Recovery of Logged Tropical Montane Rainforests as Potential Habitats for Hainan Gibbon

Kexin Fan 1,2, Yue Xu 2,3,*, Pengcheng Liu 2,3 and Runguo Zang 2,3

1 State Forestry and Grassland Administration Key Laboratory of Silviculture in Downstream Areas of the Yellow River, Forestry College of Shandong Agricultural University, Taishan Mountain Forest Ecosystem Research Station, Taian 271018, China; kexin@sdau.edu.cn
2 Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China; liupe@caf.ac.cn (P.L.); zangrung@caf.ac.cn (R.Z.)
3 Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China
* Correspondence: xuyue@caf.ac.cn

Abstract: As the world’s rarest ape, the main threat facing Hainan gibbon (Nomascus hainanus) is habitat degradation and loss caused by human disturbances. The insufficient area and continuous human disturbance in most of the existing habitats can hardly maintain the future recovery and development of the gibbon population. A large area of secondary tropical montane rainforest in recovery was retained in Bawangling National Nature Reserve after disturbance. Therefore, it is of great significance to study the recovery of these secondary forests for the protection and restoration of Hainan gibbon habitat. To explore the recovery of secondary tropical rainforests after different disturbances, and whether they have the potential to serve as the future habitats for Hainan gibbon, we calculated four dynamic indexes (including recruitment rate, mortality/loss rate, relative growth rate and turnover rate) of abundance and basal area for the total community and for food plants of Hainan gibbon based on data from two censuses of secondary forests recovered nearly 45 years after different disturbances (clear-cutting and selective-logging) and old-growth forest of tropical montane rainforest. The results are as follows: (1) There were no significant differences in recruitment rates, mortality rates and turnover rates of abundance and basal area between recovered clear-cutting forests, selectively logged forests and old-growth forests. (2) Abundance, basal area and species of small (1 < DBH ≤ 10 cm) and medium (10 ≤ DBH < 30 cm) food plants in the two disturbed forests were higher, while those of large food plants (DBH ≥ 30 cm) in the two forests were lower than in old-growth forests. (3) For the common food species occurring in all three kinds of communities, the relative growth rate of most small trees in clear-cutting forest was higher than that of old-growth forest. Our research demonstrates that the lack of large food plants is the key limiting factor for the development of the secondary mountain rainforest as habitats for Hainan gibbon at present. However, it has great potential to transform into suitable habitats through targeted restoration and management due to the high recruitment rate and relative growth rate of the small- and medium-sized food plants.

Keywords: selective-logging; clear-cutting; food plants; population demography; turnover rate; relative growth rate; phenological periods

1. Introduction

Hainan gibbon (Nomascus hainanus) is the most representative flagship species and an important indicator of the effectiveness of tropical rainforest protection in Hainan, South China [1–4]. However, it is also listed as one of the 25 most endangered primate species in the world by the Species Survival Commission of International Union for Conservation of Nature (SSC of IUCN) and the International Primate Society (IPS) due to its extremely low population; in addition, it is considered to be the most likely extinct primate species in the
21st century [5–7]. Once widespread across the island, the relic population is confined to a single forest patch of 16 km\(^2\) in Hainan Bawangling National Nature Reserve (BNNR) [7]. Therefore, the protection of Hainan gibbon will play a crucial guiding role in improving the conservation efficiency of the National Park of Hainan Tropical Rainforest. In recent years, field census and long-term monitoring field research on the known population of Hainan gibbon have been carried out and paid attention to [2,3]. At present, the number of Hainan gibbon in BNNR has increased from seven individuals among two groups in the 1980s to 33 individuals among five groups [2–4,8]. Hovering on the brink of extinction due to the extremely small populations and low genetic diversity [9], it has been found that habitat degradation and loss caused by high disturbance are the main threats facing Hainan gibbon [10]. The remaining habitats are scattered across a large area of secondary forest and plantation [11], which are unable to support the population in recovery, while dispersal barriers due to forest degradation and conversion restrict the range expansion necessary for recovery [12].

Hainan gibbon usually forage and rest in mature and unlogged montane rainforests below 1300 m [7], whereas large areas of old-growth montane tropical forests in Bawangling have been logged in the 1960s, which are now in the process of secondary succession [13–15]. Compared to primary forest, secondary forest is also diverse in primate food species, but large fruit trees are rare [16]. The decrease in the number of large food plants and the relatively simple community structure of secondary forests may be insufficient in supporting the resting and feeding activities of Hainan gibbon [7,10]. However, tropical forests usually have very high resilience after disturbance, and studies have proved that human-disturbed forests can still provide potential habitats for ecosystem functioning and conserving biodiversity [17,18]. An exciting discovery was made at the end of 2019 that a newly formed gibbon population was detected in a well-recovered secondary forest outside the known gibbon range [19]. Therefore, the secondary forests of tropical montane rainforest in recovery may become the habitats for Hainan gibbon again. Additionally, directional restoration of the available secondary forests for Hainan gibbon is of great importance [10].

Whether the recovering tropical montane rainforest can provide food sources for Hainan gibbon is still highly uncertain [11]. Some studies have discussed whether secondary forests can become potential habitats for primates, but most of them focus on the recovery of community structure and species richness, while few focused on the recovery of food plants in secondary forests [10,16,20]. Zhang and Zang [10] compared the distribution and diversity of food plants between different recovery stages of secondary forests and plantations, argued that secondary forests at medium-recovering stage (25 to 60 years) are most likely to become potential habitat of Hainan gibbon, due to their high similarity with old forest community structure and species richness. Studies of primate habitats in other areas also found no significant differences in primate food plant species between secondary forests and natural forests, e.g., see Bryson-Morrison et al. [20]. For Hainan gibbon, although the rapid recovery of the community structure of tropical montane rainforests may provide good shelter conditions, the lack of food supply may become the key barrier to the survival and reproduction of gibbon population [3]. Hence, the demography of food plants can determine the possibility of secondary forests as future habitats for the species, and it is necessary to include them in the analysis of the recovering processes of gibbon habitat.

Forest dynamics arise from the interplay of chronic drivers and transient disturbances with the demographic processes of recruitment, growth and mortality [21–23]. Analyzing community dynamics is essential for a better understanding of the mechanisms of succession in tropical forests and for the subsequent development of strategic measures for forest conservation and restoration [24]. The turnover of a community refers to the relative ratio of variations in the abundance of species or stem growth, recruitment and mortality indicators to the total amount in a certain period [21–23]. Studying the dynamics in the turnover of stems or species of a given community can reveal the changes in the abundance pattern in the community and the performance of the population over time [25]. This
dual individual–community model can also help to understand the driving mechanism of specific factors in the succession or recovery process and the response mechanism of a given community to external disturbances such as human activities and climate change [26].

There is a large area of secondary mountain rainforests in recovery after commercial logging in the BNNR [27], along with changes in community composition and structure [28]. The hope that they will recover to match the character of old-growth forests that they have replaced through natural succession has increased significantly [29]. However, there is a long-term debate about the recovery degree and limited information is available for secondary forests after more than 20 years’ harvesting [30]. For example, the mature stem density, species richness and diversity indices showed no differences between post-cutting forest and old-growth forest in a Brazilian tropical forest after 5 years of recovery [31]. There was no significant difference in the turnover rates between logged forests and old-growth forests in Uganda [32]. In contrast, the negative effect of logging was still distinct 150 years after logging, and species loss was irreversible in the tropical forests of Madagascar [33]. Thus, it is of great importance to study the recovery process and its potential for animal habitats of tropical rainforests logged using different practices based on relatively long-term data.

In Bawangling forest region, two different logging methods (selective-logging and clear-cutting) have caused different disturbance intensities to tropical mountain rainforests [27]. Few studies have compared the impacts of these two logging approaches on tropical forest recovery, so it is unclear whether there are significant differences in dynamics, diversity and structure between logged forests recovered for several decades and old-growth forests. Here, based on monitoring data of ca. 45-year-old selectively logged; ca. 45-year-old clear-cutting; old-growth tropical montane rainforest in Bawangling National Nature Reserve on Hainan Island, we compared the differences of recovering dynamics of community structure and food plants between these secondary forests and old-growth forests. The conservation prospects for these disturbed forests as potential habitats for Hainan gibbon were also evaluated.

2. Materials and Methods

2.1. Study Site

This study was carried out in the BNNR on Hainan Island, which is the largest tropical island in China (18°52′–19°12′ N, 108°53′–109°20′ E). The tropical montane rainforest has an average elevation of roughly 1000 m. The study area has an annual average temperature of 19.4 °C and an annual average precipitation of 2806 mm. Precipitation is distributed seasonally with a wet season (precipitation ≥ 100 mm/month) from May to October and a dry season (precipitation < 100 mm/month) from November to April [27].

The tropical montane rainforest is one of the main vegetation types in BNNR, and currently plays an important role in conserving biodiversity and providing ecosystem services on Hainan Island [11]. Clear-cutting took place in 1966, and all trees were felled except for a few parent trees. Subsequently, two species with high commercial value (Vatica mangachapoi and Homalium ceylanicum) were planted. Due to their natural distribution in low-altitude environments and intolerance to low temperatures in winter, the planted trees were replaced by montane rainforest species gradually during the natural recovery process in the 1970s. The selectively logged forest was felled in 1975. According to the selective-logging regulations, the tree species were categorized into six classes based on the diameter at breast height (DBH). At least 15 seed trees from the top class to the third class must be retained per hectare as seed trees. About 60% of the timber volume was harvested during this process.

2.2. Data Collection

According to the historical data and logging records of Hainan Bawangling Forestry Bureau, we established 6 forest dynamic plots of tropical montane rainforest all with an area of 1 ha (100 m × 100 m) near the Hainan gibbon habitats, including 2 clear-cutting
forests after 45 years’ recovery (CC), 2 selectively logged forest plots after 45 years’ recovery (SL) and 2 old-growth forest plots (OG). The distance between the edge of each plot and the forest margin was more than 100 m in order to avoid edge effect. In each plot, all individuals with DBH more than 1 cm were tagged, mapped, measured and identified to species. Tree species nomenclature was standardized followed the Flora of China (http://www.efloras.org, accessed on 23 November 2019). We also identified food plants and their edible organs (including fruit, petals and leaves) amongst the surveyed species according to food plant lists from long-term studies of the Hainan gibbon in BNNR [10,34,35].

Five years after the first census, all trees in the 6 plots were re-censused, and DBH was re-measured at the same location of first census. The newly recruited trees with DBH ≥ 1 cm were tagged, mapped, measured and identified following the same procedure, and trees that had died over this interval were also recorded.

2.3. Calculation Formula

Recruitment rate, mortality/reduction rate and turnover rate of abundance and basal area were quantified between the first census and the re-census after 5 years. Results regarding the basal area were put in the Supplementary Information. The methods from Condit et al. [36] was used to calculate these indexes. The calculation formulas are as follows:

The recruitment rates of abundance:

\[ \lambda_{\text{indr}} = \frac{\ln(N_2) - \ln(N_{2\text{sur}})}{t} \times 100\% \]  

where \(N_2\) is the total number of individuals at the re-census, \(N_{2\text{sur}}\) is the total number of survival individuals during the 5-year period, and \(t\) is the 5-year interval.

The mortality rates of abundance:

\[ \lambda_{\text{indm}} = \frac{\ln(N_1) - \ln(N_{2\text{sur}})}{t} \times 100\% \]  

where \(N_1\) is the total number of individuals at the first census.

The turnover rates of abundance:

\[ T_{\text{ind}} = \frac{(M + R)}{2} \times \frac{1}{(N_1 + N_2)} \times t \times 100\% \]  

where \(M\) and \(R\) are the total numbers of dead and newly recruited individuals at the re-census, respectively.

The recruitment rates of basal area:

\[ \lambda_{\text{bar}} = \frac{\ln(B_2) - \ln(B_{2\text{sur}})}{t} \times 100\% \]  

where \(B_2\) is the total basal area at the re-census, \(B_{2\text{sur}}\) is the total basal area of survival individuals during the 5 years at the second census.

The loss rates of basal area:

\[ \lambda_{\text{bam}} = \frac{\ln(B_1) - \ln(B_{1\text{sur}})}{t} \times 100\% \]  

where \(B_1\) is the total basal area at the first census, \(B_{1\text{sur}}\) is the total basal area of survival individuals during the 5-year period at the first census.

The relative growth rates of basal area:

\[ \lambda_{\text{bag}} = \frac{\ln(B_{2\text{sur}}) - \ln(B_{1\text{sur}})}{t} \times 100\% \]
The turnover rates of basal area:

\[ T_{ba} = \frac{B_r + B_m + B_g}{\frac{1}{2} \times (B_1 + B_2) \times t} \times 100\% \]  

(7)

where \( B_r \) is the total basal area of newly recruited individuals at the re-census, \( B_m \) is the total basal area of dead individuals at the re-census, \( B_g \) is the total relative growth basal area of survival individuals during the 5-year period.

2.4. Statistical Analysis

In order to compare the demographic dynamics of woody plants with different DBH classes in the three forest types, all woody plants with DBH \( \geq 1 \) cm in the plots were divided into three size groups: small trees (1 \( \leq \) DBH < 10 cm), medium trees (10 \( \leq \) DBH < 30 cm) and large trees (DBH \( \geq \) 30 cm). The relative growth rate, mortality/loss rate and turnover rate of abundance and basal area of the tropical montane rainforest communities and the food plants of different groups were calculated. Additionally, significant tests were conducted by means of analysis of variance (ANOVA) and Tukey’s honest significant difference (HSD) test. In addition, standardized major axis regression (SMA) was used to compare the relative growth rate of food plants that commonly existed in all three forest types of the total and three different-sized groups between the two logged forests and the old-growth forest. According to the seasonal availability of the edible organs of the food plants mentioned above, we divided the abundance of food sources in different seasons. Then, abundance distributions of food plants of montane rainforests under different disturbance intensities in different seasons were compared. The above analyses were all conducted in R program (https://www.R-project.org/, R Core Team, accessed on 10 October 2020), where SMA was performed with the R package ‘smatr’.

3. Results

3.1. Recovery of Community of Secondary Tropical Montane Rainforests after Different Disturbances

Comparing the turnover dynamics among the three different disturbances, we found that old-growth forests had the highest turnover rates except for big trees. In the selectively logged forests, the recruitment rates were lower, and the mortality rates were higher for small and medium trees, which was consistent with the trend of the whole community but contrary to the big trees. In terms of size groups, the small trees and medium trees had similar dynamic patterns, while the large trees tended to have the opposite pattern among different disturbances. No matter the recruitment rates, mortality rates or turnover rates, there was no significant difference among different disturbances. In addition, the mortality rates were larger than the recruitment rates for small and medium trees, while smaller than the recruitment rates for large trees (Figure 1).

As for dynamic changes of basal area, the whole community and large trees showed the same trend, while small trees and medium trees showed a similar trend. The result is understandable since the biggest contribution of the basal area comes from the large trees in a community. By comparing the dynamics of the basal area after different disturbances, we found that clear-cutting forests had the highest turnover rates except for the medium trees, although the differences were not significant. The basal area turnover rates of the big trees increased along disturbance intensity, and the recruitment rates and turnover rates of the medium trees in selectively logged forests were significantly lower than those in the old-growth forests (Figure S1).
Figure 1. Variations in recruitment rates, mortality rates and turnover rates of abundance among forests after three disturbances (clear-cutting, CC; selectively logged, SL; old-growth forests, OG) for the total community (A–C), small trees (1 cm ≤ DBH < 10 cm, D–F), medium trees (10 cm ≤ DBH < 30 cm, G–I) and large trees (DBH ≥ 30 cm, J–L). DBH, diameter at breast height. Different lowercase letters indicated significant differences between three disturbances at p < 0.05 according to ANOVA and HSD test.

3.2. Recovery of Food Plants of Secondary Tropical Montane Rainforests after Different Disturbances

The ratios of food plants in terms of abundance in clear-cutting, selectively logged and old-growth forests were 37.09%, 27.38% and 18.57%, respectively. Additionally, the ratios of food plants in terms of basal area were 31.80%, 29.26% and 53.14%, respectively. There were great differences amongst forest types regarding abundance and basal area of the three group sizes. The relative ratios of abundance and basal area were lower in
old-growth forests than those in the secondary forests for small food plants, while the opposite was true for big food plants. As for species richness, the secondary forests had already reached to the richness level of old-growth forests in both the whole community and each size group (Figure 2).

Figure 2. Abundance, basal area and species richness distribution of food plants for gibbons in clear-cutting forests (CC), selectively logged forests (SL) and old-growth forests (OG) for the total community (A–C), small trees (1 cm ≤ DBH < 10 cm, D–F), medium trees (10 cm ≤ DBH < 30 cm, G–I) and large trees (DBH ≥ 30 cm, J–L). DBH, diameter at breast height.

The old-growth forests had the greatest abundance mortality rates and turnover rates of food plants, and selectively logged forests generally had the lowest abundance recruitment rates and turnover rates, although the differences were not significant except for mortality rates of large trees. The mortality rates of the small food plants were higher
than the recruitment rates among different disturbances, but this tendency was reversed for the medium and large food plants (Figure 3).

Figure 3. Recruitment, mortality and turnover rates of food plant abundance among forests after three disturbances (clear-cutting, CC; selectively logged, SL; old growth forests, OG) for all individuals (A–C), small trees (1 cm ≤ DBH < 10 cm, D–F), medium trees (10 cm ≤ DBH < 30 cm, G–I) and large trees (DBH ≥ 30 cm, J–L). DBH, diameter at breast height. Different lowercase letters indicated significant differences between three disturbances at p < 0.05 according to ANOVA and HSD test.

In terms of the basal area of food plants, the clear-cutting forests had the greatest recruitment rates, although the differences were not significant. The old-growth forests had the greatest mortality rates. Turnover rates of selectively logged forests were smaller
than that of the other two forest types, and the difference was significant for large trees. The mortality rates of selectively logged and old-growth forests were always larger than recruitment rates (Figure S2).

Generally, for common food plants, their relative growth rates in clear-cutting forests were higher than those in selectively logged forests, and this pattern was consistent in small and medium food plants. For example, small food plants such as *Psychotria Rubra*, *Gironniera subaequalis*, *Syzygium chunianum*, *Gironniera subaequalis* and *Xanthophyllum hainanense* had much higher relative growth rates in clear-cutting forests than in selectively logged forests. However, in the medium and large food plants, the ratios of the relative growth rates of the secondary forests to old-growth forest converged to 1, and the distribution was relatively uniform (Figure 4).

![Figure 4](image-url)

**Figure 4.** The relative growth rates of food plants in three different disturbances (clear-cutting, CC; selectively logged, SL; old-growth forests, OG) for all individuals (A), small trees (1 cm ≤ DBH < 10 cm, B), medium trees (10 cm ≤ DBH < 30 cm, C) and large trees (DBH ≥ 30 cm, D). Red points and light gray words indicate species in CC forests, while green points and dark gray words indicate species in SL forests. Species represented by abbreviations in this figure can be seen for detailed information in Table S1.

The frequency distribution of food plants in the three size groups among different disturbances showed that there were plants available for gibbons to eat in all four seasons throughout the year, and spring generally had the smallest ratios of food plants. The ratios of small food plants in clear-cutting and selectively logged forests were greater than those in old-growth forests all year round. The gap of food plant ratios between old-growth forests and secondary forests decreased and even reversed as the tree grew. For large trees, the ratios of food plants in secondary forests became smaller than that in old-growth forests in all seasons (Figure 5).
4. Discussion

Current studies have found that the diversity and density of vertebrates in large areas of tropical forests (especially those heavily affected by human activities) are much lower than they should be at the natural level [37,38]. In these forests, the plant species that mainly rely on animals for seed dispersal has been declining due to the decreasing of frugivorous animals that adversely affect the species diversity and the long-term stability of the community [39–41]. Therefore, the core issue of this study is whether the tropical montane rainforests recovered for 45 years after human disturbances can become potential habitats for Hainan gibbon. We assessed two important indicators for the recovery of gibbon habitats, including the recovery of the whole community and the food plants [10,42].

4.1. The Recovery of Community Structure in Secondary Forests

The recovery of the community structure in tropical montane rainforest is a precondition for the survival and settlement of gibbons. By analyzing our dynamic data, the results illustrated that the community structure of logged tropical montane rainforests after 45 years of natural recovery was very similar to that of the old-growth forests. Especially for the small and medium trees, both their community structure and dynamics were similar to those of old-growth forests. The same conclusion has been proven in studies of other tropical rainforests, for example, selective logging only had a significant impact on the abundance of mature trees (DBH ≥ 30 cm) in tropical rainforests of Indonesia [43,44] and Brazil [31], the abundance and species richness there had reached the level of the mature forests only after less than 30 years of recovery. Species numbers with DBH greater than 1 cm in a tropical secondary forest in Bolivia could reach levels of old-growth forests only after 20–25 years [45], while in Puerto Rico, after 35–40 years [46]. Therefore, a large

Figure 5. Distribution of abundance ratio of food plants in communities among seasons classified by phenological period of edible parts in the three forest types (clear-cutting, CC; selectively logged, SL and old-growth forest, OG) for all individuals (A), small trees (1 cm ≤ DBH < 10 cm, B), medium trees (10 cm ≤ DBH < 30 cm, C) and large trees (DBH ≥ 30 cm, D).
number of studies showed that tropical secondary forests have high resilience and recovery rates after commercial logging [47,48], and they are able to take only several decades to reach the pre-logged level [32]. This may follow from the fact that both fast-growing and light-demanding tree species typically dominate at the early successional stage. In contrast, it takes a longer time for dominant species with large DBH to grow and for saplings of shade-tolerant species to reach the max limit at later stages of succession [49]. After more than 45 years of recovery, the plant recruitment, mortality, relative growth and turnover dynamics in secondary forests showed no significant difference with old-growth forests, which also indicated that the recovering tropical montane rainforests are very stable. This has a direct impact on tropical forest biodiversity conservation and global climate change on a large scale and provides a relatively stable habitat environment for the future migration and survival of Hainan gibbon.

4.2. The Recovery of Food Plants in Secondary Forests

An important reason why many forest types (such as the tropical coniferous forests and tropical lowland rainforests recovered after slash-and-burn cultivation) in BNNR will not become primate habitats is the lack of food plants [3,10]. In contrast, tropical montane rainforests show a high ratio of food plants and a high community stability after logging (Figure 2; Figure 3). Studies of forests in Uganda showed that primates’ preferences for certain forest habitats are mainly determined by the abundance of food resources rather than the forest structure [42].

Recovering forests were becoming more similar to old-growth forests in terms of community structure and species composition with time. The higher density of trees with a smaller size than that of the large size also indicates the sustainable and good regeneration potential of forests [50]. However, the large trees that DBH ≥ 30 cm, that are resting places and main food supplies for gibbons, are still insufficient and cannot meet the needs of gibbons in the short term. Our results showed that although the ratios of food plants in all seasons in the disturbed forests could reach the level of the old-growth forests, there was still a considerable gap in the composition of the large trees (DBH ≥ 30 cm) (Figure 2; Figure 5). In addition, variations in food supplies such as seasonal fluctuation, especially for diversity and distribution of food plants, are also major factors affecting gibbon population [20,51–53]. The lack of high quality food resources may be the main obstacle to habitat recovery of gibbons to date, which is also likely the main factor limiting the population growth of gibbons [53]. However, due to the considerable abundance of small and medium food plants, as well as the high relative growth rate of food plants, these secondary forests have a high conservation value and will become potential habitats for gibbons in the near future. Moreover, the results indicated that planting suitable food plants in this area could be an effective measure to restore and improve the existing habitats for gibbons.

The results also provide us with targeted ecological restoration strategies to better conserve Hainan gibbon. For example, introduction of food species, especially large-sized food plants in the secondary forests can be an efficient action. Planting food plants is helpful to attract gibbons to feed here. Hainan gibbon can disperse seeds in their droppings, which may further attract secondary seed dispersers and post-dispersal seed predators [40]. This positive circle can enhance the regeneration of plant species which rely on animals for seed dispersal. In the long term, the stability of the community will also be increased.

4.3. The Recovery of Secondary Forests with Different Disturbance Intensities

At present, both the ratios and the seasonal supply of food plants among small- and medium-sized groups have recovered well in the two secondary forests, but this study revealed some interesting results. Species richness, basal area and abundance of food plants in clear-cutting forests were higher than that in selectively logged forests except for large trees (Figure 2). At the same time, the recruitment rates of the food plants were higher while the mortality rates were lower in clear-cutting forests than those in the selectively
logged forests. In addition, the recruitment rates were always smaller in selectively logged forests than that in clear-cutting forests no matter of size group (Figure 4). These results indicated that the recovery of food plants in clear-cutting forests may be better than that in selectively logged forests.

It is believed that clear-cutting caused much more significant disturbance to community structure and species composition than selectively logging. Therefore, the natural recovery of selectively logged forests would be faster and better than clear-cutting forests after the same period of recovery [27,54]. However, the results of our study suggested that clear-cutting forests might be better recovered than selectively logged forests. This is consistent with a study in Uganda, which showed that selective logging is not necessarily better than clear-cutting for the recovery and management of secondary forests by analyzing the dynamics of stems, species and functional traits of tropical forests [32]. Our results may be due to the following reasons. Firstly, the intensity of selective logging on Hainan island is much higher than in other tropical regions, with at least 60% of the timber volume harvested during the logging process [27]. Secondly, seeds from old-growth forest spread easily into clear-cut areas, and the high available light after clear-cutting creates better conditions for the recruitment of long-lived pioneer species. Moreover, the practice of controlled burning after clear-cutting further provides abundant nutrients for these rapid resource-use pioneer species. Thirdly, selectively logged forests have better initial conditions (such as the number of mother trees, regional species pool, etc.) than clear-cutting forests. This suggested that competition caused by the density-dependent factors may play a more important role in regulating community dynamics in selectively logged forests, which was consistent with the higher mortality rates in selectively logged forests than in clear-cutting forests. Lastly, due to the lower disturbance intensity of selectively logged forests, these secondary forests had gradually stepped into the later successional stage after 45 years of recovery. At this time, the forests had large abundance, high community density and the intense inter-/intra-specific competition, which could cause low relative growth rates. Meanwhile, clear-cutting forests may be in the initial stage of recovery with a small abundance and a fast growth rate (Figure 2). However, the instantaneous results of this study do not represent permanent conclusions, and we think that more research is needed to determine the longer-term effects of logging on tree communities, particularly the effects of logging intensity on demographic rate.

5. Conclusions

Using data from secondary forests recovered 45 years after different disturbances (clear-cutting and selective-logging) and old-growth forest of tropical montane rainforest, we found that there were no significant differences in the recruitment rates, mortality rates and turnover rates of abundance and basal area between recovered clear-cutting forests, selectively logged forests and the old-growth forests. Abundance, basal area and species of small and medium food plants (DBH < 30 cm) in the two disturbed forests were higher than in old-growth forests. For the common food species that occurred in all three kinds of communities, the relative growth rate of small and medium trees in clear-cutting forest was higher than that in selectively logged forest. In conclusion, the lack of large food plants is the key defect in the development of secondary forests to be Hainan gibbon habitats in the BNNR. However, due to the good recovery of small and medium food plants, this area is poised to become future gibbon habitats with proper management and guidance. It is also necessary to take further long-term monitoring and effective managements to ensure better development of the gibbon habitats in the future. In order to restore the food resources and attract gibbons to live in this area, we can implement targeted ecological restoration strategies in the tropical secondary forests and consider the introduction of food species.
Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/forests1207071/s1, Figure S1: Variations in recruitment rates, mortality rates, and turnover rates of basal area among forests after three disturbances for the total community, small trees, medium trees and large trees. Figure S2: Recruitment, mortality and turnover rates of food plants basal area among forests after three disturbances for all individuals, small trees, medium trees and large trees. Table S1: The list of food plants.

Author Contributions: R.Z. conceived and designed the experiments; K.F. conducted the field work; K.F. and P.L. performed the data compilation and analyzed the data; K.F., P.L., Y.X. and R.Z. contributed to the writing of the paper. All authors have read and agreed to the published version of the manuscript.

Funding: The research was supported by the National Nonprofit Institute Research Grant of the Chinese Academy of Forestry (CAFYBB2019ZB010).

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Stone, R. Last-Ditch Effort to Save Embattled Ape. Science 2011, 331, 390. [CrossRef] [PubMed]
2. Bryant, J.; Turvey, S.; Wong, M.; Traylor-Holzer, K. Conserving the world’s rarest ape: Action planning for the Hainan gibbon. Oryx 2015, 49, 391–392. [CrossRef]
3. Fan, P. The past, present, and future of gibbons in China. Biol. Conserv. 2017, 210, 29–39. [CrossRef]
4. Deng, H.; Zhang, M.; Zhou, J. Recovery of the Critically Endangered Hainan gibbon Nomascus hainanus. Oryx 2017, 51, 161–165. [CrossRef]
5. Geissmann, T.; Bleisch, W. Nomascus hainanus. IUCN Red List of Threatened Species, Version 2011.1. Available online: https://www.iucnredlist.org/ (accessed on 23 November 2019).
6. Mootnick, A.R.; Chan, B.P.L.; Moisson, P.; Madler, T. The status of the Hainan gibbon Nomascus hainanus and the Eastern black gibbon Nomascus nasutus. Int. Zoo Yearb. 2012, 46, 259–264. [CrossRef]
7. Zhang, M.; Fellowes, J.; Jiang, X.-L.; Wang, W.; Chan, B.; Ren, G.-P.; Zhu, J. Degradation of tropical forest in Hainan, China, 1991–2008: Conservation implications for Hainan Gibbon (Nomascus hainanus). Biol. Conserv. 2010, 143, 1397–1404. [CrossRef]
8. Guo, Y.; Peng, D.; Han, L.; Liu, T.; Li, G.; Garber, P.A.; Zhou, J. Mitochondrial DNA control region sequencing of the critically endangered Hainan gibbon (Nomascus hainanus) reveals two female origins and extremely low genetic diversity. Mitochondrial DNA Part B 2021, 6, 1355–1359. [CrossRef]
9. Liu, H.; Ma, H.; Cheyne, S.M.; Turvey, S.T. Recovery hopes for the world’s rarest primate. Science 2020, 368, 1074.
10. Zhang, Z.; Zang, R. Diversity and distribution of food plants: Implications for conservation of the critically endangered Hainan gibbon. Nat. Conserv. 2018, 31, 17–33. [CrossRef]
11. Zang, R.; Ding, Y.; Zhang, Z.; Deng, F.; Mao, P. Ecological Foundation of Conservation and Restoration for the Major Functional Groups in Tropical Natural Forests on Hainan Island; Science Press: Beijing, China, 2010; pp. 17–38.
12. Turvey, S.T. International Conservation Workshop for the Hainan Gibbon: Final Report; Journal of Wildlife Rehabilitation: London, UK, 2015.
13. Hansen, M.C.; Potapov, P.; Moore, R.; Hancher, M.; Turubanova, S.; Tyukavina, A.; Thau, D.; Stehman, S.; Goetz, S.; Loveland, T.; et al. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science (N. Y.) 2013, 342, 850–853. [CrossRef]
14. Berry, N.; Phillips, O.; Lewis, S.; Hill, J.; Edwards, D.; Tawatao, N.; Ahmad, N.; Magintan, D.; Khen, C.; Mohamed, M.; et al. The high value of logged tropical forests: Lessons from northern Borneo. Biodivers. Conserv. 2010, 19, 985–997. [CrossRef]
15. Arroyo-Rodríguez, V.; Melo, F.; Martinez-Ramos, M.; Bongers, F.; Chazdon, R.; Meave, J.; Norden, N.; Santos, B.; Leal, I.; Tabarelli, M. Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 2017, 92, 326–340. [CrossRef] [PubMed]
16. Bryson-Morrison, N.; Matsuzawa, T.; Humle, T. Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa. Am. J. Primatol. 2016, 78, 1237–1249. [CrossRef]
17. Rozendaal, D.; Bongers, F.; Aide, T.M.; Alvarez Davila, E.; Ascarrunz, N.; Balvanera, P.; Becknell, J.; Bentos, T.; Brancalion, P.; Cabral, G.; et al. Biodiversity recovery of Neotropical secondary forests. Sci. Adv. 2019, 5, eaau3114. [CrossRef]
18. Chazdon, R.L.; Peres, C.A.; Dent, D.; Sheil, D.; Lugo, A.E.; Lamb, D.; Stork, N.E.; Miller, S.E. The potential for species conservation in tropical secondary forests. Conserv. Biol. 2009, 23, 1406–1417. [CrossRef] [PubMed]
19. Chan, B.; Lo, P.; Mo, Y. New hope for the Hainan gibbon: Formation of a new group outside its known range—ERRATUM. Oryx 2020, 54, 296. [CrossRef]
20. Mammides, C.; Cords, M.; Peters, M. Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. Afr. J. Ecol. 2009, 47, 87–96. [CrossRef]
21. Phillips, O.L.; Gentry, A.H. Increasing turnover through time in tropical forests. Science 1994, 263, 954–958. [CrossRef]
22. Lewis, S.L.; Phillips, O.L.; Sheil, D.; Vinceti, B.; Baker, T.R.; Brown, S.A.; Graham, A.W.; Higuchi, N.; Hilbert, D.W.; Laurance, W.F. Tropical forest tree mortality, recruitment and turnover rates: Calculation, interpretation and comparison when census intervals vary. J. Ecol. 2004, 92, 929–944. [CrossRef]
23. Phillips, O.L.; Baker, T.R.; Arroyo, L.; Higuchi, N.; Killeen, T.J.; Laurance, W.F.; Lewis, S.L.; Lloyd, J.R.; Malhi, Y.; Monteagudo, A. Pattern and process in Amazon tree turnover, 1976-2001. Philos. Trans. R. Soc. B 2004, 359, 381–407. [CrossRef]
24. Wang, J.; Lu, H.; Lin, Y.; Campbell, D.E.; Hongyue, C.; Ren, H. Dynamics of community structure and bio-thermodynamic health of soil organisms following subtropical forest succession. J. Environ. Manag. 2020, 280, 111647. [CrossRef]
25. Norden, N.; Letcher, S.; Boukili, V.; Swenson, N.; Chazdon, R. Demographic drivers of successional change in phylogenetic structure across life-history stages in plant communities. Ecology 2012, 93, S70–S82. [CrossRef]
26. Meiners, S.J.; Cadotte, M.W.; Fridley, J.D.; Pickett, S.T.A.; Walker, L.R. Is successional research nearing its climax? New approaches for understanding dynamic communities. Funct. Ecol. 2015, 29, 154–164. [CrossRef]
27. Ding, Y.; Zang, R.; Lu, X.; Huang, J. The impacts of selective logging and clear-cutting on woody plant diversity after 40 years of natural recovery in a tropical montane rain forest, south China. Sci. Total Environ. 2017, 579, 1683–1691. [CrossRef] [PubMed]
28. Edwards, D.P.; Tobias, J.A.; Sheil, D.; Meijaard, E.; Laurance, W.F. Maintaining ecosystem function and services in logged tropical forests. Trends Ecol. Evol. 2014, 29, 511–520. [CrossRef] [PubMed]
29. Putz, F.E.; Zuidema, P.A.; Sznott, T.; Pea-Claros, M.; Pinard, M.A.; Sheil, D.; Vanclay, J.K.; Sist, P.; Gourlet-Fleury, S.; Griscom, B. Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. Conserv. Lett. 2012, 5, 296–303. [CrossRef]
30. Xu, H.; Li, Y.; Liu, S.; Zang, R.; He, F.; Spence, J. Partial recovery of a tropical rainforest a half century after clear-cut and selective logging. J. Appl. Ecol. 2015, 52, 1044–1052. [CrossRef]
31. Villela, D.M.; Nascimento, M.T.; Aragao, L.E.O.C.; Gama, D.M.D. Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest. J. Biogeogr. 2006, 33, 506–516. [CrossRef]
32. Osazuwapeters, O.L.; Jimenez, I.; Oberle, B.; Chapman, C.A.; Zanne, A.E. Selective logging: Do rates of forest turnover in stems, species composition and functional traits decrease with time since disturbance?—A 45 year perspective. For. Ecol. Manag. 2015, 357, 10–21. [CrossRef]
33. Brown, K.; Gurevitch, J. Long-term impacts of logging on forest diversity in Madagascar. Proc. Natl. Acad. Sci. USA 2004, 101, 6045–6049. [CrossRef]
34. Zhou, J. The Ecology and Behavior Traits of Hainan black-crested Gibbon (Nomascus hainanus). Ph.D. Thesis, Northeast Normal University, Changchun, China, 2008.
35. Deng, H.; Jiang, Z. Thirteen years observation on diet composition of hainan gibbons (Nomascus hainanus). North West. J. Zool. 2018, 14, e171703.
36. Condit, R.; Ashton, P.S.; Manokaran, N.; Lafrankie, J.V.; Hubbell, S.P.; Foster, R.B. Dynamics of the forest communities at Pasoh and Barro Colorado: Comparing two 50-ha plots. Philos. Trans. R. Soc. B 1999, 354, 1739–1748. [CrossRef]
37. Harrison, R.; Tan, S.; Plotkin, J.; Slik, F.; Detto, M.; Brenes, T.; Itoh, A.; Davies, S. Consequences of defaunation for a tropical tree community. Ecol. Lett. 2013, 16, 687–694. [CrossRef]
38. Harrison, R.D. Emptying the Forest: Hunting and the Extirpation of Wildlife from Tropical Nature Reserves. BioScience 2011. [CrossRef]
39. Stevenson, P.R. The Abundance of Large Ateline Monkeys is Positively Associated with the Diversity of Plants Regenerating in Neotropical Forests. Biotropica 2011, 43, 512–519. [CrossRef]
40. Vanthomme, H.; Bellé, B.; Forget, P.M. Bushmeat Hunting Alters Recruitment of Large-seeded Plant Species in Central Africa. Biotropica 2010, 42, 672–679. [CrossRef]
41. Mcconkey, K.R. Influence of faeces on seed removal from gibbon droppings in a dipterocarp forest in Central Borneo. J. Trop. Ecol. 2005, 21, 117–120. [CrossRef]
42. Furuichi, T.; Hashimoto, T. Botanical and Topographical Factors Influencing Nesting-Site Selection by Chimpanzees in Kalinzu Forest, Uganda. Int. J. Primatol. 2004, 25, 755–765. [CrossRef]
43. Cannon, C.H.; Pearson, D.R.; Leighton, M. Tree species diversity in commercially logged Bornean rainforest. Science 1998, 281, 1366–1368. [CrossRef] [PubMed]
44. Slik, J.; Verbarg, R.W.; Keler, P.J.A. Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. Biodivers. Conserv. Lett. 2002, 11, 85–98. [CrossRef]
45. Claros, M.P. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 2003, 35, 450–461. [CrossRef]
46. Aide, T.M.; Zimmerman, J.K.; Pascarella, J.B.; Rivera, L.; Marcano-Vega, H. Forest Regeneration in a Chronosequence of Tropical Abandoned Pastures: Implications for Restoration Ecology. Restor. Ecol. 2000, 8, 328–338. [CrossRef]
47. Carrero-Rocabado, G.; Pea-Claros, M.; Bongers, F.; Alarcón, A.; Poorter, L. Effects of disturbance intensity on species and functional diversity in a tropical forest. J. Ecol. 2012, 100, 1453–1463. [CrossRef]
48. Martin, P.A.; Newton, A.C.; Pfeifer, M.; Kho, M.S.; Bullock, J.M. Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. For. Ecol. Manag. 2015, 356, 224–233. [CrossRef]
49. Oberleitnera, F.; Eggberb, C.; Oberdorrerc, S.; Dullingerd, S.; Waneke, W.; Hietz, P. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For. Ecol. Manag. 2021, 479, 118580. [CrossRef]
50. Bhatta, S.P.; Devkota, A. Community structure and regeneration status of Sal (Shorea robusta Gaertn.) forests of Dadeldhura district, Western Nepal. *Community Écol.* **2020**, *21*, 191–201. [CrossRef]

51. Rode, K.D.; Chapman, C.A.; Mcdowell, L.R.; Stickler, C. Nutritional Correlates of Population Density Across Habitats and Logging Intensities in Redtail Monkeys (*Cercopithecus ascanius*). *Biotropica* **2010**, *38*, 625–634. [CrossRef]

52. Worman, C.O.; Chapman, C.A. Densities of Two Frugivorous Primates with Respect to Forest and Fragment Tree Species Composition and Fruit Availability. *Int. J. Primatol.* **2006**, *27*, 203–225. [CrossRef]

53. Du, Y.; Li, D.; Yang, X.; Peng, D.; Tang, X.; Liu, H.; Li, D.; Hong, X.; Song, X. Reproductive phenology and its drivers in a tropical rainforest national park in China: Implications for Hainan gibbon (*Nomascus hainanus*) conservation. *Glob. Ecol. Conserv.* **2020**, *24*, e01317. [CrossRef] [PubMed]

54. Chazdon, R.L.; Letcher, S.G.; van Breugel, M.; Martinez-Ramos, M.; Bongers, F.; Finegan, B. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. B Biol. Sci.* **2007**, *362*, 273–289. [CrossRef] [PubMed]