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Macaranga and *Mallotus* species (Euphorbiaceae) as indicators for disturbance in the mixed lowland dipterocarp forest of East Kalimantan (Indonesia)

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Abstract

The indicator value (IV) of *Macaranga* and *Mallotus* species (Euphorbiaceae) for different types of disturbance in lowland dipterocarp forest was assessed by counting and identifying all individuals of species of these genera taller than 30 cm in 45 (10 m × 300 m) plots at nine locations. Twelve *Macaranga* and nine *Mallotus* species were found. The main forest disturbance types (primary forest, secondary forest, selectively logged forest, forest burned once, and repeatedly burned forest used for shifting-cultivation) each had their own set of indicator species. The level of disturbance in the forest types was assessed by measuring nine forest structural parameters. The occurrence of *Macaranga* and *Mallotus* species was closely related to the level of disturbance in a forest. Most *Macaranga* species were characteristic of high disturbance levels, while most *Mallotus* species preferred intermediate to low levels of disturbance. However, both genera had species at both disturbance extremes. Using multiple regression analysis, combinations of *Macaranga* and *Mallotus* species were formed and used to predict the separate forest structural parameters and the general level of disturbance of a forest. The *Macaranga* and *Mallotus* species could be grouped into (1) primary forest 'remnant' species; (2) generalist pioneer species; and (3) high disturbance pioneer species. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Indicator species; Forest structure; Forest disturbance; Tree species diversity; Life-history strategies; *Macaranga*; *Mallotus*

1. Introduction

Kalimantan (the Indonesian part of Borneo) was mainly covered with primary forest until the start of mechanised logging at the end of the 1960s. Since then, large parts of the mixed lowland dipterocarp forest have been selectively logged (Kartawinata, 1980; Kartawinata and Vayda, 1984; Appanah and Ratnam, 1992; MacKinnon et al., 1996). Logging was often followed by settlement of trans-migrants who practised destructive shifting-cultivation activities

because of the poor quality of the soils in Kalimantan (Kartawinata et al., 1981b; Kartawinata and Vayda, 1984). This has resulted in a large variety of secondary forests which cover extensive parts of the island. These secondary forests form a mosaic of different vegetation types, depending on the kind and severity of the disturbance, on the time elapsed since the disturbance, and on the vicinity of primary forest. They range from grasslands, to forests dominated by pioneer tree species, to forests that are hardly distinguishable from primary forest.

Currently the amount of secondary forest forms such an important part of the total forested area of East Kalimantan that information on its extent and regeneration potential has become essential for effective

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forest management, land use and conservation planning. To identify and map these secondary forests, data are needed on species composition, forest structure, and environmental conditions. This is very laborious work, especially since forest inventories are dependent on a small group of specialists to identify all the collected plant material. For large scale rapid assessment of tree species diversity and forest regeneration potential, other methods are needed to estimate these forest properties via faster and easier to measure parameters (Boyle and Boontawee, 1994; Koop et al., 1994; Lammerts van Buren and Duivenvoorden, 1996; Dallmeier and Comiskey, 1998). The use of indicator species is one such an approach (Pearson, 1995; World Bank, 1998; Lindenmayer et al., 2000).

In this paper we study the possible indicator role of *Macaranga* Thou. and *Mallotus* Lour. species for forest disturbance (fire, selective logging and shifting-cultivation). *Macaranga* and *Mallotus* are two closely related genera belonging to the Euphorbiaceae (Webster, 1994; Slik and Welzen, 2001). The species in these two genera are relatively easy to identify, even when sterile, and useful keys to the species of Borneo and East Kalimantan are available (Airy Shaw, 1975; Whitmore, 1975; Slik et al., 2000; Davies, 2001). Based on the fact that many *Macaranga* and *Mallotus* species are characteristic of secondary forests in southeast Asia (Whitmore, 1967, 1969; Primack and Lee, 1991; Keßler et al., 1995; Davies, 1998; Davies et al., 1998), combined with information available from labels on herbarium material and field observations, we expect the composition and the frequencies of occurrence of *Macaranga* and *Mallotus* species to change following disturbance in a forest. This change in species composition and abundance is expected to be dependent on the type and severity of the disturbance, and the life-history strategies of the studied species (climax versus pioneer).

In order to test the hypothesis that species of *Macaranga* and *Mallotus* are useful forest disturbance indicators we employed the indicator value (IV) method of Dufrière and Legendre (1997). Additionally, correlation between the forest structural variables and the occurrence of *Macaranga* and *Mallotus* species were tested using canonical correspondence analysis (CCA) (Jongman et al., 1987). Multiple regression analysis was then used to calculate the multiple comparison equations needed to predict the forest

structure variables and general level of disturbance in a plot based on the presence of certain *Macaranga* and *Mallotus* species (Sokal and Rohlf, 1995).

2. Material and methods

2.1. Study sites

The study was carried out at two locations south of the Mahakam River in East Kalimantan (Fig. 1). Both areas were originally covered with mixed lowland dipterocarp forest. Rainfall patterns and quantities in the two locations are similar (2000–2500 mm per year) and show no clearly marked dry season, although the period between June and October is slightly drier than the rest of the year (Kartawinata et al., 1981a; Kartawinata and Vayda, 1984; van Valkenburg, 1997). Temperatures range between a minimum of ca. 24 °C at night to a maximum of ca. 31 °C at midday. In both areas very dry years occur occasionally, mostly associated with the El Niño southern oscillation phenomenon (Salafsky, 1994; Walsh, 1996).

2.1.1. Wanariset

The Wanariset research area is located at 38 km along the Balikpapan–Samarinda main road. The forest has been logged in the early 1970s with extraction rates of up to 20 trees per ha. After logging, several local wood extraction teams have continued to fell trees illegally. Local farmers have used most of the area for shifting-cultivation since the beginning of the 1980s. All forest around Wanariset was burned in 1982/1983 (MacKinnon et al., 1996; Dennis, 1998), except for a 100 ha forest fragment named Wartono Kadri. Several small scale fires occur regularly in the area, mainly caused by local farmers who are clearing forested land for agricultural purposes. Fieldwork in this area was carried out in 1997, just before the large scale fires of 1997/1998 burned the whole area again (Hoffmann et al., 1999).

2.1.2. International Timber Corporation Indonesia (ITCI)-logging concession

The ITCI-concession is located south of the Mahakam River, between Kenangan, Mt. Meratus and Kotabangun. It covers an area of ca. 600,000 ha. The

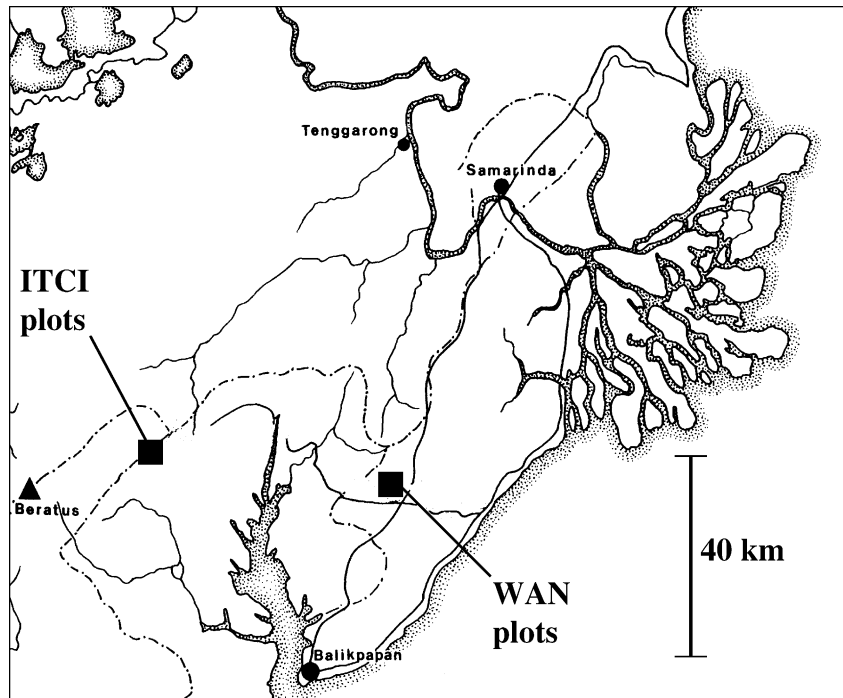


Fig. 1. Map (courtesy after Keßler and Sidiyasa, 1994) showing the proximate location of the two research locations in east Kalimantan, Indonesia: the ITCI-logging concession (ITCI) and the Wanariset research area (WAN). See also Table 1 for more detailed information.

forest is being selectively logged since the end of the 1960s, using a 35 year cutting cycle. Logging intensities vary around 10 trees per ha (MacKinnon et al., 1996). The oldest parts of the concession have been converted into timber plantations, the rest is production forest. A small area of primary forest still exists in the western part of the concession. This undisturbed forest will be selectively logged between now and ca. 2006. In 1998 extensive parts of the concession were burned (ca. 90%), so that only small areas of primary forest and selectively logged forest remain unaffected by fire (Dennis, 1998; Hoffmann et al., 1999).

2.2. Relating *Macaranga* and *Mallotus* species to the type of disturbance

At the two locations, ITCI and Wanariset, plots were established in primary forest, selectively logged forest, forest burned once, and repeatedly burned forest which was used for shifting-cultivation (Table 1). No selectively logged forest could be sampled in

Wanariset due to absence of this kind of disturbance there, while no repeatedly burned forest used for shifting-cultivation could be sampled in ITCI due to absence of this forest type in ITCI. In total 45 plots were laid out in a north–south direction, five plots for each kind of forest disturbance (Table 1). Each plot measured 300 m × 10 m and was subdivided into 30 subplots of 10 m × 10 m. The five plots within each forest disturbance type were placed as far apart from each other as possible, with a maximum distance of 2 km. However, due to the size of some of the studied forests, distances between the plots varied considerably.

Within the plots all *Macaranga* and *Mallotus* individuals taller than 30 cm were counted, identified, and their position recorded. We used the 30 cm height limit, because smaller plants of some of the species can be very difficult to identify due to their morphological variability (see Bodegom et al., 1999). The IV for each species was calculated using the method of Dufrière and Legendre (1997). This method is especially suited for identifying indicator species independently

Table 1
The studied forest disturbance types, their codes, coordinates and disturbance history

Locality	Code	Coordinates (longitude/latitude)	Disturbance
Wanariset	WAN1	116.56E/0.59S	Primary forest, sampled in 1997
	WAN2	116.55E/0.59S	Selectively logged early 1970s, repeatedly burned since 1982/1983 and used for shifting-cultivation until 1994, sampled in 1997
	WAN3	116.57E/0.59S	Selectively logged early 1970s, burned in 1982/1983, sampled in 1997
ITCI	ITCI1	116.20E/0.49S	Primary forest, sampled in 1998/1999
		116.34E/0.54S	Primary forest, sampled in 1998/1999
	ITCI2	116.21E/0.52S	Selectively logged in 1997/1998, sampled in 1998/1999
	ITCI3	116.31E/0.55S	Selectively logged in 1983, sampled in 1998/1999
	ITCI4	116.35E/0.53S	Selectively logged in 1973, sampled in 1998/1999
	ITCI5	116.27E/0.48S	Primary forest burned in 1997/1998, sampled in 1998/1999
	ITCI6	116.30E/0.51S	Selectively logged in 1983, burned in 1997/1998, sampled in 1998/1999

The forest disturbance types are located in the ITCI-concession (ITCI) and in the Wanariset research area (WAN). In each forest disturbance type five plots of 300 m × 10 m were established.

of the plant (or animal) community as a whole (Dufrière and Legendre, 1997; McGeoch and Chown, 1998). The method gives an integrated measure for the relative mean abundance and the relative frequency of the studied species in the forest disturbance types.

$$A_{ij} = \frac{N \text{ individuals}_{ij}}{N \text{ individuals}_i}$$

$$B_{ij} = \frac{N \text{ plots}_{ij}}{N \text{ plots}_j}$$

$$IV_{ij} = A_{ij} \times B_{ij} \times 100$$

A_{ij} (relative mean abundance) is the mean number of individuals of species i in disturbance type j divided by the mean number of individuals of species i in disturbance type j plus the mean number of individuals of species i outside disturbance type j . B_{ij} (relative frequency) is the number of plots in disturbance type j , where species i is present divided by the total number of plots in disturbance type j . IV_{ij} (indicator value) is the relative mean abundance of species i in disturbance type j multiplied by the relative frequency of species i in disturbance type j times 100%.

Species that are weakly associated with a certain forest disturbance type because they are either not abundant or not present in all the plots will score a low IV. Only species that have both a high mean abundance and are present in the majority of plots of

a certain disturbance type will score a high IV for that particular habitat. To test whether the observed IV of a species in a certain forest disturbance type was significantly higher than could be expected based on a random distribution, the observed IV was compared with 500 randomly generated IVs. These random IVs were generated with a random reallocation procedure of the plots among the disturbance types (see Dufrière and Legendre, 1997). If the observed IV of a species in a forest disturbance type fell within the top 2.5% of the random IVs (sorted in decreasing order), it was considered to have significantly positively deviated from the expected random mean, i.e. the species had a significant higher IV than expected.

2.3. Relating *Macaranga* and *Mallotus* species to the level of disturbance

To assess the relationship between the severity of forest disturbance and the occurrence of *Macaranga* and *Mallotus* species, nine forest structural variables were measured and calculated for all the plots. These variables were selected to reflect forest disturbance and covered a wide spectrum of the forest structure (Koop et al., 1994). Some forest structural variables (nos. 5, 6, 7, 8, and 9 mentioned below) were measured in the 10 m × 10 m subplots as present or absent (Boolean variables). These presence/absence data were averaged to get a frequency value for each plot. The forest structural variables used in the analyses are

the following.

1. The number of trees with a diameter at breast height (dbh) ≥ 10 cm, measured with a diameter tape.
2. The total basal area (m²) of all trees with a dbh ≥ 10 cm.
3. The tree species diversity expressed as the number of species present. All trees with dbh ≥ 10 cm were identified to species level or assigned to morpho-species. Vouchers are stored in the Nationaal Herbarium Nederland, Leiden University Branch, The Netherlands (L).
4. The maximum tree height in each subplot, estimated in classes of 5 m, averaged to get a value for the whole plot.
5. The presence of trees with dbh ≥ 50 cm in each subplot, scored as 0 when absent, and 1 when present, averaged to get the frequency for the whole plot.
6. Density of leaf cover between 0 and 5 m height in each subplot (undergrowth), estimated as either less than 50% coverage, scored as 0, or more than 50% coverage, scored as 1, averaged to get the frequency for the whole plot.
7. Density of leaf cover between 5 and 30 m height directly above the subplot (intermediary layer), estimated as either less than 50% coverage, scored as 0, or more than 50% coverage, scored as 1, averaged to get the frequency for the whole plot.
8. Density of leaf cover above 30 m height directly above the subplot (canopy), estimated as either less than 50% coverage, scored as 0, or more than 50% coverage, scored as 1, averaged to get the frequency for the whole plot.
9. Visible disturbance in each subplot, i.e. subplots affected by fire, skid trails, paths, land slides, or tree extraction (stumps, logs), scored as 0 when absent or 1 when present, averaged to get the frequency for the whole plot.

A CCA was used to assess the correlation between the forest structural variables (environmental variables) and the occurrence of *Macaranga* and *Mallotus* species in the plots (Jongman et al., 1987). This analysis was done with the computer programme multi variate statistical package (MVSP) 3.01 and was performed using the species frequencies of oc-

currence (based on presence/absence per subplot) in the plots. The environmental axis that best reflected the level of disturbance among the plots was used as the disturbance axis. By projecting the plots on this axis their general level of disturbance could thus be determined. The plots were scaled between 0 and 100 based on the minimum and maximum value of the projections on this axis. The disturbance preference of the *Macaranga* and *Mallotus* species was determined similarly.

A multiple regression analysis (Sokal and Rohlf, 1995) was used to find the optimum number of species needed to explain the forest structure parameters and the general level of disturbance in the plots as good as possible (i.e. with high R^2 values). We used several selection methods (forward, backward and stepwise selection) to find useful species groups (using SPSS 8.0). The resulting multiple comparison equations can be used to predict the forest structure parameters in plots where these are unknown.

3. Results

3.1. *Macaranga* and *Mallotus* as indicators for the type of disturbance

Twelve *Macaranga* and nine *Mallotus* species were found in the 45 plots (Table 2). The *Macaranga* species were usually present in both the ITCI and the Wanariset plots, while most *Mallotus* species occurred either only in ITCI or only in Wanariset (Table 2). Of the twelve *Macaranga* species, nine (75%) were significantly more common in secondary than in primary forest, while two species (17%) were significantly more common in primary forest. Of the nine *Mallotus* species, five (56%) were significantly more common in secondary than in primary forest, while three species (33%) were significantly more common in primary forest.

Most of the species showed clear relationships in distribution to forest disturbance types (Fig. 2). The best indicators for primary forest were *Mallotus penangensis* and *Macaranga lowii*. Secondary forests could be distinguished from primary forests very accurately by looking at the relative frequency and mean abundance of a small set of *Macaranga* species. The presence of *Macaranga gigantea*, *Macaranga*

Table 2

Densities (average number of individuals (n) per 0.3 ha) of *Macaranga* and *Mallotus* species taller than 30 cm in primary (IT1, WAN1) and secondary (IT2, IT3, IT4, IT5, IT6, WAN2, WAN3) forest, and the localities where they were found (ITCI or Wanariset) indicated with 'X', and the total number of individuals (taller than 30 cm) found for each species 'N'

Genus	Species	Primary forest ($n/0.3$ ha)	Secondary forest ($n/0.3$ ha)	ITCI	Wanariset	N
<i>Macaranga</i>	<i>bancana</i> (Miq.) Müll.Arg.	3.7	8.1***	X	X	319
	<i>conifera</i> (Zoll.) Müll.Arg.	0.2	4.8***	X	X	171
	<i>depressa</i> (Müll.Arg.) Müll.Arg.	0.3	0.3	X	X	12
	<i>gigantea</i> (Rchb.f. and Zoll.) Müll.Arg.	0.6	121.8***	X	X	4268
	<i>hullettii</i> King ex Hook.f.	1.3**	0.5	X	X	29
	<i>hypoleuca</i> (Rchb.f. and Zoll.) Müll.Arg.	0.8	13.9***	X	X	496
	<i>lowii</i> King ex Hook.f.	122.1***	7.9	X	X	1497
	<i>motleyana</i> (Müll.Arg.) Müll.Arg.	3.1	11.5***	X	X	434
	<i>pearsonii</i> Merr.	0	111.2***	X	X	3893
	<i>tanarius</i> (L.) Müll.Arg.	0	0.9***		X	33
	<i>trichocarpa</i> (Rchb.f. and Zoll.) Müll.Arg.	0.5	150.8***	X	X	5284
	<i>winkleri</i> Pax and K.Hoffm.	0	11.3***	X		396
	<i>Mallotus</i>	<i>dispar</i> (Blume) Müll.Arg.	3.0	5.7***	X	
<i>lackeyi</i> Elmer		1.6	4.3***	X		165
<i>macrostachyus</i> (Miq.) Müll.Arg.		0	0.4*		X	15
<i>miquelianus</i> (Scheff.) Boerl.		44.7***	9.1	X		765
<i>mollissimus</i> (Geiseler) Airy Shaw		0.1	8.6***	X		302
<i>paniculatus</i> (Lam.) Müll.Arg.		0	9.2***		X	323
<i>peltatus</i> (Geiseler) Müll.Arg.		0.5	1.5**	X		58
<i>penangensis</i> Müll.Arg.		55.0***	11.1	X	X	938
<i>wrayi</i> King ex Hook.f.		21.8***	2.8	X		315

Species found significantly (non-parametric G -test) more often than expected in primary or secondary forest are indicated with P -values.

* $0.05 \geq P > 0.01$.

** $0.01 \geq P > 0.001$.

*** $P \leq 0.001$.

hypoleuca and *Macaranga pearsonii* was important in this respect, with IVs around 90%, which indicates that they were present and common in almost all secondary forest plots. Within the secondary forests, the selectively logged forests were characterised by two *Mallotus* species, while the fire affected forests were characterised by a mixture of *Macaranga* and *Mallotus* species (Fig. 2).

3.2. *Macaranga* and *Mallotus* as indicators for the level of disturbance in a forest

The forest structural variables (environmental variables) correlated well with the first axis of the CCA (0.96) which explained 33.3% of the variance present in the data. The second axis had a correlation of 0.80 with the environmental variables and explained 22.2% of the data variance. Primary forest, selectively logged forest, forest burned once and repeatedly burned for-

est (used for shifting-cultivation) formed recognisable groups in the CCA (Fig. 3). Along the second axis of the CCA the ITCI plots were separated from the Wanariset plots.

The direction of the environmental variables is best represented by the visible disturbance variable (the 'disturb' variable in Fig. 3). A clear pattern is visible along this axis, with all the primary forest plots on the right, followed to the left by selectively logged plots, forest plots that burned once, and on the extreme left the repeatedly burned plots (shifting-cultivation). Projecting the plots on this axis gives a generalised idea of their level of disturbance (Table 3). Similarly, projecting the *Macaranga* and *Mallotus* species on this axis gives an estimate of the species disturbance level preference (Fig. 4; Table 4). It shows that most *Macaranga* species prefer intermediate to high levels of disturbance, while most *Mallotus* species prefer low to intermediate levels of disturbance. However, both

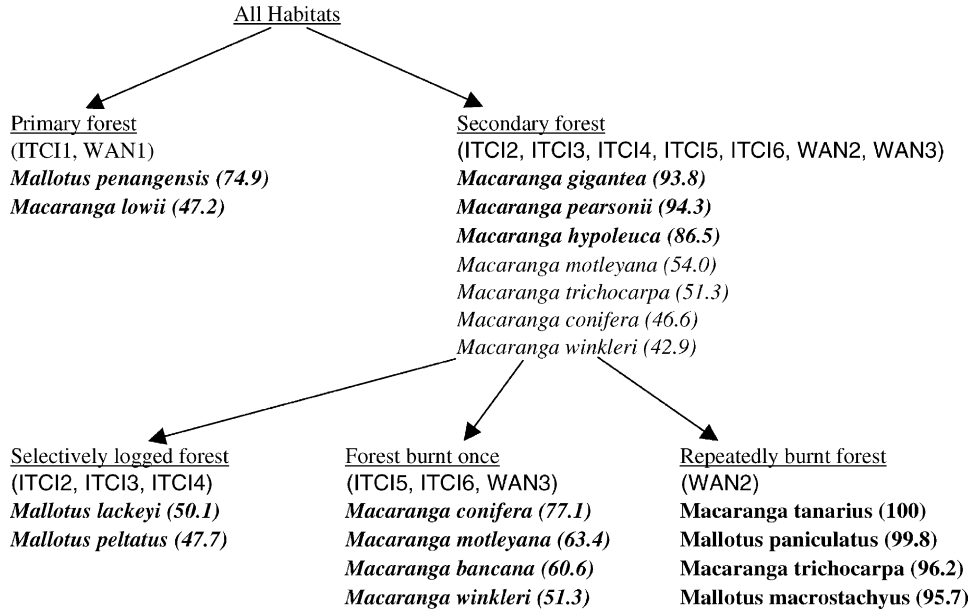


Fig. 2. Forest disturbance types and their indicator species. Each disturbance type is based on the plots in the forest types mentioned between brackets (see also Table 1). Indicator values of the species are mentioned between brackets after the species name. Only species with significant IV are mentioned. Species names are written in bold when they have their highest IV in that specific forest disturbance type. For example, *Macaranga hypoleuca* has its highest IV (86.5) for secondary forest.

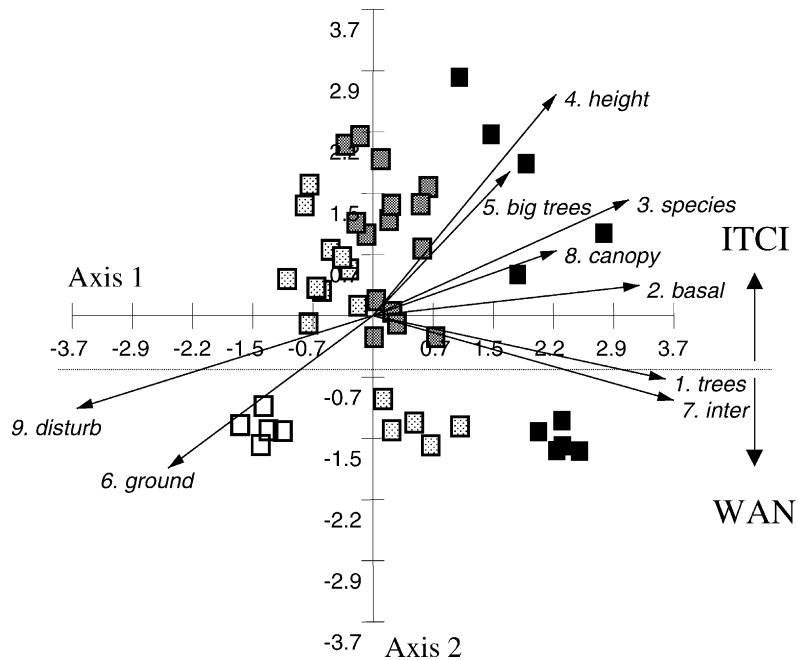


Fig. 3. CCA showing the plots and environmental variables (numbers before the variable names correspond to the numbers in Section 2). The first axis explains 33.3% of the variance in the data, the second axis 22.2%. The main forest disturbance types can be separated well. Black squares, primary forest plots; dark grey squares, selectively logged plots; light grey squares, burned once plots; white squares, repeatedly burned (shifting-cultivation) plots. Along the second CCA-axis all Wanariset (WAN) plots are separated from the ITCI plots. The general direction of the forest structure parameters is best reflected by the disturb variable.

Table 3

Mean values (\bar{x}) of the forest structure parameters per 0.3 ha with their standard deviations (σ), and the CCA scores on the disturbance axis (scaled between 0 and 100), for the nine studied forest types

Forest type		(1) Tree numbers (dbh \geq 10 cm)	(2) Basal area (m ²) (dbh \geq 10 cm)	(3) Tree species numbers (dbh \geq 10 cm)	(4) Tree height (dbh \geq 10 cm)	(5) Frequency of big trees (%) (dbh \geq 50 cm)	(6) Understorey leaf cover (%) (height < 5 m)	(7) Intermediary leaf cover (%) (5 > height < 30 m)	(8) Canopy leaf cover (%) (height > 30 m)	(9) Visible disturbance (%)	CCA disturbance axis score (%)	Disturbance level
WAN2	\bar{x}	32.6a	1.9a	17.4a	5.5a	4.8a	89.4d	16.0a	5.4a	91.6d	94.6a	High
	σ	13.5	0.8	3.8	2.1	4.5	10.3	13.4	5.1	7.8	3.8	↑
ITCI6	\bar{x}	85.6cd	4.9bc	57.2c	27.9d	17.4bc	71.4cd	12.8a	18.6abc	77.4c	73.1b	↑
	σ	21.0	0.7	13.1	2.2	7.6	31.5	8.9	12.0	9.4	6.1	↑
ITCI5	\bar{x}	58.8b	6.1cde	42.2b	26.9d	29.8e	71.4cd	30.0b	22.6abc	89.4cd	70.6b	↑
	σ	14.7	0.6	9.7	2.7	4.1	15.9	17.9	16.1	10.8	5.3	↑
WAN3	\bar{x}	144.2fg	6.8def	40.0b	20.6bc	11.8ab	69.8cd	75.2de	14.8ab	84.6cd	57.0c	↑
	σ	11.7	1.7	6.9	4.3	6.1	15.5	9.8	14.3	15.0	7.1	↑
ITCI2	\bar{x}	68.6bc	3.8ab	40.8b	18.1b	14.6b	58.0c	24.0ab	8.4a	48.6b	56.5c	↑
	σ	12.7	1.0	5.7	3.0	5.5	18.4	7.7	9.5	8.9	4.3	↑
ITCI3	\bar{x}	125.8ef	5.6bcd	70.0d	27.0d	14.2ab	29.8ab	57.2c	30.0bc	38.2b	56.1c	↑
	σ	26.0	1.3	11.9	4.4	6.7	18.8	10.9	24.5	5.2	5.9	↑
ITCI4	\bar{x}	125.8ef	6.3cde	72.0d	27.0d	20.0bcd	21.8a	62.2cd	35.4cd	43.4b	49.9c	↑
	σ	14.5	1.2	6.9	3.3	8.6	12.4	6.0	18.3	20.2	8.3	↑
WAN1	\bar{x}	151.2g	7.9ef	78.2d	24.8cd	27.2de	53.4bc	80.2e	35.2d	4.6a	22.6d	↑
	σ	21.7	2.0	6.6	2.7	8.0	8.8	5.6	15.8	3.9	4.3	↑
ITCI1	\bar{x}	107.8de	8.3f	56.6c	33.8e	26.6cde	25.4a	69.2cde	52.0d	6.8a	18.3d	↑
	σ	17.2	1.8	9.4	6.3	11.1	24.1	12.6	20.6	2.5	11.5	Low

For an explanation of the forest type names, see Table 1. The numbers in front of the forest structural variables correspond to the order in which they are treated in Section 2. The means for each forest type are based on five plots of 0.3 ha (10 m \times 300 m) each. The characters behind the means indicate group memberships within the columns (one-way ANOVA with post hoc least significant difference test).

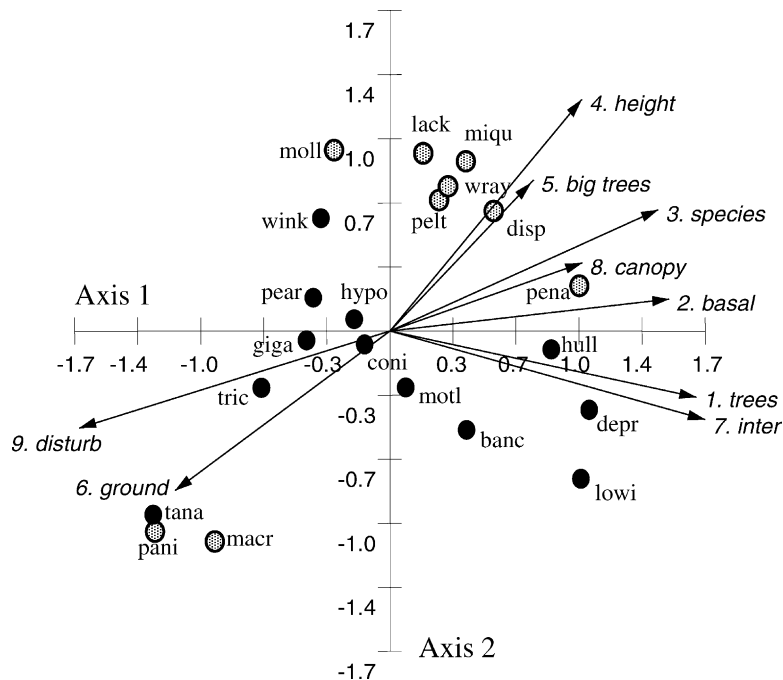


Fig. 4. CCA showing the *Macaranga* and *Mallotus* species (names abbreviated to the first four characters of their full species names, see Table 2) and the environmental variables (numbers before the variable names correspond to the numbers in Section 2). *Macaranga* species are indicated as black circles, *Mallotus* species as grey circles. The disturb axis represents the level of disturbance in the plots best (see Fig. 2). Species on the left have a high disturbance preference, while species on the right prefer undisturbed habitats.

genera do have representatives at low as well as very high disturbance levels.

The results of the multiple regression analysis are shown in Table 5. The general level of disturbance in the plots can be predicted well ($R^2 = 86.1\%$) with a subset of five *Macaranga* and *Mallotus* species. The R^2 for the relationship between the occurrence of seven *Macaranga* and *Mallotus* species and the tree species diversity in a plot is also high (80.0%), indicating that these seven species are good estimators for the tree species diversity of a plot.

4. Discussion

4.1. Indicating the type of disturbance

Only a small set of seven *Macaranga* species sufficed to tell secondary forest apart from primary forest. This set consisted of species that were found

in almost all secondary forest types that were studied, but were absent or very rare in primary forest. These species represent secondary forest generalists, establishing themselves only after disturbance irrespective of its type, severity or location. They were found immediately following until at least 25 years after disturbance, which is the time span covered by this study. Three pioneer tree species (*Macaranga gigantea*, *Macaranga hypoleuca* and *Macaranga pearsonii*) are very strongly associated with disturbance. Their secondary forest IV varied around 90%. Indeed these three species are generally considered to represent typical pioneer tree species for lowland dipterocarp forests (Whitmore, 1984; Primack and Lee, 1991; Davies, 1998, 2001; Davies et al., 1998; Slik et al., 2000, 2002).

Indicator species were also found for the three main types of secondary forest that were studied. Selectively logged forests for example were characterised by *Mallotus lackeyi* and *Mallotus peltatus*. However,

Table 4

The disturbance level preferences of the studied *Macaranga* (left) and *Mallotus* (right) species

<i>Macaranga</i>	Rescaled CCA score	<i>Mallotus</i>	Disturbance level
	100.0	<i>paniculatus</i>	High
<i>tanarius</i>	94.9		
	87.8	<i>macrostachyus</i>	
<i>trichocarpa</i>	71.2		
<i>gigantea</i>	59.9		
<i>pearsonii</i>	56.4		
<i>winkleri</i>	51.4		
<i>hypoleuca</i>	49.0		
<i>conifera</i>	47.8		
	46.1	<i>mollissimus</i>	
<i>motleyana</i>	40.8		
<i>bancana</i>	29.8		
	27.5	<i>lackeyi</i>	
	25.8	<i>peltatus</i>	Pioneers
	23.4	<i>wrayi</i>	Primary forest (remnant species)
	18.8	<i>miquelianus</i>	
	14.7	<i>dispar</i>	
<i>hullettii</i>	8.4		
<i>lowii</i>	7.6		
<i>depressa</i>	2.7		
	0.0	<i>penangensis</i>	Low

The species have been ordered between 0 (low disturbance) and 100 (high disturbance) according to their position on the disturbance axis of the CCA (re-scaled CCA score). Three ecologically different groups can be recognised based on the species preference for primary or secondary forests, the outcome of the indicator species analysis, and the CCA: (1) primary forest 'remnant' species; (2) pioneer species; and (3) high disturbance pioneers.

these two species had rather low IVs, because they were only ca. three times more common in selectively logged than in primary forest and because they were not present in all the selectively logged plots (patchy distribution). These two species either prefer only lightly disturbed forest conditions or are not resistant to fire since they were very rare to absent in burned forests.

The burned forest types were mainly characterised by *Macaranga* species. An important difference between the species found characteristic for repeatedly burned (shifting-cultivation) forest and forest that was burned once is that the species in repeatedly burned (shifting-cultivation) forest start reproducing 1–3 years after germination, while the species indicating forest that burned once start reproducing 5–15 years after establishment (Davies, 1996; Slik, personal observation). The species of repeatedly burned (shifting-cultivation) forest also have a more shrub-like habit than species found in forests burned once. The latter are all small to large trees reaching heights up to

35 m (Airy Shaw, 1975; Whitmore, 1975; Slik et al., 2000; Davies, 2001). The fast reproductive maturity of the repeatedly burned (shifting-cultivation) forest indicators, in combination with their high disturbance tolerance is probably the main reason why these species can become so extremely common in this type of forest in comparison with other *Macaranga* and *Mallotus* species.

4.2. Indicating level of disturbance

The environmental variables (forest structural variables) correlated well with the frequency of occurrence of the *Macaranga* and *Mallotus* species. This means that the occurrence of these species is closely related to these environmental variables. Some species are frequent in highly disturbed plots, while others are common in intermediately to little disturbed plots. The preference of different species for certain disturbance levels is reflected in their position on the disturbance axis in the CCA. It shows that most

Table 5

Multiple regression analysis between the frequency of occurrence (number of 10 m × 10 m subplots occupied in a plot of 10 m × 300 m) of *Macaranga* and *Mallotus* species, the forest structural variables and the re-scaled CCA scores (general level of disturbance)

	(1) Tree number (dbh ≥ 10 cm)	(2) Basal area (m ²) (dbh ≥ 10 cm)	(3) Species number (dbh ≥ 10 cm)	(4) Tree height (dbh ≥ 10 cm)	(5) Frequency of big trees (%) (dbh ≥ 50 cm)	(6) Leaf cover (%) (height < 5 m)	(7) Leaf cover (%) (5 > height < 30 m)	(8) Leaf cover (%) (height > 30 m)	(9) Visible disturbance (%)	CCA disturbance axis score (%)
Constant	128.40	7.49	62.11	31.67	25.92	23.08	62.00	53.02	15.79	37.56
<i>bancana</i>			-0.90	-0.41	-0.63	1.75	1.44			
<i>conifera</i>							-1.65		1.77	
<i>dispar</i>									1.36	
<i>gigantea</i>	-1.17								0.84	0.93
<i>hypoleuca</i>								-2.23		0.93
<i>lackeyi</i>	-2.25	-0.18	-1.37	-0.79			-1.98	-1.92		
<i>lowii</i>	1.35		0.94	-0.21		0.98		-0.82		
<i>miquelianus</i>	-4.07									
<i>mollissimus</i>								-1.58		
<i>motleyana</i>			-1.08						2.24	
<i>paniculatus</i>	-4.80	-0.20	-3.98	-1.22		3.56				
<i>pearsonii</i>		-0.14	1.17	-0.27	-1.09		-1.18		1.62	1.65
<i>penangensis</i>							1.14		-0.91	-1.09
<i>trichocarpa</i>							-1.53	-1.86	1.84	
<i>winkleri</i>			-1.68		1.00	4.00				-1.10
<i>n</i>	45	45	45	45	45	45	45	45	45	45
<i>F</i> -model	22.1	19.7	26.1	25.7	9.4	22.1	24.2	9.4	40.9	55.5
<i>R</i> ² -adjusted	65.8	56.0	80.0	73.8	36.3	65.8	76.0	48.7	86.4	86.1
S.E.	16.53	0.52	9.00	4.30	8.23	16.53	1.33	14.54	12.5	8.79

The numbers in front of the forest structural variables correspond to the order in which they are treated in Section 2. The table shows the species that can be used to predict the re-scaled CCA score (0 is low disturbance, 100 is high disturbance) and forest structural variables. For example, the general level of disturbance in a plot (re-scaled CCA score) can be predicted with the formula: general level of disturbance in a plot = 37.56 + 0.93 × number of subplots occupied by *gigantea* + 0.93 × number of subplots occupied by *hypoleuca* + 1.65 × number of subplots occupied by *pearsonii* - 1.09 × number of subplots occupied by *penangensis* - 1.10 × number of subplots occupied by *winkleri*. The standard error for this prediction is 9.00, and the *R*² is 80.0%.

Macaranga species prefer more disturbed habitats than *Mallotus* species, although both genera do have representatives in very little and very highly disturbed habitats. This general pattern agrees with the conclusions of Primack and Lee (1991), who mentioned *Mallotus* as a typical late successional to primary forest understory genus and *Macaranga* as an early successional genus. However, they lumped several species per genus together, thereby losing information for individual species. For *Macaranga* more specific data are known, and they confirm that there is considerable variation in micro-habitat preferences and life histories of the species within that genus (Davies, 1998; Davies et al., 1998). The micro-site preferences were shown to be dependent on light-environment, soil disturbance and to some extent the soil texture. These factors are all closely linked to forest disturbance and their results support the results found in this study for the shared species.

Since the CCA shows that the presence of *Macaranga* and *Mallotus* species is closely related to forest structure and the amount of disturbance in a plot, these species can also be used to predict forest structural variables and disturbance levels in the plots. Indeed most forest structural variables could be predicted quite accurately by using just a small set of *Macaranga* and *Mallotus* species. Since this multiple regression analysis is based on frequency of occurrence (number of subplots occupied) of *Macaranga* and *Mallotus* species in a plot, the method is very easy and fast to apply. Only presence/absence data are needed. However, the CCA analysis also shows that a geographical component is present in the data, so that care has to be taken in the application of this method outside the study area. Although some of the species in this study are very wide spread and common in many localities (Airy Shaw, 1975; Whitmore, 1975; Fiala et al., 1999; Slik et al., 2000; Davies, 2001), it is probably necessary or at least sensible to calibrate the method for new research areas to account for the site specific species.

The observed geographical component in the CCA is probably related to the fact that 10 of the 21 observed species were only found in one locality, i.e. either only in ITCI (seven species) or only in Wanariset (three species). This could be caused by the geographic distance between the two localities (ca. 50 km), but in this case the sampling itself might be partly due

to the observed pattern. In Wanariset no unburned selectively logged forest could be sampled because it was not present there. Similarly no repeatedly burned (shifting-cultivation) forest could be sampled in ITCI, because this type of disturbance was absent there. This means that species characteristic for these forest types are less likely to be found in both localities. Indeed all three species found only in Wanariset are indicators of repeatedly burned (shifting-cultivation) forest, while two of the seven species only found in ITCI are characteristic for selectively logged forest.

4.3. An ecological classification of the indicator species

Based on the CCA the *Macaranga* and *Mallotus* species can be ordered from low to high disturbance preferences. This continuous scale can be subdivided into three species groups with different life-history strategies (Table 4). The first group encompasses species that prefer primary, undisturbed forest. All of these species, except *Mallotus dispar*, had higher densities in primary forest than in secondary forest (Table 2). Although they preferred primary forest, these species were often also present in selectively logged forest. However, they occurred there as primary forest remnant species, not as very active colonisers (although seedlings and saplings were found near the parent trees). The second and largest group of species encompasses pioneer species. These species are all more common in secondary forest than in primary forest. However, some species are more confined to disturbed forests than others. *Mallotus peltatus*, *Mallotus lackeyi*, *Macaranga bancana*, and *Macaranga motleyana* are examples of pioneers that prefer low to intermediate disturbance levels. These species are also quite often present in primary forest. An explanation for this behaviour could be that these pioneers are adapted to small forest gaps, but no data is available to support this hypothesis. All other pioneer species are very rare or even absent in undisturbed primary forest. These species are the more typical pioneers that probably depend strongly on disturbance for successful establishment at a site (see Primack and Lee, 1991; Davies et al., 1998; Slik et al., 2002). A small group of these pioneers is confined to heavily disturbed sites, namely *Macaranga trichocarpa*, *Mallotus macrostachyus*, *Macaranga*

tanarius, and *Mallotus paniculatus*. These species are grouped together as high disturbance pioneers. As mentioned above, they are often shrubs with very fast reproductive cycles. With the exception of *Macaranga trichocarpa*, they were almost exclusively found in the repeatedly burned (shifting-cultivation) forest. The species in this group are adapted to very dynamic degraded vegetation types.

5. Conclusions

The occurrence of most *Macaranga* and *Mallotus* species was related to the type and level of forest disturbance. Different species of these genera can be ranked according to their preference for certain levels of disturbance. This ranking is related to the life-history strategies of the species: primary forest species, pioneer species, high disturbance pioneer species. As such these species can be used as forest disturbance indicators. Small sets of *Macaranga* and *Mallotus* species can be used to predict the general level of forest structure disturbance. However, a geographical component was present in the data that suggests that the method will have to be adapted to areas with different species of *Macaranga* and *Mallotus*.

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