

Two-decade changes in habitat and abundance of Japanese macaques in
primary and logged forests in Yakushima: Interim report

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Abstract Continuous, rather than discrete, data on animal population are ideal for identifying the causal relationships driving population fluctuations. In this study, we reveal the effect of forest regeneration after logging on the habitat, food availability, and abundance of Japanese macaques over two decades, spanning the period from 2000 until 2019, based on a continuous population census conducted every year. Three vegetation types, covering an area of 7.5 km², make up our study sites: primary forests, forests logged from 1984 until 1995 and then naturally regenerated (natural regeneration), and forests logged from 1975 until 1983 and then planted with cedars (plantation). In natural regeneration, both individual and total tree biomass increased, in particular naturally grown cedars. In plantation, the number of trees decreased and the total biomass did not change, mainly due to thinning (partial removal of planted cedars to harvest timber) in 2015. A state space model suggests that the relative fruit production in natural regeneration to that in the primary forest tended to be low after 2012, a condition brought about by cleaning cutting to remove non-cedar broad-leaved trees and shrubs in natural regeneration. An analysis of aerial photos detected an increase in naturally grown cedar patches in natural regeneration between 2009 and 2014. We also observed a population decrease of Japanese macaques in natural regeneration but not in primary and plantation forests. The state space model indicates that this decrease occurred in the first half of the study period, which was earlier than the replacement of cedar patches in natural regeneration. The high time resolution of our data refutes the simple scenario that macaques decreased their number in natural regeneration due to the reduced food availability there. The less frequent use of natural regeneration began as a stochastic event; i.e., the disappearance of multiple individuals from

a group ranging there, and then the subsequent changes in the habitat reinforced this tendency.

Keywords: aerial photography; *Cryptomeria japonica*; expansive afforestation; logging; *Macaca fuscata*; state space model

1. Introduction

Many wildlife species are now facing the risk of extinction due to various anthropogenic reasons, among which destruction of habitat is one of the most significant (Estrada *et al.*, 2017). On a global scale, 4.1% of the forest land was lost during the period of 1990-2020 (<https://fra-data.fao.org/WO/fra2020/home/>, data accessed in January 2023), and many of the remaining forests have deteriorated as habitat of wild animals due to fragmentation and damage to the remaining trees and soils during selective logging (Johns and Skorupa, 1987). Plantation of exotic and/or indigenous tree species is often performed after logging, which forms simple forests composed of one or a few species (Fashing *et al.*, 2012). The effects of logging have largely been examined by comparisons of animal abundance, behaviors, and food availability between logged and intact forests (Rode *et al.*, 2006; Bernard *et al.*, 2016) or between forest conditions before and after logging (Johns, 1986; Guo *et al.*, 2008). Even though these short-term studies can reveal important changes in primate behavioral ecology, long-term studies on the effects of logging are also necessary because logged forests are regenerated afterwards. Long-term research is thus necessary, in particular for clarifying the effects on long-lived animals, such as primates.

Very few studies have investigated the effects of logging and subsequent regeneration on the abundance of large animals that cover a longer

period than the lifespan of the subject species. Studies on a primate community in Kibale National Park, Uganda, offer such rare data (Chapman *et al.*, 2010; Chapman *et al.*, 2018). In Kanyawara, Kibale, logging was carried out at light and heavy intensities in different compartments in the 1960s, and the fluctuations in the abundance of five diurnal primates and their food availability up to the 2010s were studied by repeatedly conducted primate censuses and vegetation surveys. The patterns of population dynamics varied among the species, and each pattern could be explained by the changes in the habitat as a result of forest regeneration. In another long-term study site, on Barro Colorado Island, Panama, two particular pioneer fig species decreased their abundance after about a century after the clearing of their habitat, which caused a decrease in the abundance of howler monkeys (Milton *et al.*, 2019). However, not all population fluctuations have a correlation with the changes in food availability. This might be because animal populations can fluctuate over a long term due to reasons other than forest regeneration, such as disease, predation, or climate change (Altmann *et al.*, 1985; Rudran and Fernandez-Duque, 2003; Lwanga *et al.*, 2011; Bush *et al.*, 2020).

Most of the data on animal population and forest regeneration have been collected by combining the results of multiple surveys conducted intermittently over a long term. Data on population changes based on censuses conducted at regular intervals are usually available only for small isolated populations (Rudran and Fernandez-Duque, 2003) or for a particular group but not the whole population (Nishida *et al.*, 2003). If the interval between censuses is short enough relative to the reproduction of the animal species, the advantage of such data is improved time resolution, which permits detailed analyses of the

potential causes of these changes. One such example is a study on the migration of orangutans, which is a response to the mast fruiting that occurs at unpredictable and multi-year intervals (Kanamori *et al.*, 2017). Data with a high temporal resolution would be useful even for examining gradual changes, such as forest regeneration after logging. For example, in order to detect long-term trends in fruit production, continuous data are much better than intermittent data (Bush *et al.*, 2020) because fruit production per se fluctuates each year as a natural phenomenon (Noma, 1997).

Japan has one of the highest rates of forest cover in the world (68.4% in 2020; <https://data.worldbank.org/indicator/AG.LND.FRST.ZS>, accessed in January 2023), and it is home to many species of wildlife, including Japanese macaques (*Macaca fuscata*), the northernmost-living non-human primate. Expansive afforestation, clear-cutting of broad-leaved trees and subsequent plantation of conifers (Japanese cedar *Cryptomeria japonica* and hinoki cypress *Chamaecyparis obtuse*), progressed throughout Japan in the 1960s and 1970s. As a result, conifer plantations constitute 41% of the forest in Japan (<https://www.rinya.maff.go.jp/j/keikaku/genkyou/h29/>, accessed in January 2023). Because undergrowth is cleared before planting conifer saplings of ca 60 cm, many of the plantations are composed mostly of conifers. These conifers do not provide edible fruits for animals, so food availability for frugivorous animals, such as macaques, is lower than in broad-leaved forests (Hanya *et al.*, 2005). Therefore, the management of these conifer plantations is a serious conservation issue for forest-dwelling animals (Sakamaki *et al.*, 2011; Chijiwa and Nishimura, 2021). Crop raiding by wildlife, such as macaques, bears, deer, and wild boars has rapidly increased in Japan since the 1980s, which is

151 suspected of being related to the expansive afforestation that took place 10-20
152 years before (Agetsuma, 2007).

153 Our study site, Yakushima, is home to the southernmost distribution of
154 Japanese macaques and native Japanese cedar. It is a well-known region for
155 the production of timbers from large, thousands-year-old cedars (Agetsuma,
156 2007). Large-scale logging of primary forests and plantation of cedars were
157 conducted in the 1960s and 1970s (Agetsuma, 2007). In the late 1980s, when
158 forestry began to shrink as an industry in Japan, the Forestry Agency, the
159 governmental body managing national forests, started a new regeneration
160 system. In the system, they did not plant cedar saplings after clear-cutting and
161 tried to regenerate cedars naturally. We conducted a survey of the Japanese
162 macaque population and forest composition in 2000-2003 in primary, naturally
163 regenerated, and cedar plantation forests in the basin of the upper Segire River,
164 which is the last place where a primary forest was logged in Yakushima (Hanya
165 *et al.*, 2005). According to this cross-sectional study, both the abundance of
166 macaques and fruit availability were the largest in the 7-18 yr. naturally
167 regenerated forest, intermediate in the primary forest, and the lowest in the
168 19-27 yr. plantations. In this study, we report the subsequent longitudinal
169 changes in the same study site.

170 The purpose of this study is to reveal the effects of forest regeneration
171 after logging on the habitat, food availability, and abundance of Japanese
172 macaques over two decades, spanning a period from 2000 until 2019. First, as
173 background information on the population dynamics of macaques, we describe
174 the changes in forest composition at the beginning and end of the study period
175 based on the vegetation survey in naturally regenerated and plantation forests.

Second, we show the data on fruit production collected continuously in the primary and naturally regenerated forests to examine the long-term trends in fruit availability during forest regeneration. Third, we examine the changes in the area covered with cedar patches by aerial photos taken four times (every five years) during the study period. Despite the fact that neither new plantation nor clear-cutting of planted cedars took place during the study period, we observed that naturally grown (non-planted) cedar saplings grew and replaced the broad-leaved trees in logged areas. Finally, we analyze the continuous population changes of Japanese macaques based on the data of a census conducted every year. Using these data, we summarize the changes in the forest during regeneration for 20 years and discuss how they affected the population fluctuations of Japanese macaques. We also discuss the implications of our findings regarding population monitoring and forest management for the conservation of Japanese macaques.

2. Materials and Methods

2.1. Study site

Yakushima is in the south of Japan (30°N, 131°E), with its highest peak at 1,936 m above sea level. Our study site is a 7.5 km² area in the basin of the upper Segire River in the western part of Yakushima, at an altitude of 800-1,300 m. Part of the study site, mostly north of the Segire River, is the Yakushima National Park, where there has been no mechanical logging (referred to as primary forest). This is a mixed forest of conifers (*Cryptomeria japonica*, *Abies firma*, and *Tsuga sieboldii*) and warm-temperate evergreen broad-leaved trees (e.g., *Quercus acuta*, *Q. salicina*, and *Distylium racemosum*). Evergreen shrubs,

mainly *Symplocos myrtacea* and *Eurya japonica*, are very abundant in the undergrowth and provide food-fruit for macaques (Hanya, 2004). Outside of the national park, logged and non-logged compartments are mixed in a mosaic manner along a logging road (Fig. 1). The forest close to the entrance of the logging road, in the western part of the logged area (referred to as plantation), was logged and cedars were planted there from 1975 until 1983. After clear-cutting, the felling area was cleared, and 1,000–2,000 cedar saplings of about 60 cm tall were planted per hectare. Cleaning cutting (including the removal of broad-leaved shrubs) was conducted once a year a few years after logging. Thinning was conducted for a few months in 2015 in most of the plantation forest in this area, and timber was harvested from the planted cedars. The forest near the end of the logging road, in the eastern part of the logged area (referred to as natural regeneration), was logged from 1984 until 1995. Cedars were not planted, and the clear-cut forests were left to regenerate naturally. Cleaning cutting of broad-leaved shrubs was conducted for some of the naturally regenerated forest at most once during the study period to enhance the growth of naturally grown cedar saplings.

2.2. Vegetation survey in the logged forests

We set 27 5 m*5 m vegetation plots in the naturally regenerated and plantation forests in September 2002 (N=17 for natural regeneration, N=10 for plantation). We allocated the number of plots so that we could cover different forest ages equally. We positioned each plot at the approximate center of gravity of logged patches (Hanya et al., 2005). We recorded the species and diameter at breast height (DBH) of all trees taller than 1 m. We surveyed the vegetation of these

plots again in August 2019, except for one plot in the natural regeneration, which was lost in the second survey and not included in the analysis. We examined the temporal changes of the four vegetation parameters (total basal area, number of trees, number of species, per-capita basal area) by a paired t-test.

2.3. Fruit production in the primary and naturally regenerated forests

We set a 50 m*50 m vegetation plot in the primary forest (within L14 in Fig. 1) in September 1999 and monitored fruit production in this plot every year since then. We identified, marked, and measured the DBH for all trees >5 cm DBH; in 10% of the vegetation plot, we measured all trees >1 m tall. We chose the figure of 10% as a compromise between the time required to check all dense undergrowth vegetation and the precision needed to estimate fruit availability. We counted the number of fleshy fruits in all of the marked trees on one day in September every year (1999-2019). Hanya *et al.* (2005) described the details of the method as well as the reason why we monitor fruits in this season and how the data can be regarded as annual fruit production. In the naturally regenerated forests, we used the above-mentioned 5 m*5 m plots to estimate the fruit production there. The individual logged patches were too small for us to make a single large plot, as we did in the primary forest. In addition, the difficulty of making a large plot was also increased by the vegetation's very high density (e.g. >150 trees/5 m*5 m). Even though we did not mark trees in these plots, we counted the number of fleshy fruits in all of the trees in August 2002, 2003, 2006-2019. Even though fleshy fruits were available in one plantation plot in the first year, the fruiting tree was removed by cleaning cutting in the next year. Therefore, we regard the fleshy fruit production in the plantation plots as nil. In

two plots in the natural regeneration, all of the fruiting species were removed by cleaning cutting in 2010. We evaluated the fruit production as the fresh weight of the fleshy parts per unit area. Because the purpose of showing these data is to reveal yearly changes in fruit production in each habitat, a key assumption made here is that there is no temporal variation in the mass of fleshy parts. Only a few species constitute fruit production in this forest (Hanya *et al.*, 2005), and as far as these species are concerned, there seemed to be no such change during the study period, even though we did not collect quantitative data on this.

We analyzed the time-series data on fruit production in natural regeneration using state space models. A state space model is a widely used modeling framework for analyzing ecological time-series data (Auger-Méthé *et al.*, 2021). To represent the process through which the observed time-series data were generated, the state-space models consisted of two stochastic models: (1) a system model, representing changes in latent states over time that were not directly observable, and (2) an observation model, representing how the observed data were obtained from latent states through randomness in the sampling or a surveying process. By explicitly modeling temporal autocorrelation and differentiating variations in latent states from observation error, state space models allow inferences regarding changes in latent states over time, known as trend components. Based on the models using a second-order difference trend component (Matsuura, 2023), we estimated the trend of fruit production for each year and calculated the parameters representing the differences between the trend of a given year and that of the subsequent year (see Supplementary material for details on the statistical models). We then identified the years when significant increases or decreases occurred by examining the 95% credible

intervals of the parameters: If the 95% credible interval does not include zero, it can be inferred that there is a significant effect, as seen in classical statistical hypothesis testing. We conducted this analysis both for gross fruit production in the natural regeneration and its value relative to that of the primary forest in the corresponding year. Assuming there is no decreasing or increasing trend in the fruit production in the primary forest, we tried to detect any temporal change in the relative fruit production in the natural regeneration when compared with the primary forest. In addition to the state space model, we tested the difference in relative fruit production in the natural regeneration between the averages of the first two (2002-2003) and the last three (2017-2019) years by a paired t-test (paired by the plots) to detect the overall changes during the two decades.

2.4. Aerial photography

We purchased aerial photos of our study site taken in 2004, 2009, 2014 and 2019 from the collection of the Forestry Agency of Japan (https://www.rinya.maff.go.jp/j/kokuyu_rinya/kutyu_syasin/). The photos of 2009, 2014 and 2019 were provided as an orthophoto. This was not the case for the one in 2004, so we georeferenced it manually. Patches of cedars were visible and could be distinguished from broad-leaved forests by their dark color and uniform crown shape. The minimum discernable patches were ca 3 m in width. We digitized those patches on QGIS 3.28.1 (©Creative Commons). Even though cedars also exist in the primary or other unlogged forests, they do not form a patch and are mixed with broad-leaved trees at the level of tree individuals, and thus they are difficult to distinguish. Therefore, we neglected these single-grown cedars. We calculated the areas of the cedar patches at around 200 m from the

census points of the macaques (below) using QGIS. We use 200 m as a criterion because it is the range that observers can detect macaque groups from the census points (Hanya *et al.*, 2003).

2.5. Census of Japanese macaques

We conducted a census of Japanese macaques in August 2000-2019, and it lasted 15-25 days each year. Our method was point census with group follows (Hanya *et al.*, 2003). We divided the 7.5 km² census area into 30 500 m*500 m quadrats and positioned one observer in each quadrat at a fixed point. If we define the vegetation type as that occupying the largest area within 200 m from the point, the numbers of census points were 12 for the primary forests, 8 for the natural regeneration (but only six in 2000), and 10 for the plantation forests. The observers stayed at the point for one day (6-10 hours) and recorded all of the vocalizations or direct detections of macaques. We surveyed about half of the census area on a same day. We repeated these point observation 3-7 times for each point for each year. In addition to these point observers, some of the census members tracked macaque groups that they encountered in the census area and recorded the location every 30 minutes. The group trackers recorded the composition of the group whenever possible.

We counted the number of groups detected within each hour (6:00-6:59, 7:00-7:59, etc.) at each point. We assumed that a group was detected only when a point observer saw any adult female or juvenile or heard vocalizations of multiple individuals of macaques. The number of groups detected each hour was averaged for each day, and then the day's average value was averaged for all of the census days of the year for each point. We refer to this value, *n*, as the

number of groups detected at the point. If the duration of point observation was less than 6 hours in the day, we discarded the data of that day for the point. By combining the location data of the tracked macaque groups and the detection of the group by the point observers, we calculated the proportion of groups detected by point observers (detectability) at a given distance. We regressed the relationship between point-group distance y and detectability $g(y)$ on a half-normal model: $g(y) = e^{-\lambda y^2}$ (Buckland *et al.*, 1993) and calculated λ as the ‘detectability constant.’ Then, group density D was calculated as $D = \frac{\lambda n}{\pi}$ (Hanya *et al.*, 2003). Since detectability may vary among different vegetations and among different periods, we separated the data into three groups by the vegetation (primary, natural regeneration, and plantation) and into four groups by period (2000-2004, 2005-2009, 2010-2014, and 2015-2019) and then calculated detectability separately for the 12 conditions. We calculated population density as the product of group density and the mean group size counted in the year for the vegetation type. However, because males tend to range alone or stay in the periphery of the group spread (Otani *et al.*, 2013; Otani *et al.*, 2014), it may be difficult to count all of the individuals in a group. Therefore, we also calculated the population density of adult females in a group, which occupy the central position in a group (Nishikawa *et al.*, 2014), as the product of group density and the average number of adult females in a group in the vegetation type (referred to as female density).

Using a state space model, we analyzed the time-series fluctuations of group, population, and female densities for each of the primary, naturally regenerated, and plantation forests. We estimated a trend component for each

year and identified the years when significant increases or decreases in the abundance of macaques took place compared to the subsequent year. We ran a similar model to that for fruit production. See the Supplementary material for details on the statistical models. As well as fruit production, we tested the difference in density indices between the averages of the first and the last three years by a paired t-test.

3. Results

3.1. Forest composition

Forest composition changed during the study period, and one notable change was the increase of cedars in natural regeneration (18% in 2002 to 43% in 2019 in the basal area). Comparing the results of the vegetation survey in 2002 and 2019, total tree biomass (total basal area) increased 4.9 times, and the average size of individual trees (per-capita basal area) increased 9.1 times in natural regeneration (Fig. 2). In plantations, the number of trees decreased and the total basal area did not change. Total basal area is composed mostly of cedars both in 2002 (94%) and 2019 (96%). Tree species diversity did not differ in either natural regeneration or plantation (Fig. 2d).

3.2. Fruit production

Relative fruit production in natural regeneration tended to be lower around the latter half of the study period compared with that in the primary forest. Gross fruit production fluctuated considerably by year in both primary (Fig. 3a) and naturally regenerated forests (Fig. 3b), and we observed both significant decreases and increases (Fig. 3b). However, relative fruit production significantly decreased

from 2011 to 2012 and then did not further recover. Compared to the relative fruit production in the first two years (2002-2003), that of the last three years (2017-2019) was significantly lower ($t = 5.31$, $p < 0.0001$). However, this tendency did not appear when we excluded the two plots where fruiting trees were removed by cleaning cutting ($t = 1.47$, $p = 0.15$).

3.3. Expansion of cedar patches

Analysis of aerial photos indicates that the area occupied by cedar patches increased in natural regeneration from 2009 (4.8%) to 2014 (19.0%) (Fig. 4). The proportion of cedar patches of natural regeneration reached as high as 56% of that of plantation in 2014, and 60% in 2019. The proportion of cedar patches in plantation did not fluctuate so much (31-33%; Fig. 4).

3.4. Abundance of Japanese macaques

All three measures (group density, population density, female density) indicated that the abundance of Japanese macaques decreased only in natural regeneration (Table 1). According to the state space models, a significant decrease of abundance in natural regeneration occurred from 2004 to 2008 for group density (Fig. 5), from 2004 to 2005 for population density (Fig. 6), and from 2002 to 2003 for female density (Fig. 7). We did not detect any significant increasing or decreasing drift in the primary and plantation forests.

4. Discussion

4.1. Change in habitat

Not surprisingly, in natural regeneration, both the size of individual trees and total

biomass increased while the number of tree individuals did not decrease. This suggests that self-thinning process has not started in which trees cover the canopies and suppress the growth and survival of each other (Yoda *et al.*, 1963). In plantation, the number of trees decreased, and this was likely to be due to the harvest of planted cedars by thinning in 2015. It is not known how much biomass was removed by the thinning, but the remaining biomass (total basal area) in 2002 and 2019 was almost the same.

Another conspicuous change during the two decades was the increase in naturally grown cedars in natural regeneration. An extensive survey using aerial photos indicated that the areas occupied by cedar patches increased from 5% in 2004 to 19% in 2014 and 2019. Even though cedar flowers are food for Japanese macaques (Hanya, 2004), other parts of the tree are not eaten. An increase of cedars is usually regarded as deterioration of the habitat, evidenced by the avoidance of cedar plantation observed in various populations of Japanese macaques (Furuichi *et al.*, 1982; Hanya *et al.*, 2005; Yamada and Muroyama, 2010; Sakamaki and Enari, 2012). The increase in cedar patches was partly due to cleaning cutting that removed broad-leaved trees, but we observed that cedars grew naturally and densely even without cleaning cutting, particularly near the logging road. The establishment of cedar seedlings is enhanced under good light conditions and on mineral soil without litter (Hirayama and Sakimoto, 2005). The area near the logging road is ideal for the establishment of cedars, where dirt from road construction was threw away. In fact, most of the bare lands, where provided edible herbs and shrubs for macaques (Hanya, 2004; Hanya *et al.*, 2005) in the aerial photos in 2004 and 2009, were replaced with cedar patches in 2014 and 2019. Aerial photos provide

information on crown conditions but not on undergrowth. The naturally grown cedar patches are still short (< 5m), and the undergrowth remains poor (Hanya et al., unpublished data), so we can assume that food availability there is low, as well as in cedar plantations. Interestingly, in northern Japan, undergrowth vegetation is rich in cedar plantation because the canopy is not closed due to the slow growth of the cedars given the area's low temperatures as well as damage by snowfall (Sakamaki et al., 2011). There seems a large difference in regeneration patterns following the logging over the habitat of Japanese macaques and the cedars.

The most important environmental determinant of the abundance of Japanese macaques is known to be fruit production in Yakushima (Hanya et al., 2004b). During the initial period of our long-term study, the reason that the abundance of macaques was highest in natural regeneration was that the fruit production was even larger there than in the primary forest (Hanya et al., 2005). Shrubs, mainly *Eurya japonica* and *Symplocos myrtacea*, provide food-fruit for macaques (Hanya, 2004), and their reproduction is enhanced when canopy trees are removed by logging (Hanya et al., 2005).

Fruit production was also varied over the past two decades. The ratio of fruit production in natural regeneration to that in the primary forest was lower in the last three years than in the initial two years. One reason for this decrease might be due to cleaning cutting conducted in 2010 when all of the fruiting shrubs in two plots in natural regeneration were removed. The periods of decrease in relative fruit production and the cleaning cutting did not match exactly, but this is understandable considering that the relative fruit production is affected by fruiting both in the primary and naturally regenerated forests.

Excluding these two plots, the relative fruit production in the first two (2002-2003) and the last three (2017-2019) years did not differ significantly. Therefore, relative fruit production may not have been reduced yet in naturally regenerated stands where broad-leaved shrubs have not been replaced with cedars. Fruit production may or may not start decreasing as trees continue to grow, the self-thinning process starts, and the number of trees begins to decrease.

4.2. Change in abundance of Japanese macaques

Analyses of the habitat indicated that the deterioration of the habitat's quality in natural regeneration, in terms of replacement of cedar patches, occurred in the earlier half of the 2010s. The abundance of Japanese macaques in natural regeneration was also apparent over the two decades, as evidenced by the lower abundance in the first three than in the last three years. However, the state space model indicated that a decrease occurred in 2008 or earlier in group density, and even earlier in other abundance measures (from 2004 to 2005 for population density and from 2002 to 2003 for female density). We did not detect any conspicuous change in the distribution of the identified groups, except one group fission that occurred in 2005 for a group whose home range was mostly plantation. The decrease was related to the sudden disappearances in 2003 of four out of seven adult females from the PE group, one of the two groups ranging in natural regeneration. During the census in 2003, we did not observe any change in its home range, and we did not detect any two groups simultaneously in the range of the PE group in 2000-2002. Therefore, we believe that those females happened to die at the same time. It may take several years for resident

males to emigrate from the group (Suzuki *et al.*, 1998), and it may also take several years for the group to accommodate themselves to their home range with their now smaller group size. Therefore, even though the decrease in female density occurred shortly in 2002-2003, the group may have changed their range use gradually, probably in the form of decreasing the use of natural regeneration. After the macaques began to use the natural regeneration less frequently than during the initial period, food availability in the natural regeneration decreased, and the tendency of the range use was maintained or reinforced by the change in the habitat.

The advantage of our current study is the availability of data on population changes having temporally high resolution. Thanks to this high resolution, we could dismiss a simple causal relationship of reduced food availability decreasing the abundance of the macaques. We suggest that a stochastic event, in which multiple individuals disappeared within a short period, triggered this population change. Here, the role of reduced food availability may have been to reinforce this change.

4.3. Conservation implications

Previous studies on the long-term changes in primate populations indicate that both stochastic and deterministic factors could drive population fluctuations. A series of studies on the primate community in Kibale is an example of a deterministic process of forest regeneration (Chapman *et al.*, 2010; Chapman *et al.*, 2018). A considerable (95%) decline in the population of baboons in Amboseli, Kenya, is another example of a deterministic scenario of population fluctuations, which was caused by rapid change in the habitat due to climate

change (Altmann *et al.*, 1985). A population of red howler monkeys increased
due to the regeneration of their habitat during the first half of the 30-year study
period but then declined as a result of disease (Rudran and Fernandez-Duque,
2003). It is difficult to generalize these findings, for example, in identifying the
most prevalent mechanism of primate population dynamics, since long-term data
are still sufficient. However, our study suggests one important aspect of the
mechanism: the synergetic effects of stochastic events and deterministic
processes. Sudden disappearances of many individuals, such as in the PE
group in 2003, can happen by various reasons, such as disease, predation and
severe climate (Hanya, 2009). In the lowland of Yakushima, we observed a
mass mortality caused possibly by epidemics in 1998-1999, killing all of the
individuals in two groups and 56% of individuals living in an area of 3 km²
(Hanya *et al.*, 2004a). After the mass mortality, neighboring groups migrated and
occupied the empty area in only 2-3 years, and the low-density state did not last
long (Hideki Sugiura *et al.*, unpublished data), which was different from the case
of the current study. Whether a sudden change triggered by stochastic events is
maintained over a long term may depend on food availability, which itself
changes over a long term.

 This study suggests the importance of continuous data in population
monitoring. To understand the environmental factors that make animal
populations fluctuate, continuous data are more valuable. Even if conducting
surveys every year is difficult, we recommend the collection of data at intervals
as short as possible.

 Our data indicate that natural regeneration is a cost-effective way to
regenerate cedars without planting cedar saplings, but at the same time, even

without plantation, food availability for macaques deteriorates, in particular when it is combined with cleaning cutting. In northern Japan, it has been pointed out that foods for macaques can grow in the undergrowth of plantation when light penetrates to the ground as a result of thinning (Sakamaki *et al.*, 2011). In the plantations of the current study site, we did not observe obvious changes in the land use and food availability of Japanese macaques. Our study on the longitudinal changes in the habitat and macaque population is still ongoing after 2019. Further monitoring is needed, for example, of changes in food availability in the undergrowth of plantation, changes in fruit production in natural regeneration by future self-thinning, and the corresponding population-level response by macaques to these future habitat changes.

In conclusion, during the study period spanning two decades, food availability decreased in natural regeneration along with the expansion of naturally grown cedar patches in the latter half of the study period. The abundance of Japanese macaques decreased in natural regeneration in the earlier half of the study period but not in the primary and plantation forests. Their less frequent use of natural regeneration than during the initial period started as a stochastic event, namely the disappearance of multiple individuals in a group ranging in the natural regeneration, and then the subsequent changes in the habitat reinforced this tendency.

Acknowledgements

This study would not have been possible without the hard work of the participants of the 'Yakuzaru-chosa-tai' (Yakushima Macaque Research Group),

who voluntarily joined the census in 2000-2019. We dedicate this paper to Masaru Otake, Masafumi Oshima, and Mii Tanaka, participants in the census who have passed away during the past two decades. We would like to thank the villagers in Onoaida, Kurio, Isso and Nagakubo for their help during our stay in Yakushima. The Yakushima Forest Ecosystem Conservation Center and Yakushima National Park approved our study.

Funding: This study was supported by the Cooperation Research Programs of the Primate Research Institute and Wildlife Research Center, Kyoto University.

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682

683

Figure Legends

Fig. 1. Vegetation and the distribution of points where we conducted census of Japanese macaque groups. Thick lines indicate the census area. Vegetation in areas north and east of the national park's border is primary forest. Modified from the Fig. 1 of Hanya et al. (2005).

Fig. 2. Changes in forest composition in natural regeneration and plantation between 2002 and 2019.

Fig. 3. (a) Fruit production in the primary forest, (b) in natural regeneration, and (c) ratio of fruit production in natural regeneration to primary forest. Arrows in (b) and (c) indicate significant decreases or increases detected by the state space model.

Fig. 4. Changes in the average proportion of cedar patches in the area 200 m from the macaque census points detected by aerial photos.

Fig. 5. Changes in group density in the (a) primary forest, (b) natural regeneration, and (c) plantation over the study period. Arrows indicate significant decreases detected by the state space model.

Fig. 6. Changes in population density in the (a) primary forest, (b) natural regeneration, and (c) plantation over the study period. Arrows indicate significant decreases detected by the state space model.

Fig. 7. Changes in female density in the (a) primary forest, (b) natural regeneration, and (c) plantation over the study period. Arrows indicate significant decreases detected by the state space model.

Supplementary material: Detailed protocol of state space model analyses for fruit production and the abundance of macaques

710

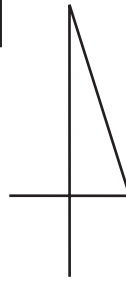
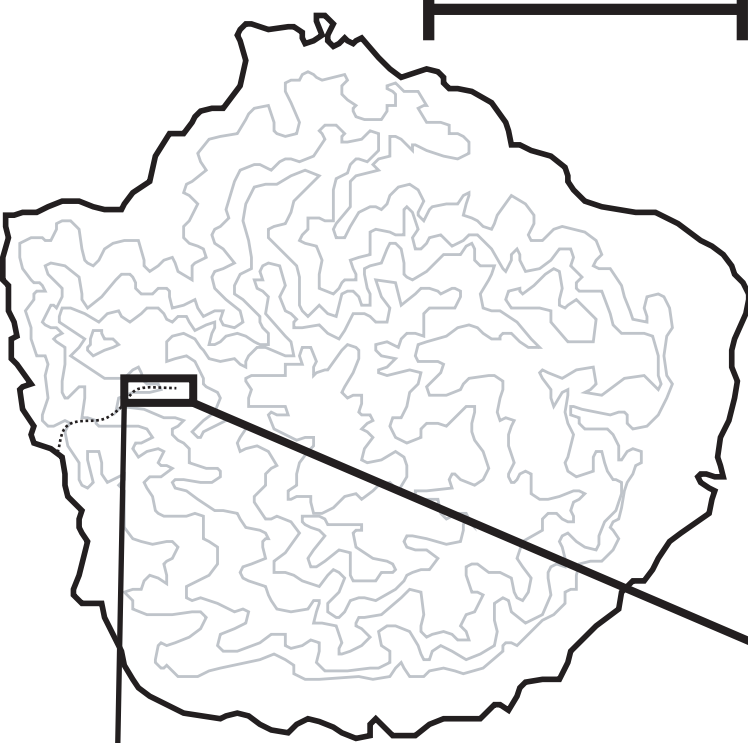
Table 1. Comparisons of abundance of Japanese macaques between the first (2000-2003) and the last (2017-2019) three years

Vegetation	Abundance measures	t	p
Primary	Group density	0.99	0.33
	Population density	1.56	0.13
	Female density	0.41	0.69
Natural regeneration	Group density	2.69	0.024
	Population density	2.83	0.020
	Female density	3.11	0.013
Plantation	Group density	0.25	0.81
	Population density	0.30	0.77
	Female density	0.04	0.97

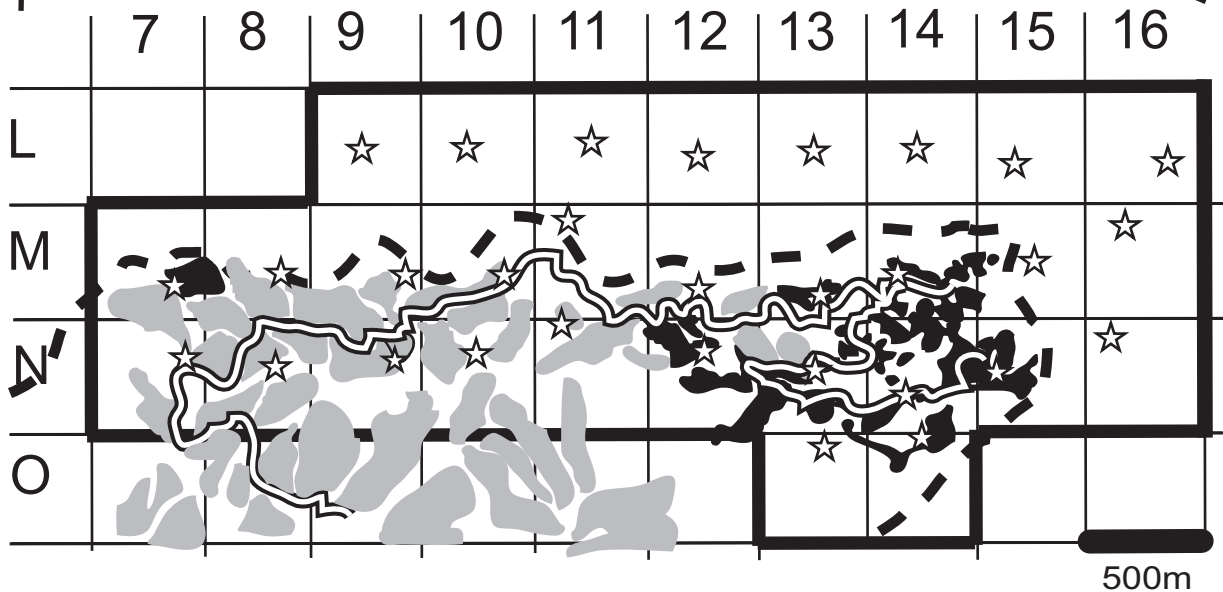
711

Yakushima

10km



..... Segire River



--- Border of the National Park

== Logging road

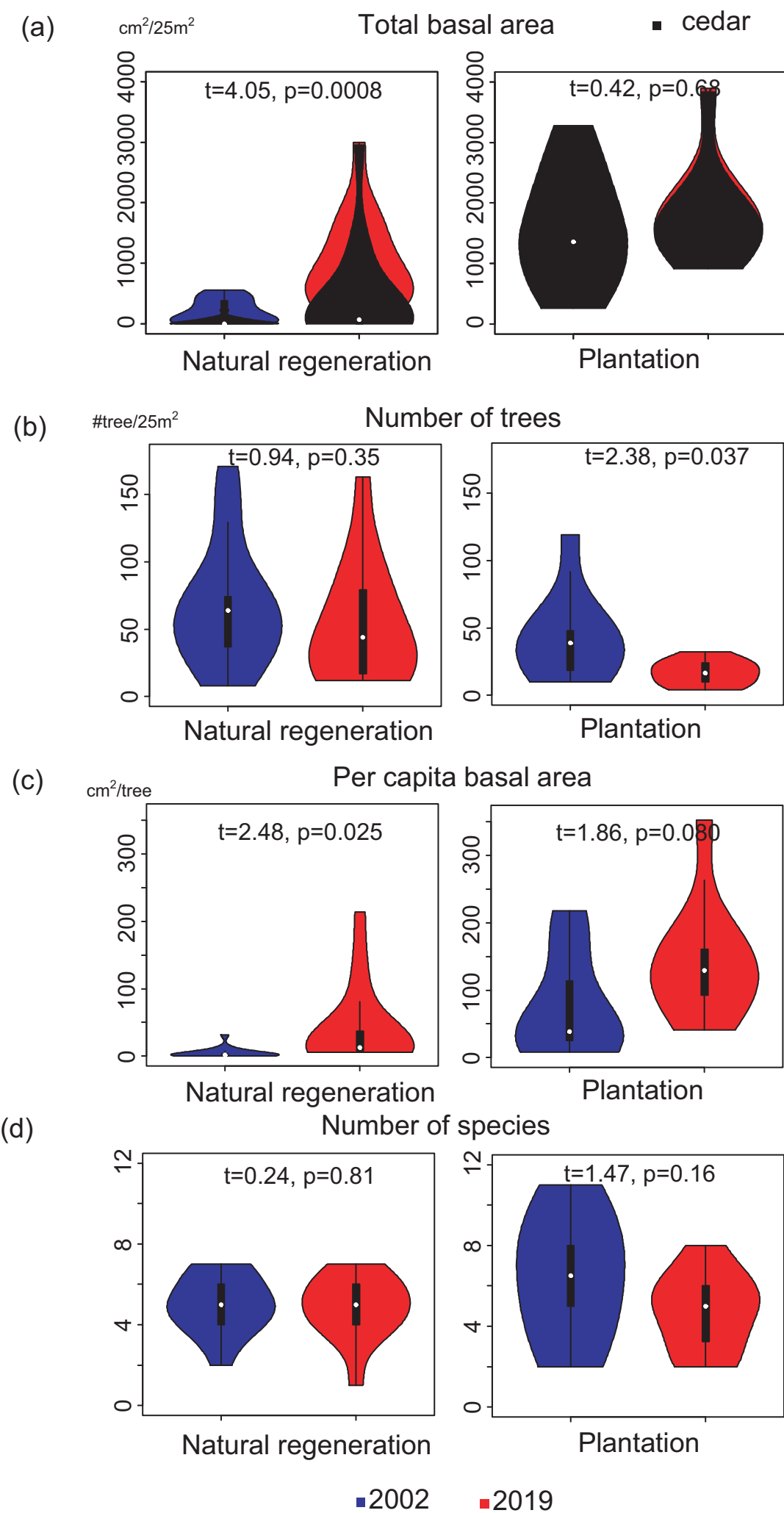
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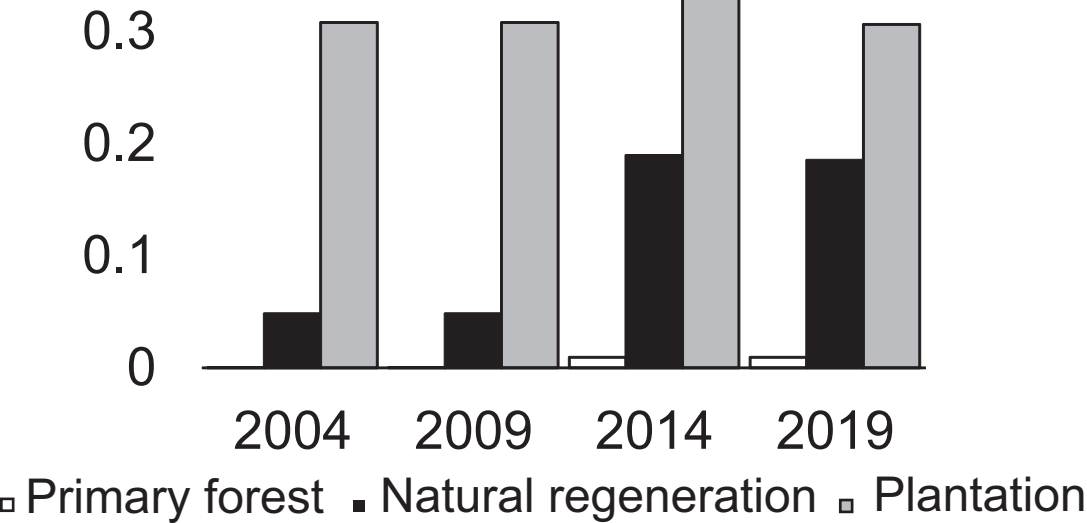


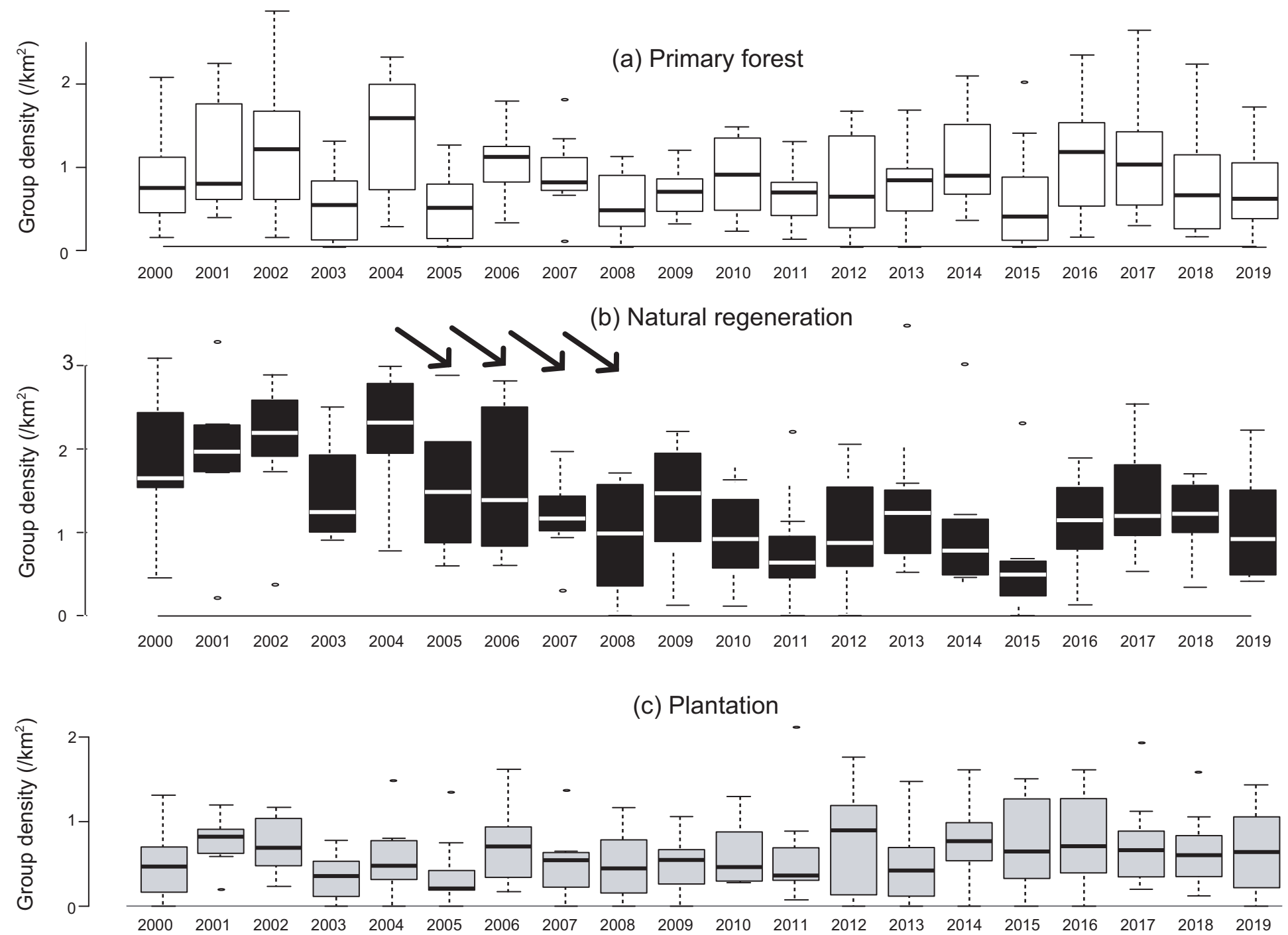
Plantation

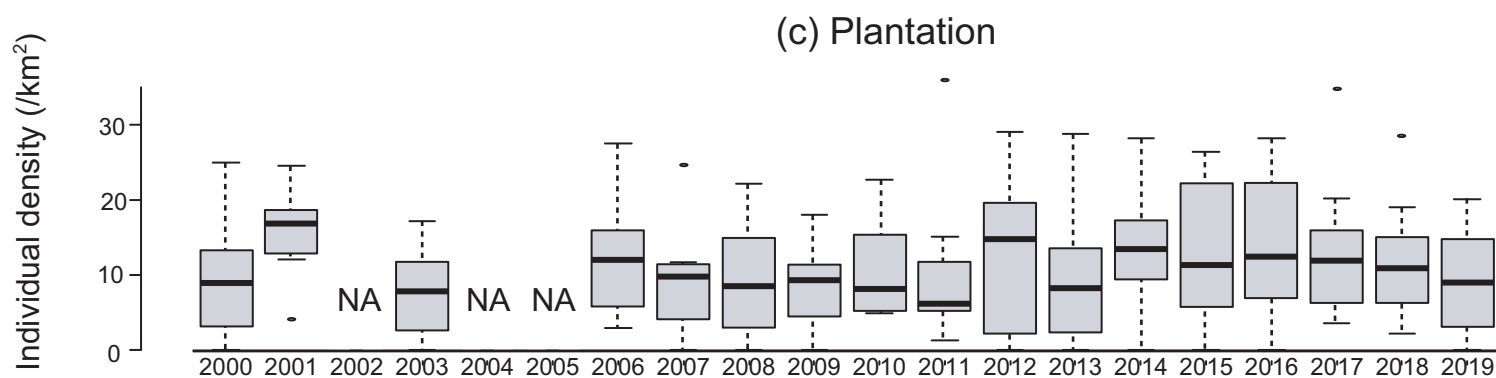
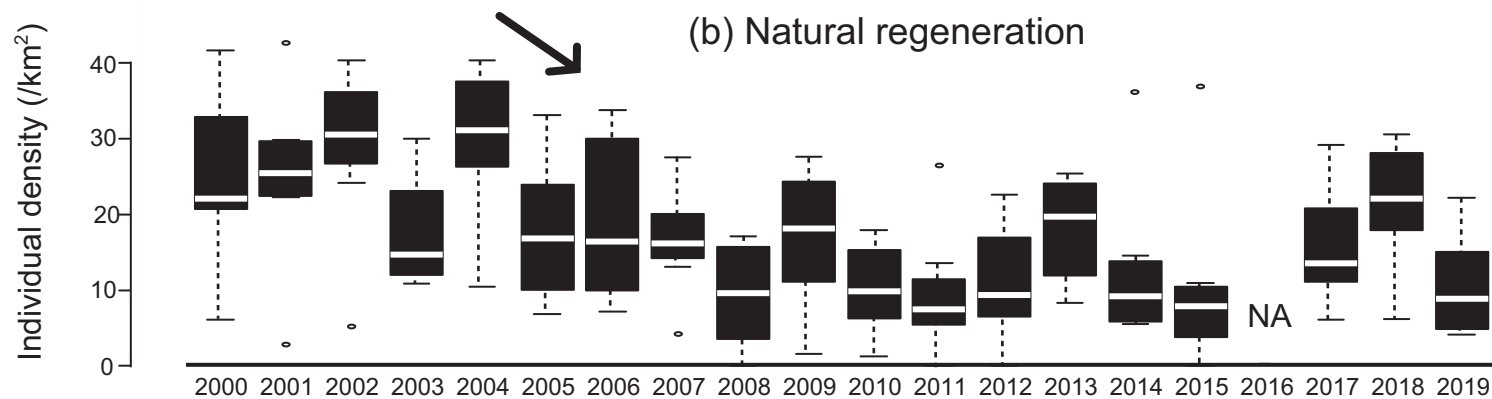
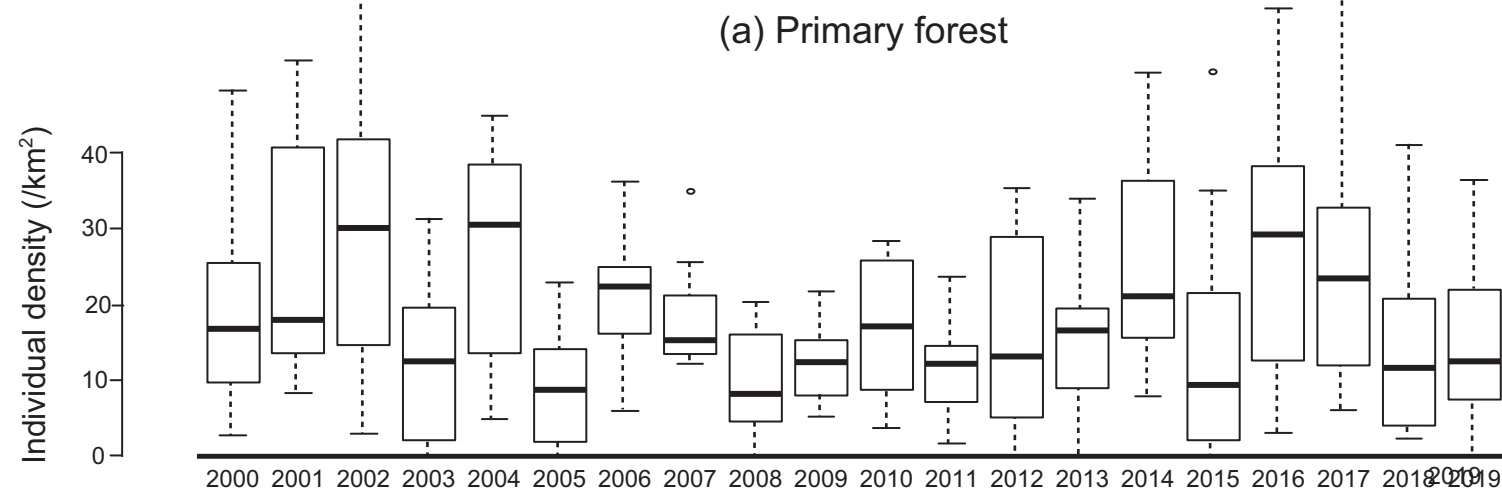


Natural regeneration

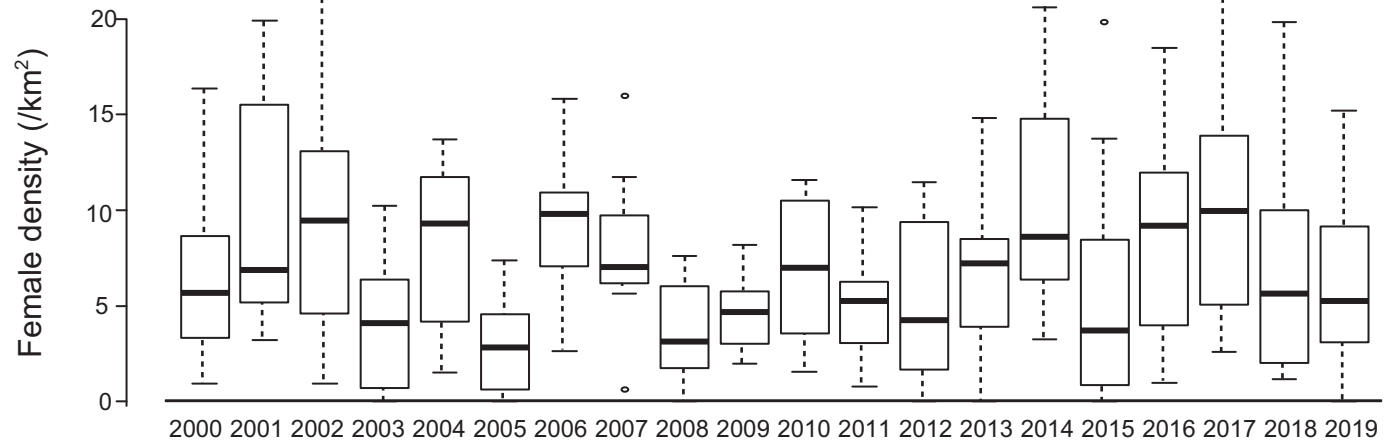




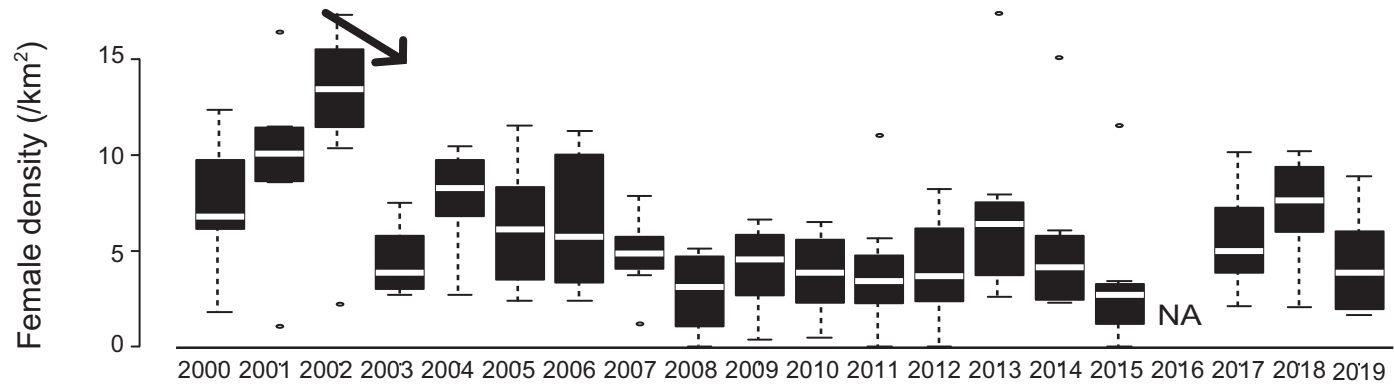




(a) Primary forest



(b) Natural regeneration



(c) Plantation

