Research Article

Effect of Logging on the Ficus Community at Batu Timbang Research Station, Imbak Canyon Conservation Area, Sabah

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Abstract

We investigated the effect of logging on *Ficus* species at a community level in the Imbak Canyon Conservation Area (ICCA) in Sabah, Malaysian Borneo. We made comparisons of species composition, density, fig size, and host-tree size (DBH) between heavily logged and relatively old forests, and assessed factors affecting the size of hemi-epiphytic species. There were no significant differences in species composition, density, and fig size between the two habitats. There were significant differences between the DBH of host and non-host trees in both young and old forests as well as between those of host trees in young and old forests. The DBH of hemi-epiphytic species was negatively affected by the DBH of host trees. The results obtained in this study indicate that *Ficus* species, particularly hemi-epiphytes, can survive in degraded habitats that have recently been logged as well as in undegraded forests, and that their growth is not greatly affected by prior logging activities. Thus, *Ficus* exhibits both flexibility and adaptability to habitat change. This indicates that *Ficus* species make ideal plants for the restoration of logged forests considering that figs are an important food resource for numerous animal species, and can promote seed dispersal of other plants by attracting these animals into degraded habitats.

Keywords: Moraceae, hemi-epiphytic figs, forest logging, rainforest, Borneo

Introduction

Ficus is one of the most species-rich plant genera, containing approximately 750 species that are pantropically distributed (Janzen, 1979), with around 150 species on Borneo alone (Berg & Corner, 2005). Hemi-epiphytic species account for one-third to more than a half of all *Ficus* species in any given locality and are an important component of forest ecosystems (Harrison et al., 2003). Their seeds are dispersed among the branches of host trees by arboreal and/or volant animals, where these plants start their life as epiphytes, until their aerial roots grow and connect them to the ground (Putz & Holbrook, 1986). Climbers also need host trees for physical support. Owing to the large crop size produced by hemi-epiphytic species and their seasonal fig (inflorescence) availability, *Ficus* are keystone plants in terms of food resources for more than 1,000 animal species worldwide (Shanahan et al., 2001). Thus, *Ficus* is an ecologically important genera and is closely related to the survival of other plants and animals in forest communities.

Forest logging is the critical factor in forest degradation in Bornean rainforests (Reynolds et al., 2011). Mechanical logging drastically alters forest structure and species composition of the dominant plant family, which in rainforests comprises dipterocarps (Ancrenaz et al., 2010), leading to a reduction in food resources for frugivorous and folivorous animals (Johns, 1986, 1988). Therefore, the effects of logging on *Ficus* may directly impact both plant and animal species diversity and composition in any given forest ecosystem. The spatial distribution of fleshy-fruited plants following logging is determined by seed dispersal via animals (Wunderle Jr, 1997). Most animals that feed on figs are potential seed dispersers for this plant, because fig seeds are numerous, tiny (ca. 1 mm) and mostly egested in faeces without destruction, with the exception of some animals, e.g. mice and green pigeons (Compton et al., 1996; Lambert, 1989a; Shanahan et al., 2001). However, only large animals can disperse the seeds of large fig species, e.g. *Ficus punctata*, because these species usually have thick outer flesh, and most small animals leave the seeds inside, untouched (Shanahan, 2016). Given that large animals are usually negatively affected by logging (Meijaard et al., 2005; Ancrenaz et al., 2010), fig size could also influence *Ficus* species composition and spatial distribution, especially in degraded habitats. Therefore, the species composition, spatial distribution, and fig size of each species will reflect the effect logging has on *Ficus*. For host-dependent species, the host tree is a key factor for their survival and growth (Putz & Holbrook, 1986), so the characteristics of host trees should also be considered.

Despite the importance of this matter, to the best of our knowledge there are no such data available. Therefore, in this study, we investigated the effect of logging on *Ficus* species at a community level in the Imbak Canyon Conservation Area (ICCA), in Sabah, Malaysian Borneo. We specifically addressed the following: 1) a comparison of species composition, density, fig size and host-tree size between heavily logged and relatively old forests, and 2) factors affecting the size of hemi-epiphytic *Ficus* individuals.

Materials and Methods

Study site

This study was conducted between 18 and 23 August 2017 in the forests around Batu Timbang Research Station (BTRS, 5°00'N, 117°04'E), near the border of Imbak Canyon Forest Reserve and Mt. Magdalena Forest Reserve, in the south-eastern section of the Imbak Canyon Conservation Area (ICCA, 5°04'N, 117°06'E). The ICCA covers an area of approximately 30,000 hectares. Most of the habitat within the ICCA comprises lowland dipterocarp rainforest and upper montane forest, including montane heath forest patches (Sugau et al. 2012, Suleiman et al. 2012). The ICCA was formerly a part of the Yayasan Sabah Concession Area, and in the past the habitat around the periphery of the ICCA was heavily logged. The forests around the BTRS were logged several times during the 1980s and the 2000s (Yap, S.W. personal communication). Logging activity was totally prohibited when the ICCA became a Class I (Protection) Forest Reserve in 2009. The forests inside the canyon are relatively pristine (Latif & Sinun, 2012).

Survey methods

We established plots consisting six transects (250 × 250 m at 50 m intervals) andsearched for *Ficus* species along the transects in heavily logged (hereafter referred to as 'young') forest and old forest habitats (Figure 1). In addition to these plots, we also searched them using transects in each area. When we detected a *Ficus* species, we recorded the species name, coordinates (using a GPS: Garmin 64S, Garmin International, Olathe, Kansas, USA), diameter at breast height (DBH, cm), height (using a laser range finder: Laser 550AS, Nikon, Tokyo, Japan), host-tree species, and the host tree's DBH. For hemi-epiphytes, we also measured the DBH of the largest aerial roots that reached the ground. We regarded the height of the position of colonisation as the height of hemi-epiphytes, while for climbers we regarded the height of the crown as the height. The nomenclature of plant species, plant growth form, and taxonomic rank followed Berg & Corner (2005).
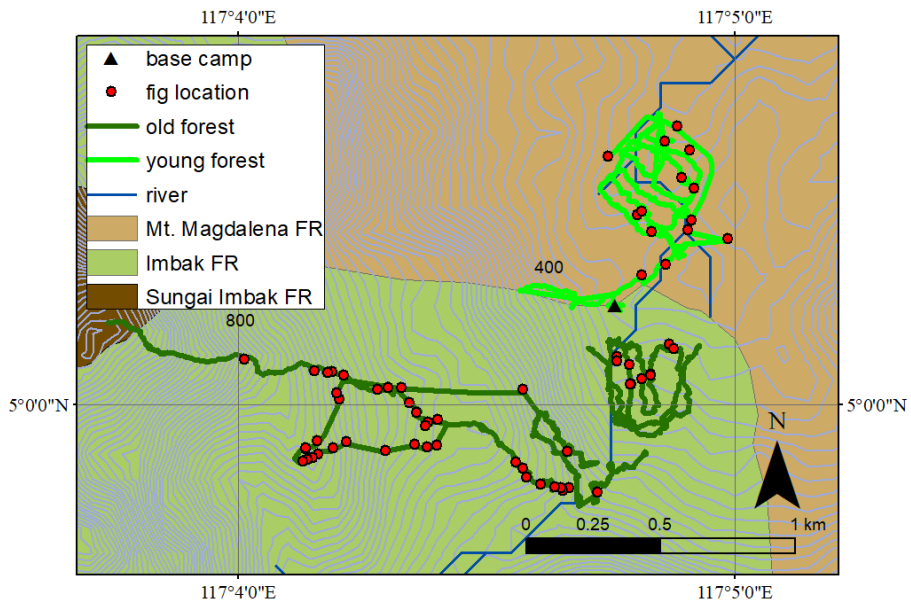
Figure 1. Map of the surveyed area and all fig locations

Data analysis

We assessed the similarity of *Ficus* species composition between the two habitats (young and old forest) using Jaccard's similarity index (Jaccard, 1912; Koleff et al., 2003). A value of zero indicates completely dissimilar sets; a value of 1 indicates identical sets. The difference in densities between the two habitats was assessed by comparing the number of *Ficus* individuals in each habitat with the expected number of individuals if they were distributed equally in the two habitats, using Fisher's exact test.

We investigated whether there were differences in fig size between the two habitats using a simulated distribution of indices that would be expected if there was no effect of habitat differences, by performing an exact permutation test estimated by Monte Carlo (9,999 replications) using the perm package in R 3.4.2 software (R Development Core Team, 2017). We calculated the fig size index as diameter (mm)*length (mm)/100 for each species. Fig sizes were based on Lambert (1989b) and Nakabayashi (2015, including unpublished data). We also compared the DBH of host trees of host-dependent species, such as hemi-epiphytes and climbers, with that of non-host trees, and also the DBH of host

trees between the two habitats, by using exact permutation tests with Bonferroni corrections.

We assessed the factors affecting the size (DBH) of hemi-epiphytic species using generalised linear mixed models (GLMMs) with Gamma distributions. We used the restricted maximum likelihood with the lmer function to fit the GLMMs. Random effect was individual, and the fixed effects were habitat type (young or old forest), colonisation height, fig species, and DBH of host trees. We evaluated the support for all models using the Akaike information criterion (AIC) and found the best fit models with the lowest AIC value. We tested whether the coefficient estimates in the best model deviated from zero using the Wald test. GLMMs and the Wald test were executed using the lme4 package in R 3.4.2 software.

Results

In total, we surveyed 8.1 km in young forest areas and 12.6 km in old forest areas. We defined 5 m on either sides of a transect as the visible range, and therefore the total surveyed area in young and old forests was 8.1 and 12.6 ha, respectively. We found 14 and 20 (total 27) *Ficus* species in young and old forests, respectively (Table 1, 2). There were three and 12 unidentified species in young and old forests, respectively. It was unclear whether these unidentified species included the same species. The growth form of 18 out of 27 identified species was hemi-epiphytic (66.7%), five species were climbers (18.5%), two species were shrubs (7.4%) and two species were trees (7.4%). We found 18 and 51 (total 69) individuals, including 15 unidentified species, in young and old forests, respectively. The growth form of 44 out of 55 species-identified individuals was hemi-epiphytic (80.0%), seven were climbers (12.7%), two were shrubs (3.6%) and two were trees (3.6%).

Table 1. Attributes of *Ficus* species detected during this expedition; N = number of individuals

subgenus section subsection	species	growth form[a]	N	DBH±SD (cm)	height±SD (m)	density (ha⁻¹) surveyed area[b]	density (ha⁻¹) Sarawak[c]
Urostigma							
Urostigma							
Conosycea	*F. binnendijkii*	H	2	6.0	38.8±11.3	0.10	0.15
	F. callophylla	H	2	103.8±96.3	20.0	0.10	0.02
	F. consociata	H	3	14.2±11.3	23±7.9	0.15	0.08
	F. delosyce	H	1			0.05	0.42
	F. dubia	H	2	12.3±4.8	35.0±10.0	0.10	
	F. globosa	H	1			0.05	
	F. kerkhovenii	H	6	11.6±10.1	32.0±5.0	0.29	0.27
	F. microcarpa	H	1	100	30.0	0.05	
	F. pellucido-punctata	H	2	4.5±1.5	29.0±13.0	0.01	0.05
	F. pisocarpa	H	2	10.5±4.5	28.5±10.5	0.01	0.08
	F. spathulifolia	H	2	16.5±7.5	27.8±0.8	0.01	
	F. stricta	H	5	7.0±6.6	27.3±8.7	0.24	
	F. stupenda	H	5	24.0±21.3	25.2±11.2	0.24	0.12
	F. subcordata	H	1	11.0	22.0	0.05	0.08
	F. subgerderi	H	2			0.01	0.4
	F. sundaica	H	4	37.8±33.9	37.7±4.8	0.19	
Urostigma	*F. caulocarpa*	H	2	53.5±46.5	17±10	0.01	0.02
	F. virens	H	1	50.0	26.0	0.05	0.05
total of H	18 species		44			2.13	2.99

Table 1. *Continued*

Ficus						
Ficus						
Frutescentiae						
	F. deltoidea	C	1			0.05
Synoecia						
Kissosycea						
	F. punctata	C	2	12.0		0.10
Rhizocladus						
Punctulifoliae						
	F. spiralis	C	1	1.5	21.5	0.05
Trichocarpeae						
	F. trichocarpa	C	1	7.0	25.0	0.05
Sycidium						
Palaeomorphe						
	F. tinctoria gibbosa	C	2	4.5±1.5	19.0±3.0	0.10
Sycomorus						
Sycocarpus						
	F. beccarii	S	1	1.0	3.0	0.05
	F. treubii	T	1	25.0	6.0	0.05
	F. uncinata	S	1	11.0	7.0	0.05
Sycomorus						
Sycomorus						
	F. variegata	T	1			
-	unidentified spp	H/C	15			
Total	27 species		55 (70)			2.66 (3.43)

a: H, hemi-epiphyte; C, climber; S, shrub; T, tree
b: 20.7ha
c: 120 ha, only hemi-epiphytes at Lambil Hills National Park. Harrison et al. (2003)

Table 2. Attributes of *Ficus* species detected in each habitat. The numbers in parentheses in the N column indicate surveyed area.

growth form	species	N		fig size index
		young (8.1 ha)	old (12.6 ha)	
H				
	F. binnendijkii		2	4.0
	F. callophylla		2	0.6
	F. consociata	1	2	2.9
	F. delosyce		1	0.4
	F. dubia		2	7.9
	F. globosa		1	4.2
	F. kerkhovenii		6	1.6
	F. microcarpa	1		0.7
	F. pellucido-punctata		2	2.1
	F. pisocarpa	1	1	1.4
	F. spathulifolia		2	0.4
	F. stricta	2	3	2.5
	F. stupenda	2	3	42.5
	F. subcordata	1		15.8
	F. subgerderi		2	1.3
	F. sundaica	1	3	2.7
	F. caulocarpa	1	1	0.3
	F. virens		1	0.5
C				
	F. deltoidea		1	0.1
	F. punctata	1	1	56.1
	F. spiralis	1		0.4
	F. trichocarpa	1		2.5
	F. tinctoria gibbosa		2	-
S				
	F. beccarii	1		-
	F. uncinata		1	0.8
T				
	F. treubii	1		-
	F. variegata	1		3.8
	unidentified spp.	3	12	
	Total species	**14**	**20**	
	Total N	**19**	**51**	
	density (ha^{-1})	**2.35**	**4.05**	

Density (individuals/ha), including unidentified species, was 2.35 and 4.05, (total 3.43), in young forest and old forest, respectively. There was no significant difference in density between the two habitats (p=0.11), although the density in the old forest tended to be higher than that in the logged forest. The Jaccard similarity index between the species composition of the two habitats was 0.75. The fig size index was 11.0±5.1 (mean±SD) in the young forest, while that in the old forest was 7.2±3.6 (Figure 2). There was no significant difference in fig size index between the two habitats (p=0.14).
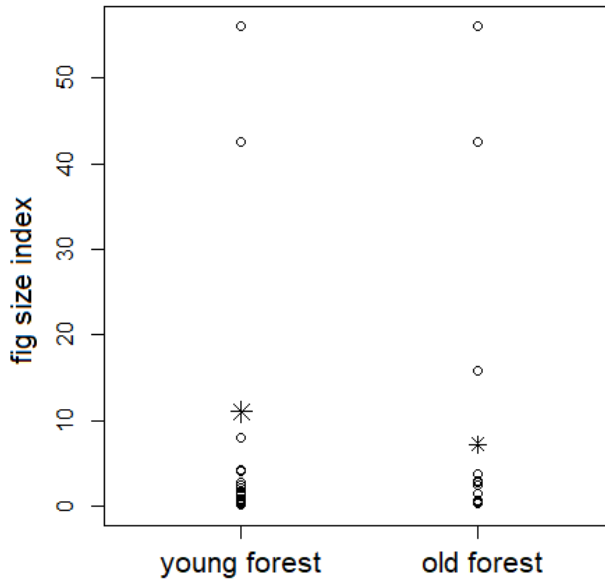
Figure 2. Fig size index of the two habitats. Asterisks indicate mean values.

Table 3. Attributes of the host trees of hemi-epiphytic and climber *Ficus* species

Family	species	N	%	DBH ± SD (cm)	family N	family %
Achariaceae	*Ryparosa acuminata*	1	2.7	30.0	1	2.7
Calophyllaceae	*Calophyllum* spp.	2	5.4	42.0±21.0	2	5.4
Dipterocarpaceae					24	64.9
	Dipterocarpus spp.	4	10.8	93.3±20.5		
	Dryobalanops lanceolata	1	2.7	170.0		
	Parashorea spp.	2	5.4	80.0±30.0		
	Shorea johorensis	1	2.7	68.0		
	Shorea pauciflora	3	8.1	176.7±17.0		
	Shorea platyclados	5	13.5	161.7±12		
	Shorea spp.	6	16.2	131.7±43.7		
	Vatica oblongifolia	1	2.7	170.0		
	Vatica sp.	1	2.7	180.0		
Fagaceae	*Lithocarpus* spp.	3	8.1	63.3±18.9	3	8.1
Lauraceae	*Eusideroxylon zwageri*	3	8.1	53.3±11.8	3	8.1
Myrtaceae	*Decaspermum fruticosum*	3	8.1	30.0	3	8.1
Rubiaceae	*Neonauclea* sp.	1	2.7		1	2.7
	Total	37	100.0	93.1±55.4		100

We found 37 host trees belonging to seven families (Table 3). Due to the small sample size of identified host trees (n=5), we excluded host species or genus from the analysis. The most common host was the genus *Shorea* of the Dipterocarpaceae, which accounted for 40.5% of all host trees. Family Dipterocarpaceae accounted for 64.9%, followed by Fagaceae, Lauraceae, and Myrtaceae (all 8.1%). The DBH of the host trees was 93.1±55.4 cm (mean±SD), but 40 to 50 cm was the most common size in both habitats (Figure 3). The DBH in the young and old forests was 51.1±30.5 cm (mean±SD, n=10) and 111.2±59.2 cm (n=32), respectively. The DBH of non-host trees in young and old forests was 17.9±19.6 (n=39) and 33.0±41.8 (n=284). There were significant differences between the DBH of host and non-host trees in both young (p < 0.01) and old forests (p < 0.01), as well as between those of host trees in young and old forests (p < 0.01) (Figure 4).
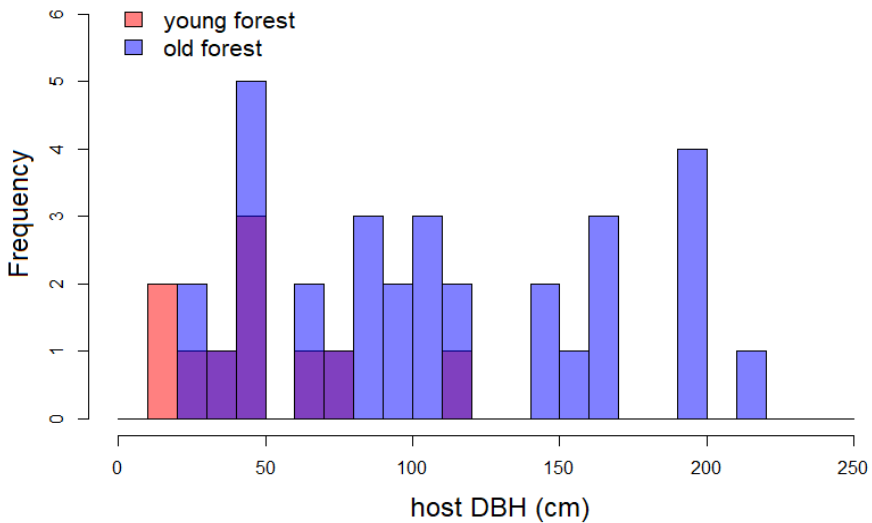

Figure 3. Distribution of DBH of the host trees. Overlapped areas show different colour (purple).

The GLMM analysis showed that the size (DBH) of hemi-epiphytic species was affected by the DBH of host trees, habitat type, and colonisation height, with an AIC value of -354.5, followed by the model with height as its fixed effect, with an AIC value of -351.1. The third best model was the null model, with an AIC value -347.6. The species did not affect the DBH of hemi-epiphytes. Only the DBH of host trees was a significant fixed effect in the best model according to the Wald test, but the colonisation height was marginally significant (Table 4).
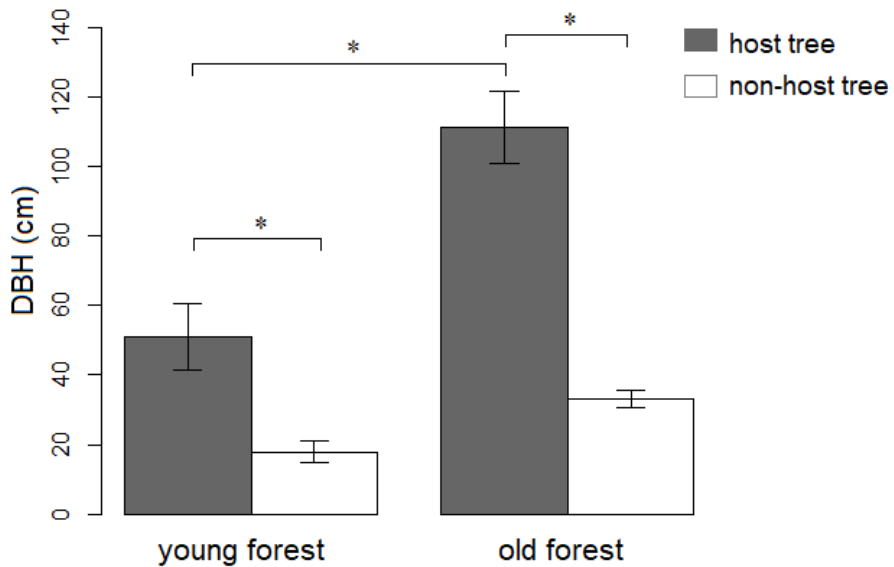

Figure 4. DBH of the host trees of hemi-epiphytic and climber *Ficus* species and non-host trees in the two habitats (mean ± SE). Asterisks indicate significant differences (p < 0.01).

Table 4. Attributes of the best model of the GLMM analysis on the DBH of the hemi-epiphytic *Ficus* species

parameter	coefficient±SE	t-value	p value
intercept	0.41±0.19	2.22	0.03
young forest	0.08±0.15	0.56	0.58
colonisation height	0.01±0.001	1.76	0.07
DBH of host tree	-0.004±0.001	-2.9	0.004

Discussion

Although the species diversity and richness around Batu Timbang Research Station (BTRS) cannot simply be compared with other sites, because of the short survey period (six days) and small area surveyed (20.7 ha), we found quite a diverse range of *Ficus* species, especially those belonging to subsection Conocycea, which comprises only hemi-epiphytic species (Table 5). The density of hemi-epiphytic species in the BTRS, in terms of both species and community level, and the *Ficus* species richness around the BTRS during the study period, were basically the same as seen at other sites on Borneo, except for the subgenus *Ficus* (Table 5). These results indicate that the *Ficus* species richness and density of hemi-epiphytic species found around the BTRS is very common on Borneo (Table 1, 5).

Table 5. *Ficus* species richness in five sites on Borneo. GP, Gunung Palung National Park; KP, Kutai National Park; MK, Mount Kinabalu National Park; LH, Lambir Hills National Park. Data from Laman & Weiblen (1998).

subgenus and section (N species on Borneo)	GP	KP	MK	LH	Batu Timbang
survey effort	1996 & 1997	-	3.5 months	120 ha	6 days 20.7 ha
Urostigma					
Urostigma (5)	1	2	2	1	2
Conosycea (36)	27	23	16	19	16
Malvanthera (1)	0	0	0	0	0
Pharmacosycea					
Oreosycea (5)	0	1	0	0	0
Sycomorus					
Sycomorus (3)	0	1	0	0	1
Ficus	28	25	60	34	8
Total	56	52	78	54	27

Based on the high value of the Jaccard similarity index, the young and old forest habitats had similar *Ficus* species composition. The density and fig size did not differ between the two habitats, and species producing large figs (*F. punctata* and *F. stupenda*) were found in both habitats. There were relatively young individuals of *F. stupenda* in both young (DBH = 4 cm) and old (7 cm) forests, and therefore the seed dispersal system of large fig species is working in these areas, regardless of their logging history. Habitat degradation by logging can negatively affect most animals, including important seed dispersers such as

hornbills (Meijaard et al. 2005), but some animals, for example palm civets (Nakabayashi et al., 2014), take advantage of the higher levels of light in these habitats in terms of the food resources available, such as flowers, fruits, new leaves and herbivorous insects (Fowler et al., 1993). Such animals are important seed dispersal agents in degraded habitats (Corlett, 2017). The similar species composition and lack of differences in tree density and fig size between the young and old forests in the BTRS indicate that, in this area, animals act as seed dispersal agents for *Ficus* species, including large-fig species.

Dipterocarpaceae comprised the most common hosts in the BTRS area; this result is consistent with results from other study sites (Harrison et al., 2003). Several studies have indicated that DBH is the most important host factor for some hemi-epiphytic *Ficus* species, rather than bark roughness or host species (Laman, 1996, Harrison et al., 2003), and the results of the present study corroborate this pattern, as the size of host trees (DBH) was significantly larger than that of non-host trees in both habitats. Although preferred host size varies among hemi-epiphytic species (Laman, 1996), we were unable to assess this because of the small sample size. Host size seems to be determined by relative tree size in a given environment, because the host DBH in the old forest was significantly larger than that in the young forest (Figure 3, 4), and there was a similar species composition between the two habitats. The results of the current study suggest that even in recently logged forests, host-dependent species depend on relatively large trees rather than specific species as their host. Considering that habitat type (old or young forest) did not affect density or species composition in the BTRS area, it appears that host-dependent species can colonise relatively disturbed habitats if there are suitable potential host trees and seed dispersal agents.

The size (DBH) of host-dependent species was negatively affected by the DBH of host trees. This result indicated that host-dependent species grow well when they colonise relatively small host trees. Water stress is the critical limiting factor for the germination of hemi-epiphytic *Ficus* species seeds, but once they are established on their hosts, the level of light is the most important factor for seedling growth (Laman, 1995). Although not significant, the parameters of young forest and colonisation height were selected as the fixed effects of the best model (Table 4), and both of these factors are linked to a high level of light. Other than light level, physical factors of large hosts might also affect the size of host-dependent species, especially hemi-epiphytes. Once the aerial roots from epiphytic hemi-epiphytes reach the ground, they begin to thicken. They then usually produce horizontally growing roots around their host tree to

increase their physical support (Putz & HolBrook, 1986). When hosts are large, they may consume energy to obtain horizontal support, inhibiting diameter growth. Our results suggest that logging history would not strongly affect the growth of hemi-epiphytes across species, and that their growth is dependent on host size.

Conclusion

The results obtained in this study indicate that *Ficus* species, particularly hemi-epiphytes, can survive in degraded habitats that have recently been logged as well as in undegraded forests, and that their growth is not greatly affected by prior logging activities. Thus, this genus exhibits both flexibility and adaptability to habitat change. This indicates that *Ficus* species make ideal plants for the restoration of logged forests. In an Indian agricultural mosaic landscape, sapling density and species richness of plants growing under isolated *Ficus* trees was higher than under non-*Ficus* trees (Cottee-Jones et al., 2016). Successful seed dispersal is one of the critical factors that limits tropical forest restoration (Wunderle Jr 1997, Cole et al., 2010, Holl et al., 2013). Figs are an important food resource for numerous animal species (Shanahan et al., 2001) and can promote seed dispersal of other plants by attracting these animals into degraded habitats. However, the present study was based on a short-term survey; therefore, more long-term, fundamental studies in this area are needed to obtain a greater understanding of the ecology and ecological roles of *Ficus* in this region and on Borneo as a whole.

Acknowledgements

References

Ancrenaz M, Ambu L, Sunjoto I, Ahmad E, Manokaran K, Meijaard E, Lackman I. 2010. Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *PLoS ONE* **5(7):** e11510.

Ashton P. 2014. *On the forests of tropical Asia: lest the memory fade*. London: Kew Publishing

Berg CC, Corner EJH. 2005. *Moraceae - Ficus. Flora Malesiana Series I (Seed Plants) Volume 17/Part 2*. Leiden: National Herbarium of the Netherlands

Cole RJ, Holl KD, Zahawi RA. 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecological Applications* **20:** 1255–1269.

Compton S, Craig A, Waters I. 1996. Seed dispersal in an African fig tree: birds as high quantity, low quality dispersers? *Journal of Biogeography* **23(4):** 553-563.

Corlett RT. 2017. Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. *Global Ecology and Conservation* **11:** 1-22.

Cottee-Jones HEW, Bajpai O, Chaudhary LB, Whittaker RJ. 2016. The Importance of *Ficus* (Moraceae) trees for tropical forest restoration. *Biotropica* **48:** 413–419.

Fowler HG, Silva-Carlos A, Venticinque E. 1993. Size, taxonomic and biomass distributions of flying insects in central Amazonia: forest edge vs. understory. *Revista de Biologia Tropical* **47:** 755-760.

Gentry AH, Emmons LH. 1987. Geographical variation in fertility, phenology, and composition of the understory neotropical forests. *Biotropica* **19:** 216-227.

Harrison RD, Hamid AA, Kenta T, Lafrankie J, Lee HS, Nagamasu H, Nakashizuka T, Palmiotto P. 2003. The diversity of hemi-epiphytic figs (*Ficus*; Moraceae) in a Bornean lowland rain forest. *Biological Journal of the Linnean Society* **78 (4):** 439-455.

Holl KD, Stout VM, Reid JL, Zahawi RA. 2013. Testing heterogeneity-diversity relationships in tropical forest restoration. *Oecologia* **173:** 569–578.

Jaccard P. 1912. The distribution of the flora in the alpine zone. *New Phytologist* **11:** 37–50.

Janzen DH. 1979. How to be a fig. *Annual Review of Ecology and Systematics* **10:** 13–51.

Johns AD. 1986. Effects of selective logging on the behavioral ecology of West Malaysian primates. *Ecology* **67(3):** 684–694.

Johns AD. 1988. Effects of "selective" timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* **20:** 31-37.

Koleff P, Gaston KJ, Lennon JJ. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72:** 367–382.

Laman TG, Weiblen GD. 1998. Figs of Gunung Palung National Park (West Kalimantan, Indonesia). *Tropical Biodiversity* **5(3):** 245-297.

Laman TG. 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. *Ecology* **76:** 2617-2626.

Laman TG. 1996. Specialization for canopy position by hemiepiphytic *Ficus* species in a Bornean rain forest. *Journal of tropical ecology* **12(6):** 789-803.

Lambert FR, Marshall AG. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *The Journal of Ecology* **79:** 793-809.

Lambert FR. 1989a. Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* **131(4):** 521-527.

Lambert FR. 1989b. Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology* **5(4):** 401-412.

Latif A, Sinun W. 2012. *Imbak Canyon Conservation Area, Sabah: Geology, Biodiversity and Socio-economic Environment.* Kota Kinabalu: Academy of Sciences Malaysia and Yayasan Sabah, Sabah

Leighton M, Leighton DR. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. pp. 181–196. In: Sutton SL, Whitmore TC, Chadwick AC. (eds.). *Tropical rain forests: ecology and management.* Oxford: Blackwell Scientific Publications

Meijaard E, Sheil D, Nasi R, Augeri D, Rosenbaum B, Iskandar D, Setyawati T, Lammertink M, Rachmatika I, Wong A. 2005. *Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo.* Bogor: CIFOR

Nakabayashi M, Nakashima Y, Bernard H, Kohshima S. 2014. Utilisation of gravel roads and roadside forests by the common palm civet (*Paradoxurus hermaphroditus*) in Sabah, Malaysia. *Raffles bulletin of zoology* **62:** 379-388.

Nakabayashi M. 2015. Feeding ecology of three frugivorous civets in Borneo. Ph.D. thesis, Kyoto University, Kyoto, Japan.

Putz FE, Holbrook NM. 1986. Notes on the natural history of hemiepiphytes. *Selbyana* **9:** 61-69.

R Development Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. www.R-project.org.

Reynolds G, Payne J, Sinun W, Mosigil G, Walsh RPD. 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **366(1582):** 3168–3176.

Shanahan M, So S, Compton SG, Corlett R. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews of the Cambridge Philosophical Society* **76(4):** 529-572.

Shanahan M. 2016. *Gods, wasps and stranglers. The secret history and redemptive future of fig trees.* White River Junction: Chelsea Green Publishing

Soepadmo E, Saw L.G. 2000. *Tree flora of Sabah and Sarawak, Volume3*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Saw LG, Chung RCK, Kiew R. 2007. *Tree flora of Sabah and Sarawak, Volume6*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Saw LG, Chung RCK, Kiew R. 2011. *Tree flora of Sabah and Sarawak, Volume7*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Saw LG, Chung RCK. 2002. *Tree flora of Sabah and Sarawak, Volume4*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Saw LG, Chung RCK. 2004. *Tree flora of Sabah and Sarawak, Volume5*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Wong KM, Saw LG. 1996. *Tree flora of Sabah and Sarawak, Volume2*. Kepong: Forest Research Institute Malaysia

Soepadmo E, Wong KM. 1995. *Tree flora of Sabah and Sarawak, Volume1*. Kepong: Forest Research Institute Malaysia

Sugau JB, Muin PJ, Sabran S, Majawal U. 2012. Study on diversity and distribution of Dipterocarp in imbak Canyon Conservation Area around Gunung Kuli Research Station. pp. 305–313. In: Latif A, Sinun W. (eds.). *Imbak Canyon Conservation Area, Sabah: Geology, Biodiversity and Socio-economic Environment*. Kota Kinabalu: Academy of Sciences Malaysia and Yayasan Sabah

Suleiman, M., Chua, M.S. and Kanak, F.A. 2012. Mosses from the southern part of Imbak Canyon Conservation Area. pp. 269-281. In: Latif A, Sinun W. (eds.). *Imbak Canyon Conservation Area, Sabah: Geology, Biodiversity and Socio-economic Environment*. Kota Kinabalu: Academy of Sciences Malaysia and Yayasan Sabah

Terborgh J. 1986. Keystone plant resources in the tropical forest. pp 330-344. In: Soule ME. (ed.). *Conservation biology, the science of scarcity and diversity*. Sunderland: Sinauer

Todzia C. 1986. Growth habits, host tree species, and density of hemi-epiphytes on Barro Colorado Island, Panama. *Biotropica* **18:** 22-27.

Wunderle Jr JM. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest ecology and management* **99:** 223-235.