(65.37–135.64)		1.38	(0.87–2.20)	
Young deciduous broadleaf forests	15.70	(13.00–19.00)		62.80	(43.38–90.92)		0.77	(0.42–1.42)	
Young evergreen coniferous forests	9.16	(7.28–11.50)		30.88	(21.33–45.15)		0.31	(0.17–0.57)	
AIC	301.93			958.42			116.90		
Percentage of deviance explained	24.30			36.42			11.18		

^a We standardized the value in variables with continuous data type

^b CI = confidence interval

^c $AIC_{\text{(model built with all variables)}} - AIC_{\text{(model built with all variables excluding the variable concerned)}}$

^d To calculate the coefficients and 95% CI of all forest types, the current models were developed without an intercept