BIODIVERSITAS ISSN: 1412-033X
Volume 23, Number 3, March 2022 E-ISSN: 2085-4722
Pages: 1576-1587 DOI: 10.13057/biodiv/d230348

Composition and diversity of tree species after fire disturbance in a lowland tropical forest in East Kalimantan, Indonesia

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Manuscript received: 19 January 2022. Revision accepted: 26 February 2022

Abstract. *Sakai A, Arbain, Sugiarto, Rahmawati K, Mirmanto E, Takahashi M, Ueda A. 2022. Composition and diversity of tree species after fire disturbance in a lowland tropical forest in East Kalimantan, Indonesia. Biodiversitas 23: 1576-1587.* Lowland dipterocarp forests in East Kalimantan have suffered severe forest fires after prolonged drought at least twice in recent decades. We investigated species richness, stand structure and species composition in Sungai Wain Protection Forest using circle plots (each 0.04 ha) along multiple long transects (0.5 - 4.5 km long) from the edge to the interior of this forest. The impact of forest fires remained in the form of significantly smaller tree sizes in burnt areas, although species richness and the number of stems appeared to be recovering. NMDS (non-metric multidimensional scaling) ordination revealed that the species composition of burnt areas was still considerably different from that of intact forest. However, nearly 20 years have elapsed, suggesting that it takes a long time for species composition to recover, if at all. The species composition was affected by the basal area ratio of pioneer trees, the basal area ratio of dipterocarp trees and maximum diameter at breast height, in order of its strength. Distance from the edge of the Protection Forest also had a minor effect on species composition, suggesting that forest fires had damaged marginal areas of the forest.

Keywords: Dipterocarp, forest fire, NMDS, pioneer tree, species composition

Abbreviations: CV: coefficient of variance; NMDS: non-metric multidimensional scaling; SWPF: Sungai Wain Protection Forest

INTRODUCTION

Due to anthropogenic activities and the subsequent decline in biodiversity, deforestation and degradation of tropical rain forests continue to be a major concern (Barlow et al. 2016; Ehrlich and Wilson 1991). Forest fire is one of the primary factors degrading tropical forests globally (Goldammer et al. 1996; Goldammer 1999; Hammond and ter Steege 1998; Mori 2000). Although forest fires have always been a natural part of tropical rain forest ecology, unconnected with human activities (Sanford et al. 1985; Whitmore 1984), increasing population has heightened the extent and frequency of forest fires induced by logging and conversion to agricultural land (Laurance 1998; Mori 2000; Nepstad et al. 1999; Siegert et al. 2001; Xaud et al. 2013; Yamashina et al. 2020). Impacts of a forest fire on stand structure, species composition, and biodiversity have been investigated in tropical rainforests across the world (Sagar et al. 2003; Toma et al. 2000; Slik et al. 2002; Slik et al. 2003b; Woods 1989; Xaud et al. 2013; Yeager et al. 2003).

The lowland area of East Kalimantan was almost completely covered by tropical rainforest until the 1970s, but this area experienced huge forest fires at least twice in1982-83 and 1997-98 that were attributable to the El Niño Southern Oscillation (ENSO) event (Eichhorn 2006; Mori 2000; Taylor et al. 1999). It is reported that the land area affected by the 1982-83 fire reached 3.5 million ha in East Kalimantan alone (Goldammer et al. 1996). The next major fire, in 1997-98, burned a total of 5.2 million ha which included 2.2 million ha of lowland dipterocarp forests (Siegert et al. 2001; Yamaguchi and Tsuyuki 2001). As a result, only a few forest reserves with relatively little damage remain, such as those in Bukit Bangkirai, Wanariset and Sungai Wain. The impacts of forest fires on stand structures and species composition of plants and insects have been investigated in and around Sungai Wain Protection Forest (Eichhorn 2006; Slik et al. 2002; Ueda et al. 2017; van Nieuwstadt et al. 2001; Yeager et al. 2003). Here, since nearly 20 years have passed since the last major fire, it would be expected that plant succession has been progressing, showing a changing stand structure and species composition. Therefore, it is important to evaluate the current situation and observe to what extent these stand variables have recovered since the most recent disturbance. It would also be expected that the impact on the forest will vary in relation to distance from the forest edge (e.g., Cochrane and Laurence 2002; Euskirchen et al. 2001; Harper et al. 2005; Murcia 1995). However, conventional random plot design may fail to detect any unique effects in the context of landscape ecology. We, therefore, conducted a study in which we ran multiple long transects from the edge to the deep interior of the Sungai Wain Protection Forest.

The objective of this study was to evaluate the impact of disturbance in a lowland dipterocarp forest in East Kalimantan, Indonesia, that has experienced major fires in the past few decades. We focused on (1) how species richness, stand structures, and tree species composition have changed as results of such fires; (2) how closely these variables have returned to those of intact forest over approximately 20 years; and (3) what elements of the landscape (i.e., distance from the forest edge and topography) affected stand structure and species composition after fire disturbance. We then discussed the species-specific habitat preference of several major tree species that were found in the process of this study.

MATERIALS AND METHODS

Study area

The study was carried out in Sungai Wain Protection Forest (SWPF), located approximately 15 km north of Balikpapan in East Kalimantan, Indonesia (Figure 1). SWPF is composed of lowland dipterocarp forests covering approximately 10,000 km^2. It acts as a water catchment area for a petroleum company and neighboring Balikpapan (Fredriksson 2002; Eichhorn 2006). This area suffered huge forest fires resulting from the severe and prolonged droughts associated with the ENSO event in 1982-83 and 1997-98, as noted in the Introduction. As a result, approximately 4,000 ha were left intact in Sungai Wain Protection Forest. It is the last remnant of any size in East Kalimantan (Eichhorn 2006; Fredriksson 2002; Slik et al. 2010) (Figure 1). Since 1998, small-scale forest fires have sporadically occurred in or around SWPF (Figure 1). Local residents have reclaimed the burned lands, and even small-scale illegal logging has taken place in or around SWPF (Eichhorn 2006; Yamaguchi and Tsuyuki 2001).

This area has no pronounced dry seasons and receives between 2,000 and 2,500 mm of rain annually (Slik and Eichhorn 2003). Air temperature is almost constant throughout the year, ranging from a minimum of 24ºC at night to a maximum of 31ºC during the day (Slik and Eichhorn 2003). The topography of the SWPF is gentle overall but includes some steep slopes created by the erosive action of the many small rivers that intersect across SWPF (Eichhorn 2006). The soil type comprises mainly Alisols: very deep, acid and infertile soils with high fractions of loam and clay (Eichhorn 2006).

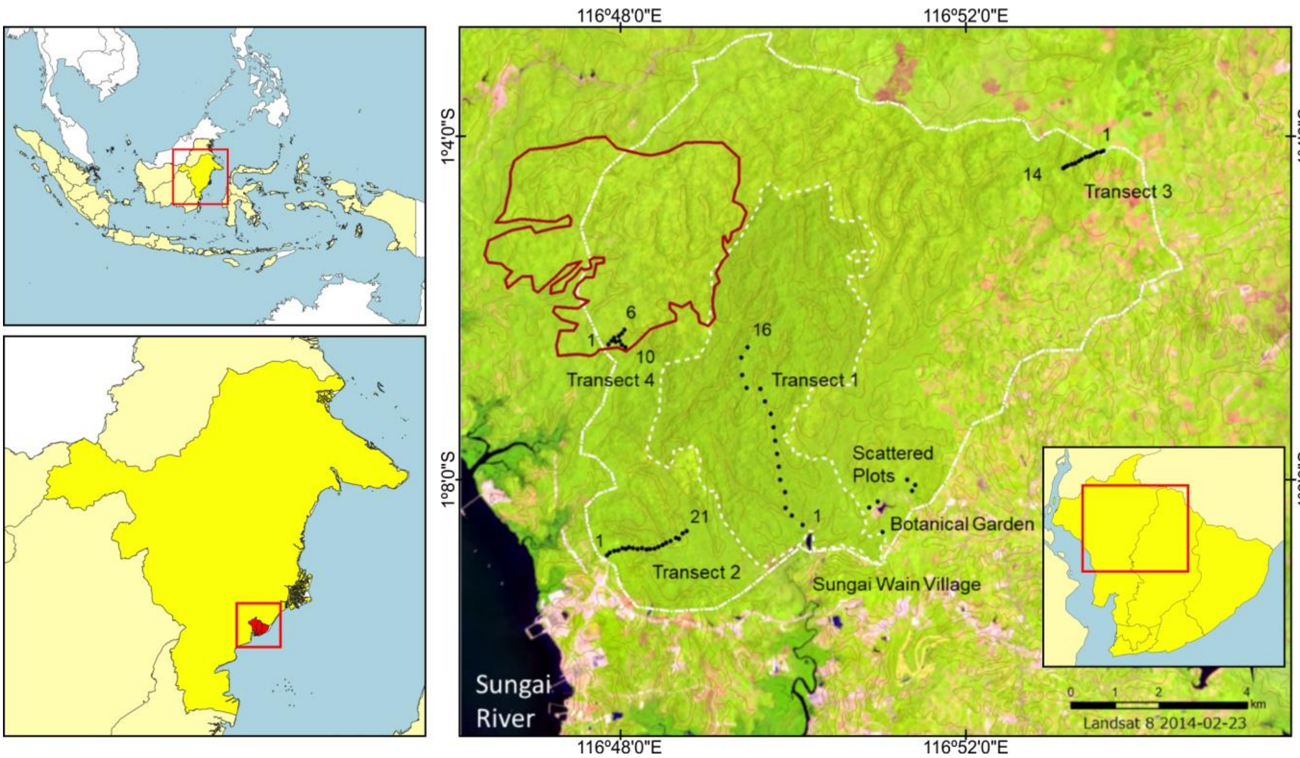

Figure 1. Map indicating the location of study plots in Sungai Wain Protection Forest in East Kalimantan, Indonesia. The Protection Forest is shown as the area surrounded by a white solid line. Unburned areas are surrounded by broken lines. Recently burnt areas are surrounded by a red line. Circle plots are shown as lines of dots within the Protection Forest and as dots distributed around the Balikpapan Botanic Gardens

Field survey

We ran four transects (T1, T2, T3, and T4) of various lengths from the boundary towards the interior of SWPF in 2016 and 2017 (Figure 1). Circle plots with a radius of 11.28 m (area = 0.04 ha) were positioned along the transects or randomly in the SWPF. Transect 1 (T1) was 4.5 km long, consisting of 16 circle plots placed approximately 300 m in the north-south direction. Transect 2 (T2) was 2.0 km long, consisting of 21 circle plots placed approximately every 100 m in the east-west direction. Transect 3 (T3) was set in a degraded forest in the northeast of SWPF. T3 was approximately 900 m long, consisting of 14 circle plots arranged approximately every 50-100 m along the transect. Transect 4 (T4) crossed a recently burned area (in 2015), consisting of 10 circle plots along an approximately 500 m-long main transect and an approximately 400 m-long branch transect (Figure 1). Six circle plots were distributed around Balikpapan Botanic Gardens to supplement the number of sample plots (hereinafter 'Scattered Plots'). A total of 67 circle plots were therefore placed in the SWPF.

The diameter at breast height (DBH) of living trees (DBH ≥10 cm) was measured in each circle plot, and the height of major canopy trees was measured using an ultrasonic measuring instrument (Vertex IV, Haglof). All dicot trees were identified, but palm trees (monocotyledons) were excluded from the survey. The latitude and longitude of the centers of the circle plots were recorded using GPS instruments (Garmin, GPSmap 62S). We surveyed the topography along T1 and T2 using a laser surveyor (Laser Technology, TruPulse360) and visually classified the topography of all the circle plots into three categories: ridge or upper slope, hillside slope, and valley or lower slope.

Data analysis

We classified tree species into pioneer, dipterocarp, and others. Here, we defined 'pioneer' as a typical light-demanding tree that develops after the disturbances of a tropical rain forest (Swaine and Whitmore 1988); i.e., *Macaranga* spp., *Endospermum diadenum* and *Vernonia arborea*. *Macaranga lowii* was exceptionally excluded from the pioneer group because it occurs in primary rather than secondary forests in East Kalimantan (Slik et al. 2003a). 'Dipterocarps' included all Dipterocarpaceae trees: *Dipterocarpus* spp, *Hopea* spp., *Shorea* spp., and *Vatica* spp. Basal area was calculated based on DBH and aggregated for each tree species and each class (pioneer, dipterocarp and others) in each circle plot.

We performed non-metric multidimensional scaling (NMDS) on our data set for the basal area to look for compositional similarity among the plots (transects) and explore specific tree species that might reveal the degree of disturbance or successional stage in a lowland tropical forest. Prior to the analysis, rare species (Frequency < 3) were excluded from the data set. We employed PC-ORD Version 6.08 (McCune and Mefford 1999) for NMDS. Sørensen distance was used as a measure of compositional dissimilarity between the circle plots. Low and thorough autopilot mode (step length = 0.2, stability criterion = 0.00001, 400 iterations maximum) was selected to generate solutions, and the lowest stress solution was picked to interpret. To examine the compositional similarity or dissimilarity among the circle plots or transects, we drew an ordination diagram using the result of NMDS ordination. Maximum DBH of each circle plot, maximum tree height, total basal area, basal area ratio of pioneer and dipterocarp, distance from the edge of SWPF, and topography (ridge, hillside slope, valley) were selected as possible variables that might indicate the degree of disturbance or successional stages. Potential variables were overlaid on the NMDS ordination using a correlation vector (joint plot) implemented in PC-ORD. The vector angles in the ordination indicate the direction of the highest correlation, and the lengths represent the strength of the correlation. Pearson's correlation coefficient was calculated between every pair of variables. Tukey's HSD test was applied to stand variables (no. of species, no. of stems, maximum DBH, maximum height, and total basal area) and specific tree dominance (basal area of pioneers and dipterocarps) for each transect and total data, pooling all transects and Scattered Plots. JMP® 12 (SAS Institute Inc., Cary, NC, USA) was used for statistical analyses except for NMDS.

RESULTS AND DISCUSSION

Tree species

A total of 301 dicot tree species was recorded in the 67 circle plots (Table 1, Table S1). The most abundant species were *Beilschmiedia madang* and *Vernonia arborea* (frequency = 20), followed by *Dipterocarpus cornutus*, *Ptenandra echinata*, *Schima walichii* (19), and *Gironiera nervosa* (18) (Table 1). At Family level, Lauraceae, Dipterocarpaceae and Euphorbiaceae were the most abundant, followed by Melastomataceae, Myrtaceae and Annonaceae (Table 1). Of the 301 species, 54 species appeared in four or more plots (Table 1), and 39 species appeared in three plots. Infrequent species accounted for most species, as 61 species appeared twice and 147 species only once (Table S1).

Transects and scattered plots

Maximum DBH, maximum height, and total basal area in Transect 1 were significantly larger than in the other transects (Figure 2). The number of species and the number of stems were also the largest class among the transects. The DBH, height, total basal area, and basal area ratio of dipterocarps became extremely large in the forest located more than 3 km from the edge of SWPF. The basal area of the pioneers was the smallest of all the transects, although there were hot spots locally (e.g., T1-9), which resulted in the high coefficient of variance (CV) of pioneer trees. In contrast, the basal area of dipterocarps was significantly large, giving the lowest CV (Table 2). Maximum DBH, total basal area, and basal area of dipterocarps were significantly larger in ridge than in valley (Tukey's HSD test, $p < 0.05$).

Both the number of species and stems in Transect 2 showed no significant difference with those in Transect 1, while the maximum DBH and height were significantly smaller than in Transect 1 (Figure 2). There were few pioneers along Transect 2, except around 1.8 km (T2-19) inside from the edge of SWPF (Figure 3). Dipterocarps were commonly found along Transect 2, dominating in some areas (0.4 to 0.8 km from the forest edge) while absent in some areas (Figure 3). Pioneers and dipterocarps showed no significant differences in the basal area among the transect (Table 2). There were no significant differences in stand variables in relation to topography.

Table 1. Frequent tree species appeared in Sungai Wain Protection Forest, East Kalimantan, Indonesia. DBH ≥ 10cm and Frequency ≥ 4 are listed

d/p*	Species name	Abbre-viation	Family name	Max. DBH (cm)	Frequency					
					T1	T2	T3	T4	SP	Total
	Alseodaphne bancana	Alba	Lauraceae	20.5	2	1		3		6
	Alseodaphne borneensis	Albo	Lauraceae	24.4		2	3			5
	Alseodaphne nigrescens	Alni	Lauraceae	41.4	2	3				5
	Alseodaphne penduncularis	Alpe	Lauraceae	19.9		3	1		2	6
	Aporosa nitida	Apni	Euphorbiaceae	36.0	4	2	1			7
	Archidendron cockburnii	Arco	Fabaceae	21.5	1	3	3	4		11
	Artocarpus anisophyllus	Aran	Moraceae	44.9	5	3	1	1	1	11
	Beilschmiedia madang	Bema	Lauraceae	38.2	1	7	4	7	1	20
	Cratoxylon arborescens	Crar	Hypericaceae	27.4	1	2		1	1	5
	Croton argiratus	Crar	Euphorbiaceae	20.7		3			1	4
	Dacryodes rostrata	Daro	Burseraceae	43.9	5	4		1		10
	Dehaasia incrassata	Dein	Lauraceae	27.1	2	1	1			4
	Dillenia indica	Diin	Dilleniaceae	22.3	1	2		3	1	7
	Dillenia reticulata	Dire	Dilleniaceae	26.8		7	4			11
d	*Dipterocarpus cornutus*	Dico	Dipterocarpaceae	84.5	4	9	3	3		19
	Drypetes kikir	Drki	Euphorbiaceae	106.1	2	1		1		4
	Drypetes polyneura	Drpo	Euphorbiaceae	30.0	2	1	2			5
	Endiandra kingiana	Enki	Lauraceae	51.4	5		2			7
p	*Endospermum diadenum*	Endi	Euphorbiaceae	53.5		2	1	1	2	6
	Eusideroxylon zwageri	Euzw	Lauraceae	95.0	6	3			2	11
	Gironiera nervosa	Gine	Ulmaceae	27.7	5	9	4			18
	Gluta aftera	Glaf	Anacardiaceae	24.3	1	2	1			4
	Geunsia pentandra	Gupe	Melastomataceae	23.2			1		3	4
	Knema hirtela	Knhi	Myristicaceae	20.7	2	1	1			4
	Litsea ferruginea	Life	Lauraceae	54.7	4					4
	Litsea lancifolia	Lila	Lauraceae	16.9		2		2		4
p	*Macaranga gigantea*	Magi	Euphorbiaceae	45.1		5	8	1		14
p	*Macaranga hypoleuca*	Mahy	Euphorbiaceae	31.7	3	3	1	1		8
p	*Macaranga kingii*	Maki	Euphorbiaceae	29.9		1	3			4
	Madhuca kingiana	Mdki	Sapotaceae	34.3	5	2				7
	Madhuca sericea	Mdse	Sapotaceae	39.3	1	5	3			9
p	*Melicope glabra*	Megl	Rubiaceae	34.2		6	4		4	14
	Memecylon borneensis	Mebo	Melastomataceae	40.6	3	1			1	5
	Monocarpia eunera	Moeu	Annonaceae	19.5	3	1				4
	Monocarpia kalimantanensis	Moka	Annonaceae	17.4	3		1			4
	Nephelium laurinum	Nela	Sapindaceae	34.8	2	2	2			6
	Nephelium noronhihianum	Neno	Sapindaceae	16.2	1	1	1		1	4
	Polyalthia glauca	Pogl	Annonaceae	25.1	3			3		6
	Polyalthia sumatrana	Posu	Annonaceae	12.3	4					4
	Ptenandra echinata	Ptec	Melastomataceae	27.1	3	8	1	6	1	19
	Rhodamnia cinerea	Rhci	Myrtaceae	20.4	3	3	1	3		10
	Schima walichii	Scwa	Theaceae	41.2		9	3	7		19
	Scorodocarpus borneensis	Scbo	Olacaceae	50.8	3	1	1	2		7
d	*Shorea fallax*	Shfa	Dipterocarpaceae	45.6	1		3	1		5
d	*Shorea laevis*	Shla	Dipterocarpaceae	127.1	8	6		2		16
d	*Shorea lamelata*	Shlm	Dipterocarpaceae	117.0	4	1				5
d	*Shorea leprosula*	Shle	Dipterocarpaceae	134.0	3	4	2			9
d	*Shorea smithiana*	Shsm	Dipterocarpaceae	66.1	2	3				5
	Sterculia foeitida	Stfo	Sterculiaceae	15.8	3		1			4
	Syzigium hertum	Syhe	Myrtaceae	53.2	2	4	1			7
	Syzigium lineatum	Syli	Myrtaceae	42.7		2	2			4
	Syzygium tetrapterum	Syte	Myrtaceae	39.8	3			2		5
p	*Vernonia arborea*	Vear	Compositae	30.9		3	10	3	4	20
	Xylopia stenopetala	Xyst	Annonaceae	28.4	4					4

Note: *; d: dipterocarp species, p: pioneer species

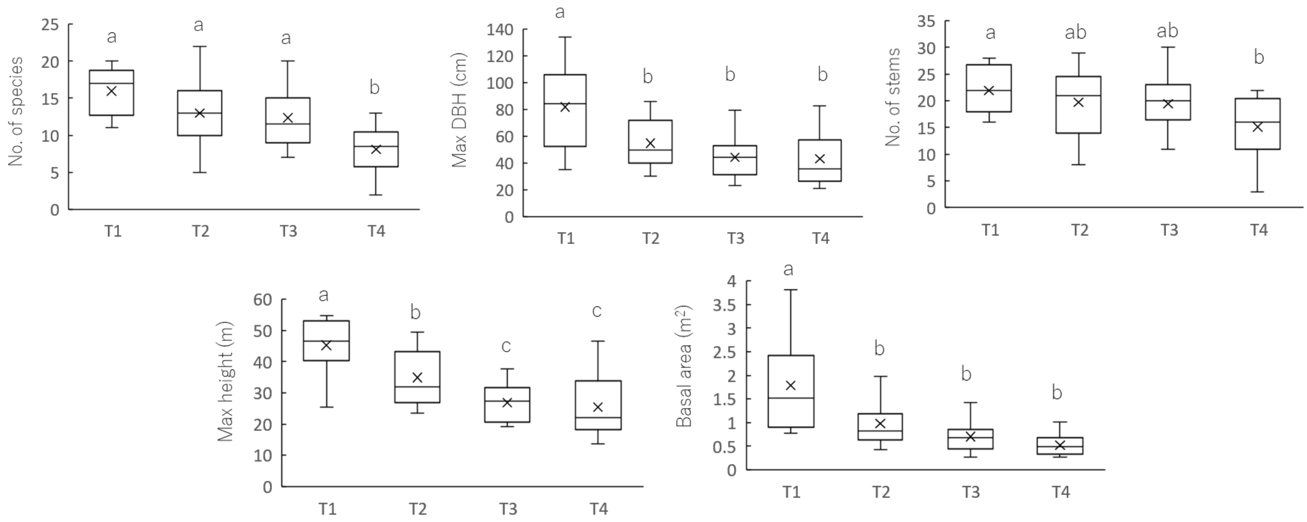

Figure 2. Box plots comparing stand variables among the transects. The different letters above the boxes indicate significant difference at the 5% level by Tukey's HSD test

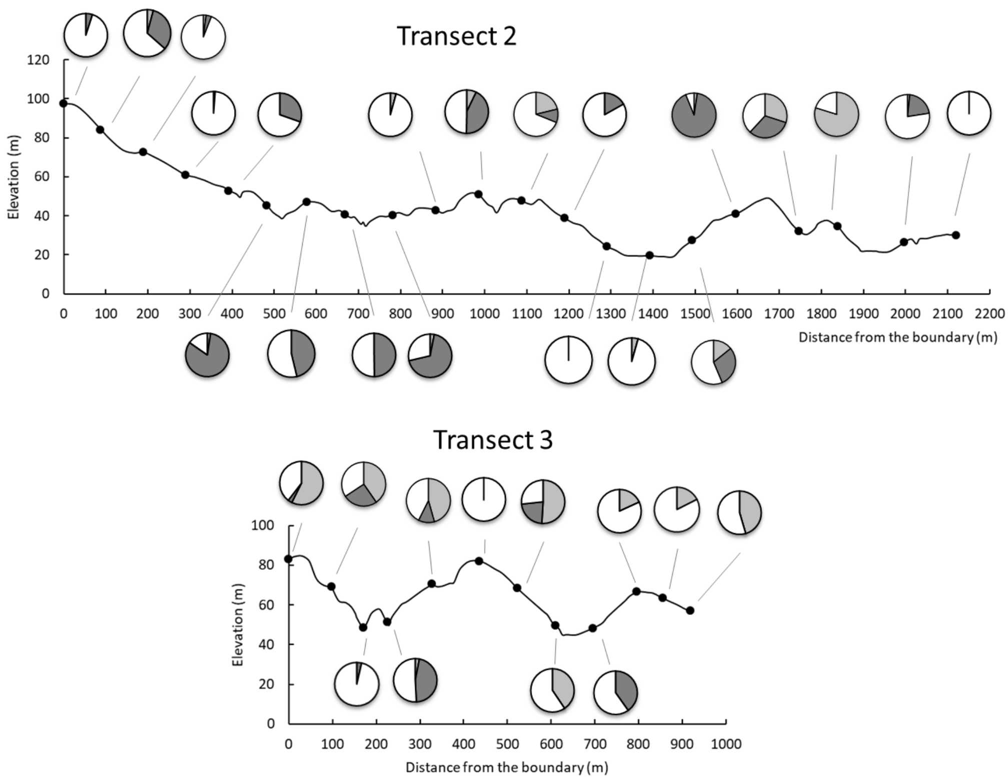

Figure 3. Cases of terrain profiles along the transects (Transects 2 and 3). Each small circle on the profile indicates an investigated circle plot. Ratios of basal area are shown as pie charts: light grey as pioneer trees, dark grey as dipterocarps and blank as other species

Both the number of species and stems in Transect 3 were intermediate among the transects, whereas tree size and basal area were classified as smaller (Figure 2). Pioneer tree species such as *Macaranga gigantea* and *V. arborea* were abundant along Transect 3 (Table 1), and their basal area was high overall and uniform, as seen by the lowest CV (Table 2). The basal area of pioneer trees was significantly larger on ridges than in valleys (Tukey's HSD test, $p < 0.05$), although no other differences were observed in other variables. In contrast, dipterocarps appeared intermittently, and their basal area varied from approximately 40% to 0% (Figure 3) with high CV (Table 2).

The landscapes of burned forests varied considerably according to the position of the circle plots in Transect 4, where forest fires had broken out most recently. Evidence of severe burning, such as charred barks in large residual trees, was found in T4-4, T4-5, T4-6, and T4-10, whereas no recent traces of fire were found in the other plots. The number of species was the least, and other variables were the class among the Transects (Figure 2). Pioneer and dipterocarp appeared locally, indicated by their V in Table 2. We did not apply statistical analysis to the six Scattered Plots around Balikpapan Botanic Gardens because of the small number of samples. Forest stands in Scattered Plot seemed like a dense bush, and the number of species and the other variable was totally small. Pioneer species such as *V. arborea* and *E. diadenum* were found, while dipterocarp was almost absent (Table 1).

Table 3 shows a matrix of Pearson's coefficient correlations among the stand variables of all the circle plots, including the Scattered Plots. The number of species was positively correlated with maximum DBH, maximum height, and total basal area, but it was negatively correlated with pioneer basal area ratio. Maximum DBH, maximum height, and total basal area were positively and highly correlated with each other, as would be expected. The basal area ratio of pioneers had negative and low correlations with other variables. Dipterocarp basal area ratio also showed a high and positive correlation with tree size variables.

Species composition

NMDS ordination yielded a three-dimensional solution that explains 38.5% of the variation in the raw data (final stress = 16.6). Axis 1, Axis 2 and Axis 3 explained 10.2%, 14.5% and 13.9% of the variation in the data, respectively. Figure 4 shows a two-dimensional ordination diagram of the circle plots drawn with Axis 2 and 3, which are more explanatory than Axis 1. The basal area ratio of pioneers (pioneer %) was positively correlated with Axis 2 (r = 0.765), which is represented by a correlation vector that is almost parallel with Axis 2 (Figure 4). Vector of maximum DBH, maximum height, and total basal area are oriented diagonally in the above-left direction with almost the same direction and length (Figure 4). Therefore, only the maximum DBH vector, which is correlated negatively with Axis 2 (r = −0.574) and positively with Axis 3 (r = 0.410), is shown in Figure 4. The correlation vector of the basal area ratio of dipterocarps (dipterocarp %) is also oriented diagonally in the above-left direction in a negative correlation with Axis 2 (r = −0.474) and positively with Axis 3 (r = 0.482) (Figure 4). Distance from the edge of SWPF is weakly negatively correlated with Axis 2 (r = −0.401). In contrast, topography (ridge, hillside slope and valley) is not significantly correlated with any Axis, showing that species composition is unaffected by topography.

The scores of the circle plots are distributed over the ordination space and form weak clusters that partially overlap (Figure 4). The scores of Transect 1 are clustered in the fourth quadrant of Figure 4. Notably, the scores for 3.3 km or more inside from the edge of SWPF are densely clustered (surrounded by a dotted line in Figure 4). The correlation vectors of maximum DBH and dipterocarp % are oriented towards the cluster of Transect 1, indicating a positive correlation with maximum DBH and the ratio of dipterocarps in Transect 1. The scores of Transect 2 are widely distributed throughout the ordination space. The scores of Transect 3 and the Scatter Plots are biased to the right side of Axis 2, implying a positive correlation with the basal area ratio of pioneers. The scores of Transect 4 are clustered in the lower center of Figure 4, overlapping the scores of Transect 2. Figure 5 shows the scores for tree species distributed in the same ordination space as Figure 4. All the pioneer species with a frequency of ≥ 3 (*M, gigantea*, *M. hypoleuca*, *E. diadenumas*, and *V. arborea*) are clustered in the right-center of Figure 5 (surrounded by a dotted line). The scores of *Shorea laevis*, *S. leprosula* and *S. lamelata* are clustered in the fourth quadrant of Figure 5, far from the center, while other dipterocarps, *D. cornutus*, *Shorea smithania*, and *S. fallax* appeared near the center of Axis 2 or Axis 3 (Figure 5).

Table 2. Mean basal area (m^2) of pioneer trees and dipterocarp tree per circle plot (0.04 ha). Different letters to the right of the value indicate significant difference at 5% level by Steel-Dwass test. CV: coefficient of variance

Transect	Pioneer		Dipterocarp	
	Basal area	CV	Basal area	CV
Transect 1	0.0218 b	2.74	0.8936 a	1.03
Transect 2	0.0704 ab	1.85	0.3555 ab	1.47
Transect 3	0.1911 a	0.81	0.1128 b	1.68
Transect 4	0.0205 b	1.84	0.1476 ab	1.58

Table 3. Matrix of Pearson's coefficient of correlation among stand variables of the circle plots (0.04 ha)

	No. of species	No. of stem	Max DBH	Max height	Basal area (BA)	Pioneer BA %	Dipterocarp BA %
No of species	1.0000	0.6926***	0.4258***	0.4292***	0.4695***	-0.4056***	-0.1967
No of stem		1.0000	0.0821	0.0800	0.2531*	-0.1717	-0.0621
Max DBH			1.0000	0.8884***	0.8983***	-0.4390***	-0.7536***
Max height				1.0000	0.8006***	-0.3754**	0.7211***
Basal area (BA)					1.0000	-0.3436**	0.6735***
Pioneer BA %						1.0000	-0.3709
Dipterocarp BA %							1.0000

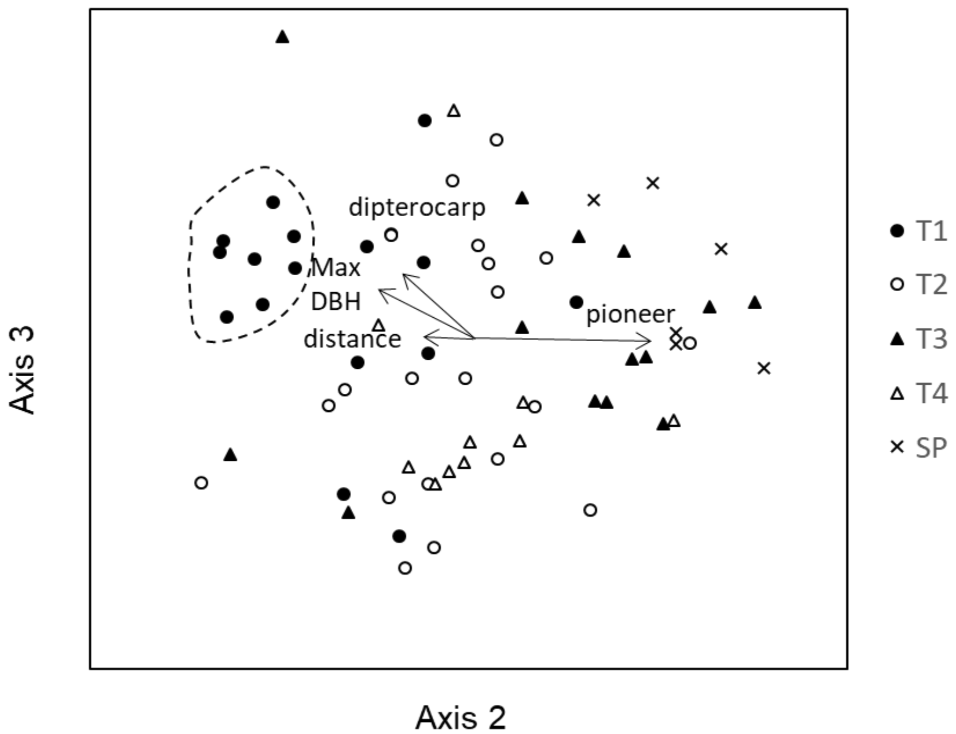

Figure 4. NMDS ordination diagram with correlation vectors of stand variables showing the ordination scores of the transects and the Scattered Plots. The correlation vectors of maximum height and basal area are not shown because their directions and strengths coincide with those of maximum DBH

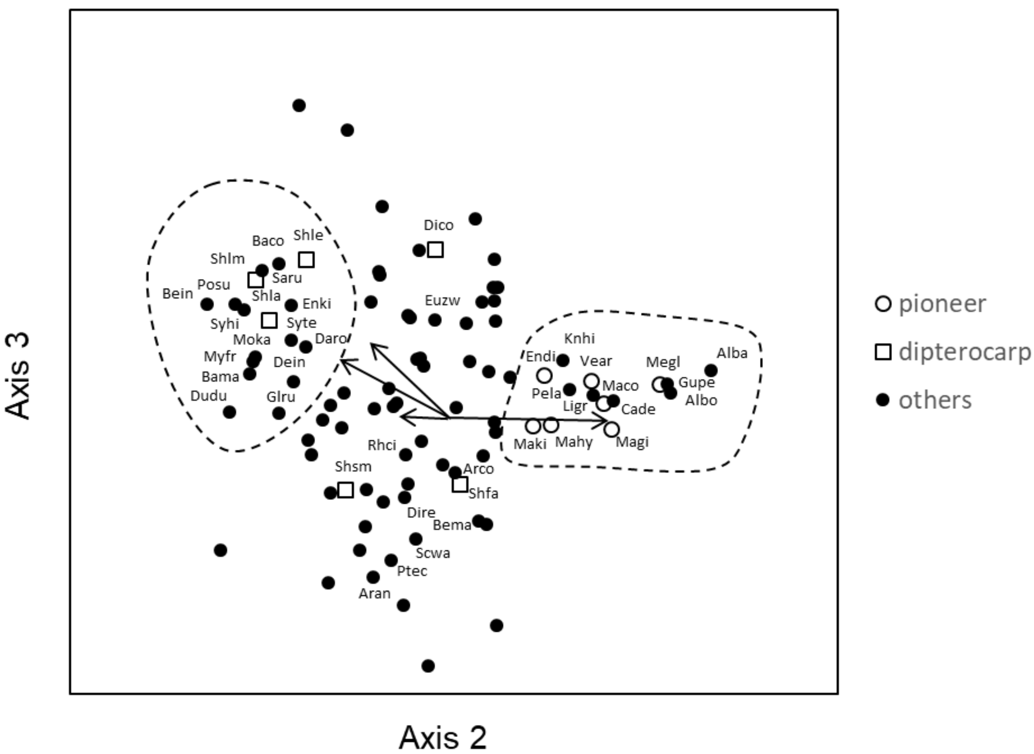

Figure 5. NMDS ordination diagram showing the ordination scores of tree species (pioneers, dipterocarps and others). The correlation vectors are the same as those in Fig. 3. Tree species (frequency ≥ 10 or surrounded by dotted lines) are shown using the abbreviation listed in Table 1. Abbreviations not listed in Table 1 are as follows, Bama: *Barringtonia macrostachya*, Cade: *Canarium denticulatum*, Dein: *Dehaasia incrassata*, Dudu: *Durio dulcis*, Glru: *Glochidion rubrum*, Maco: *Macaranga conifera*, Myfr: *Myristica fragrans*

Discussion

Large *Shorea* trees with a DBH exceeding 1 m and height of up to 50 m appeared in the core area 3 km or more inside the forest edge (Figure 1), which must be the primary forest landscape across East Kalimantan. Kartawinata et al. (1981) reported that more than 80 % of the lowlands and hills in East Kalimantan had been covered by dense dipterocarp forests before the era of large-scale exploitation. Eichhorn (2006) reported that the tree species composition of SWPF is similar to those of vicinal lowland dipterocarp forests such as Bukit Bangkirai, which is covered by mature *Shorea* and *Dipterocarpus* trees. This statement is supported by an extensive floristic analysis of lowland dipterocarp forests across Borneo Island (Slik et al. 2003b).

Our results showed a tendency for both species richness and the number of stems to decline with more recent fire outbreaks (Figure 2), consistent with previous observations in lowland dipterocarp forests in East Kalimantan. Slik et al. (2002) demonstrated that the number of stems recovered within 10 to 20 years but the number of species neither increased nor decreased during the first 15 years after a forest fire. Eichhorn (2006) showed species richness and tree density (≥10 cm in DBH) declined at subplot level (10m x 20 m) in fire-damaged forests, but most tree species were still present at the landscape level in SWPF. Forest fires in tropical areas often rapidly spread over the forest floor, killing seedlings and saplings, but leaving some large or fire-tolerant trees alive (Kinnaird and O’Brien 1998; Okimori and Matius 2000; Slik and Eichhorn 2003; Toma et al. 2000; van Nieuwstadt and Sheil 2005). In our study plots, even in Transect 4, where a forest fire had broken out most recently, medium to large trees had survived, although their survival rate might vary with fire intensity and location. In Transect 3 and the Scattered Plots, nearly 20 years had elapsed since the last 1997-1998 fire, and the stands were in the process of recovery. However, tree size and basal area (by extension, above-ground biomass) were far from those in a deep unburned forest, although the number of species and the number of stems appeared to be catching up. Many studies indicate that it takes time to restore the primary forest in terms of biomass (Toma et al. 2000) or that it will never be restored if repeated human disturbances occur (Eichhorn 2006; van Nieuwstadt et al. 2001).

Although Transect 2 had also been exposed to fire in 1998, the species richness was at the same level as in Transect 1, and tree size (maximum height in particular) was between Transect 1 and the other transects (Figure 2). Pioneer trees were few and locally clustered, while dipterocarps were established irregularly, appearing approx. 400-800 m from the forest edge (Figure 3). We presume that past fires had burned the forest in a patchy fashion, causing the observed mosaic-like distribution of pioneers and dipterocarps.

The ordination diagram in Figure 4 shows that the scores of Transect 3 and the Scattered Plots diverge considerably from those of the core area of Transect 1, which are gathered on the opposite side of the Axis 2 (surrounded by the dotted line), apparently due to the abundance of pioneer trees which had grown due to previous fires. The species composition of Transect 3 and the Scattered Plots will therefore be unlike those of the core area, although species richness and the number of stems appear to have recovered (Figure 2). The scores of Transect 2 are widely distributed between the scores of Transects 1 and 3 along Axis 2, which indicates the abundance of pioneer trees, suggesting them to be intermediate as to species composition. The scores of Transect 4 are also distributed between Transects 1 and 3 along Axis 2 (Figure 4), indicating that the species composition is intermediate although it has experienced fire the most recently. It is likely that a considerable number of unburned or surviving trees remained in Transect 4, and small pioneer trees (<10 cm in DBH) were not detected even if they were present.

The distance from the forest edge is weakly correlated with species composition (Figure 4), indicating that marginal areas were more degraded, even at an area 2 km from the forest edge, as in Transect 2. Fragmentation of forests causes subsequent degradation, regeneration process disturbance, and decline in biodiversity, associated with immigration, transformation to agricultural lands, logging and edge-related fires (Barlow et al. 2016; Cochrane and Laurence 2002; Laurence et al. 2012; Susatya 2018; Zulfikhar et al. 2017). The absence of large dipterocarp trees in marginal areas may suggest that large trees vulnerable to fire had been killed by repeated forest fires (Goldammer et al. 1996). Otherwise, large trees were lost by logging prior to or after fires since such observations have been made in SWPT (Eichhorn 2006) and around the world (Nepstad et al. 1999; Woods 1989; Yeager et al. 2003).

Topography was not detected as a significant environmental variable by NMDS. Slik and Eichhorn (2003) demonstrated that climax tree species (mostly dipterocarps) remained in river valleys and on lower slopes, while pioneer trees were abundant on hillsides and ridges in burned forests around Sungai Wain Protection Forest. This observation coincided with the distribution in Transect 3, where pioneer trees tended to have appeared on ridges while dipterocarps remained in the valleys (Figure 3). On the other hand, no pioneer or dipterocarp dominance pattern was found along Transect 2 (Figure 3), possibly due to the mosaic distribution of fire disturbance. Forest fire often results in forest mosaics in which forest remnants are left in valleys or lower slopes, as seen along Transect 3, regardless of topography, as seen in Transect 2. This pattern can be recognized in the SPOT image (Figure 1), in which unburnt forest appears to remain along river valleys, visible as dark green in the northeast of SWPT (T3), while it is not clear in the west. (T2). We, therefore, presume the heterogeneity of the burned area to have obscured the effects of topography on species composition under the current sampling design.

The typical pioneer species *M. gigantea*, *M. hypoleuca*, and *V. arborea* indicate the occurrence of previous forest fires or logging (Swaine and Whitmore 1988; Slik et al. 2003a). It is noteworthy that *Geunsia pentandra* (Gupe) and *Alseodaphne borneensis* (Albo) appeared in a similar ordination space with these typical pioneer species (Figure 5), suggesting that they might possess similar habitat preferences to pioneer species. The presence of large dipterocarps such as *S. laevis*, *S. leprosula* and *S. smithiana* is doubtless an indicator of forest maturity in lowland dipterocarp forests (Kartawinata et al. 1981; Whitmore 1984). Meanwhile, *D. cornutus* and *Shorea fallax* are positioned at the center of Axis 2 (Figure 5), suggesting that they appear both in primary forests and moderately disturbed forests. Although studies of physiological and ecological reactions to disturbances remain limited for individual dipterocarp species, it is known that some dipterocarps such *S. fallax* and *S. parvifolia* can survive and even regenerate in gaps or logged areas (Kuusipalo et al. 1996; Niiyama et al. 2003; Okimori and Matius 2000; Tuomela et al. 1996). *Dacryodes rostrata*, *Endiandra kingiana*, and *Syzygium hirtum* appear in a similar ordination space to *S. laevis* (Figure 5), suggesting that they might be associated with primary forests; otherwise, they might be vulnerable to fire. *Eusideroxylon zwageri* is also known as Borneo ironwood timber, and is very useful in Borneo owing to its high density and durability (Kessler 1996; Kurokawa et al. 2004). It is located in the center of Axis 2 (Figure 5), although it is noted in several reports as primary forest species (Matius et al. 2000; Slik and Eichhorn 2003). This discrepancy may be attributed to fire tolerance owing to thick bark (van Nieuwstadt and Sheil 2005) and its ability to regenerate in degraded forests (Toma 2000). Although extensive studies on forest inventory have been carried out in East Kalimantan (Echhorn 2006; Slik and Eichhorn 2003; Slik et al. 2010), further efforts need to be made in tropical rainforest in which very numerous taxa are present.

ACKNOWLEDGEMENTS

We thank local staff at Sungai Wain Village for their assistance during the field survey. We are grateful to the staff of the Balikpapan Botanic Gardens, Indonesia, for permission to carry out our survey at the Botanic Gardens. We also thank the staff at LIPI for permission to engage in this research project and their kind support while it was being carried out. The help of Titis Hutama Syah of East Kutai Agricultural College in creating a species list is gratefully acknowledged. This study was financially supported by the Japan Society for the Promotion of Science (JSPS) KAKENHI (Grant No. 26304028).

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Table S1. Electronic supplementary material. Infrequent tree species (Frequency < 4) appeared in Sungai Wain Protection Forest, East Kalimantan, Indonesia

d/p*	Species	Family name	Frequency T1	T2	T3	T4	SP	Total
	Actinodaphne bancana	Lauraceae					3	3
	Actinodaphne borneensis	Lauraceae					1	1
	Actinodaphne fragilis	Lauraceae					1	1
	Actinodaphne glabra	Lauraceae			1			1
	Actinodaphne glomerata	Lauraceae		2				2
	Actinodaphne macrophylla	Lauraceae	1					1
	Actinodaphne mountana	Lauraceae		1				1
	Actinodaphne ridleyi	Lauraceae				1		1
	Actinodaphne sphaerocarpa	Lauraceae	1					1
	Adina minutiflora	Rubiaceae		1				1
	Adinandra colina	Pentaphylacaceae		2				2
	Adinandra dumosa	Pentaphylacaceae				1		1
	Aglaia dokko	Meliaceae				1		1
	Aglaia leptantha	Meliaceae	1					1
	Aglaia odoratissima	Meliaceae			1			1
	Aglaia tomentosa	Meliaceae		1			1	2
	Aglaia sp.	Meliaceae				1		1
	Allophylus cobbe	Sapindaceae		1				1
	Alseodaphne corneri	Lauraceae			2	1		3
	Alseodaphne elmeri	Lauraceae		1	2			3
	Alseodaphne glomerata	Lauraceae		1				1
	Alseodaphne macrantha	Lauraceae	1					1
	Alseodaphne macrocarpa	Lauraceae		1				1
	Alseodaphne macrophyllus	Lauraceae					1	1
	Alseodaphne madang	Lauraceae			1			1
	Alseodaphne paludosa	Lauraceae			1			1
	Alseodaphne pendulifolia	Lauraceae	1				1	2
	Alseodaphne perakensis	Lauraceae					1	1
	Alseodaphne robusta	Lauraceae			1		1	2
	Alseodaphne rubrolignea	Lauraceae		2				2
	Alseodaphne wrayi	Lauraceae		2				2
	Alseodaphne sp.	Lauraceae				1		1
	Antidesma bunius	Phyllanthaceae			2			2
	Antidesma coriaceaum	Phyllanthaceae	1	2				3
	Antidesma leucocarpa	Phyllanthaceae			1			1
	Antidesma neurocarpum	Phyllanthaceae			2			2
	Antidesma polyneura	Phyllanthaceae			1			1
	Aporosa attenifera	Euphorbiaceae		1				1
	Aporosa falcifera	Euphorbiaceae		1				1
	Aporosa galeata	Euphorbiaceae			1			1
	Aporosa granularis	Euphorbiaceae	1					1
	Aporosa nervosa	Euphorbiaceae	1	1				2
	Aporosa subcaudata	Euphorbiaceae	1		1			2
	Aquilaria malacensis	Thymelaeaceae	1					1
	Artocarpus campedens	Moraceae	1	2				3
	Artocarpus comedo	Moraceae		2				2
	Artocarpus comunis	Moraceae	3					3
	Artocarpus elasticus	Moraceae			1			1
	Artocarpus glaucus	Moraceae		1				1
	Artocarpus lanceifolius	Moraceae		1	1			2
	Artocarpus nitidus	Moraceae	2					2
	Artocarpus rigidus	Moraceae					1	1
	Atuna racemose	Chrysobalanaceae		1				1
	Baccaurea cordata	Phyllanthaceae	1	1	1			3
	Baccaurea deflexa	Phyllanthaceae		1				1
	Baccaurea kustleri	Phyllanthaceae		1	1		1	3
	Baccaurea sumatrana	Phyllanthaceae		1				1
	Baringtonia pendula	Lecythidaceae			1			1
	Baringtonia reticulata	Lecythidaceae		1	1			2
	Barringtonia lanceolata	Lecythidaceae	1					1
	Barringtonia macrostachya	Lecythidaceae	3					3
	Barringtonia sp.	Lecythidaceae	1					1
	Beilschmiedia brevipes	Lauraceae			1			1
	Beilschmiedia glabra	Lauraceae			2			2
	Beilschmiedia insignis	Lauraceae	3					3
	Beilschmiedia micrantha	Lauraceae	2					2
	Blumeodendron tokbrai	Euphorbiaceae		1	1			2
	Bridelia minutiflora	Phyllanthaceae	1					1
	Buchanania sessifolia	Anacardiaceae		1				1
	Calophyllum nodosum	Calophyllaceae	1					1
	Camnosperma squamatum	Anacardiaceae	1		1			2
	Camnosperma auriculata	Anacardiaceae	1	1				2
	Canarium comuni	Burseraceae	2					2
	Canarium denticulatum	Burseraceae		2	1			3
	Chaetocarpus castanocarpus	Peraceae		1				1
	Cleistanthus faxii	Phyllanthaceae		1				1
	Cleistanthus myrianthus	Phyllanthaceae	1		1			2
	Cleistanthus pubens	Phyllanthaceae	1		1			2
	Cleistanthus rufescens	Phyllanthaceae		1				1
	Cratoxylon formosum	Hypericaceae	1	1				2
	Cratoxylon sumatranum	Hypericaceae		1	1			2
	Cryptocaria costata	Lauraceae	1					1
	Cryptocarya ferrea	Lauraceae		1				1
	Cryptocarya glabra	Lauraceae			2			2
	Cryptocaria griffithiana	Lauraceae	1					1
	Cryptocarya impressa	Lauraceae	3					3
	Cryptocarya lanceolata	Lauraceae		1	1			2
	Cryptocarya nitens	Lauraceae		1				1
	Cryptocarya polyneura	Lauraceae			1			1
	Cryptocarya stricifolia	Lauraceae		3				3
	Dacryodes incurvata	Burseraceae		1	1			2
	Dehaasia glabra	Lauraceae			1			1
	Dehaasia lancifolia	Lauraceae		1				1
	Dehaasia polyneura	Lauraceae		3				3
	Dendrocnide eliptica	Urticaceae		2				2
	Dendrocnide stimulan	Urticaceae	1					1
	Dialium indum	Fabaceae		2	1			3
	Dictyoneura acuminata	Sapindaceae	2					2
	Dillenia bornensis	Dilleniaceae	1				2	3
	Dillenia ciberiana	Dilleniaceae		1				1
	Dillenia excelsa	Dilleniaceae	1	1				1
	Dillenia reticulata	Dilleniaceae			1			1
	Dillenia tomentela	Dilleniaceae			1			1
	Diospyros bornensis	Ebenaceae	1					1
	Diospyros confertifolia	Ebenaceae		1				1
	Diospyros onfolius	Ebenaceae	1					1
d	*Dipterocarpus confertus*	Dipterocarpaceae	1					1
d	*Dipterocarpus crinitus*	Dipterocarpaceae	1				1	2
d	*Dipterocarpus grandiflorus*	Dipterocarpaceae	2					2
	Drypetes cactilloi	Euphorbiaceae	2					2
	Durio dulcis	Malvaceae	3					3
	Durio grandiflorus	Malvaceae			1			1
	Durio graveolens	Malvaceae			2			2
	Durio grifitii	Malvaceae	2	1				3
	Durio lanceolata	Malvaceae	2	1				3
	Durio oxleyanus	Malvaceae		1	1			2
	Dyospyros bornensis	Ebenaceae		1				1
	Dyospyros onfolius	Ebenaceae	1		1			2
	Elmerilia molis	Magnoliaceae			1			1
	Endiandra ochraceae	Lauraceae	1					1
	Endiandra rubescens	Lauraceae				1		1
	Endiandra wrayi	Lauraceae	1					1
	Eurya trichocarpa	Pentaphylacaceae		1				1
	Fahrenhetia macrophylla	Euphorbiaceae	2					2
	Ficus madurensis	Moraceae		1				1

	Foristia macrophyla	Commelinaceae		1				1
	Foristia molisima	Commelinaceae	1					1
	Garcinia microphylla	Clusiaceae	1					1
	Garcinia nervosa	Clusiaceae		1				1
	Garcinia benthani	Clusiaceae	1					1
	Garcinia celebica	Clusiaceae	2					2
	Glochidion lutescens	Phyllanthaceae		1				1
	Glochidion obscurum	Phyllanthaceae			1			1
	Glochidion rubrum	Phyllanthaceae	1			2		3
	Gluta macrocarpa	Anacardiaceae			1			1
	Gluta renghas	Anacardiaceae		1				1
	Gluta velutina	Anacardiaceae		1				1
	Gordonia borneensis	Theaceae		1				1
	Guettarda speciosa	Rubiaceae		1	1			2
d	*Hopea mangarawan*	Dipterocarpaceae		1				1
d	*Hopea nervosa*	Dipterocarpaceae		1				1
	Horsfieldia grandis	Myristicaceae		1				1
	Hydnocarpus pentale	Achariaceae	1					1
	Timonius coordersii	Rubiaceae				1		1
	Knema galeata	Myristicaceae			1			1
	Knema glauca	Myristicaceae	2			1		3
	Knema glaucescens	Myristicaceae	1	2				3
	Kokoona coriacea	Celastraceae		1	1			2
	Lindera caesia	Lauraceae	1			1		2
	Lindera reticulosa	Lauraceae		1				1
	Lithocarpus conocarpus	Fagaceae	1		1			2
	Lithocarpus gracilis	Fagaceae			3			3
	Lithocarpus sundaicus	Fagaceae	1	1				2
	Litsea accendens	Lauraceae	2					2
	Litsea angulata	Lauraceae	1					1
	Litsea curtisii	Lauraceae		1				1
	Litsea firma	Lauraceae		2	1			3
	Litsea gracilipes	Lauraceae	1					1
	Litsea grandis	Lauraceae	2					2
	Litsea lucida	Lauraceae		1				1
	Litsea nidularis	Lauraceae	1			1		2
	Litsea robusta	Lauraceae			1			1
	Litsea tomentosa	Lauraceae	1					1
	Litsea wrayi	Lauraceae	1					1
	Litsea sp.	Lauraceae		1				1
	Macaranga anceps	Euphorbiaceae				1		1
p	*Macaranga conifera*	Euphorbiaceae	1		2			3
	Macaranga lowii	Euphorbiaceae	1					1
	Madhuca spectabilis	Sapotaceae		1				1
	Maranthes corimborsa	Chrysobalanaceae			1			1
	Mezzettia parviflora	Annonaceae	1	2				3
	Moultonianthus leembruggianus	Euphorbiaceae			1			1
	Myristica fragrans	Myristicaceae	1	1	1			3
	Myristica maxima	Myristicaceae			1			1
	Myristica villosa	Myristicaceae		1				1
	Nauclea subdita	Rubiaceae				1		1
	Neolitsea sp.	Lauraceae				1		1
	Neonauclea oficinalis	Rubiaceae	1					1
	Neonauclea sp.	Rubiaceae		1				1
	Neouvaria foetida	Annonaceae	1					1
	Nephelium cuspidatum	Sapindaceae	3					3
	Nephelium glauca	Sapindaceae	1					1
	Nephelium ramboutan-ake	Sapindaceae		1				1
	Nephelium subfalcatum	Sapindaceae		1				1
	Nephelium xestophylum	Sapindaceae			1			1
	Nepheliun laurinum	Sapindaceae					1	1
	Octanostachys amentacea	Olacaceae			2			2
	Palaquium hexandrum	Sapotaceae	1					1
	Palaquium quercifolium	Sapotaceae		2				2
	Paranepheliun xestophylum	Sapindaceae					1	1
	Parkia speciosa	Fabaceae	1					1
	Payena acuminata	Sapotaceae		1				1

	Payena lucida	Sapotaceae	2	1				3
	Pentace laxiflora	Malvaceae	1	1		1		3
	Phoebe grandis	Lauraceae	1					1
	Planchonella obovata	Sapotaceae		1				1
	Planchonella sp.	Sapotaceae			1			1
	Planchonia valida	Lecythidaceae			1			1
	Podocarpus sp.	Podocarpaceae		1			1	2
	Polyalthia cauliflora	Annonaceae		2				2
	Polyalthia glauca	Annonaceae		1				1
	Polyalthia lanceolata	Annonaceae			1			1
	Polyalthia xantophetala	Annonaceae	2	1				3
	Prunus nodosa	Rosacea		1				1
	Pteleocarpa lamponga	Boraginaceae		2				2
	Ptenandra rostrata	Melastomataceae	1		1			2
	Quercus argentata	Fagaceae	1					1
	Quercus elmeri	Fagaceae		1				1
	Quercus gaharuensis	Fagaceae					1	1
	Quercus sagitata	Fagaceae	1	1		1		3
	Sandoricum beccarianum	Meliaceae	1	1				2
	Santiria rubiginosa	Burseraceae	3					3
	Santiria tomentosa	Burseraceae	2		1			3
	Scaphium macropodum	Malvaceae		1				1
	Semecarpus sp.	Anacardiaceae		1				1
d	*Shorea eliptera*	Dipterocarpaceae			1			1
d	*Shorea gibbosa*	Dipterocarpaceae		1				1
d	*Shorea guiso*	Dipterocarpaceae		1				1
d	*Shorea ovalis*	Dipterocarpaceae	1					1
d	*Shorea parvifolia*	Dipterocarpaceae			2			2
d	*Shorea pauciflora*	Dipterocarpaceae	2					2
d	*Shorea seminis*	Dipterocarpaceae	2					2
d	*Shorea* sp.	Dipterocarpaceae		1	1	1		3
	Sindora walichii	Fabaceae		1				1
	Stemonorus scorpioides	Icacinaceae			1			1
	Strombosia javanica	Olacaceae	1					1
	Symplocos fasciculata	Symplocaceae		1				1
	Syzigium formosum	Myrtaceae			1			1
	Syzigium haifii	Myrtaceae			1			1
	Syzigium javanichum	Myrtaceae		1	1			2
	Syzigium lanceifolium	Myrtaceae		1				1
	Syzigium leucoxcylum	Myrtaceae		2				2
	Syzigium longiflorum	Myrtaceae	2	1				3
	Syzigium pendens	Myrtaceae		1				1
	Syzigium pendulum	Myrtaceae			3			3
	Syzigium rejangensis	Myrtaceae			1			1
	Syzigium rostadonis	Myrtaceae	2					2
	Syzigium stafianum	Myrtaceae		1				1
	Syzigium tapingensis	Myrtaceae		1				1
	Syzigium tawahense	Myrtaceae		1	2			3
	Syzigium zeylanicum	Myrtaceae			1			1
	Syzygium hirtum	Myrtaceae	3					3
	Syzygium hoseanum	Myrtaceae	1					1
	Syzygium nemestrinum	Myrtaceae				1		1
	Syzygium papillosum	Myrtaceae				1		1
	Syzygium pellidulum	Myrtaceae	1					1
	Syzygium pendens	Myrtaceae				1		1
	Syzygium rostadonis	Myrtaceae	1					1
	Trigonostemon villosus	Euphorbiaceae			2			2
	Triomma malaccensis	Burseraceae	2					2
	Tristania whiteana	Myrtaceae		1				1
d	*Vatica micrantha*	Dipterocarpaceae	1					1
d	*Vatica oblongifolia*	Dipterocarpaceae		1				1
d	*Vatica umbonata*	Dipterocarpaceae		1				1
	Vitex pinnata	Lamiaceae			1			1
	Xylopia ferruginea	Annonaceae		3				3
	Xylopia malayana	Annonaceae			1	1		2

Note: *d: dipterocarp species, p: pioneer species