

## Limited Edge Effects Along a Burned-Unburned Bornean Forest Boundary Seven Years after Disturbance

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### ABSTRACT

Large parts of the everwet tropics have been burned, leaving many unburned–burned forest edges. Here we studied a Bornean forest edge to determine: (1) how unburned and burned forest differ in vegetation structure, diversity, composition and plant functional traits 7 yr after fire, and (2) if these variables showed significant edge effects. Environmental and inventory data from 120 plots (0.01 ha each), covering both sides of a ~1.3 km forest boundary were sampled. Differences in vegetation structure, diversity, composition and plant functional traits were analyzed in relation to disturbance type (Mann–Whitney tests) and edge distance (partial correlation analysis that controlled for confounding effects of elevation, slope and fire intensity). Seven years after fire, burned forest differed significantly from unburned forest in most measured variables while few significant edge effects were detected, *i.e.*, there existed a sharp delimitation between the two forest types. The regeneration of the burned forest depended almost entirely on *in situ* recruitment with little input of late successional species from the neighboring old growth forest. On the other hand, old growth forest showed few signs of edge degradation. A possible explanation for these results might be related to the absence of a mast fruiting event during these first 7 yr of forest recovery, resulting in low levels of late successional species seed input into the burned forest, combined with the quick development of a closed canopy in the burned forest by early successional species that shielded the unburned forest from adverse edge effects.

*Key words:* canopy development; dispersal limitation; functional traits; mast fruiting; regeneration; tropical forest fire.

TROPICAL FORESTS HAVE BECOME INCREASINGLY FRAGMENTED IN RECENT DECADES, resulting in a huge increase in forest edge length and associated edge dynamics (Didham & Lawton 1999, Laurance *et al.* 2002, Broadbent *et al.* 2008). Many studies have shown that old growth forests near these margins can experience serious degradation (Laurance *et al.* 2006a, b, Tabarelli *et al.* 2008), raising the troubling prospect of an accelerating erosion of undisturbed forests due to edge effects. The problem of forest fragmentation and subsequent edge effects is especially pressing in Southeast Asia because this region is characterized by the highest relative levels of deforestation and fragmentation in the tropics (Sodhi *et al.* 2004). Unfortunately, most studies on edge effects have been performed in the Neotropics, with very few examples from Asia (see reviews by Didham & Lawton 1999, Laurance *et al.* 2002, Broadbent *et al.* 2008). Asian forests differ substantially in structure and composition from Neotropical forests, with a more open upper canopy and higher density of tall, large diameter trees (Dial *et al.* 2004, Paoli *et al.* 2008). Southeast Asian forests in particular also differ in reproductive and seed dispersal behavior, with community-wide mast fruiting events

(Appanah 1985, Primack & Corlett 2005) and high frequency of wind dispersal (Gentry 1988; Primack & Corlett 2005).

Previous edge dynamics studies often did not simultaneously examine both sides of the forest edge. In most cases, edge effects on the undisturbed forest side are studied (see reviews by Didham & Lawton 1999, Laurance *et al.* 2002, Broadbent *et al.* 2008). Rarely the forest edge in relation to the disturbed vegetation is considered (Gorchov *et al.* 1993, Cubina & Aide 2001, Dickie *et al.* 2005, Gunter *et al.* 2007). However, edge dynamics depend strongly on the interaction between the undisturbed forest and the neighboring disturbed vegetation matrix (Osunkoya 1994, Camargo & Kapos 1995, Newmark 2001, Ries *et al.* 2004, Cleary & Priadhati 2005, Lawes *et al.* 2005, Frederiksson *et al.* 2007, Schedlbauer *et al.* 2007) and a large fraction of the reported variability in forest edge dynamics can be attributed to differences in disturbance levels of the vegetation matrix (Didham & Lawton 1999, Ries *et al.* 2004). Furthermore, edge effects work in both directions, *i.e.*, undisturbed forest species colonize the disturbed vegetation while successional or exotic species can invade the undisturbed forest. For a good understanding of forest edge dynamics, it is therefore essential to include both sides of the forest edge.

In this study, we examine the result of 7 yr of forest dynamics along a sharp boundary created by a major fire in 1998 which

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followed a severe drought (Slik & Eichhorn 2003, Cleary & Priadjati 2005, Nieuwstadt & Sheil 2005, Frederiksson *et al.* 2007, Slik *et al.* 2008). Our research design incorporated equal representation of burned and unburned forest area, while controlling for topography, slope and fire intensity. We address the following questions: (1) How do these two forest conditions differ in structure, tree species diversity, tree species composition and plant functional traits? (2) Can we detect edge effects and if so, are they biased in one direction or the other, *i.e.* does the forest interior become more like burned forest or vice versa?

## METHODS

**FIELD SITE AND PLOT LAYOUT.**—The study site ( $1^{\circ} 5' 52.8''$  S,  $116^{\circ} 49' 8.4''$  E) was located in the Sungai Wain Protection Forest near the city of Balikpapan in East Kalimantan Province, Borneo, Indonesia. The area consists mostly of lowland dipterocarp forest typical for eastern lowland Borneo (Slik *et al.* 2009). The area receives  $\sim 2400$  mm of rain annually spread equally over the year with rainfall exceeding evaporation in all months. Soils are generally poor and sandy, and the area is characterized by fresh water swamps, river valleys and low hills varying in elevation between 0 and 100 m asl. For a more detailed site description see Nieuwstadt (2002) and Eichhorn (2006). The region was severely hit by the 1997/98 El Nino-Southern Oscillation (ENSO) drought and subsequent fire (Siegert *et al.* 2001). Although the fires were slow-moving surface fires of low intensity, the damage to the forest understory was catastrophic with mortality rates of near 100 percent for saplings and small trees with a diameter at breast height (dbh)  $< 10$  cm (Slik & Eichhorn 2003, Nieuwstadt & Sheil 2005). Additionally, fire intensity and damage were highly variable, depending on topography, slope and soil moisture content, with some river valleys and swamp areas escaping fire altogether (Slik & Eichhorn 2003). In our research area, the fires were actively extinguished, creating an edge between burned and unburned forest that was created by human activity, instead of any inherent characteristics of the forest that would otherwise complicate interpretation of persistent post-fire differences between burned and unburned forests.

The study was carried out in lowland dipterocarp forest between late 2004 and early 2005, almost 7 yr after the fires that hit the area in April 1998. We chose an area with a relatively straight, North-South oriented unburned–burned forest edge to minimize possible edge shape effects on our study. We made 60 transects of 600 m length perpendicular to the forest edge, with the burned–unburned forest edge located in the middle of each transect. Transects were spaced at 20 m intervals, covering a forest edge length of *ca* 1300 m. On each transect we established two plots of  $10 \times 10$  m, one in unburned and one in burned forest, both at an equal distance from the forest edge. Distance of the plots from the forest edge along transects was determined randomly (10 m intervals). However, to make sure that each edge distance was represented by an equal number of samples we introduced the constraint that each distance was only allowed to be selected twice. This resulted in the spatial array of plots shown in Figure 1.

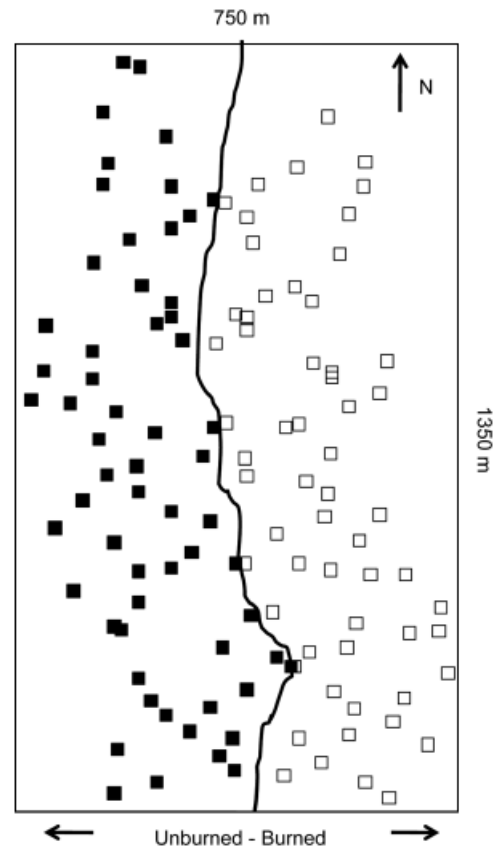


FIGURE 1. Location of the plots in relation to the unburned–burned forest edge in our study area.

**PLOT AND TREE MEASUREMENTS.**—For each  $10 \times 10$  m plot, we determined elevation, slope, canopy openness, leaf area index (LAI) and fire disturbance. Canopy openness and LAI were determined from hemispherical photographs taken in the center of each plot in a North-South direction at 2 m height. These photographs were analyzed with Winphot software (Steege 1996). Fire disturbance was classified into: (0) no fire disturbance, (1) light fire disturbance if only part of the plot had been burned, (2) medium fire disturbance if the whole plot had burned but most pre-fire poles (trees with dbh between 5 and 10 cm, *i.e.*, large enough not to be recruited after the fire) had survived, (3) heavy fire disturbance if the whole plot had burned with no or few surviving pre-fire poles.

Within each  $10 \times 10$  m plot, we measured the dbh of all trees  $> 5$  cm dbh, including dead standing trees, while all stems taller than 1.3 m and a dbh  $\leq 5$  cm were measured in a  $5 \times 5$  m subplot that was located in the same corner for each  $10 \times 10$  m plot. All living trees were identified by checking leaf samples against herbarium collections in the Wanariset (WAN, Samboja, East Kalimantan, Indonesia) and Leiden (NHN-L, Leiden University, Leiden, The Netherlands) herbaria. For all species we subsequently measured a suite of functional traits based on at least ten herbarium specimens and the information on their labels in the Leiden herbarium. These traits were: (1) minimum reproductive diameter, determined by ranking the dbh values scored from herbarium labels

of fertile specimens from small to large, plotting them in a scattergraph ( $Y = \text{dbh}$ ;  $X = \text{rank}$ ), fitting an exponential function through the graph, and scoring the  $Y$ -intercept of this function as the minimum reproductive dbh; (2) maximum adult diameter, determined in the same way as minimum reproductive diameter, but this time with the dbh values ranked from high to low; (3) oven-dry wood density, based on reported values in the literature (Oey 1990; Suzuki 1999; Osunkoya *et al.* 2007), or if no literature values were available, based on the average wood density of the genus to which the species belonged because this explains up to 59–70 percent of species-specific wood density in Indonesian trees (Slik 2006); (4) leaf shape, defined as blade length divided by blade width; (5) fruit size, defined as the longest length of the fruit (including wings, if present); (6) seed size, defined as longest length of the seed (excluding appendages such as wings or hairs when present); (7) flower size, defined as maximum flower diameter; (8) dispersal mode, either animal (fruits/seeds with edible parts and/or bright colors), gravity (fruits/seeds with no visible animal or wind dispersal adapted structures) or wind (fruits/seeds with wings, long hairs or broad flattened appendages). These characters were selected because they provide important information on tree life-history strategies, especially in relation to tree species successional status (Westoby *et al.* 2002, Reich *et al.* 2003, Moles *et al.* 2005, Slik 2005, Poorter & Bongers 2006, Wright *et al.* 2007).

**DATA PREPARATION.**—We subdivided our stem data in three diameter classes to compare differences between tree regeneration classes: (1) saplings, height taller than 1.3 m and dbh  $\leq 5$  cm; (2) poles, dbh 5.1–10 cm; and (3) trees, dbh  $> 10$  cm. Preliminary analysis of stem density and basal area in each  $10 \times 10$  m plot showed that many burned forest plots contained very few stems, making it difficult to compare diversity, composition and functional traits among plots directly. To overcome this we based our analysis on equal numbers of stems, not area, by sorting all stems according to their distance along the 600 m transect lengths. We then selected groups of 20 stems, without replacement, going from 0 to 600 m along the unburned–burned forest gradient. This procedure was repeated for each of the three tree diameter classes. While this solves the problem of low and unequal plot stem densities, it introduces unequal variance in transect length covered per sample in unburned vs. burned forest because stem densities differed between these forest types. This could result in more  $\beta$ -diversity included in burned than in unburned forest samples, and might thus slightly over-estimate diversity in burned forest while under-estimating compositional differences between unburned and burned forest. However, these biases are limited compared with those introduced by the alternative method of using equal area comparisons (plots) with variable stem numbers.

For each 20 stem sample we determined basal area and species based averages of minimum reproductive diameter, maximum adult diameter, oven-dry wood density, leaf shape, fruit size, seed size, and flower size. Additionally, we determined percentage of wind-, gravity- and animal-dispersed species. Except for basal area, which was calculated using all 20 stems in each sample, the other traits were calculated using species averages to avoid biases caused

by very abundant species. Sample stem density, slope, elevation, canopy openness, LAI, distance from forest edge and fire intensity were determined by assigning each stem the value of the plot where it was found and then calculating the average value for these parameters based on the 20 stems in each sample.

Species compositional values for each sample of 20 stems were based on detrended correspondence analysis (DCA), using the samples as cases and the species presence/absence as variables. We combined the samples of all diameter classes in one analysis to make compositional values comparable between diameter classes. The analysis revealed that the first DCA-axis corresponded strongly with disturbance with a clear separation between burned and unburned forest samples. Therefore, we compared compositional differences between samples using their loading on the first DCA-axis.

**DETECTING DIFFERENCES BETWEEN UNBURNED AND BURNED FOREST.**—We compared all variables between unburned and burned forests using the nonparametric Mann–Whitney test. Nonparametric testing was used because data variance levels between unburned and burned forests were usually significantly different and could not be corrected by standard data transformations.

**EDGE EFFECT ANALYSIS.**—Since edge effects can be confounded by variation in elevation, slopes and especially fire intensity we applied partial correlation analysis to detect significant correlations between distance from the forest edge and the study variables. Partial correlation produces correlation coefficients that have been corrected for co-variation with other variables included in the analysis, *i.e.*, any confounding effect of elevation, slope and fire intensity on the correlation coefficient between the study variable and distance from the forest edge is controlled for by this type of analysis. We performed the partial correlation using both the original edge distance data and the log transformed edge distance data to test for linear and nonlinear (logarithmic) relationships with the test variables, respectively.

## RESULTS

**UNBURNED–BURNED FOREST COMPARISONS.**—Almost 7 yr after fire we still detected highly significant differences between unburned and burned forest in most measured variables (Figs. 2, 3 and 4) and many either increased or declined with increasing diameter class. Of the forest structural variables (Fig. 2) differences between burned and unburned forest with increasing diameter class declined for stem density and basal area, remained constant for canopy openness and increased for LAI and the number of dead standing trees. Tree diversity, composition and dispersal strategies mostly showed increasing differences between burned and unburned forest with increasing diameter class (Fig. 3). Functional traits (Fig. 4) show increasing differences between burned and unburned forest with diameter class for wood density, seed size, leaf shape and reproductive dbh, while no change was detected for flower size and a decline for maximum dbh and fruit size.

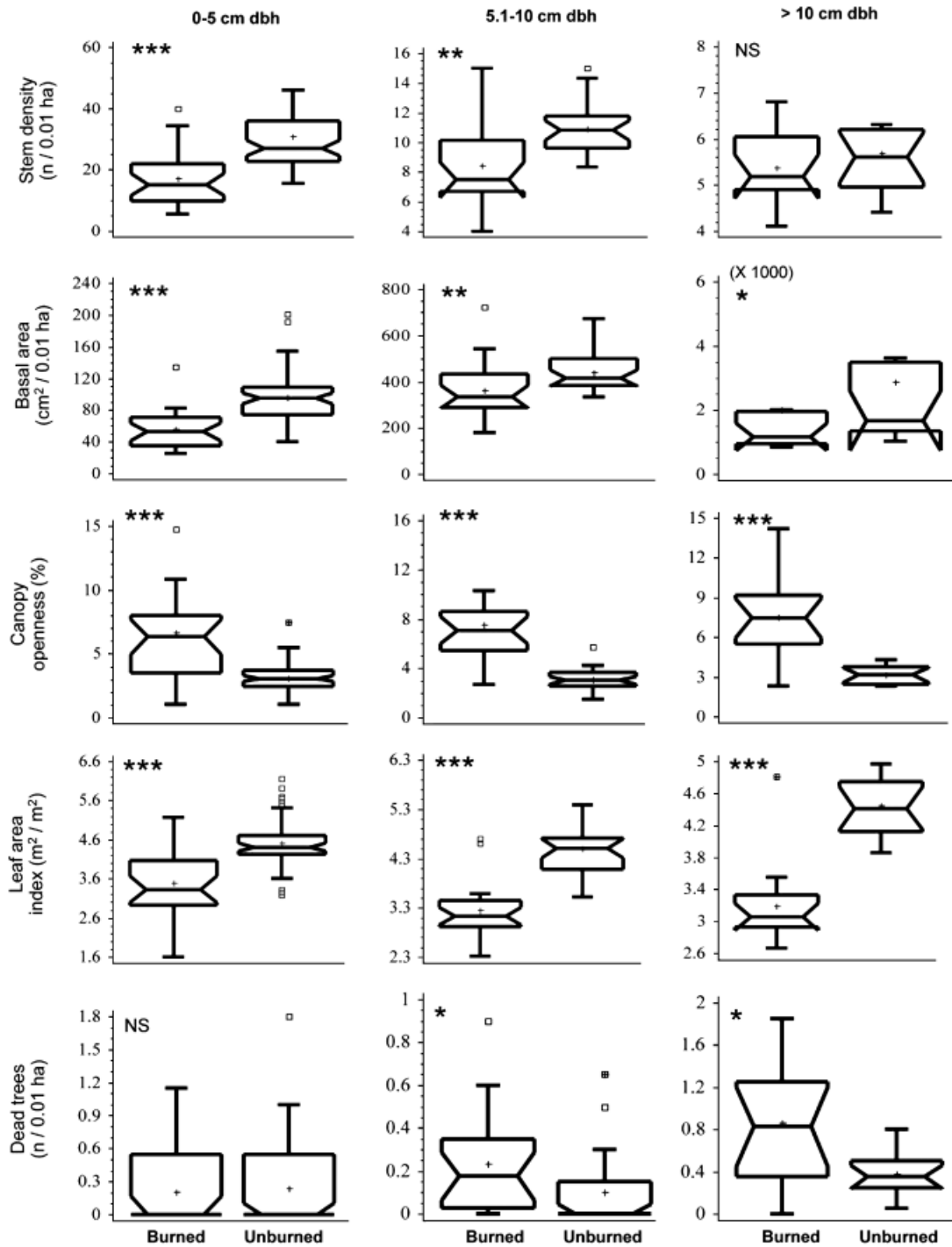


FIGURE 2. Comparison of the medians of several forest structural variables between burned and unburned forest as measured for three tree size classes. Significance levels indicated with stars (\* $0.05 < P < 0.01$ ; \*\* $0.01 < P < 0.001$ ; \*\*\* $P < 0.001$ ).

Composition and abundances of the top ten most common species in each diameter class differed dramatically between unburned and burned forest (Table 1). Only a few of the top ten abundant species in unburned forest were still found among the top ten common species in burned forest, while many of the top ten species in burned forest were very rare or absent in the unburned

forest plots. Notably, differences in diversity and composition, together with pioneer species dominance, were lowest in the smallest diameter class.

EDGE EFFECTS.—We only detected a few significant edge effects (Table 2): a decreasing LAI away from the forest edge in burned

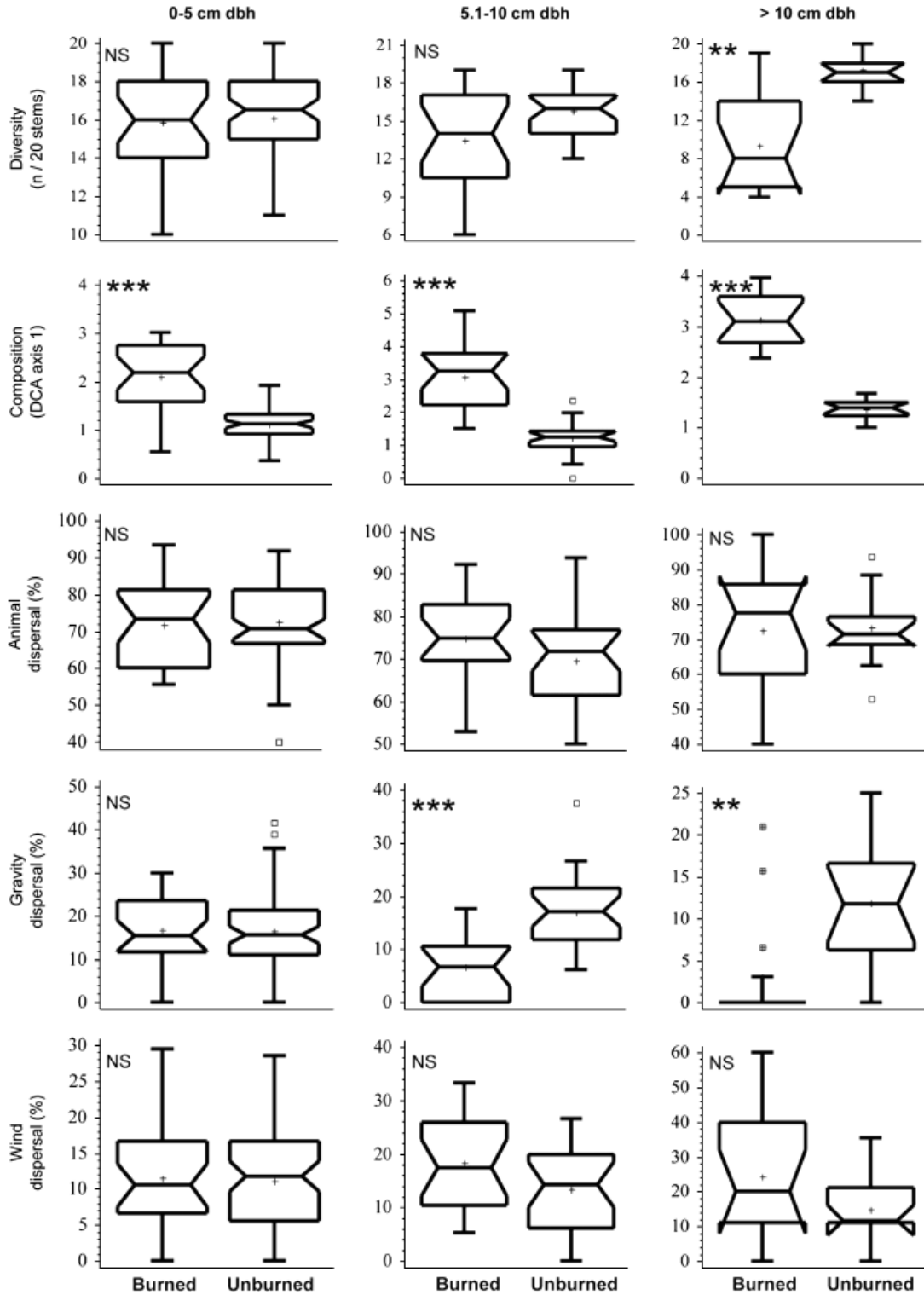


FIGURE 3. Comparison of the medians of forest diversity, composition and seed dispersal syndromes between burned and unburned forest as measured for three tree size classes. Significance levels indicated with stars (\* $0.05 < P < 0.01$ ; \*\* $0.01 < P < 0.001$ ; \*\*\* $P < 0.001$ ).

forest; an increasing number and basal area of saplings away from the forest edge in unburned forest; an increasing number of dead standing saplings away from the forest edge in both burned and unburned

forest; declining numbers of dead standing poles and trees away from the forest edge in unburned forest; increasing sapling diversity away from the forest edge in burned forest; a shift in sapling species

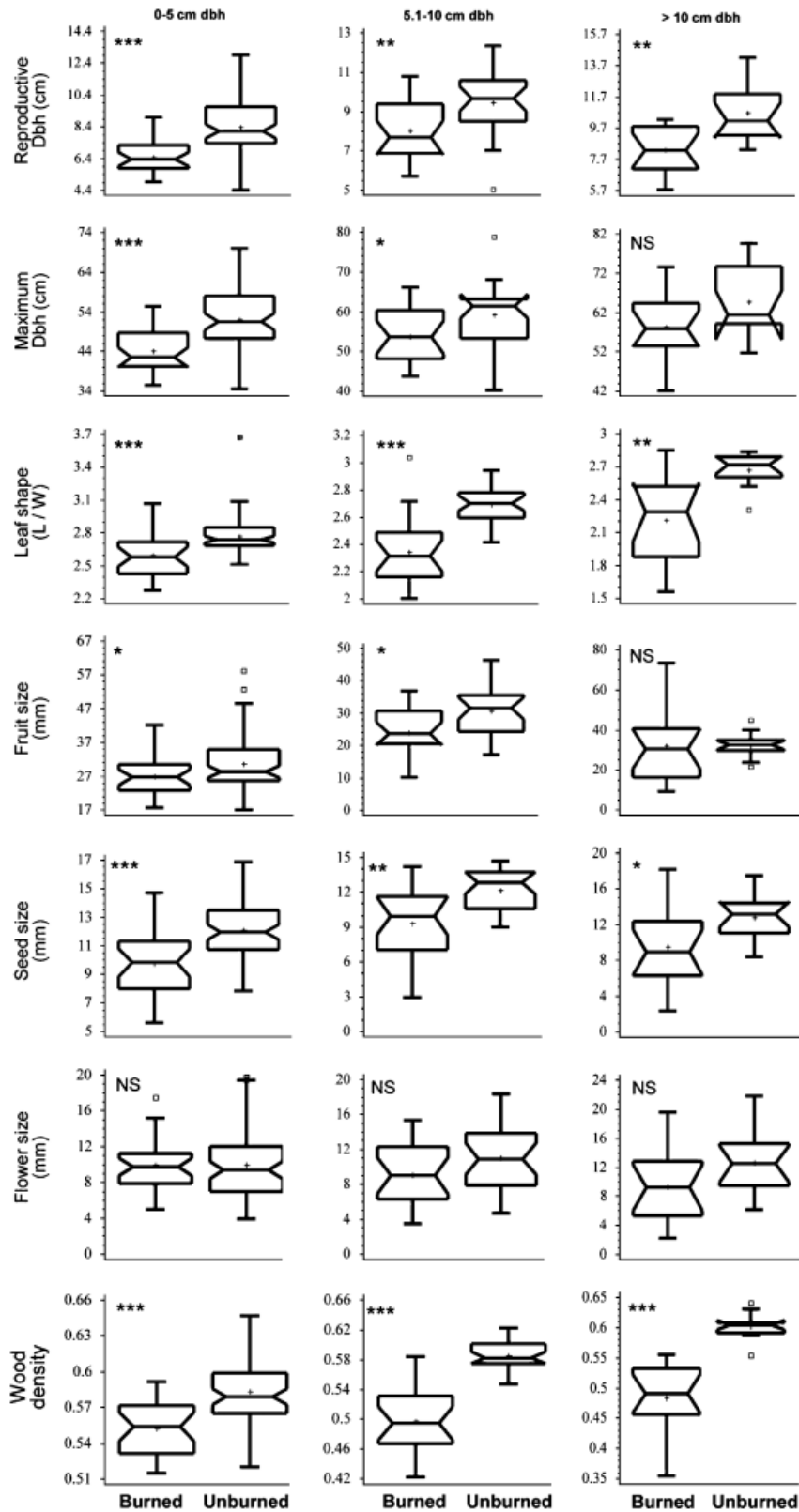


FIGURE 4. Comparison of the medians of several species functional traits between burned and unburned forest as measured for three tree size classes. Significance levels indicated with stars (\* $0.05 < P < 0.01$ ; \*\* $0.01 < P < 0.001$ ; \*\*\* $P < 0.001$ ).

TABLE 1. The ten most abundant species in number per ha and percentage of stems per diameter class in unburned and bordering burned forest, 7 yr after fire. Top ten species in unburned forest are indicated in bold in the burned forest. Species authors can be found at (<http://www.asiaplant.net>).

	Unburned (0–5.0 cm)		Unburned (5.1–10.0 cm)		Unburned (> 10.0 cm)			
	N (ha)	N (%)	N (ha)	N (%)	N (ha)	N (%)		
<i>Shorea laevis</i>	766.7	7.8	<b><i>M. lowii</i></b>	98.3	10.4	<b><i>M. lowii</i></b>	30.0	6.3
<i>Macaranga lowii</i>	500.0	5.1	<i>Madhuca kingiana</i>	56.7	6.0	<i>G. nervosa</i>	20.0	4.2
<i>Gironniera nervosa</i>	366.7	3.7	<b><i>D. acutifolius</i></b>	26.7	2.8	<i>M. kingiana</i>	16.7	3.5
<i>Urophyllum arboreum</i>	300.0	3.1	<i>Aporosa subcaudata</i>	25.0	2.6	<i>S. laevis</i>	16.7	3.5
<i>Fordia splendissima</i>	286.7	2.9	<i>Cleistanthus erycibifolius</i>	25.0	2.6	<b><i>D. acutifolius</i></b>	15.0	3.1
<i>Dipterocarpus confertus</i>	213.3	2.2	<i>S. laevis</i>	23.3	2.5	<i>Payena lucida</i>	13.3	2.8
<i>Durio acutifolius</i>	200.0	2.0	<i>G. nervosa</i>	21.7	2.3	<b><i>D. confertus</i></b>	11.7	2.4
<i>Melanochyla fubineris</i>	186.7	1.9	<b><i>D. confertus</i></b>	16.7	1.8	<i>Syzygium tauahense</i>	11.7	2.4
<i>Vatica umbonata</i>	186.7	1.9	<i>Dacryodes rostrata</i>	15.0	1.6	<i>D. kikir</i>	10.0	2.1
<i>Syzygium laxiflorum</i>	180.0	1.8	<i>Drypetes kikir</i>	13.3	1.4	<b><i>V. umbonata</i></b>	8.3	1.7
	Burned (0–5.0 cm)		Burned (5.1–10.0 cm)		Burned (> 10.0 cm)			
	N (ha)	N (%)	N (ha)	N (%)	N (ha)	N (%)		
<b><i>Pternandra coerulescens</i></b>	206.7	7.0	<i>Macaranga gigantea</i>	140.0	22.8	<i>M. gigantea</i>	215.0	47.7
<b><i>Dillenia grandifolia</i></b>	146.7	5.0	<i>V. arborea</i>	71.7	11.7	<i>V. arborea</i>	70.0	15.6
<b><i>F. splendissima</i></b>	140.0	4.8	<i>D. grandifolia</i>	26.7	4.3	<b><i>M. kingiana</i></b>	10.0	2.2
<b><i>M. lowii</i></b>	93.3	3.2	<b><i>D. confertus</i></b>	16.7	2.7	<i>E. diadenum</i>	6.7	1.5
<b><i>U. arboreum</i></b>	93.3	3.2	<i>Macaranga bancana</i>	15.0	2.4	<b><i>D. confertus</i></b>	5.0	1.1
<b><i>Anthocephalus chinensis</i></b>	86.7	3.0	<i>P. coerulescens</i>	13.3	2.2	<i>Knema pallens</i>	5.0	1.1
<b><i>Crudia reticulata</i></b>	86.7	3.0	<i>Barringtonia macrostachya</i>	11.7	1.9	<i>M. bancana</i>	5.0	1.1
<b><i>Vernonia arborea</i></b>	86.7	3.0	<i>Ficus aurata</i>	11.7	1.9	<i>Chaetocarpus castanocarpus</i>	3.3	0.7
<b><i>G. nervosa</i></b>	66.7	2.3	<i>Endospermum diadenum</i>	10.0	1.6	<i>Cratogeomum sumatranum</i>	3.3	0.7
<b><i>Glochidion glomerulatum</i></b>	66.7	2.3	<b><i>M. kingiana</i></b>	10.0	1.6	<b><i>D. acutifolius</i></b>	3.3	0.7
						<i>Knema psilantha</i>	3.3	0.7
						<i>Macaranga hypoleuca</i>	3.3	0.7
						<i>Madhuca sericea</i>	3.3	0.7
						<i>Pentace laxiflora</i>	3.3	0.7
						<b><i>V. umbonata</i></b>	3.3	0.7
						<i>Xylopia malayana</i>	3.3	0.7

TABLE 2. Correlation coefficients of variables with linear and log-transformed (between brackets) distance to the forest edge in both burned and unburned forest and for three tree size classes, based on a partial correlation test that controlled for the confounding effects of fire intensity, slope and topography. Significance levels indicated with stars (\*0.05 < P < 0.01; \*\*0.01 < P < 0.001; \*\*\*P < 0.001).

Variable	Dbh < 5.0		Dbh 5.1–10		Dbh > 10	
	Unburned (n = 66)	Burned (n = 27)	Unburned (n = 26)	Burned (n = 20)	Unburned (n = 13)	Burned (n = 14)
Canopy openness	0.15 (0.18)	– 0.08 (0.02)	0.12 (0.19)	0.11 (0.22)	0.21 (0.37)	0.07 (0.25)
Leaf area index	– 0.20 (– 0.17)	– 0.25 (– <b>0.45*</b> )	– 0.12 (– 0.12)	– <b>0.44*</b> (– <b>0.60**</b> )	– 0.06 (– 0.17)	– 0.34 (– <b>0.56*</b> )
Stem density	<b>0.25*</b> ( <b>0.31*</b> )	0.09 (– 0.14)	0.21 (0.28)	0.16 (0.09)	– 0.48 (– 0.31)	0.07 (0.00)
Basal area	0.12 ( <b>0.25*</b> )	0.10 (– 0.10)	0.20 (0.18)	0.27 (0.26)	– 0.20 (– 0.08)	0.36 (0.34)
Dead trees	<b>0.38**</b> ( <b>0.25*</b> )	<b>0.36*</b> ( <b>0.51**</b> )	– <b>0.49**</b> (– <b>0.45*</b> )	0.31 (0.29)	– <b>0.58*</b> (– <b>0.63**</b> )	0.17 (0.18)
Diversity	– 0.11 (– 0.10)	<b>0.38*</b> (0.33)	– 0.06 (0.13)	– 0.16 (– 0.24)	– 0.22 (– 0.37)	0.03 (0.11)
DCA axis 1	– 0.11 (– <b>0.24*</b> )	0.05 (0.22)	0.25 (0.20)	0.24 (0.35)	– 0.42 (– 0.15)	0.45 (0.36)
Animal dispersal	0.00 (0.04)	– 0.20 (– 0.15)	– <b>0.45*</b> (– 0.39)	– 0.16 (– 0.18)	0.12 (0.15)	0.23 (0.29)
Gravity dispersal	0.00 (– 0.12)	0.16 (0.12)	0.35 (0.25)	– 0.01 (– 0.12)	– 0.15 (0.00)	– <b>0.64*</b> (– <b>0.68*</b> )
Wind dispersal	0.00 (0.09)	0.13 (0.10)	0.36 (0.37)	0.17 (0.26)	– 0.03 (– 0.17)	– 0.09 (– 0.15)
Reproductive dbh	– 0.06 (0.02)	– 0.21 (– 0.22)	0.38 ( <b>0.40*</b> )	0.18 (0.12)	0.48 (0.35)	0.18 (0.11)
Maximum dbh	– 0.07 (0.07)	– 0.18 (– 0.16)	0.03 (0.08)	0.08 (0.05)	– 0.11 (– 0.27)	0.25 (0.13)
Leaf shape	0.03 (– 0.05)	– 0.09 (– 0.11)	0.03 (– 0.01)	– 0.02 (– 0.05)	– 0.12 (– 0.10)	0.05 (0.06)
Fruit size	– 0.10 (– 0.08)	– 0.02 (– 0.05)	0.33 (0.34)	0.00 (– 0.01)	0.13 (– 0.09)	0.42(0.50)
Seed size	– 0.12 (– 0.06)	– 0.14 (– 0.20)	0.30 (0.36)	0.01 (0.03)	– 0.01 (– 0.14)	– 0.11 (– 0.07)
Flower size	– 0.16 (– 0.13)	0.03 (0.05)	– 0.17 (– 0.21)	0.26 (0.37)	– 0.30 (– 0.44)	– 0.36 (– 0.31)
Wood density	– 0.10 (– 0.09)	0.28 (0.16)	– 0.13 (– 0.17)	0.03 (– 0.02)	0.25 (0.30)	– 0.25 (– 0.26)

composition toward the forest edge in unburned forest; declining percentage of animal-dispersed poles away from the forest edge in unburned forest; and declining percentage of gravity-dispersed trees away from the forest edge in burned forest. Of the functional traits only reproductive dbh showed a significant edge effect for poles in unburned forest.

## DISCUSSION

THE LASTING IMPACT OF FIRE.—We observed large and significant differences between unburned and burned forest in almost all measured variables 7 yr after fire. This is not surprising given the huge impact that the fires had on the forest ecosystem in our study area, resulting in overall tree mortality rates of ~70 percent, and almost 100 percent mortality for trees with a diameter <10 cm shortly after the 1998 fires (Slik & Eichhorn 2003, Cleary & Priadjati 2005, Nieuwstadt & Sheil 2005, Slik *et al.* 2008). Despite the fact that stem densities and basal areas of trees (dbh >10 cm) were comparable between the two forest conditions, the burned forest canopy remained underdeveloped, as indicated by greater canopy openness and lower LAI. This was mainly caused by the low density and basal area of understory vegetation and the dominance of a few fast growing pioneer species that had already reached the canopy since the 1998 fires. These species were generally characterized by relatively large, rounded leaves placed terminally on the branches producing a wide but shallow crown, creating a relatively open and single-layered canopy.

The dominance of pioneer species in burned forest was also reflected in the large difference in species composition with un-

burned forest, even though species diversity among saplings and poles (dbh <10 cm) did not differ. The lower stem densities in the small diameter classes (dbh <10 cm) together with the large compositional difference with unburned forest indicate that regeneration toward an old growth forest species composition in the burned forest is slow, confirming similar long-term observations from burned forests around the tropics (Riswan *et al.* 1985, Slik *et al.* 2002, Chazdon 2003, Cochrane 2003, Barlow & Peres 2008). However, the smaller compositional difference between burned and unburned forest in the smallest diameter class, as compared with the larger diameter classes, indicates an increasing dominance of old growth forest species. This apparent recovery, however, is most likely caused by the fact that the pioneer trees started to grow into the larger diameter classes while the slower growing old growth species that had survived the fire remained behind in the smallest diameter class.

The strong shift toward an early successional vegetation type in burned forest was also clear from the pronounced difference in tree species functional traits compared with unburned forest. Trees in the burned forest were characterized by lower wood densities, indicative of fast growth rates (King *et al.* 2005), which together with the relatively small maximum stature and small reproductive diameter suggest reproductive maturity at an early age. Contrasting with the narrow leaves found in the unburned forest, the burned forest was dominated by species with more rounded leaves, indicating higher photosynthetic capacity (Popma *et al.* 1992, Westoby *et al.* 2002, Falster & Westoby 2003). Also, fruit and seed sizes were smaller in burned forest, indicating lower shade tolerance



(Osunkoya *et al.* 1994, Coomes & Grubb 2003, Slik 2005), higher fruit and seed production, combined with better colonizing ability (Hammond & Brown 1995, Westoby *et al.* 2002, Coomes & Grubb 2003) compared with the species in unburned forest. Many of the newly established and now dominant tree species in the burned forest also produced seeds capable of dormancy, meaning that they can, unlike most species in the unburned forest, survive in the soil seed bank (Ng 1980, Nieuwstadt 2002).

IMPACT OF NEIGHBORING OLD GROWTH FOREST ON BURNED FOREST REGENERATION.—Very few variables showed a correlation with distance from forest edge in burned forest. This emphasizes the importance of local processes such as stump or root sprouting, seed rain from locally surviving adult trees, and germination from the soil seed bank for the initial regeneration of the old growth forest species in burned forests and agrees with other studies that indicate very limited impact of and species exchange between undisturbed and bordering disturbed forest (Osunkoya *et al.* 1994, Ries *et al.* 2004, Lawes *et al.* 2005, Schedlbauer *et al.* 2007). However, it contradicts general ideas about the importance of proximity of old growth forests for secondary forest compositional recovery (Chazdon *et al.* 2009), and observations on the importance of remnant trees and vegetation for seed dispersal from undisturbed into disturbed vegetations (Zahawi & Augspurger 2006). In this case a possible explanation for this discrepancy might be related to the mast fruiting strategy of most late successional tree species in Asian forests, *i.e.*, trees fruit synchronously but irregularly at intervals of several years (Appanah 1985, Primack & Corlett 2005). No large mast fruiting event was recorded for our study site and Borneo in general between 1998 and 2005 (G. M. Frederiksson, pers. comm., and comments posted on Mastwatch: <http://www.phylodiversity.net/mastwatch/>), meaning that seed rain from the undisturbed forest into the burned forest has been limited.

More generally valid explanations across the tropics might be related to adverse seedling establishment conditions in burned forests for old growth forest tree species. The dominating early successional species usually produce a thick litter layer consisting mainly of large leaves which can inhibit establishment of seedlings (Molofsky & Augspurger 1992). Even if young seedlings manage to reach the soil they will find that the mycorrhizal fungi community differs between undisturbed and disturbed forest (Dickie *et al.* 2005) providing unsuitable establishment conditions for some species. Also, several studies have found that seed predator and herbivore densities differ between undisturbed and disturbed forests, especially near the forest edge (Osunkoya *et al.* 1994, Galetti *et al.* 2003). Successful re-establishment of pre-fire species will therefore be a slow process that depends not only on seed input of old growth species, but also on processes related to litter dynamics, plant–herbivore interactions, seed predation levels and soils. However, we like to emphasize that some recovery was already taking place in the burned forest, as was indicated by the nonexistent difference in diversity and reduced compositional difference in the smallest diameter class compared with adjacent unburned forest. Our results indicate that this recovery is currently more driven by processes in the burned forest itself than by colonization from the unburned forest.

IMPACT OF BURNED FOREST ON OLD GROWTH FOREST INTEGRITY.—Our data indicates that the forest edge has very limited impact on light conditions, tree diversity, functional traits and species composition in unburned forest, contrasting sharply with studies from the Neotropics (Laurance *et al.* 2002). The limited impact of light and micro-climate related edge effects on old growth forest in our study is probably related to the fact that the most adverse edge effects were reduced by the development of a closed canopy of considerable height (15–20 m) in the bordering secondary forest within 7 yr. Furthermore, Bornean old growth forests are characterized by a relatively tall, but open canopy structure, possibly making them more resilient to edge effects than their Neotropical counterparts.

Although edge effects were limited in the undisturbed forest, we did observe some edge effects, such as decreasing numbers of dead standing saplings (dbh  $\leq$  5 cm) toward the forest edge, a pattern that was also observed in the burned forest. In the case of the unburned forest the decline in dead standing saplings was accompanied by a decline in live sapling density toward the forest edge. This suggests higher sapling survival accompanied by lowered sapling recruitment rates near the forest edge. This pattern of lowered recruitment might be explained by hampered seed input, *i.e.*, seed input of old growth forest species can only arrive from one direction, the forest interior, as opposed to sites further from the forest edge that may receive seeds from all directions. Indeed, seed rain has been shown to be less diverse, especially for large seeds, in forest edges (Lopes de Melo *et al.* 2006).

The reduced mortality for saplings was opposite to the pattern observed for larger diameter trees (dbh > 5 cm) which showed increasing mortality toward the forest edge, corresponding to results from other studies that report increased tree mortality up to 1200 m from the forest edge (Laurance *et al.* 2001a, b; D'Angelo *et al.* 2004; Frederiksson *et al.* 2007). This increased tree mortality has been linked to increased wind disturbance, causing more tree falls near the forest edge. In our study area it is more likely that the tree mortality is caused by increased drought susceptibility near the forest edge, with higher insolation, more wind and lower air humidity, especially during infrequent but severe ENSO-associated droughts that occur in eastern Borneo (Laurance *et al.* 2001a, b, Nieuwstadt & Sheil 2005). This is in accordance with the high tree mortality observed in the more exposed burned forest. Earlier studies have already shown that drought especially affects large trees during severe droughts (Slik & Eichhorn 2003, Nieuwstadt & Sheil 2005).

Another noticeable long distance edge effect in unburned forest concerned the increasing percentage of animal dispersed tree species in the 5.1–10 cm diam class. As most of these trees were already established before the 1998 fire, this change may result from selective mortality of gravity and wind dispersed plant groups near the forest edge rather than an increase in animal dispersed trees. Many gravity dispersed trees are extremely shade-tolerant understory to sub-canopy species and are susceptible to the micro-climatic changes associated with edge effects (Benitez-Malvido & Lemus-Albor 2005). Also, wind dispersal is a typical dispersal strategy of old growth forest trees (*e.g.*, Dipterocarpaceae) in Borneo (Primack & Corlett 2005), unlike most other tropical regions where it is usually associated with a pioneer strategy.

## CONCLUSIONS

Our results show that forest fires in Asian tropical rain forests have a lasting impact on forest structure and tree species composition, with very limited exchange of late successional species from the undisturbed to the neighboring burned forest during the first few years of regeneration. This might be a common pattern in Asian tropical rain forests which are characterized by mast fruiting, meaning that seed input from undisturbed forest into disturbed forest is irregular and can be completely lacking for many years. Other studies have shown that this lack of recovery or even deterioration in species composition and forest structure can last at least 20 yr (Slik *et al.* 2002, Barlow & Peres 2008, Slik *et al.* 2008). However, there is also a lot of evidence showing that almost all old growth tropical forests around the world are affected by rare fire events (Power *et al.* 2008), from which they apparently recovered. Our own data suggests that compositional recovery was already happening in the smallest diameter class, although this recovery is most likely not driven by colonization from the neighboring undisturbed forest but by growth of pioneer species into the larger diameter classes thus leaving the slower growing climax species that survived the fire in the burned forest understory. Therefore it is extremely important to maintain strict protection for burned forests so that the *in situ* regeneration process is not disturbed. Since most climax tree species were still present in the burned forest, these forests have the potential for full recovery and actions to prevent further fires, such as creation of fire breaks, should be considered as a management option.

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