Patterns of species diversity are not consistent between shifting cultivation in Bawangling Nature Reserves and selective logging in Diaoluoshan Nature Reserves, Hainan Island, China.

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Abstract

Examining changes in plant species diversity after shifting cultivation and logging has taken place in a system can help generate an understanding of the differences in species' responses to these human disturbances. We established 17 plots (each 0.25 hm^2) in young, middle-aged and old-growth forests (i.e. three recovery stages) in Bawangling and Diaoluoshan on Hainan Island, China, after shifting cultivation and selective logging had taken place. We divided each plot into four vertical communities. Changes in the species diversity of each plot (i.e. the overall community) and within the vertical communities were assessed across the three recovery stages. Results showed that, after shifting cultivation, species diversity increased across the three recovery stages for the overall community and for the four vertical communities. Species abundance decreased for the overall community but change was inconsistent for the four vertical communities. After selective logging, however, there was generally little change in species diversity and abundance across the three recovery stages, either overall or within the vertical communities. This suggests that patterns of species diversity between communities are different after shifting cultivation has occurred and when selective logging has taken place. Furthermore, Non-Metric Multidimensional Scaling showed differences in species composition across the three stages in the four vertical communities after shifting cultivation, but no differences in species composition across the three stages after selective logging. We also divided species dissimilarity coefficients into two parts, showing changes in species composition and abundance between the vertical communities under canopies and the canopy communities. We found that after shifting cultivation the coefficients between young-aged and old-growth forests, and middle-aged and old-growth forests were more than 0.77, but that they did not differ after selective logging had occurred. This suggests that changes in species turnover is unpredictable after shifting cultivation, but predictable after selective logging.

Keywords: anthropogenic disturbance; forest succession; species dynamics; tropical rain forest.

Introduction

Natural forest succession usually undergoes a regeneration process whereby species composition and community structure recovers to a condition similar to that of primary forests [1, 2]. Whether or not forests can fully recover from fragmentation and the degradation caused by human disturbances, however, has been of concern for many years [3-5]. Exploring the changes in species diversity and community structure in different disturbance regimes can help us to understand the dynamics of forest succession, and enables us to suggest pertinent objectives for forest management [6].

The monoclimax hypothesis believes that as long as topography and soil conditions are similar, climatic factors are the only forces driving community succession [1]. Given sufficient time, communities under the same climatic conditions will thus grow into a stable and mature climax forest. But it is clear that human activities also have a critical impact on community succession [7]. Assuming that community succession is driven by both anthropogenic and climatic factors, it is expected that successional trajectories will be modified by human-generated disturbances [4, 8-10]. Shifting cultivation and logging are the two most common types of land use in the tropics. Studies have found that these two anthropogenic disturbances drive tropical forest degradation [11, 12], bringing about dramatic changes in environmental conditions and resource availability, and imposing strong constraints on species establishment, growth and recruitment [13, 14]. It is evident that the rate of community recovery depends on the availability of plant seeds and on dispersal distance. However, where shifting cultivation has occurred there is little biological legacy left after burning and several cycles of cultivation [15, 16]. Additionally, after shifting cultivation community environments become dry due to lack of forest cover, and soil degradation is rapid because of the loss of soil nutrients and the reduction of the soil's water-holding capacity [13]. Although selective logging disrupts forest structures and reduces mass [17], saplings, young trees, stumps and soil seed banks are often preserved if proper logging methods have been used [14, 18]. As a consequence, the rate of forest recovery after selective logging is different from the rate of recovery after shifting cultivation [19].

In some cases, environmental gradients influence vertical vegetation patterns both at a micro- and macro-scale, and trees in different levels of the canopy adapt to these gradients more or less sharply [20]. In the secondary forest succession process, canopy trees do not suddenly appear, but have a close relationship with seedlings and saplings under forest canopies. Overstory seedlings and saplings are the regeneration potential of the forest and they affect the future course of succession and canopy composition [21]. Exploring the patterns of species replacement among different vertical communities enables us to generate data about species dynamics, and thus predict the direction of forest succession [22].

Most studies investigate either the impact of shifting cultivation or of logging on patterns of species diversity and composition [15, 23]. Few studies have compared the consequences simultaneously [24, 25]. Since shifting cultivation and logging represent the two major land use types in tropical forest ecosystems, examining them together in a single study can enhance our insights into the recovery processes of secondary tropical forests. This was our objective in our study on Hainan Island, China.

The tropical rainforest on the Island is an important part of the India-Malaysia rainforest. Long-term shifting cultivation and large-scale commercial logging (mainly selective logging) have brought about the fragmentation of primary forests, with the result that there are now large areas of secondary forests.

Our hypothesis was that shifting cultivation and selective logging would lead to different patterns of species diversity, and that the succession trajectories would be different [26]. We studied young, middle-aged and old-growth forests after shifting cultivation in Bawangling Nature Reserve and after selective logging in Diaoluoshan Nature Reserve. We used a space-for-time substitution method [27] and divided each plot into four vertical communities. We then measured species diversity within the overall community as well as separately within each vertical one. We asked two questions: (1) were the patterns of species diversity within each vertical community consistent with those of the overall community after shifting cultivation and after selective logging and (2) were the changes in species turnover between the vertical communities under the canopies and within the canopy communities similar after both shifting cultivation and selective logging?

Methods

Study sites

This study was conducted in both the Bawangling Nature Reserve (BWL, 18°52' — 19°12' N, 108°53' — 109°20' E) and the Diaoluoshan Nature Reserve (DLS, 18°40' —18°49' N, 109°45' — 109°57' E) in Hainan Island, China (Fig. 1). BWL is ca. 500 km², with an altitude range of ca. 100 — 1654 m. The mean annual temperature is 23.6℃, and the precipitation range is 1676 — 2553 mm. DLS is ca. 380 km², with an altitude range of ca. 50 — 1499 m. It has a mean annual temperature of 24.4℃, and the precipitation range is 1870 — 2760 mm. Both the Reserves are characterized by tropical monsoon climates, with a distinct wet season from May to October and a dry season from November to April. Soil types in both places are mountain red soil and mountain yellow soil. Vegetation, from low to high altitude, is tropical lowland rainforest, tropical montane rainforest, tropical montane evergreen forest and tropical montane dwarf forest [28].

Data Collection

We established 8 plots in the forests in BWL in areas where shifting cultivation had taken place, and 9 plots in DLS after selective logging had occurred. Each plot was 0.25 hm². We determined the vegetation and land use history for each plot using forestation materials provided by the local Forestry Bureau. We then divided the plots into three successional stages comprising young forest (about 30 years old: BWL1, BWL2, BWL3, DLS1 and DLS2), middle-aged forest (about 60 years old: BWL4, BWL5, BWL6, DLS3, DLS4, DLS5, DLS6 and DLS7) and old-growth forest (more than 120 years old: BWL7, BWL8,

DLS8 and DLS9) (See fig. 1). The elevation of plots ranged from 300 m to 700 m in BWL and DLS, while the gradient ranged from 12° to 21°. Before shifting cultivation and selective logging had taken place, the primary vegetation in each site was tropical lowland rain forest, and the dominant species included *Vatica mangachapoi* and *Cyclobalanopsis patelliformis*. Each plot underwent natural restoration and there was no evidence of any additional disturbances. Because shifting cultivation had destroyed canopy cover and led to degraded, dry soils, both the young and middle-aged forests in BWL were dominated by drought-resistant deciduous trees, such as *Syzygium cumini* and *Liquidambar formosana*. The dominant species in old-growth forests in BWL, however, were evergreen trees such as *Vatica mangachapoi, Koilodepas hainanense*, and *Cyclobalanopsis patelliformis* because soil moisture had improved as the forest community recovered. The dominant species in plots in DLS, on the other hand, were evergreen trees such as *Schefflera heptaphylla* and *Sarcosperma laurinum* in the young forests, *Vatica mangachapoi, Gonocaryum lobbianum, Gironniera subaequalis* and *Maclurodendron oligophlebium* in the middle-aged forests, and *Vatica mangachapoi* and *Cyclobalanopsis patelliformis* in the old-growth forests.
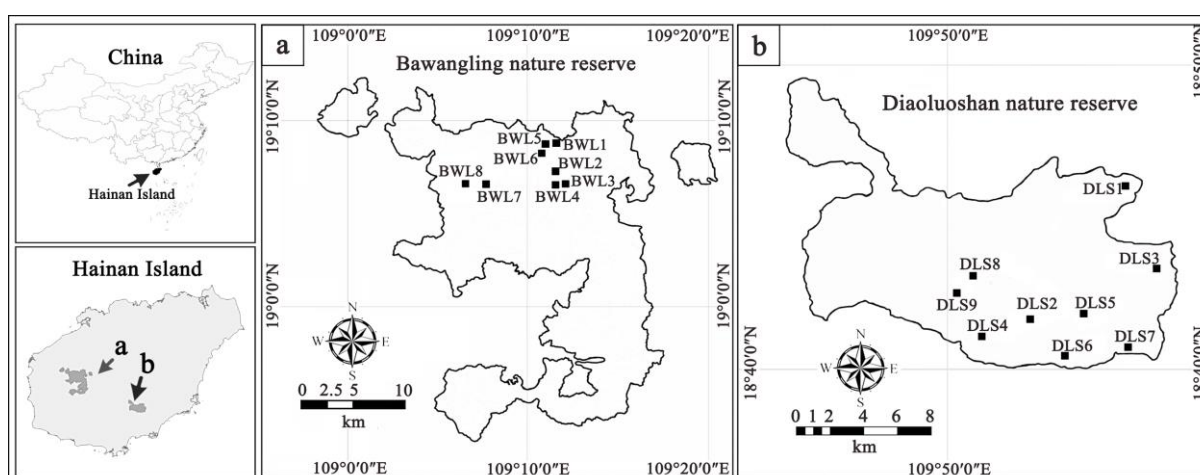
Fig. 1. A map showing the locations of the seventeen 0.25-hm² plots in Bawangling Nature Reserve (BWL) and Diaoluoshan Nature Reserve (DLS) .

We measured the height of all individual trees and shrubs (to the height of the highest sucker or shoot) in each of the study plots (excluding those clearly suckering from other trees), with DBH ≥ 1 cm. We used a clinometer to measure from the base to the highest point on a tree. Species names and their growth form were recorded in accordance with *Flora of China* (English edition: http://www.efloras.org).

Following standard vertical stratification division classification in tropical forests methods [29], and using Whittaker's Growth Form Classification System [30], the vertical community was divided into four sub-communities. These comprised the ground layer, where plant height was more than 1 m but less than 3 m; the regeneration layer, where plant height was more than 3 m but less than 5 m; the succession layer, where plant height was more than 5 m but less than 10 m; and the canopy layer, where plant height was more than 10 m. Species in each community were grouped, according to their growth forms, into 1) hierarchy species (plants which grow in a layer under canopies but do not appear in the canopy layer when they are mature), 2) regeneration species (plants that grow in low layers but also appear in the canopy layer), and 3) succession species (plants which grow in low layers but can also potentially appear in the canopy layer).

Data Analysis

Hypothesis 1: Were the patterns of species diversity within each vertical community consistent with those of the overall community after shifting cultivation and selective logging?

Species diversity within the overall community and within each of the four vertical communities were measured for the three successional stages using the *Observed Species Richness* (*OSR*) system, the *Shannon-Wiener Index* (*SW*) and the *Inverse-Simpson Index* (*I.Sim*), respectively. The abundance (*N*) of each species in the overall community and in each of the four vertical ones was measured. Species dominance and evenness of growth within each vertical community were assessed using a Species Rank-Abundance Distribution Curve with data $\log_e$ transformed. During the three successional stages differences in species diversity in the overall community and within each vertical community were assessed using a Randomization-Based Unilateral Test.

Hypothesis 2: Were the changes in species turnover between the vertical communities under the canopies and within the canopy communities similar after shifting cultivation and after selective logging?

First we took the Chao-Jaccard and Bray-Curtis dissimilarity coefficients to calculate Non-Metric Multidimensional Scaling (NMDS) in order to assess species dissimilarity in the three successional stages and in the different vertical communities. Next, we disaggregated the species dissimilarity coefficient into one part that showed changes in species composition and another part that shows changes in species abundance between vertical communities under canopies and canopy communities. Calculation of species dissimilarity coefficients is typically based either on binary data or on current species abundance estimations. Errors may appear when the two methods are used to calculate species dissimilarity between different vertical communities, as more species can be counted in low layers while higher layers are less accessible or even impenetrable. For example, the Sørensen and Bray-Curtis dissimilarity coefficients may count the species in low layers but, because of problems of access, cannot properly calculate the number of the species in the higher layers. This results in an overestimate of the dissimilarity between the layers. The Sørensen and Bray-Curtis dissimilarity coefficients used in this study, therefore, were divided into one part caused by constraints on species growth and another part caused by species replacements. The disaggregation processes were listed as follows.

The formulas for calculating the Sørensen dissimilarity coefficient (β_S, [31]) and the Bray-Curtis dissimilarity coefficient (β_B, [32]) were $\beta_S = \dfrac{b+c}{2a+b+c}$ and $\beta_B = \dfrac{\sum Bi + \sum Ci}{2\sum Ai + \sum Bi + \sum Ci}$, respectively. 'a' indicated the *OSR* common to two plots while $\sum Ai$ indicated the sum of *N* of the species common to two plots. 'b' indicated the *OSR* that appeared in the first plot but not in the second one, while $\sum Bi$ indicated the sum of *N* of the species that appeared in the first plot but not in the second one. 'c' indicated the *OSR* which appeared in the second plot but not in the first, while $\sum Ci$ indicated the sum of *N* of species which appeared in the second plot but not in the first. For the formulas, we first defined 'a' as the *OSR* of regeneration species and $\sum Ai$ as the sum of *N* of regeneration species in this study. Second, we let $b = b_1 + b_2$, $\sum Bi = \sum Bi_1 + \sum Bi_2$, and defined b_1 as the *OSR* of succession species and $\sum Bi_1$ as the sum of *N* of succession species. We also defined b_2 as the *OSR* of hierarchy species and $\sum Bi_2$ as the sum of *N* of hierarchy species. Third, we defined 'c' as the *OSR* of species which appear in high layers but not in lower ones, and $\sum Ci$ as the sum of *N* of species which appear in high layers but not in low ones. Finally, the Sørensen dissimilarity coefficient was divided into β_{S1} and β_{S2} using binary data, and the Bray-Curtis hierarchy dissimilarity coefficient was divided into β_{B1} and β_{B2} using community abundance data. $\beta_S = \beta_{S1} + \beta_{S2}$, and $\beta_B = \beta_{B1} + \beta_{B2}$, β_{S1} indicated the dissimilarity in species composition and abundance caused by species replacements, and β_{S2} showed dissimilarities in composition and abundance caused by growth form restriction.

According to the definition above, we calculated β_{S1} and β_{B1} between vertical communities under canopies (the ground layer, the regeneration layer and the succession layer) and canopy communities (the canopy layer) for each of the plots, in order to explore dissimilarities in both species richness and community abundance during forest succession. The β_{S1} and β_{B1} formulas were as follows:

$$\beta_{S1} = \frac{(b-b_2)+c}{2a+(b-b_2)+c} = \frac{b_1+c}{2a+b_1+c}$$

$$\beta_{B1} = \frac{(\sum Bi - \sum Bi_2)+\sum Ci}{2\sum Ai+(\sum Bi - \sum Bi_2)+\sum Ci} = \frac{\sum Bi_1+\sum Ci}{2\sum Ai+\sum Bi_1+\sum Ci}$$

We used presence-absence data to establish plot × species matrices showing species in the vertical communities under canopies and canopy communities, respectively, to calculate β_{S1}. The calculation not only included dissimilarities in species richness between the vertical communities under canopies and canopy communities of the same plots, but also included dissimilarities in species richness between the vertical communities under canopies of one plot and the canopy communities of the rest of the plots. For the plot in the old-growth forests, β_{S1} only referred to the dissimilarities in species richness between the vertical communities under canopies and canopy communities of the same plots. Also, we used abundance data to create matrices showing species in the vertical communities under canopies and canopy communities, respectively, in order to calculate β_{B1}. Differences in β_{S1} and β_{B1} among the three successional stages after shifting cultivation and selective logging had occurred were assessed using Randomization-Based Unilateral Tests. All data were analyzed in the statistical package R version 3.2.3.

Results

Patterns of overall species diversity after shifting cultivation and selective logging respectively.
Where shifting cultivation had occurred, *N* of the old-growth forest was significantly lower than young and middle-aged forests (Randomization-Based Unilateral Test, *P* = 0.002, *P* = 0.03; Appendix 1). However, the *OSR* and *SW* of the former were significantly higher than the latter (Randomization-based unilateral test, *OSR*, *P* = 0.002, *P* = 0.04; *SW*, *P* = 0.01, *P* = 0.03; Appendix 1), although *I.Sim* in old-growth forests was only significantly higher than in middle-aged forests (Randomization-Based Unilateral Test, *P* = 0.03; Appendix 1). In the plots where selective logging had occurred, *N* in middle-aged forests was significantly higher than in old-growth forests (Randomization-Based Unilateral Test, *P* = 0.02), and there were no significant differences in species diversity among the three recovery stages (see Appendix 1).

The *OSR*, *SW* and *I.Sim* of each forest community after shifting cultivation were significantly lower than after selective logging at each the recovery stages, while *N* of the former was significantly higher than the latter (Randomization-Based Unilateral Test, *P* < 0.001).

Patterns of species diversity in the four vertical communities after both shifting cultivation and selective logging.
For each of the four vertical communities in old-growth forests species evenness was higher while species dominance was lower, compared to growth in young and middle-aged forests after shifting cultivation had occurred (Fig. 2). The rank of species abundance in the three communities under canopies was young forest > middle-aged forest > old-growth forest, and the rank of abundance of canopy communities was middle-aged forest > young forest > old-growth forest. *N* of each vertical community in old-growth forests was significantly lower than in both young and middle-aged forests, and *N* of canopy communities in the young forests was significantly lower than in the middle-aged forests (Appendix 1 and 2; Fig. 3). The *OSR* and *SW* of each vertical community in old-growth forests,

however, were generally significantly higher than in young and middle-aged forests (Appendix 1 and 2; Fig. 3). The first axis of non-metric multidimensional scaling (NMDS) showed changes in species compositions in the three recovery stages after shifting cultivation, while the second axis showed changes in composition among the four vertical communities (Chao-Jaccard: stress = 0.11; Bray-Curtis: stress = 0.11, Fig. 4 a and c).

Where selective logging had occurred, abundance did not differ in the three successional stages of the four vertical layers (Fig. 2). N of the canopy communities in old-growth forests was significantly lower than in the young and middle-aged forests (Appendix 1 and 2; Fig. 3). No differences in the OSR, SW and $I.Sim$ of each vertical community were found in the three recovery stages (Appendix 1 and 2; Fig. 3). The first axis of NMDS showed changes in species composition among the four vertical communities (Chao-Jaccard: stress = 0.22; Bray-Curtis: stress = 0.21; Fig. 4 b and d). But the second axis did not show any patterns in species composition in the different stages.

Patterns of the $β_{S1}$ and $β_{B1}$ after shifting cultivation and selective logging
Both the $β_{S1}$ and $β_{B1}$ between young and middle-aged forests were lower than those between middle-aged and old-growth forests after shifting cultivation had occurred (Fig. 5; Appendix 3). Additionally, the $β_{S1}$ and $β_{B1}$ between both the young and middle-aged forests and the old-growth forest were greater than 0.77 and 0.93, respectively. However, neither of these dissimilarity coefficients differed between young and old-growth forests after selective logging (Fig. 5; Appendices 3 and 4). There were also no significant differences in $β_{S1}$ and $β_{B1}$ between the ground layer in middle-aged forests and the canopy layers in both middle-aged and old-growth forests after selective logging (Appendix 4).
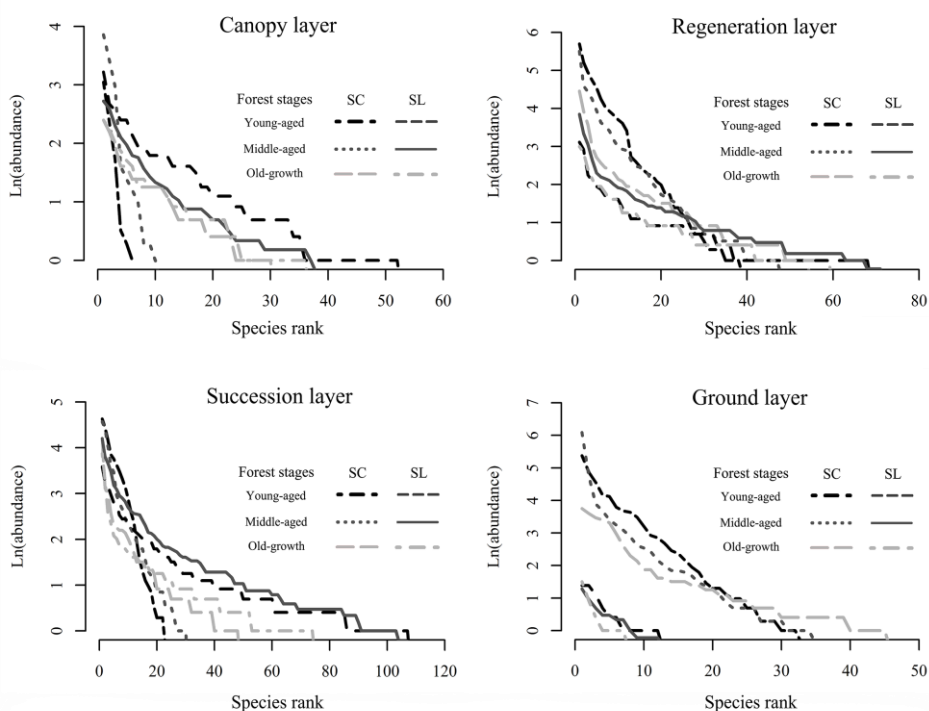
Fig. 2. Species rank-abundance distribution curves showing species dominance and evenness in each vertical community after shifting cultivation (SC) and selective logging (SL), respectively, have occurred.
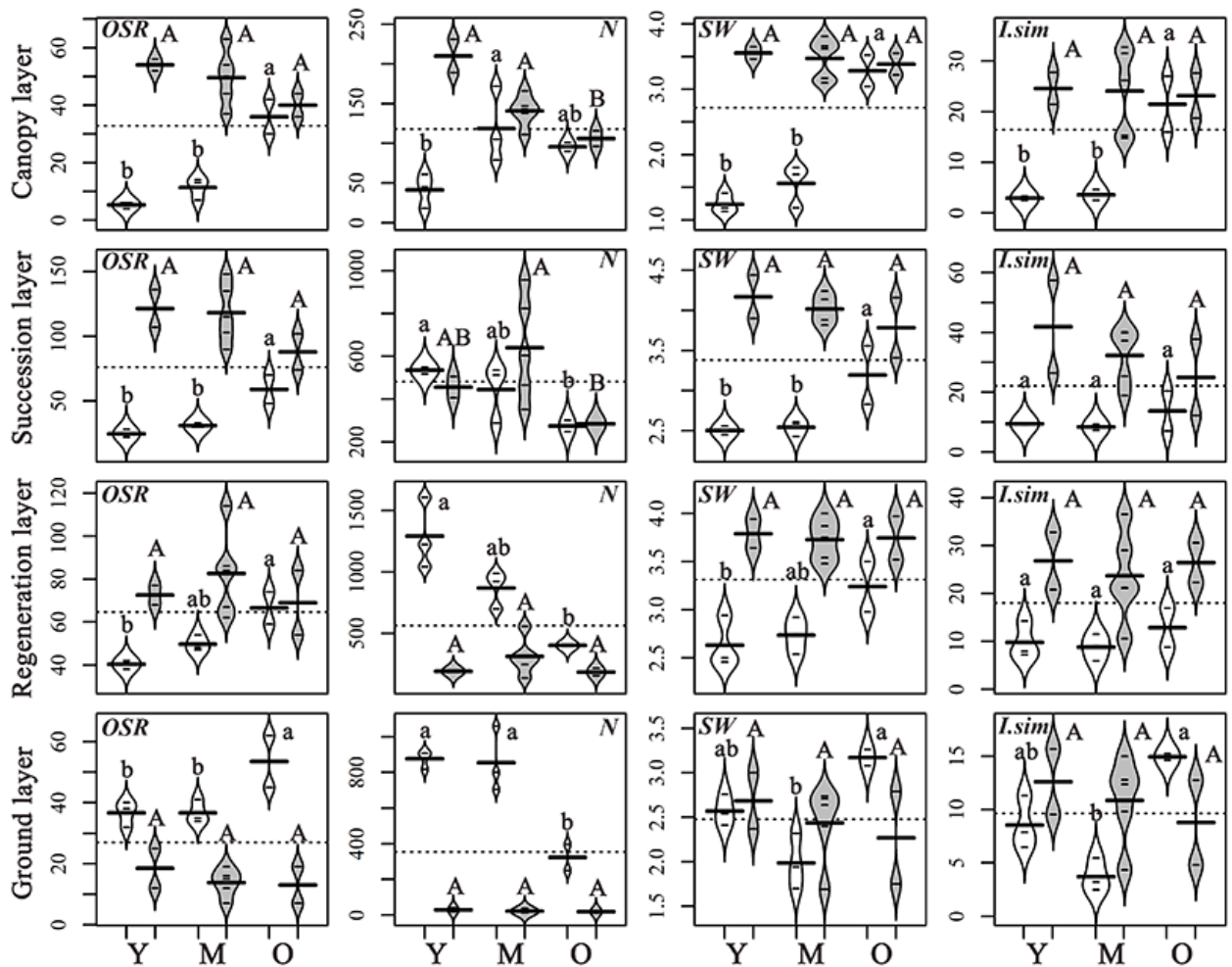
Fig. 3. Comparisons in Observed Species Richness (*OSR*), Number of individuals (*N*), Shannon Wiener's diversity index (*SW*) and Inverse Simpson's diversity index (*I.Sim*) in ground layer, regeneration layer, succession layer and canopy layer among young forest (Y), middle-aged forest (M) and old-growth forest (O) after shifting cultivation (in white) and selective logging (grey).
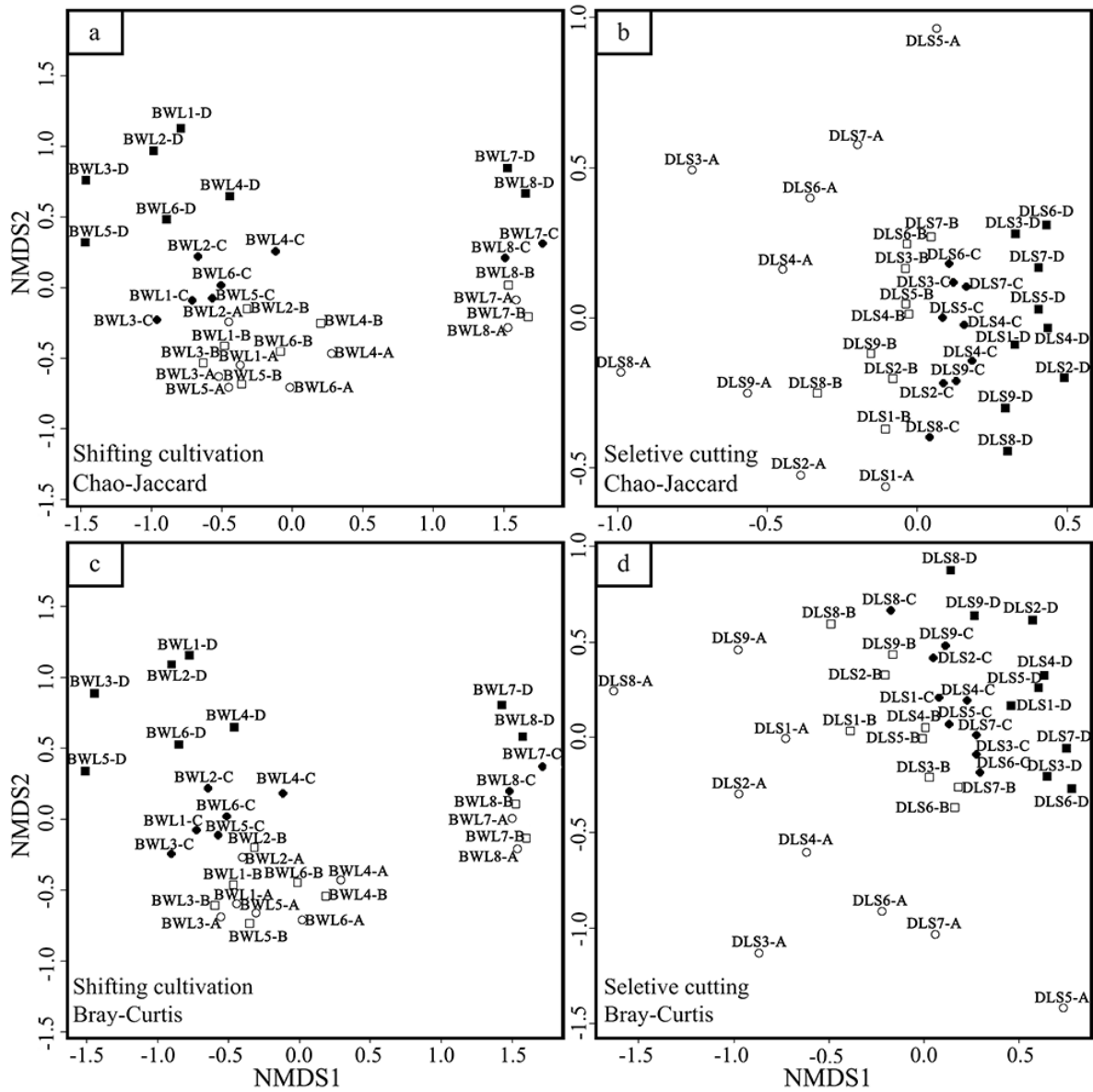
Fig. 4. Non-Metric Dimensional Scaling (NMDS) plots showing species composition in ground layer (A, ○), regeneration layer (B, □), succession ayer (C, ●), and canopy layer (D, ■) in each successional stage after shifting cultivation and selective logging have occurred. BWL1-8 and DLS1-9 show the plots after shifting cultivation and selective logging, respectively.
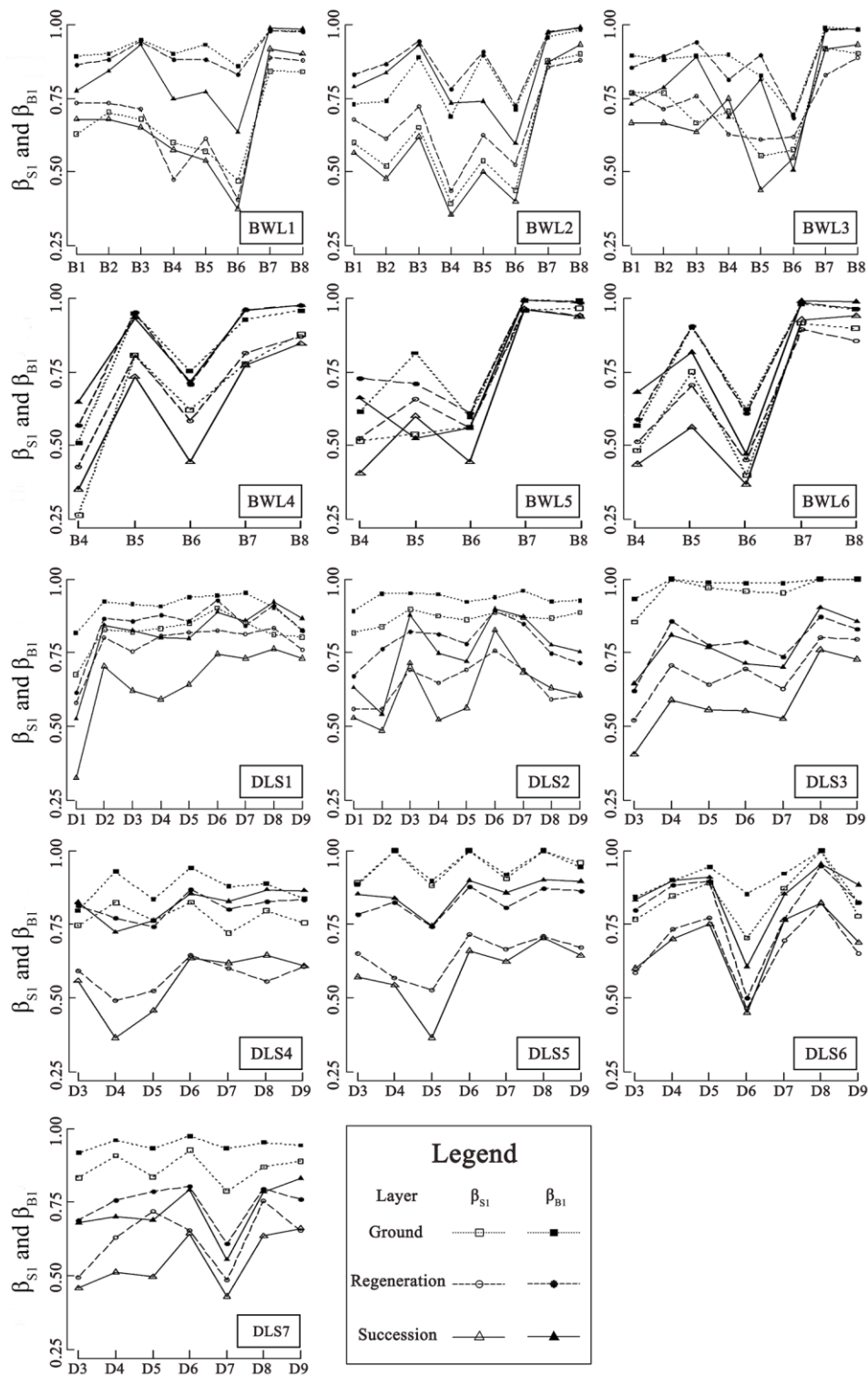
Fig. 5. Plots showing the changes in β_{S1} and β_{B1} between three vertical communities under canopies and canopy communities after shifting cultivation and selective logging, respectively. BWL1-8 and DLS1-9 show the plots where the vertical communities under canopies were after shifting cultivation and selective logging, respectively, and B1-8 and D1-9 show the plots where the canopy communities were.

Discussion

Hypothesis 1: Were the patterns of species diversity of each vertical community consistent with those of the overall community after shifting cultivation and selective logging respectively?
Overall species diversity increases after shifting cultivation but does not differ in the three recovery stages after selective logging.

While overall species diversity increases with community recovery after shifting cultivation, species abundance decreases. This pattern can be explained by the niche differentiation hypothesis. For example, in young and middle-aged forests, pioneer species with powerful sprouting ability [33, 34] rapidly colonize abandoned fields [35], so that although there is an abundance of growth, species diversity is limited. Because of intense competition, plant species in old-growth forests make more efficient use of ecosystem resources by reducing the abundance of their growth in favor of quality and richness. Hence, a large number of species may be more efficient in occupying niches, but niche differentiation stabilizes the coexistence of species [36]. On degraded soils in South China, the succession process is directly related to soil nutrition [37]. Environmental conditions become more heterogeneous during the late stages of succession (that is, in old-growth forests) and create more diverse opportunities for seedling and sapling growth than in previous stages. Thus, old-growth forest is associated with an increase in species diversity in all successional stages. These findings reinforce the point that diversity can increase asymptotically through succession [38] and further demonstrate that diversity increases asymptotically not only in primary succession processes [39] but also in secondary succession processes after shifting cultivation. We found no differences in overall species diversity after selective logging across the three successional stages. One possible reason is that the biological legacy (the seedlings and saplings) left after logging can quickly develop into canopy communities during the forest recovery process. Furthermore, most of the seed bank is usually well preserved [18], and seeds germinate quickly in vertical communities under canopies in young and middle-aged forests.

The fact that overall species diversity at each recovery stage after shifting cultivation is significantly lower than after selective logging shows that the recovery rate of species diversity after selective logging is faster than after shifting cultivation. A possible reason for this is that shifting cultivation in the tropical lowland rainforest of BWL not only destroys plants and propagules on the forest floor, but also damages the seed bank in the soil through repeated burning. The seed source for species recovery therefore comes mainly from the dispersal of seeds from surrounding forest plants, with a correspondingly small recovery rate [40]. In the case of selective logging in the tropical lowland rainforest in DLS, however, stumps, saplings and seedlings on the ground and seeds in the soil are well preserved. These propagules are sufficient for relatively rapid forest recovery, and have a high recovery rate [14, 18]. Our study therefore proves that anthropogenic disturbances (shifting cultivation and selective logging) influence the recovery rate of forest communities differently (Appendix 1): Secondary forests will take longer to return to climax forest after shifting cultivation than after selective logging [25, 41].

Patterns of species diversity in vertical communities are not consistent after shifting cultivation and after selective logging.
We found that after shifting cultivation changes in species abundance in the three vertical communities under canopies are consistent with that of the overall community (Fig. 2; Appendix 2). From early to late stages during community recovery the canopy density increases while understory light decreases. Accordingly, the competition for light among the species in vertical communities under canopies increases, and thus the density of plant individuals in these communities decreases [42], which leads to a decrease in species abundance. The evidence is that species abundance increases from young forests to middle-aged forests and this is probably due to improvements in community environments which favor deciduous and heliophilous evergreen plants that grow up into the canopy communities and enable the number of individual plants to increase. Conversely, the fact that species abundance in

the canopy communities decreases from middle-aged to old-growth forests may be due to the effects of competition, which result in stable species coexistence in old-growth forests. In the case of selective logging, species abundance in ground and canopy layers decreases from young to old-growth forests (Appendix 1), which is consistent with patterns of species abundance overall. In young and middle-aged forests, there is a biological legacy left after selective logging. When growing into forest communities, the recruitment of this biological legacy results in an increase in individual plant density. Plants in old-growth forests, however, show a uniform distribution pattern because of the effects of competition (Fig. 2), with a relatively low individual density.

The species rank-abundance distribution curves showed that less abundant species are still widespread in forest communities after selective logging but not after shifting cultivation (Fig. 2). Less abundant species have been proven to prefer special habitats [43]. The high DLS richness in these species suggests that environments recovery rapidly after selective logging, enabling the re-establishment of a diverse habitat. Our study also shows that rare species are important in structuring communities after selective logging, and reinforces the point that less abundant species play important roles in the natural ecosystem [44].

Hypothesis 2: Were the changes in species turnover between the vertical communities under canopies and the canopy communities similar after shifting cultivation and after selective logging?
The species composition in the canopy communities in middle-aged forests were similar to that of the vertical communities under canopies in young forests (Fig. 5; Appendix 3), demonstrating that the species in the canopy community in a late recovery stage have usually been regenerated from an earlier stage [45, 46]. In the plots recovering from shifting cultivation in BWL, we also found that the dissimilarity coefficients between the three vertical communities under canopies in young and middle-aged forests and the canopy communities in old-growth forests were more than 0.77 and 0.93 (Fig. 5) respectively. This suggests that there were great differences in species composition between early and middle recovery stages and late stages.

Once tropical lowland forests have been degraded by shifting cultivation in BWL they are classified as 'transformed monsoon rainforests' until they become restored to climax forests, with some deciduous species in the communities [47]. In this study, the young and middle-aged forests were transformed monsoon rainforests, and were dominated by *Syzygium cumini* and *Liquidambar formosana*. It has been demonstrated that the pattern of species diversity in these degraded forests is closely related to dry environments and poor soil conditions [25]. The dominant species in the old-growth forests are evergreen broad-leaved tree species, such as *Vatica mangachapoi*, *Koilodepas hainanense,* and *Cyclobalanopsis patelliformis*. Through analyzing the patterns of species dissimilarity between old-growth forests and the recovery stages after shifting cultivation, we predict that the present forest communities will succeed according to one of the following two paths, depending on the environmental recoveries: (1) the present forest community can probably recover to climax forest once soil moisture and nutrient levels have recovered, and deciduous species have been replaced by evergreen plant species [13]; or that (2) the present forest community will never recover to climax forest, and will stay in a disturbance climax (i.e. tropical monsoon rainforest) due to difficulties in environmental recovery [48].

Unlike after shifting cultivation, there was a high similarity in species composition between vertical communities under canopies in both young and middle-aged forests and canopy communities in old-growth forests (Fig. 5; Appendix 3 and 4). Seedlings, saplings and small trees in vertical communities under canopies in both early and middle stages have the potential to join canopy communities in late stages. The similarity in species diversity proves that species regeneration after selective logging is unproblematic in DLS. This helps us predict that the present forest communities in DLS can, according to the monoclimax hypothesis, recover to the state of old-growth forests [1]. Also, because the

saplings, young trees, stumps and soil seed bank in logged forests are well preserved in DLS, we can predict the rate of forest recovery after selective logging will be higher than after shifting cultivation in BWL [19].

Implications for conservation

The tropical rainforest on Hainan Island is an important part of the India-Malaysia rainforest, and it has been recognized as one of the hot spots of biodiversity distribution in China. Exploring changes in species diversity and community structure after shifting cultivation and selective logging has taken place can help inform objectives for forest management. In this study, we have shown that species replacement is compromised in young and middle-aged forests after shifting cultivation has occurred, whereas after selective logging it is not. Thus, our results indicate that there should be different forest management strategies for forest recovery after shifting cultivation and after selective logging.

First, shifting cultivation destroys plants and propagules on the ground and damages the seed bank in the soil through repeated burning. The surrounding forests are therefore critically important as a seed source for secondary forest recovery, and thus should be protected. Second, because shifting cultivation makes the forest environment dry and results in soil degradation, it is more difficult for deciduous species to be replaced by evergreen species, which is essential for the forest environment to recover. Third, the biological legacy: the saplings, young trees, stumps and the soil seed bank, is essential for forest recovery in logged forests, and thus should be well protected.

Acknowledgements

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Appendix 1. α species diversity in each vertical community at different successional stages after shifting cultivation and selecting logging, respectively. *OSR*, *SW*, *I.Sim* and *N* indicate the observed species richness, Shannon-Wiener Index, Inverse-Simpson Index and abundance, respectively. Y, M and O

indicate young forest, middle-aged forest and old-growth forest, respectively. DI, DT and VC indicate diversity indices, disturbance types and vertical communities, respectively.

DI	DT	VC	α species diversity		
			Y	M	O
OSR	Shifting cultivation	Ground layer	36.67±4.16	36.67±3.79	53.5±12.02
		Regeneration layer	40.33±2.08	49.67±3.79	66.5±10.61
		Succession layer	24.67±36	31±1.73	59±15.56
		Canopy layer	5.33±1.15	11.33±3.79	36±8.49
		Overall community	49.33±4.51	60±2.65	97.50±13.44
	Selective logging	Ground layer	18.5±9.19	13.8±4.55	13±8.49
		Regeneration layer	72.5±6.36	82.6±20.42	69±21.21
		Succession layer	121.5±20.51	118.2±23.49	88±19.8
		Canopy layer	54±2.83	49.6±9.86	40±5.66
		Overall community	156±19.8	151±26.7	132±21.21
N	Shifting cultivation	Ground layer	876.67±51.68	854.6±184.19	322.5±103.94
		Regeneration layer	1291.67±288.51	870.33±151.05	402.5±7.78
		Succession layer	535.33±16.5	444.67±137.03	274.5±37.48
		Canopy layer	41.33±21.73	118.67±47.98	95.5±7.78
		Overall community	2745±289.14	2288.33±116.47	1095±125.87
	Selective logging	Ground layer	28.5±14.85	21.2±10.5	18.5±9.19
		Regeneration layer	191±1.2	313.2±153.65	186.5±43.13
		Succession layer	455.5±70	640.2±249.89	284.5±3.54
		Canopy layer	210±29.7	141±19.84	106±14.14

		Overall community	882.5±84.15	1115.4±410.19	595±35.36
SW	Shifting cultivation	Ground layer	2.57±0.18	1.98±0.31	3.17±0.12
		Regeneration layer	2.63±0.27	2.74±0.19	3.24±0.36
		Succession layer	2.5±0.06	2.54±0.1	3.2±0.52
		Canopy layer	1.24±0.15	1.56±0.33	3.28±0.34
		Overall community	2.76±0.22	2.66±0.25	3.56±0.27
	Selective logging	Ground layer	2.69±0.45	2.44±0.44	2.27±0.73
		Regeneration layer	3.79±0.22	3.73±0.22	3.74±0.32
		Succession layer	4.17±0.38	4.02±0.18	3.79±0.53
		Canopy layer	3.55±0.14	3.47±0.31	3.39±0.24
		Overall community	4.31±0.29	4.14±0.2	4.2±0.34
I.Sim	Shifting cultivation	Ground layer	8.56±2.49	3.7±1.56	14.94±0.46
		Regeneration layer	9.79±3.88	8.81±2.82	12.85±5.78
		Succession layer	9.37±0.34	8.31±1.02	13.66±9.47
		Canopy layer	2.88±0.44	3.54±1.07	21.48±7.8
		Overall community	11.64±3.77	8.02±2.89	18.32±7.88
	Selective logging	Ground layer	12.6±4.35	10.86±4.09	8.78±5.63
		Regeneration layer	26.81±8.44	23.69±9.74	26.44±5.88
		Succession layer	41.86±21.94	32.26±9.63	24.91±18.07
		Canopy layer	24.59±4.48	24.09±8.65	23.14±6.3
		Overall community	43.54±19.77	34.16±11.44	36.84±17.92

Appendix 2. Differences in species diversity in each vertical community among the three successional stages using a Randomization-Based Unilateral Test. OSR, SW, I.Sim and N indicating the observed species richness, Shannon-Wiener Index, Inverse-Simpson Index and abundance, respectively. Y, M and O indicate young forest, middle-aged forest and old-growth forest, respectively. DI, VC and SS indicate diversity indices, vertical communities and successional stages.

DI	VC	SS	Shifting cultivation		Selective logging	
			Observation	*P*	*Observation*	*P*
OSR	Ground layer	Y-M	0.00	0.50	-4.70	0.82
		M-O	16.83	0.03	-0.80	0.55
		Y-O	16.83	0.03	-5.50	0.81
	Regeneration layer	Y-M	9.33	0.20	10.10	0.27
		M-O	16.83	0.07	-13.60	0.81
		Y-O	26.17	0.002	-3.50	0.57
	Succession layer	Y-M	6.33	0.38	-3.30	0.55
		M-O	28.00	0.04	-30.20	0.92
		Y-O	34.33	0.002	-33.50	0.92
	Canopy layer	Y-M	6.00	0.32	-4.40	0.72
		M-O	24.67	0.03	-9.60	0.89
		Y-O	30.67	0.002	-14.00	0.94
N	Ground layer	M-Y	-22.00	0.47	-7.30	0.21
		O-M	-532.17	0.02	-2.70	0.41
		O-Y	-554.17	0.02	-10.00	0.19
	Regeneration layer	M-Y	-421.33	0.11	122.20	0.91
		O-M	-467.83	0.11	-126.70	0.09
		O-Y	-889.17	0.002	-4.50	0.49
	Succession layer	M-Y	-90.67	0.21	184.70	0.80
		O-M	-170.17	0.09	-355.70	0.01
		O-Y	-260.83	0.02	-171.00	0.26
	Canopy layer	Y-M (Shifting cultivation) M-Y(Selective logging)	77.33	0.01	-69.00	0.03
		M-O	-23.17	0.70	-35.00	0.17
		Y-O	54.17	0.13	-104.00	0.003

SW	Ground layer	Y-M	-0.58	0.90	-0.25	0.69
		M-O	1.18	0.002	-0.17	0.62
		Y-O	0.60	0.12	-0.42	0.80
	Regeneration layer	Y-M	0.10	0.38	-0.06	0.65
		M-O	0.50	0.07	0.02	0.45
		Y-O	0.61	0.03	-0.04	0.58
	Succession layer	Y-M	0.04	0.48	-0.15	0.71
		M-O	0.65	0.03	-0.23	0.80
		Y-O	0.69	0.01	-0.39	0.89
	Canopy layer	Y-M	0.32	0.34	-0.08	0.63
		M-O	1.72	0.04	-0.09	0.64
		Y-O	2.04	0.004	-0.17	0.75
I.Sim	Ground layer	Y-M	-4.85	0.88	-1.75	0.65
		M-O	11.24	0.001	-2.08	0.71
		Y-O	6.38	0.08	-3.83	0.80
	Regeneration layer	Y-M	-0.98	0.62	-3.11	0.67
		M-O	4.04	0.14	2.75	0.37
		Y-O	3.05	0.21	-0.36	0.51
	Succession layer	Y-M	-1.06	0.59	-9.60	0.79
		M-O	5.34	0.18	-7.35	0.73
		Y-O	4.29	0.25	-16.95	0.89
	Canopy layer	Y-M	0.66	0.49	-0.50	0.54
		M-O	17.94	0.03	-0.94	0.56
		Y-O	18.60	0.01	-1.45	0.59

Appendix 3. β_{S1} showing the dissimilarity in species compositions and β_{B1} showing the dissimilarity in species abundance between vertical communities under canopies and canopy communities. Y, M and O indicated young forest, middle-aged forest and old-growth forest, respectively. DT, DC, VC and SS indicate disturbance types, dissimilarity coefficients, vertical communities and successional stages, respectively.

DT	DC	VC	Successional stages	Canopy communities		
				Y	M	O
shifting cultivation	β_{S1}	Ground layer	Y	0.67±0.08	0.54±0.09	0.88±0.03
			M	—	0.55±0.17	0.9±0.07
			O	—	—	0.46±0.06
		Regeneration layer	Y	0.72±0.05	0.55±0.09	0.87±0.02
			M	—	0.58±0.12	0.89±0.06
			O	—	-	0.46±0.09
		Succession layer	Y	0.63±0.07	0.5±0.12	0.91±0.02
			M	—	0.48±0.12	0.9±0.07
			O	—	—	0.43±0.09
	β_{B1}	Ground layer	Y	0.86±0.08	0.82±0.1	0.98±0.01
			M	—	0.7±0.16	0.97±0.02
			O	—	-1	0.66±0.02
		Regeneration layer	Y	0.89±0.04	0.82±0.08	0.98±0
			M	—	0.71±0.14	0.98±0.01
			O	—	-	0.67±0.16
		Succession layer	Y	0.84±0.07	0.69±0.1	0.99±0.01
			M	—	0.67±0.14	0.98±0.01
			O	—	—	0.64±0.19
selective logging	β_{S1}	Ground layer	Y	0.79±0.08	0.86±0.03	0.84±0.04
			M	—	0.87±0.09	0.9±0.1
			O	—	—	0.87±0.1
		Regeneration layer	Y	0.63±0.12	0.75±0.07	0.7±0.12
			M	—	0.62±0.09	0.7±0.09
			O	—	-	0.64±0.11
		Succession layer	Y	0.51±0.16	0.66±0.09	0.68±0.08
			M	—	0.55±0.11	0.69±0.07

			O	—	—	0.56±0.05
	β_{B1}	Ground layer	Y	0.9±0.06	0.94±0.02	0.89±0.05
			M	—	0.93±0.06	0.94±0.07
			O	—	—	0.94±0.05
		Regeneration layer	Y	0.73±0.11	0.85±0.04	0.8±0.09
			M	—	0.77±0.09	0.84±0.05
			O	—	—	0.76±0.09
		Succession layer	Y	0.64±0.15	0.83±0.06	0.83±0.08
			M	—	0.77±0.1	0.87±0.05
			O	—	—	0.65±0.08

Appendix 4. Differences in β_{S1} and β_{B1} among different successional stages using a Randomization-Based Unilateral Test after shifting cultivation and selecting logging have occurred. Y, M and O indicate young forest, middle-aged forest and old-growth forest, respectively. DT, VC and CC indicate disturbance types, vertical communities and canopy communities, respectively.

DT	VC	CC	β_{S1}	P	β_{B1}	P
shifting cultivation	Ground layer	M-Y	-0.13	0.04	-0.04	0.19
		M-O	0.34	<0.001	0.16	<0.001
		Y-O	0.22	0.003	0.12	0.01
		M-O	0.35	<0.001	0.27	<0.001
	Regeneration layer	M-Y	-0.17	0.01	-0.07	0.04
		M-O	0.32	<0.001	0.16	<0.001
		Y-O	0.15	0.02	0.09	0.02
		M-O	0.31	<0.001	0.27	<0.001
	Succession layer	M-Y	-0.13	0.07	-0.14	0.01
		M-O	0.41	<0.001	0.29	<0.001
		Y-O	0.29	0.001	0.15	0.02
		M-O	0.42	<0.001	0.32	<0.001
selective logging	Ground layer	Y-M	0.07	0.01	0.04	0.05
		O-M	-0.02	0.23	-0.04	0.06
		Y-O	0.05	0.09	<0.001	0.51
		M-O	0.04	0.14	0.01	0.29
	Regeneration layer	Y-M	0.12	0.02	0.12	0.01
		M-O	-0.05	0.8	-0.05	0.85
		Y-O	0.07	0.16	0.07	0.12
		M-O	0.09	0.01	0.07	0.01
	Succession layer	Y-M	0.15	0.02	0.19	0.004
		M-O	0.02	0.42	<0.001	0.51
		Y-O	0.17	0.02	0.19	0.01

		M-O	0.14	<0.001	0.10	<0.001