Chapter 2
The Extent of Biodiversity Recovery During Reforestation After Swidden Cultivation and the Impacts of Land-Use Changes on the Biodiversity of a Tropical Rainforest Region in Borneo

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Abstract Whereas many studies have addressed the effects of deforestation on biodiversity, few have focused on the recovery of diversity during reforestation. This study aimed at evaluating the recovery of, or chronosequential changes in, the biodiversity in the fallows (i.e., secondary vegetation or forests that form during the resting periods following harvest in shifting cultivation) of a tropical rainforest region in Borneo. We also aimed at determining the impacts of forest fragmentation and other land-use changes on biodiversity.

We established several study plots in fallows at different stages of succession, specifically, new fallows (rested for 1–3 years), young fallows (rested for 5–13 years), and old fallows (rested for 20–60 years). We also established study plots in a continuous primary forest and fragmented primary forests, extensive rubber gardens, and other land-use types. In addition, we investigated the diversity of trees, fungi, and animals, and compared the values obtained among the different land-use types.

With each progression in forest stage, the species richness, species density, and encounter rates increased for trees, fungi, army ants, and ants attending hemipterans. However, even after fallow periods of 20–60 years, the levels of diversity had not fully recovered to those recorded in primary forests. The biodiversity indices of fragmented primary forests were lower compared to those of the continuous primary forest for army ants. The biodiversity indices of extensive rubber gardens and the other land-use types were also lower compared to those of the continuous primary forest for bats. Such trends were also observed for aphyllophoraceous fungi and some insects.

These results indicate the irreplaceable value of continuous primary forests for conserving biodiversity. In contrast, the species richness of small mammals and phytophagous scarabaeid beetles was similar or even higher in fragmented primary forests and the other land-use types compared to the continuous primary forest. Further studies are necessary to investigate how the characteristics of each taxonomic group (e.g., disturbance tolerance, dispersal ability, and the life history traits) are related to the different types of disturbance (intensity, spatio-temporal configurations, and the consequent changes in the environmental factors of each habitat type).

Keywords Biodiversity • Fallow and secondary forest • Lambir Hills National Park • Sarawak • Swidden, shifting, and slash-and-burn agriculture

2.1   Introduction

A number of parameters contributing to the loss of biodiversity in tropical forests have been extensively studied, including the effects of forest fragmentation (e.g., Debinski and Holt 2000; Tscharntke et al. 2007), conventional and reduced-impact logging (RIL: e.g., Samejima et al. 2012), and land-use changes from primary forests to secondary forests or plantations (e.g., Barlow et al. 2007).

However, very few studies have focused on the recovery of biodiversity as forests regenerate to form old secondary forests (but see, e.g., Veddeler et al. 2005).

For centuries, swidden cultivation (i.e., shifting or slash-and-burn cultivation) has been an integral part of landscapes in tropical forests, which are crucial for biodiversity conservation (Mertz et al. 2009b; Padoch and Pinedo-Vasquez 2010). Some scholars regard swidden cultivation as a primary cause of deforestation and forest degradation (Freeman 1955; Lanly 1982). In contrast, other scholars claim that some traditional swidden cultivation is a sustainable practice for maintaining ecosystem services because of the complex patterns of fallow mosaics, which contain a mixture of vegetation at various stages of regrowth (Rerkasem et al. 2009; Padoch and Pinedo-Vasquez 2010).

To devise better strategies for biodiversity conservation in tropical forest regions, it is important to determine (1) the extent to which biodiversity recovers during the reforestation process in fallow periods of swidden cultivation and (2) the impacts of land-use changes and forest fragmentation on biodiversity.

2.1.1 The Tropical Rainforest of the Lambir Hills National Park (LHNP)

The primary lowland forests of the Southeast Asian tropics are characterized by extremely species-rich biodiversity (Whitmore 1998). The current project was conducted in and around the Lambir Hills National Park (LHNP; 4°08–12′ N, 114°00′–07′ E, 20–465 m a.s.l.), which is situated approximately 20 km south of Miri City and 10 km from the northwest coast of Borneo, in the northern part of the state of Sarawak, Malaysia (Fig. 2.1). The LHNP was established in 1975, and forms part of a forest reserve in a water catchment area for Miri City, covering 6,949 ha of land (Hazebroek and Abang Kashim bin Abang Morshidi 2000; Ichikawa 2007). The average annual rainfall and mean air temperature in the LHNP from 2000 to 2009 were 2,600 mm and 25.8 °C, respectively (Kume et al. 2011). The region is subject to irregular and short-term droughts; however, there is no regular dry season, as such (Kume et al. 2011). The national park is mainly covered with a primary lowland mixed dipterocarp forest (Hazebroek and Abang Kashim bin Abang Morshidi 2000), which is formed on nutrient-poor sandy or clay soil (Watson 1985). The forest is multi-layered, with a canopy approximately 35–50 m in height and emergent trees (i.e., trees rising above the canopy) reaching a maximum height of 70 m (Kato et al. 1995). The forest potentially contains the richest tree diversity in the Old World, with a record number of 1,175 tree species in a 52-ha plot (Condit et al. 2000; Ashton 2005; Corlett 2009). Arthropod assemblages are also highly diverse. For example, 347 butterfly species have been reported to occur in the primary forest and surrounding areas of the LHNP (Itioka et al. 2009).
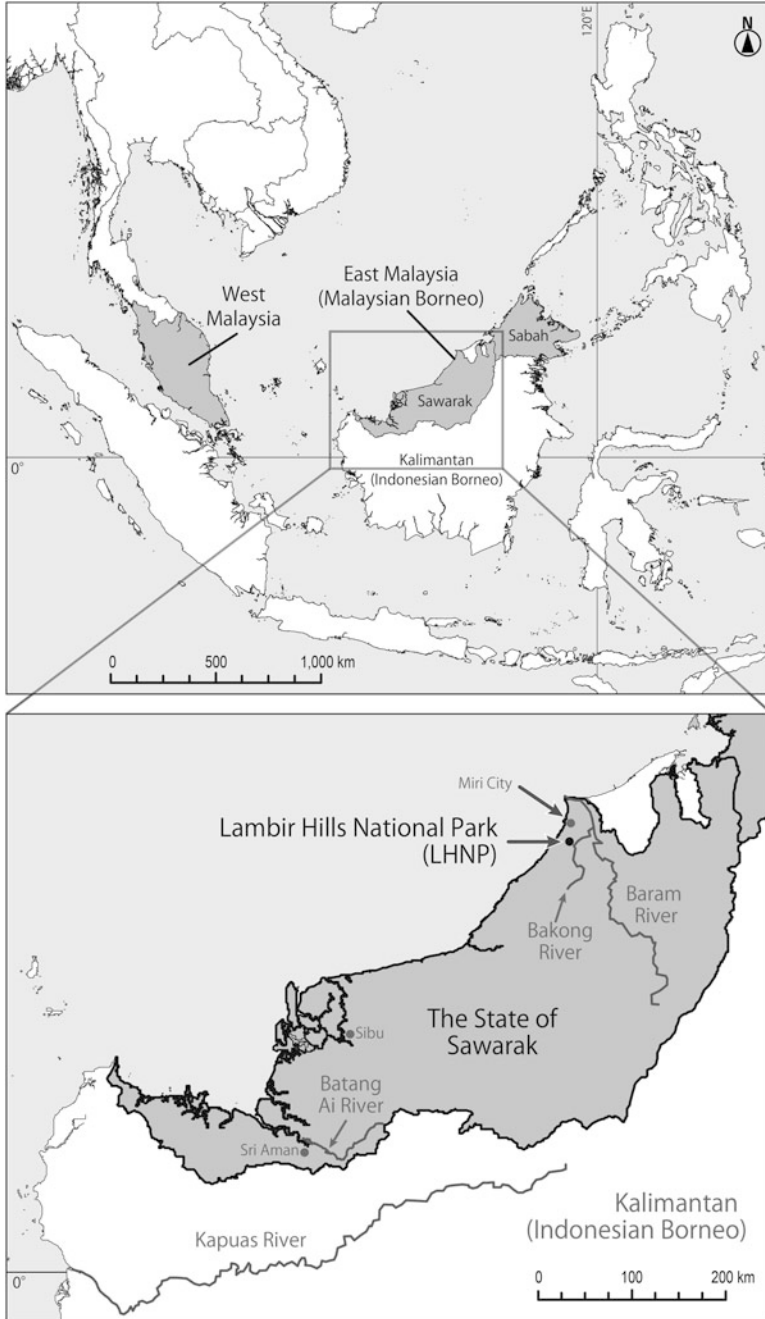
Fig. 2.1 The location of the Lambir Hills National Park in Sarawak, Malaysian Borneo

2.1.2   Traditional Swidden Cultivation by the Iban Around the LHNP

Swidden cultivation in Malaysian Borneo is mainly practiced by more than 50 ethnic groups that have traditionally inhabited rural areas, including the Iban, Bidayuh, Kayan, Murut, and Dusun tribes (Mertz et al. 2009a). Ichikawa (2010) described the practice of swidden cultivation by the Iban who inhabit villages near the LHNP in 1995. In the author's description, forest stands (0.46 ha on average, $n = 14$) of fallows that had rested for periods of 7–10 years were cleared with bush-knives, axes, and fire. Rice and other crops (e.g., maize, cassava, and vegetables) were cultivated for just 1 year. Subsequently, the fields were allowed to revert into secondary forests.

Freeman (1955) reported that, after the clearance of a primary forest stand, the Iban of Sarawak continue cropping for a few years until the productivity of the land declines. In contrast, when a secondary forest stand is cleared, the area is only cropped for 1 year (but see Sect. 2.4.1 of this chapter). A wide range in fallow lengths has been reported, lasting from 3 to more than 25 years (Freeman 1955; Padoch 1982; Cramb 1993). Since the speed of forest succession differs at each location, Iban farmers usually judge where to open a new swidden based on the girth of trees and other forest structures, rather than the duration of fallow periods (Padoch 1982; Dove 1985).

2.1.3   Indigenous Categories of Land-Use by the Iban

The Iban have several land-use categories, specifically: (1) *kampong*, which is a primary forest that has not been farmed within historical memory, including a previously farmed forest that is currently difficult to distinguish from primary forests; (2) *umai*, which is a currently cultivated swidden field; (3) *jeremi* or *redas*, which is a recently fallowed field that has rested for 1 year following the last harvest; (4) *temuda*, which is a young secondary forest with a fallow period of 2–10 years; (5) *damun*, which also refers to a young secondary forest that regenerated during fallow periods of 10–20 years, depending on the nature of the soil and human population pressure; (6) *pengerang, which is an old secondary forest, where* the vegetation resembles that of a primary forest, having been left uncultivated for 20 years or more; (7) *pulau galau*, which is a special tree reserve designated to ensure the availability of logs for house construction; and (8) *kebun*, which contains rubber and fruit tree groves (Table 2.1, Fig. 2.2; Freeman 1955; Wadley et al. 1997; Ichikawa 2007).

Under customary land-use by the Iban, a household that clears a stand of a primary forest gains ownership of the land, and the title of the land is inherited by the family's descendants (Ngidang 2005). However, the Sarawak Land Code limits the right to land first-cut to before 1958 (Ngidang 2005). Therefore, current

Table 2.1 The classification of the study plots in relation to the indigenous categories of land-use by the Iban

Classification of plots in the current study	Continuous primary forest	Not studied	New fallow	Young fallow	Old fallow	Fragmented primary forest	Extensive rubber garden	Fruit tree grove
Explanation	The primary forest in the national park	Currently cultivated swidden fields	Recently fallowed fields rested for 1–3 years after cropping	Younger secondary forests regenerated during fallow periods of 5–13 years	Older secondary forests regenerated during fallow periods of 20–60 years	Special tree reserves for logs for house construction	Small-scale extensive rubber gardens	Fruit tree groves
Indigenous category	*kampong*	*umai*	*jeremi* or *redas*	*temuda*	*damun pengerang*	*pulau galau*	*kebun*	
Years after swidden cultivation	No significant disturbance within historical memory	0 year	1 year	2–10 years	10–20 years ≥20 years	No significant disturbance within historical memory	Variable	
Swidden cycle	⇠···→	→	→	→	→			
Customary rights	Open access	Individual (household) tenure						

Fig. 2.2 General view of the study plots at different stages of regeneration or subject to different types of land use. (**a**) Currently cultivated swidden field (dissemination after slash and burn). (**b**) New fallow. (**c**) Young fallow. (**d**) Old fallow. (**e**) Continuous primary forest of the Lambir Hills National Park. (**f**) Fragmented primary forest. (**g**) Extensive rubber garden. See Table 2.1 for details about each land-use type. Photographs by Kato Y. (**a**) and Tanaka H.O. (**b–g**)

swidden cultivation is basically repeated within secondary forests, where the customary rights were established before 1958 (but see Ichikawa 2010).

2.1.4 History of Land-Use Alterations in the Study Area

Ichikawa (2003, 2007, 2010) documented the history of land-use change around the LHNP, which is summarized in the following text.

2.1.4.1 Immigration of the Iban

Sarawak is home to approximately 2.7 million inhabitants (Department of Statistics Malaysia 2004) and has a population encompassing various ethnic groups. The largest native ethnic group is the Iban, who represent more than 30 % of the population (Department of Statistics Malaysia 2004). The Iban are believed to have emigrated from the Kapuas River basin, currently West Kalimantan, Indonesia, and settled in Sarawak, on the Malaysian side of Borneo. Sandin (1967) reported that the Iban settled in the Batang Ai River basin, which is close to today's Sri Aman and Sibu Divisions, 14 generations ago. The Iban then emigrated from Sri Aman and Sibu Divisions and settled in the Bakong River basin, which is where the LHNP is located, from the end of the ninetieth century to the early twentieth century (Pringle 1970; Sandin 1994). Before the Iban settled in this region, much of the Bakong area was the territory of hunter-gatherers and was covered with primary forests (Ichikawa 2007).

2.1.4.2 Swidden Cultivation

The immigrants collected forest products to sell, such as wild rubber and rattan, while cutting the primary forest around their longhouses for swidden cultivation. Until the 1960s, hill swiddens were important for the Iban and were larger in size compared to paddy fields established in the swamps. This is because hill rice tasted and smelled better than wet rice at that time, and because other products from hill swiddens were important for subsistence under an economy that was more self-sufficient compared to that of today. The area covered by hill swiddens decreased from 1963 to 1997 (Ichikawa 2007), with almost no swidden cultivation being observed around the LHNP after 2000 (Ichikawa, personal observation). The reasons for the reduction in hill swiddens include (1) an increase in rice production from paddy fields in the swamps after the 1970s and (2) a decrease in the importance of hill swidden products, since it became possible to buy vegetables and root crops from nearby markets(Ichikawa 2007).

2.1.4.3 Other Types of Land Uses

Small-scale patches of Para rubber (*Hevea brasiliensis*, Euphorbiaceae) were planted after swidden cultivation in the 1950s and early 1960s (Ichikawa 2003). Rubber was planted when the international market prices were high; however, the trees were not adequately harvested and managed when rubber prices dropped. Various tree species grow naturally in rubber gardens where rubber tapping has not been conducted for several years.

Commercial selective logging on a relatively small scale was conducted by small Chinese companies after the mid-1970s. Immediately after areas were subjected to logging activity, the Iban cut and burned the remaining trees to create swiddens. The Chinese companies continued to operate until the end of the 1980s, cutting all remaining large-trunked trees.

The Iban began to sell fruit in Miri City after the 1980s. Groves containing various types of fruit trees have been created around work huts that are primarily used for the preparation of rice. From the late 1980s onward, fruit trees were planted around the huts and in any location where secondary forests had been opened.

After 2000, several patches of oil palm gardens (1–2 ha in size) were created near roads to sell the products to nearby oil processing factories at reasonable prices. The oil palm gardens were cultivated by some Iban who had a certain amount of capital and land near roads, from which the products could be easily transported out. In Malaysia, the oil palm area has increased rapidly from 1.8 million ha in 1990 to 4.2 million ha in 2005 (FAO 2010), during which time 1.1 million ha of primary forest have been lost (Fitzherbert et al. 2008).

Consequently, primary forests outside the LHNP had almost completely disappeared by 1997 (97 % of the study area of Ichikawa 2007). Currently, the LHNP is surrounded by a mosaic of fallows, fragmented primary forests, extensive rubber gardens, fruit tree groves, small- to large-scale oil palm plantations, logged forests, and wet paddies.

2.2 Study Design

In total, 46 study plots were established in and around LHNP between 2003 and 2011. The area of each plot ranged in size from approximately 0.1 ha to 0.5 ha (Fig. 2.3). We interviewed land-holders and classified the plots into the following categories: (1) new fallows, rested for 1–3 years after cropping; (2) young fallows, rested for 5–13 years; (3) old fallows, rested for 20–60 years; (4) fragmented primary forests, which have not been significantly disturbed for 100 years or more; and (5) continuous primary forest, which is the protected tropical rainforest in the national park. We also established study plots in extensive rubber gardens, fruit tree groves, and oil palm plantations (Table 2.1, Fig. 2.2).
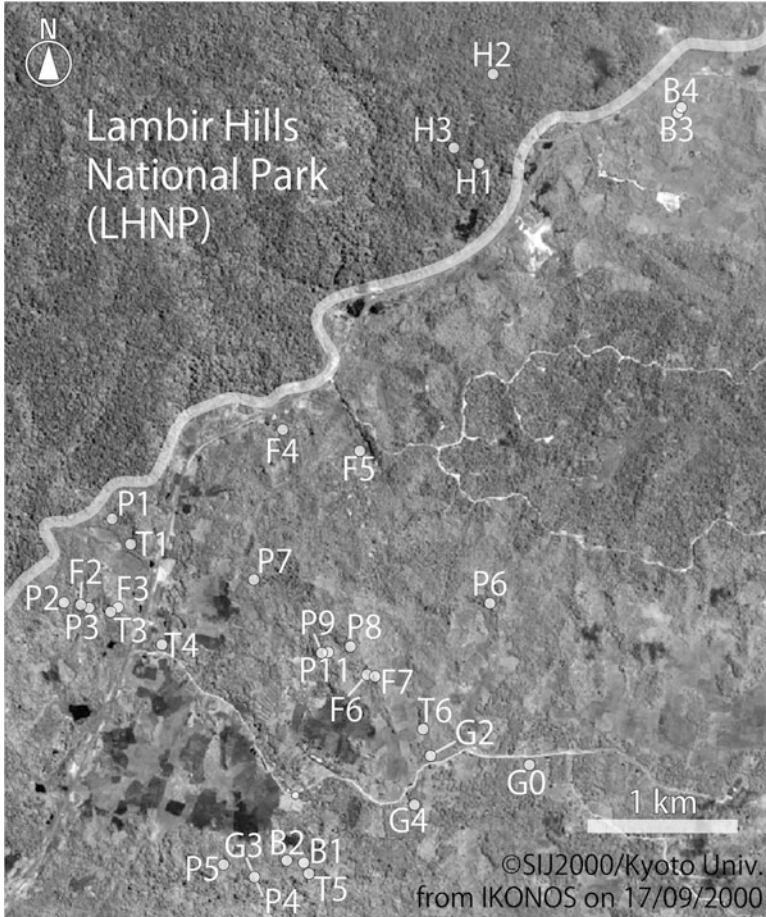
Fig. 2.3 Spatial distribution of the study plots in and around the Lambir Hills National Park (LHNP). Different letters indicate different types of land use: (H) continuous primary forest in the LHNP, (P) fragmented primary forest, (F) old fallow, (T) young fallow, (B) new fallow, and (G) extensive rubber gardens. The locations of fruit tree groves and oil plantations are not shown. See Table 2.1 for details about each land-use type

In these plots we investigated the diversity of trees, aphyllophoraceous fungi, small mammals, bats, phytophagous scarabaeid beetles, army ants, and ants that interact mutually with plants and hemipterans. The combination of study plots differed for each investigation (Table 2.2).

Subsequently, biodiversity indices were estimated for each taxonomic group and were compared among those obtained for the different stages of regeneration or land-use types. See the original published articles for detailed information about each taxon, sampling methods, and estimation of biodiversity indices.

Table 2.2 Number of study plots for each land-use type in each of the studies, presenting the diversity indices affected by swidden cultivation

Taxon/biological group	Land-use type								Diversity indices affected by swidden cultivation	References
	New fallow	Young fallow	Old fallow	Fragmented primary forest	Continuous primary forest	Extensive rubber plantation	Fruit tree grove	Oil palm plantation		
Trees		10	13	9	9	5			Species diversity, species composition, and the abundance of rare, endemic, and upper-layer trees	Nakagawa et al. (2013)
Aphyllophoraceous fungi		2	2	2	2	2			Species density and species composition in new fallows	Yamashita et al. (2008)
Small mammals	3	3	3	6	2	3			Species composition in new fallows, but not for the other land-use types	Nakagawa et al. (2006)
Bats	1	1	1		6		3	5	Simpson's index of diversity	Fukuda et al. (2009)
Phytophagous scarabaeids	3	3	3	5	3	3			Evenness and species composition in new fallows, but not for the other land-use types	Kishimoto-Yamada et al. (2011)
Army ants	2	2	2	2	2				Encounter rates	Matsumoto et al. (2009)
Trees with extrafloral nectaries	4	5	6		6				Species richness	Tanaka et al. (2007)
Trees with hemipterans	4	5	6		6				Species richness	Tanaka et al. (2007)
Trees with hemipteran-attending ants	4	5	6		6				Species richness	Tanaka et al. (2007)

(continued)

Table 2.2 (continued)

Taxon/biological group	Land-use type								Diversity indices affected by swidden cultivation	References
	New fallow	Young fallow	Old fallow	Fragmented primary forest	Continuous primary forest	Extensive rubber plantation	Fruit tree grove	Oil palm plantation		
Macaranga myrmecophyte	4	5	6	6	6				Species richness, frequency	Tanaka et al. (2007)
Extrafloral nectaries-attending ants	4	5	6	6	6				Species richness	Tanaka et al. (2007)
Hemipteran-attending ants	4	5	6	6	6				Species richness	Tanaka et al. (2007)
Tree with weaver ants	4	5	6	6	6				Frequency	Tanaka et al. (2007)

2.3   Recovery of Biodiversity During Fallow Periods and the Effect of Land-Use Changes on the Biodiversity of Each Taxonomic Group

2.3.1   Trees

Forest structure and tree species composition are fundamentally important habitat characteristics for a diverse range of animals and fungi. Nakagawa et al. (2013) conducted a census in 39–46 study plots and recorded 2,828 trees, representing 552 species from 58 families. Subsequently, the authors analyzed tree community structure (including trunk density, trunk basal area, tree diversity, abundance of rare, endemic, and upper-layer trees, and species composition).

A comparison of species composition implied that succession progresses steadily during fallow periods. Little distinction in species composition was observed among young and old fallow plots, indicating the relatively quick recovery of the tree community during the early stages of succession. However, the values of stem density, basal area, tree diversity, and the abundance of rare, endemic, and upper-layer trees were smaller in old fallows compared to continuous and fragmented primary forests.

The results of this study indicate that the tree communities of secondary forests had not fully recovered, even after fallow periods of 20–60 years.

2.3.2   Aphyllophoraceous Fungi

Yamashita et al. (2008) collected 155 fruiting bodies, representing 67 species of polypores, hydnoid fungi, and stereoid fungi. The authors reported that the species density (Gotelli and Colwell 2001), which was represented by the number of fungus species per 200 m^2, gradually increased from young fallows, old fallows, fragmented primary forests, and extensive rubber gardens to continuous primary forests. This observation indicates how fungal diversity partly recovers during the process of forest succession. However, the level of species density in old fallows was approximately one-third that of the primary forest.

Several environmental variables were also recorded (including canopy openness, water potential, amount and composition of coarse woody debris, litter mass, tree basal area, and tree species composition), of which the amount of coarse woody debris was significantly and positively correlated with fungal species density. Fungal species density was also correlated with principal component analysis scores for tree species composition. However, only the amount of coarse woody debris significantly affected the species composition of fungi.

2.3.3   Small Mammals

Nakagawa et al. (2006) collected 283 individuals of small mammals, representing 22 species belonging to the orders of Scandentia, Rodentia, and Insectivora. Small mammals in new fallows formed a distinctive group in an analysis of species composition, with a high emergence of human-associated rats and arboreal tree shrews. However, the structure of small mammal communities was similar in the other forest types, indicating that the various forest uses, except for new fallows, do not have a major impact on the structure of small mammal communities.

2.3.4   Bats

Fukuda et al. (2009) collected 495 bats, representing 28 species. The authors compared bat diversity for different land-use types, including the primary forest, fallows (new, young, and old fallows combined), fruit tree groves, and oil palm plantations. Simpson's index of diversity was relatively high in the primary forest (7.86) compared to fallows (3.38), fruit tree groves (3.65), and oil palm plantations (1.24). The authors also investigated the feeding habits of megachiropterans (i.e., large bats) by collecting pollen samples from the heads of captured bats. The authors suggested that many species of bats rarely use fruit tree groves and oil palm plantations for feeding. These results indicate that fruit tree groves and oil palm plantations are not suitable for maintaining bat diversity; however, these habitats may provide important food sources for a few species of megachiropterans.

2.3.5   Phytophagous Scarabaeid Beetles

Kishimoto-Yamada et al. (2011) used light traps and collected 3,230 beetles, which represented at least 51 morpho-species of phytophagous scarabaeids (Coleoptera). Estimated species richness did not differ significantly among forest types. The results of this study indicate that fallows at various stages of succession, except for new fallows, tend to maintain phytophagous scarabaeid diversity at a similar level to that found in the primary forest. The authors suggested the roles of complex mosaic landscapes, containing combinations of continuous and fragmented primary forests and fallows, should be re-evaluated in terms of biodiversity conservation.

2.3.6   Army Ants

Matsumoto et al. (2009) assessed the encounter rates of army ant *Aenictus* spp. (Hymenoptera: Formicidae) colonies present in different forest types. This genus

represents one of the top predators in litter-arthropod assemblages. Encounter rates were the highest in continuous and fragmented primary forests, intermediate in old and young fallows, and lowest in new fallows. This finding indicates that the abundance of top leaf-litter predators, which are rare and likely to be vulnerable to disturbance, did not fully recover even after fallow periods of 20 years. In terms of forest management strategies to sustain biodiversity, the study suggests it is necessary to preserve primary forests, rather than extending fallow periods, in tropical forest regions where traditional swidden cultivation is performed.

2.3.7   Mutually Interacting Plants, Ants, and Hemipterans

Tanaka et al. (2007) investigated the frequency of occurrence and composition of species involved in ant-associated mutualistic interactions with plants and hemipterans. Species richness was higher in the primary forest compared to fallows for trees bearing extrafloral nectaries, for trees with hemipteran-attending ants, and for ants attending both extrafloral nectaries and hemipterans. More than 80 % of species observed in the primary forest were not recorded in fallows. Myrmecophyte *Macaranga* spp. exhibited higher species richness and the frequency of occurrence in the primary forest compared to fallows. The number of myrmecophyte *Macaranga* species observed in fallows was approximately one-third of the number in the primary forest. In contrast, the weaver ant, *Oecophylla smaragdina*, which tends to exclude other arboreal ant species, was significantly more abundant in fallows compared to the primary forest. These results indicate swidden cultivation drastically decreases the diversity of species involved in ant-plant or ant-hemipteran mutualistic interactions.

2.4   Discussion

2.4.1   Recovery of Biodiversity During the Reforestation Process and the Effects of Swidden Cultivation on Biodiversity

In the current study, species richness, species density, and encounter rates increased from new (or young) to old fallows for trees (Nakagawa et al. 2013), fungi (Yamashita et al. 2008), army ants (Matsumoto et al. 2009), and ants attending hemipterans (Tanaka et al. 2007). This trend was also observed for forest-edge-dwelling butterflies (Itioka et al. 2014) and beetles that use coarse woody debris.

In contrast, even after fallow periods of 20–60 years, the levels of species diversity in old secondary forests had only recovered to approximately one-third

to two-third of that recorded in continuous and fragmented primary forests for trees (Nakagawa et al. 2013), fungi (Yamashita et al. 2008), army ants (Matsumoto et al. 2009), trees bearing extrafloral nectaries (Tanaka et al. 2007), and ants attending both extrafloral nectaries and hemipterans (Tanaka et al. 2007). These trends were also observed for forest-edge-dwelling butterflies (Itioka et al. 2014) and beetles that use coarse woody debris (Takano et al., unpublished data). These results indicate that swidden cultivation has significant impact on the biodiversity of the tropical forest region in Borneo. Preserving primary forests is essential to sustain the biodiversity of landscape mosaics created from the crop-fallow cycles of swidden cultivation.

Chazdon et al. (2009) hypothesized that the conservation of primary-forest species in secondary forests would be maximized in older secondary forests that have persisted where anthropogenic disturbance after abandonment is relatively low. The authors also suggested how the conservation value of such secondary forests would increase over time, due to the accumulation of species arriving from remaining primary forest patches.

In the practice of swidden cultivation, the fallow-forest phase serves the function of restoring carbon and nutrient stocks in the biomass, improving soil physical properties, and suppressing weeds (Palm et al. 2005). The length of fallow periods has been reported to vary widely from 3 years to more than 25 years in Malaysian Borneo and Indonesian Kalimantan (Freeman 1955; Padoch 1982; Cramb 1993; Mertz and Christensen 1997; Ichikawa 2010). Recently, the length of fallow periods has mainly declined in Southeast Asia (Schmidt-Vogt et al. 2009), while the length of cropping periods has increased in some parts of Sarawak (Ichikawa 2010). This change is probably due to population pressure (Hansen and Mertz 2006), shortage of farmland for certain households (cf. Coomes et al. 2000), and a need for shorter travel distance to the fields (Nielsen et al. 2006; Ichikawa 2010). Shortened fallow periods and elongated cropping periods are realized by the use of herbicides and fertilizers in some parts of Sarawak (Ichikawa 2010). However, the shortening of fallow periods may have further negative impacts on the biodiversity of these secondary forests.

2.4.2 Effects of Other Land-Use Changes on Biodiversity

Hattori et al. (2012) suggested that older secondary forests, reduced-impact logged forests, and matured tree plantations might be of some importance for the conservation of some fungal species. In the current study, the biodiversity indices of aphylloraceous fungi in extensive rubber gardens were lower than those in the continuous primary forest, but were higher compared to those in the fallows (Yamashita et al. 2008). This trend was also observed for phytophagous scarabaeid beetles (Kishimoto-Yamada et al. 2011) and beetles that use coarse woody debris (Takano et al., unpublished data). The amount of coarse woody debris was the important environment factor that explained fungal species density in different

study plots (Yamashita et al. 2008). In general, the amount of coarse woody debris in the rubber gardens was intermediate between the amounts in fallows and in primary forests. Hence, this environmental factor might explain the relatively higher biodiversity of aphyllophoraceous fungi and beetles using coarse woody debris in the extensive rubber gardens.

Fukuda et al. (2009) reported that the species richness of bats did not differ between fallows (new, young, and old fallows combined) and the continuous primary forest. In comparison, the lowest bat species richness was recorded in oil palm plantations, followed by fruit tree groves. The authors suggested that secondary forests in fallows potentially maintain bat diversity, whereas fruit tree groves and oil palm plantations provide inadequate habitats for most frugivorous and insectivorous bats.

Oil palm plantations are known to support far fewer wildlife species compared to primary forests and often have fewer species compared to other tree crops and secondary forests (Fitzherbert et al. 2008). There were not enough data available for the current study to compare the biodiversity in fallows, rubber gardens, and oil palm plantations. Further studies are necessary to evaluate the biodiversity conservation value of different types of land use to identify better strategies for balancing human activity and biodiversity conservation.

2.4.3 Effects of Fragmentation and Distance from Continuous Primary Forests on Biodiversity

Encounter rates of army ants decreased in fragmented primary forests compared to continuous primary forest (Matsumoto et al. 2009). The species density of aphyllophoraceous fungi was also slightly lower in fragmented primary forests compared to continuous primary forest (Yamashita et al. 2008). Such trends were also observed for the species richness of forest-edge-dwelling butterflies (Itioka et al. 2014) and beetles that use coarse woody debris (Takano et al., unpublished data). These results indicate how the fragmentation of the primary forest has a negative impact on biodiversity.

Recent analyses of the current study have also revealed how increasing distance from the continuous primary forest (i.e., the LHNP) has had a negative effect on species richness in fallows and fragmented primary forests for forest-edge-dwelling butterflies (Itioka et al. 2014) and beetles using coarse woody debris (Takano et al., unpublished data). These results indicate that the continuous primary forest also serves as a source population (MacArthur and Wilson 1967; Mittelbach 2012) for local wildlife populations inhabiting nearby areas.

In comparison, species richness was higher in fragmented primary forests compared to continuous primary forest for trees and phytophagous scarabaeids. Many biodiversity studies, including the current study, are conducted in small plots

that are vulnerable to edge effects from adjacent sites. Such study design may have resulted in the overestimation of the biodiversity indices in fragmented primary forests (Barlow et al. 2007).

2.4.4 Diversity in Landscape Mosaics

Nakagawa et al. (2013) verified that tree diversity is maintained across various spatial scales in and around the LHNP, specifically within plots, between plots of the same forest type, and among plots of different forest types. The authors used additive partitioning of diversity, which is a useful tool for understanding the distribution pattern of diversity in a hierarchically structured landscape (Veech and Crist 2010). The highest diversity was found among forest types, indicating that the complete forested landscape comprises a suitable scale for the conservation of tree diversity in the region.

However, there was a significant increase in the numbers of (1) singleton species (i.e., rare species recorded by a single sample or observation), (2) tree species that are endemic to Borneo, and (3) canopy and emergent trees in primary forests compared to fallows and rubber gardens (Nakagawa et al. 2013). Hattori et al. (2012) also suggested the preservation of primary forests is essential for conserving rare wood-inhabiting fungi in Malaysia. If species that are rare, endemic, and restricted to primary forests are considered, biodiversity conservation should focus on primary forest patches in landscape mosaics.

Kishimoto-Yamada et al. (2013) determined how the proportion of fragmented primary forests in a landscape affects the species diversity and species composition of ants and dung beetles in the *Macaranga*-dominated secondary forests of Sarawak. The proportion of fragmented primary forests within a 100-m radius had a significant positive effect on ant species diversity, with fragments within 100-, 300-, and 500-m radii significantly affecting species compositions. These findings indicate that ant species diversity could be enhanced in secondary forests by retaining primary forests occurring within a range of 100 m. It is also important to protect primary and secondary forests at larger spatial scales, such as in range of 100–1,000 m, which would maximize the species diversity of dung beetles in local areas of the landscape (Kishimoto-Yamada et al. 2013).

2.4.5 Variation Among Taxonomic Groups in Response to Disturbance

For small mammals and phytophagous scarabaeid beetles, species richness was similar, or even slightly lower, in the continuous primary forest compared to fragmented primary forests, fallows, and rubber gardens (Nakagawa et al. 2006;

Kishimoto-Yamada et al. 2011). Changes in land use, forest structure, and tree species composition appear to affect animal communities differently depending on the taxonomic groups (Barlow et al. 2007; Chazdon et al. 2009).

Barlow et al. (2007) compared the biodiversity indices of tropical primary, secondary, and plantation forests. The authors reported that different taxa vary markedly in their response to patterns of land use, in terms of species richness and the percentage of species restricted to primary forests (ranging from 5 % to 57 %); however, almost all between-forest comparisons showed marked differences in community structure and composition. Gibson et al. (2011) conducted a meta-analysis of 138 studies on tropical forests. The authors reported that biodiversity indices were substantially lower in degraded forests, but that these indices varied considerably with respect to geographic region, taxonomic group, and disturbance type.

Such variation or discrepancies were also observed for the results of the current study compared to Gibson et al. (2011). For example, Gibson et al. (2011) reported that Coleoptera are more sensitive to disturbance compared to Hymenoptera and Lepidoptera. However, in the current study, army ants (Matsumoto et al. 2009) and forest-edge-dwelling butterflies (Itioka et al. 2014) were sensitive to land cover changes, whereas phytophagous scarabaeid beetles (Kishimoto-Yamada et al. 2011) were less sensitive in terms of encounter rates and species richness.

Butterflies may be roughly classified into herb, liana, and tree specialists and generalists, with different guild probably exhibiting different responses to the same type of disturbance (Cleary et al. 2005). In the case of Coleoptera, phytophagous scarabaeids, which are generalists preferentially feeding on newly emerged leaves, may be attracted to new fallows with young trees, whereas beetles using coarse woody debris are more likely to prefer primary forests and old fallows. These results indicate that we must consider the biological characteristics (e.g., plasticity in feeding habits, dispersal ability, and life history traits) which affect differences in the disturbance tolerance of various species.

2.4.6 Disturbance Tolerance Through Plasticity in Feeding Habits

Gibson et al. (2011) reported that mammals are less sensitive to disturbance and, in some instances, actually benefit from human disturbance. The authors suggested some mammals might have a high tolerance to degraded forests and forest edges (Daily et al. 2003), particularly small mammals and bats which dominate most mammal studies.

To evaluate the trophic levels of small mammals, Nakagawa et al. (2007) compared the stable isotope $\delta^{15}N$ values of the toes of small mammals collected in fallows and primary forests. Higher $\delta^{15}N$ values indicate higher trophic levels (Minagawa and Wada 1984; Deniro and Epstein 1981). The $\delta^{15}N$ values for tree shrews and squirrels were similar among land-use types. However, the $\delta^{15}N$ values

of rats and mice in new and young fallows were more enriched compared to those in old fallows and primary forests. This increase in ^{15}N indicates that rats and mice inhabiting areas at the early stage of forest succession are likely to feed on more consumers, such as insects, than plant organs compared to rodents inhabiting old fallows or primary forests. These results indicate that some rats and mice are able to adjust their diet and, thus, are potentially tolerant to the conditions in degraded forests.

2.5   Future Studies

The current study, along with previous studies (e.g., Barlow et al. 2007; Chazdon et al. 2009; Gibson et al. 2011), highlights the fundamental issues associated with quantifying biodiversity in anthropogenically altered habitats. Consequently, more data on the characteristics of each taxon (e.g., habitat range, plasticity in feeding habits, dispersal ability, and life history traits) and the types of anthropogenic disturbance (intensity, spatio-temporal configuration, and consequent changes in habitat environment) are required (e.g., Liow et al. 2001; Yamashita et al. 2008). Access to such information would help toward understanding the ecological mechanisms underlying the varying vulnerability of different taxonomic groups to different types of human disturbance. Finally, it is also important to investigate the relationships between the changes in biodiversity and ecosystem functions and dynamics (e.g., decomposition services and nutrient cycles, natural enemy services and agricultural productivity, pollination services and plant reproductive success, and dispersal services and forest succession).

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