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Impacts of El Niño related drought and forest fires on sun bear fruit resources in lowland dipterocarp forest of East Borneo

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Abstract Droughts and forest fires, induced by the El Niño/Southern Oscillation (ENSO) event, have increased considerably over the last decades affecting millions of hectares of rainforest. We investigated the effects of the 1997-1998 forest fires and drought, associated with an exceptionally severe ENSO event, on fruit species important in the diet of Malayan sun bears (Helarctos malayanus) in lowland dipterocarp forest, East Kalimantan, Indonesian Borneo. Densities of sun bear fruit trees (≥ 10 cm DBH) were reduced by ~80%, from 167±41 (SD) fruit trees ha⁻¹ in unburned forest to 37 ± 18 fruit trees ha⁻¹ in burned forest. Densities of hemi-epiphytic figs, one of the main fallback resources for sun bears during periods of food scarcity, declined by 95% in burned forest. Species diversity of sun bear food trees decreased by 44% in burned forest. Drought also affected sun bear fruit trees in unburned primary forest, with elevated mortality rates for the duration of 2 years, returning to levels reported as normal in region in the third year after the ENSO event. Mortality in unburned forest near the burn-edge was higher $(25\pm5\%)$ of trees ≥ 10 cm DBH dead) than in the forest interior (14±5% of trees), indicating possible edge effects. Combined effects of fire and drought in burned primary forest resulted in an overall tree mortality of $78\pm11\%$ (≥10 cm DBH) 33 months after the fire event. Disturbance due to fires has resulted in a serious decline of fruit resources for sun bears and, due to the scale of fire damage, in a serious decline of prime sun bear habitat. Recovery of sun bear populations in these burned-over forests will depend

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on regeneration of the forest, its future species composition, and efforts to prevent subsequent fire events.

Keywords Disturbance · Drought · ENSO · Figs · Fires · *Helarctos malayanus* · Kalimantan · Species diversity · Tree mortality

Introduction

Severe droughts, associated with increased occurrences of El Niño/Southern Oscillation (ENSO) events, have become more frequent over the past decades (e.g., Timmermann et al. 1999). These droughts have created conditions conducive for uncontrolled fires, which have damaged extensive areas of forest throughout the tropics, with fires in Southeast Asia being particularly severe on the islands of Borneo and Sumatra (Goldammer and Mutch 2001; Tacconi 2003). In recent years, forest fires have caused more deforestation than intentional clearing in some tropical regions (e.g., Cochrane et al. 1999). On Borneo between 3 million ha and 5 million ha of primary forest were affected by fires in 1982-1983 during a severe ENSO related drought (Lennertz and Panzer 1984; Malingreau et al. 1985). Smaller fire events occurred in 1990, 1992 and 1994, all coinciding with ENSO episodes (Salafsky 1998). During the severe 1997–1998 ENSO event primary forest areas burned easily (Siegert et al. 2001) as prior drought stress led to the shedding of leaves by evergreen species and accumulation of dry litter on the forest floor (GMF pers. obs.). In 1997-1998 in the Indonesian province of East Kalimantan alone, 5.2 million ha of land were affected by the fires, 2.6 million ha of which were forest, including several protected lowland reserves (Hoffman et al. 1999; Siegert et al. 2001; Fuller et al. 2004). Areas previously affected by fires have also become susceptible to more intense fires due to higher fuel loads and rapid desiccation, now even during "normal" dry seasons (Cochrane and Schulze 1999; Cochrane et al. 1999; Laurance 2003).

Several studies have investigated the effects of the 1997-1998 drought and fires on tree mortality and forest structure (e.g., Nakagawa et al. 2000; Williamson et al. 2000; van Nieuwstadt 2002; Slik et al. 2002; Potts 2003; Slik and Eichhorn 2003; Slik 2004). Their findings showed that drought significantly increased mortality rates in unburned forest (Nakagawa et al. 2000; van Nieuwstadt 2002; Potts 2003; Slik 2004; van Nieuwstadt and Sheil 2005), that overall tree mortality was extremely high in burned areas (van Nieuwstadt and Sheil 2005), that fire resulted in a strong reduction of climax tree density (Slik and Eichhorn 2003), and that species composition changed after fire damage due to disproportionate mortality of certain tree species groups and tree size classes (Slik et al. 2002; Slik 2004). Shifts in species composition in natural forest occur slowly under "normal" conditions (Swaine et al. 1987), but catastrophic disturbances like repeated fires can reduce structural and biological complexity in forests (Schindele et al. 1989). Fire-return intervals of less than 90 years can eliminate rainforest tree species, whereas intervals of less than 20 years may eradicate tree growth entirely resulting in savanna-like landscapes (Cochrane et al. 1999).

Few studies however have investigated the effects of drought and forest fires on wildlife or their food resources in Indonesia (Doi 1988; Anggraini et al. 2000; O'Brien et al. 2003). Forest-dependent species tend to become less abundant or even locally extinct and other, less-forest-dependent species invade the area or increase in abundance (Doi 1988; Anggraini et al. 2000; see also Barlow et al. 2002; Peres et al. 2003). Some of the larger, long-lived species persist, reluctant or unable to relocate themselves (Suzuki 1992; Anggraini et al. 2000), although effects on their life-history remain largely unknown (but see O'Brien et al. 2003). Furthermore, the proximate causes of why individual species perish or flourish—e.g., decreased or increased food-availability, reduced nest-sites—remain unstudied.

We studied the effects of fires on a variety of food resources important in the diet of one of the largest extant mammals on Borneo, the Malayan sun bear. Sun bears are partly frugivores (McConkey and Galetti 1999; Wong et al. 2002; Fredriksson et al. in press), although during periodic mast-fruiting events fruit makes up almost 100% of the diet (Fredriksson et al. in press). These mast-fruiting events provide the opportunity for sun bears to gorge themselves on large amounts of succulent fruits, probably enabling them to build up, or recover, fat and energy reserves for the prolonged period of fruit lows preceding and following these supra-annual mastfruiting events (Fredriksson et al. in press). Sun bears are considered important actors in forest dynamics, in part due to their seed dispersal abilities (McConkey and Galetti 1999), especially of large-seeded fruits (Fredriksson, unpubl. data). Preliminary data suggests that sun bears make little use of burned forest areas for several years after a fire event (Doi 1988; Fredriksson, unpubl. data).

The aims of this study were (i) to investigate the effect of forest fires on the density of sun bear fruit resources; (ii) to quantify the effect of forest fires on species diversity of sun bear fruit resources; and (iii) to study the effect of drought on mortality of sun bear food trees in unburned forest and based on the above (iv) discuss the effects of these changes on sun bear populations in fire affected areas.

Methods

Study area

The study was carried out in the lowland dipterocarp forest of the Sungai Wain Protection Forest (SWPF), a reserve near Balikpapan, East Kalimantan, Indonesian Borneo (1°16' S and 116°54' E) (Fig. 1). The reserve covers a watercatchment area of ca 100 km². Average annual rainfall was 2740±530 mm (1998–2003). The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by many small rivers. The area varies in altitude from 30 m to 150 m a.s.l. Trees with stems greater than 10 cm DBH (diameter at breast height) are dominated by the families Euphorbiaceae, Dipterocarpaceae, Sapotaceae, and Myrtaceae. The relative dominance of Dipterocarpaceae increases substantially in the larger size classes. Due to an altitudinal gradient, with rivers running in a north–south direction, the southern part of the reserve is moister. Dipterocarpaceae, dominant in the northern part of the reserve (above 10 cm DBH) decrease in abundance towards the moister south where Sapotaceae and Euphorbiaceae become more dominant. The 25 most common tree species form 40% of the total stem density (van Nieuwstadt 2002). Several palm genera (*Borassodendron, Oncosperma, Polydocarpus, Licuala*) are



Fig. 1 Map showing the location of Sungai Wain forest on the island of Borneo. The enlargement shows the Sungai Wain forest, indicating the unburned area (dark grey), and burned areas (light grey). The location of pairs of burned and unburned edge plots is shown. The circular inset shows an example of the lay out of one pair burned-unburned edge plots over the fire edge

common in the subcanopy and understory (especially rattans), and ginger species (Costaceae and Zingiberaceae) as well as Marantaceae, Araceae, and Pandanaceae are common in the understory. This paper only deals with trees ≥ 10 cm DBH. All growth forms of figs (*Ficus* spp.) were included. Only hemi-epiphytic figs with a diameter of ≥ 3 cm were included as potential food resources, as these were observed to bear fruits and to be fed upon by sun bears (Fredriksson, pers. obs).

History of forest fires at the study site

Most of the reserve was unaffected by fires at the start of the study in 1997, except for a small area near the eastern border that had burned in 1982-1983. The prolonged drought of the 1982–1983 ENSO, and several subsequent shorter ENSO droughts, probably caused elevated levels of mortality among large trees, resulting in an irregular canopy cover. Consequently the primary forest became increasingly vulnerable to desiccation during droughts and more susceptible to fires. Drought in the region started in May 1997 and continued intermittently till late April 1998, with 6 out of 12 months having no rainfall at all, or well below 100 mm. Fires entered the SWPF in March 1998, initially from a neighbouring state-owned logging concession, but subsequently also from surrounding agricultural fields. Fires moved slowly through the leaf litter and remained mainly in the undergrowth. Occasionally the fire reached into the crowns of older trees with hollow trunks, or dead standing trees with resin residues. In burned areas, all leaf litter and surface soil humus was reduced to ash, and mortality of seedlings and saplings was close to 100% (Fredriksson, pers. obs.). Fire breaks were created over a period of 2 months but nevertheless approximately 50% of the reserve was affected by the fires (Fredriksson 2002), leaving an unburned central core of some 4,000 ha of primary forest.

Permanent sampling plots

In the SWPF, 18 permanent sample plots (PSP), of 20×200 m (0.4 ha) each, were established in once-burned forest and adjacent unburned forest after the fire event in

1998 (Fig. 1) by the Wanariset Research Station (Tropenbos-Kalimantan Project). The set-up of the PSPs was designed around man-made firebreaks of ~1.5 m wide (see van Nieuwstadt 2002). Because the fire-breaks did not correspond to any topographical feature in the places where the PSPs were positioned, this allowed for a random sampling scheme with paired plots of unburned and burned forest at a short distance from each other. The PSPs were laid out in nine pairs, each pair of PSPs adjacent to each other over the firebreak between burned and unburned forest, forming one contiguous transect of 20×400 m, half in burned and half in unburned forest. The unburned PSPs lie adjacent to the burn edge and these plots are labelled "unburned edge plots." The PSPs were nested in three groups and spread over a total area of circa 20 km² (Fig. 1).

The distance between two pairs of PSPs was more than 500 m. We counted and measured all trees (≥ 10 cm DBH) in the PSPs 33 months after the fires, and calculated the percentage of live trees in both burned and unburned edge PSPs. Liana's were not sampled, as they only make up a small proportion (1%) of fruits encountered in the diet of sun bears at the study site (Fredriksson et al. in press).

Mortality rates

Annual mortality rates were calculated from ten 0.1-ha phenology plots (total 1 ha, all trees ≥ 10 cm DBH, n = 549 trees at the start of the study) which were monitored on a monthly basis between January 1998 and July 2004. These phenology plots were positioned in unburned forest at least 1 km from the burn edge, and are subsequently called "unburned interior" plots. Annual mortality rates for the interior plots are calculated based on exact 12 month periods (Jan–Dec).

Mortality rate was determined as: $m = \{1 - (N_t/N_0)^{1/t}\}^*100$

where "*m*" is mortality per year, N_0 is the initial number of live individuals and N_t is the number of live individuals at re-census interval t (e.g., Sheil and May 1996). Percentage of live trees was calculated for the interior plots for the same time interval as for the burned and unburned edge plots.

Densities of tree species important in the diet of the sun bear

A list of 115 fruit species eaten by sun bears in the study area was available from Fredriksson et al. (in press). All trees (\geq 10 cm DBH) that provided these fruits were subsequently labelled "sun bear fruit trees." Densities of sun bear fruit trees and all *Ficus* spp. were subsequently calculated for the three subsets of plots.

Two common species-rich genera, which occur in the diet of the sun bear (*Syzigium* spp. [Fam. Myrtaceae]; *Diospyros* spp. [Fam. Ebenaceae]) posed a problem for density calculations as identification to species level is difficult. Only certain species from these genera were fed upon by the bears, whereas others were consistently ignored. In order to avoid overestimation of the density of these genera, we first calculated the percentage of trees from these genera in the 1 ha interior plots that belonged to species actually fed upon by sun bears, based on leaf and fruit samples collected during direct feeding observations of sun bears. For both genera this was found to be approximately 50% of the individual trees in the 1 ha interior plots. Therefore, the density of these taxa as potential sun bear food resources was reduced

by 50% for further analyses in all plots. Two other taxa, *Madhuca kingiana* [Fam. Sapotaceae] and *Pternandra* spec. [Fam. Melastomataceae], were infrequently encountered in the diet of the bears, but are common in the forest. In order to avoid overestimating the densities of sun bear fruit trees, we reduced the density of these species also by 50% in the analyses.

Statistical analysis

Differences between burnt and unburned forest plots were compared with paired *t*-tests. A one-way ANOVA, with a Bonferroni multiple comparison test, was used to check for differences in mortality rates between sampling regimes and years. Standard deviation is always given when the average is presented (average \pm SD). An α -level 0.05 was chosen to indicate statistical significance.

Results

Density of fruit resources

Density of live fruit trees important in the sun bear diet, 33 months after the fire was 167 ± 41 trees ha⁻¹ in unburned edge plots and 37 ± 18 trees ha⁻¹ in burned plots, indicating a drought and fire-related reduction of nearly 78% (paired *t*-test: t = 8.7, df = 8, P = 0.001) (Table 1). Densities of sun bear fruit trees in the unburned interior plots was 144 trees ha⁻¹ (total area sampled 1 ha) at the start of the study in 1998 and declined to 133 trees ha⁻¹ 33 months after the drought.

Densities of all important sun bear fruit genera were lower in burned forest compared to unburned edge plots, although this was only significant for 8 out of 19 genera (Table 1). Several genera, generally occurring at low-medium densities, were not represented by any live trees in burned plots (e.g., *Monocarpia* [Fam. Annonaceae], *Quercus* [Fam. Fagaceae], *Litsea, Cryptocarya* [Fam. Lauraceae]). The difference in densities for these genera was not significant due to the large variation in number of trees encountered in the 9 unburned edge plots (Table 1).

Two of the main sun bear fruit genera, *Artocarpus* and *Dacryodes*, which contribute the bulk of fruit eaten by bears during masting events, declined significantly in densities, respectively from 11.9 ± 6.6 trees ha⁻¹ to 1.9 ± 2.4 trees ha⁻¹ and 11.4 ± 7.8 trees ha⁻¹ to 2.5 ± 2.5 trees ha⁻¹ (Table 1). The palm *Oncosperma horridum*, whose fruits are favoured by sun bears, declined from 8.1 ± 4.2 trees ha⁻¹ in unburned edge plots to zero in burned areas (Table 1).

The most important plant genus for sun bears which provides fruits during intermast periods, *Ficus* spp., declined significantly in burned forest. Most epiphytic, hemi-epiphytic and climber figs were encountered in the unburned edge plots, with only 4 of 74 figs (all sizes combined) observed in burned plots (paired *t*-test: t = 6.5, df = 8, P = 0.001). Densities of figs important in the sun bear diet declined significantly from 5.6±1.6 figs ha⁻¹ in unburned edge plots and 0.3±0.3 figs ha⁻¹ in the burned plots (paired *t*-test: t = 3.7, df = 8, P = 0.006), corresponding to a reduction of ~95% following fire.

No significant differences were found in densities for the variably common genera *Madhuca* and *Diospyros. Madhuca kingiana* is a dominant tree species in the permanent sample plots in the south of the reserve, which is the moister part of the

Table 1 Densities (stems ≥ 10 cm DBH, average \pm SD ha⁻¹) calculated from 18 vegetation plots (total 7.2 ha) of the main fruit-bearing genera important in the sun bear diet in unburned edge forest (UBF-edge) and burned forest (BF) 33 months after the 1997–1998 fire event. Genera only include species that have been found to occur in the bear diet. *Densities of *Ficus* mainly comprise of hemi-epiphytic stranglers ≥ 3 cm diam. *P* indicates significance level for paired *t*-test (df = 8)

Genera	Family	Density				
		UBF-Edge	SD	Burned	SD	Р
Madhuca	Sapotaceae	16.5	21.3	2.9	4.4	ns
Artocarpus	Moraceae	11.9	6.6	1.9	2.4	0.003
Dacryodes	Burseraceae	11.4	7.7	2.5	2.5	0.017
Syzigium	Myrtaceae	11.4	7	3.1	3.4	0.011
Baccaurea	Euphorbiaceae	8.1	3.7	0.6	1.1	0.001
Oncosperma	Palmae	8.1	10.5	0	_	ns
Diospyros	Ebeneceae	7.8	6.4	3.3	2.8	ns
Santiria	Burseraceae	6.1	4.9	0.6	1.1	0.013
Ficus*	Moraceae	5.6	3.9	0.3	0.8	0.006
Litsea	Lauraceae	5.6	5.3	0	_	0.013
Lithocarpus	Fagaceae	4.7	3.2	0.8	1.8	0.005
Garcinia	Guttiferae	3.6	3.3	0.8	1.8	ns
Polyalthia	Annonaceae	3.3	2.5	1.1	1.8	ns
Durio	Bombacaceae	2.5	3.8	0.6	1.1	ns
Quercus	Fagaceae	1.4	2.8	0	_	ns
<i>Cryptocarya</i>	Lauraceae	1.1	1.8	0	-	ns
Mangifera	Anacardiaceae	0.6	1.7	0.3	0.8	ns
Monocarpia	Annonaceae	0.6	1.1	0	-	ns
Tetramerista	Tetrameristaceae	0	_	0.6	1.1	ns
All sun bear fru	it species combined	166.9	40.7	36.8	17.8	0.001

forest due to topography. One unburned edge plot in the southern part of the forest (0.4 ha) contained 22 trees (≥ 10 cm DBH) of this species compared to several unburned edge plots in the western or northern part of the forest which contained zero trees of this species.

Species diversity of fruit trees in burned and unburned forest

Species diversity of sun bear fruit resources declined significantly following fire (paired *t*-test: t = 11.9, df = 8, P = 0.001). At least 66 species which feature in the diet of sun bear occurred in unburned edge plots, whereas only 37 of these were observed in burned plots, representing a decrease of ~44% in richness of sun bear fruit species in burned forest areas (Appendix). The family Lauraceae, representing the sun bear fruit genera *Cryptocarya* and *Litsea*, as well as the family Caesalpiniaceae with the sun bear fruit genus *Dialium* were not encountered with any live trees in burned sampling plots, whereas in the unburned edge plots the genus *Litsea* (all species combined) occurred in 8 out of 9 plots and was represented with 20 trees. The genus *Dialium* was found in 6 out of 9 unburned edge plots. A total of 46 sun bear food tree species were encountered in the unburned interior plots (total area sampled 1 ha vs. 3.6 ha sampled of burned and unburned edge plots each).

Tree mortality

Overall tree mortality (both sun bear fruit trees and tree species not fed upon by bears) in burned forest was extremely high, with $77.5\pm10.8\%$ trees dead 33 months

after the fire event (range 58.2-90.0%, n = 9 plots). In unburned edge plots mortality was also high with $24.9\pm5.4\%$ of trees dead (range 17.7-35.6%, n = 9 plots). Cumulative percentage of dead trees in the unburned interior plots 33 months after the drought was $14.1\pm5.2\%$, some 40% lower than encountered in the unburned edge plots.

Mortality rates between years differed significantly (one-way ANOVA F = 6.6 df = 5, P = 0.001) although only mortality in 1999 was significantly different (higher) than all other years (Bonferroni, t > 3.8, P = 0.006 for all comparisons). Mortality remained elevated for 2 years in the interior plots and approached "normal" rates reported for the region in the third year after the drought (Table 2). Mortality rates did not differ significantly between sun bear fruit species and species that do not occur in the diet of bears in the interior plots (*t*-test, t = 2.3, df = 5, P = 0.067), although the *P*-value suggested a tendency. No significant difference was found in mortality of sun bear food trees and non-food trees between burned and edge plots 33 months after the fire (paired *t*-test, t > 0.04, df = 8, P > 0.3).

Discussion

The 1997–1998 fires reduced the density of sun bear fruit trees by nearly 80%, 3 years after the fire. Fruit resources are important in the diet of sun bears, partly to regain energy after periods of fruit scarcity and partly to build up fat reserves to cope with prolonged intermast periods (Fredriksson et al. in press). When few fruit resources are available sun bears subsist primarily on insects although densities of these were also highly reduced in burned forest areas (Fredriksson, unpubl. data). The reduction in fruit trees measured during this study is almost double the 44% decline reported by Leigthon and Wirawan (1986) for fruit species important in the diet of frugivorous primates like Bornean gibbons (Hylobates muelleri) and orangutans (Pongo pygmaeus) after the 1982-1983 fires in Kutai National Park, East Kalimantan. Possibly the figures presented by Leigthon and Wirawan (1986) are underestimates of the true extent of damage as their sampling was carried out shortly after the fire event. We documented delayed mortality due to the fires and drought, which continued for at least 2 years after the ENSO event. Mortality rates approached "normal" rates reported for the region in the third year after the drought (average 1.7% for 9 study sites in the region see Phillips et al. 1994; Wich et al. 1999; Potts 2003).

Table 2 Annual mortality
rates (%) of trees (≥10 cm
DBH) in unburned interior
plots calculated from ten
0.1 ha phenology plots.
Mortality rates are presented
separately for sun bear food
trees and non-food trees, as
well as for all trees combined

	Non-bear trees $(n = 405)$	Bear trees $(n = 144)$	All trees combined (n = 549)
1998	4.69	3.47	4.37
1999	7.25	4.32	6.48
2000	2.79	0.00	2.04
2001	2.01	0.00	1.46
2002	2.35	2.26	2.32
2003	2.40	3.08	2.59
Average	3.58	2.19	3.21

Fire reduced the important sun bear fruit genus *Ficus* spp. by 95% 3 years after the fires. This serious decline might well have negative consequences in terms reestablishment or persistence of frugivore populations, as figs have been found to be one of the main fruit resources during periods of food lows for a variety of wildlife (e.g., Leighton and Leighton 1983). Besides the large reduction of fig densities in burned areas, Harrison (2000) reported on local extinctions of fig wasps after the ENSO drought, which affected fig fruit production, even in forest areas unaffected by fires. Putz and Susilo (1994) however reported that 10 years after the 1982–1983 forest fires regeneration of hemi-epiphytic figs by establishment of new terrestrial connections was close to 60%.

The reduction of almost 44% in species richness of sun bear fruit taxa in onceburned forest could lead to permanent changes in the composition of sun bear fruit resources in these areas, especially as certain sun bear fruit tree genera disappeared altogether from the burned plots. Fires affect dominant tree species more than rare species (Slik et al. 2002; Potts 2003), but the disappearance of rare species is more worrying as they might become locally extinct (Cochrane and Schulze 1999). Regeneration of the forest will largely depend on the crop of trees that sprouts after the fires. The proportion of seedlings that grew up 5 years after the 1982–1983 fires in Sabah showed a close resemblance to the distribution of families in primary forest, although few Dipterocarp saplings were encountered (Woods 1989). Slik et al. (2002) found that lowland dipterocarp forest, 15 years after being affected by fire, did not show an increase in species richness, although stem density increased, but these primarily belonged to a few pioneer tree species (Macaranga). The recruitment of Macaranga, both in the under- and over-storey, indicated that recovery of species composition in burnt forests takes longer than in selectively logged forest, where after 15 years pioneer species were being replaced by primary forest species (Slik et al. 2002). Whitmore (1985) reported that a lowland dipterocarp forest, extensively damaged by storm and fire in 1880, was still unusually poor in diversity of uppercanopy species when surveyed some 70 years later. Close to 18% of the burned forest in our study area has remained as unburned forest patches in swampy areas or near streams (Fredriksson and Nijman 2004), which might facilitate a more uniform regeneration due to seed dispersal of forest-interior species into the burned areas. But overall, it will take decades, if not centuries, for many slow-growing climax species to begin fruiting and provide food for wildlife (Whitmore 1985).

Fruiting phenologies of remaining fruit trees in burned areas might also deviate from fruiting patterns in unburned forest due to changes in environmental conditions and exposure to higher levels of drought. Kinnaird and O'Brien (1998) reported that occurrence of flowering and fruiting by trees in burned areas was lower than in adjacent unburned areas just after the 1998 fires. The storage of water reserves in trees, which depends on availability of subsoil water, has been found to influence flowering, although water storing capabilities differed greatly between species (Borchert 1994). The possible influences of changed environmental conditions in burned forest on phenological patterns calls for further studies.

Drought by itself had significant effects on sun bear food trees in unburned forest, with elevated mortality rates up to 2 years after the drought. Effects of the drought on trees have been found to be differential, relative to abundance and habitat factors (Potts 2003), with trees in moister areas less affected (Potts 2003;

Slik and Eichhorn 2003; Fredriksson and Nijman 2004). The combined effects of fire and drought were far more severe than the effects of drought alone. Heavily burned forest areas have become dominated by pioneer species (Woods 1989; Nykvist 1996; Toma et al. 2000; Slik et al. 2002), have lower species diversity (Matius et al. 2000; Slik et al. 2002; this study), and decreased soil fertility due to a loss of inorganic nutrients (Nykvist et al. 1994; Malmer 1996). Several studies investigated the regeneration potential of burned forest areas after the 1982–1983 fires. Above-ground biomass in a lowland forest in Sabah 8 years after the fire was still only a quarter of adjacent unburned forest (Sim and Nykvist 1991; Nykvist 1996).

The significant decrease in both density as well as species diversity of sun bear fruit resources due to fire could partially explain the reduced usage of burned forest by sun bears (Fredriksson, unpubl. data). Few fresh signs of sun bears were encountered in burned areas up to 5 years after the fire event, and radio-collared bears rarely entered burned forest. Although the extent of the home ranges of our radio-collared bears before the fire was unknown (as they were caught in unburned forest following the fire event), sun bears ranged throughout the reserve prior to fires (Fredriksson 2005; Fredriksson, unpubl. data,). Environmental conditions like an increase in temperature due to lack of canopy cover, exposure to rain, and also the inaccessible nature of burned areas due to a thicket of ferns which blocked the understory for approximately 4 years after the fires, hampering movement for large ground-dwelling mammals, probably discouraged usage by bears. Additionally, densities of various invertebrate food resources, especially termites, declined significantly after the fires (Fredriksson et al., unpubl. data). Doi (1988) reported that sun bears did not recover quickly after the 1982-1983 fires in the largest lowland conservation area in East Kalimantan, the 200,000 ha Kutai National Park, with few bear signs found even in the core of the park 3 years after the fires. Leighton and Wirawan (1986) reported a decrease in vertebrate densities after the 1982–1983 fires, although large-bodied primates reportedly seemed to be the least affected, possibly due to their generalized omnivorous diets and behavioural flexibility to switch food types (van Schaik et al. 1993). On the other hand O'Brien et al. (2003) found a significant decrease in siamang (Symphalangus syndactylus) group sizes, as well as infant and juvenile survival, after forest fires in Sumatra to a point where it seems unlikely that groups will survive for more than two generations in burned areas.

Tree mortality figures differed substantially between edge and interior plots in unburned forest. Almost 40% more dead standing trees were encountered in the unburned edge plots compared to interior plots. Although no study as yet has specifically investigated edge effects in Borneo, Laurance et al. (2000, 2001) reported that mortality along forest edges in Amazonia is higher than in the forest interior, with increased tree mortality levels penetrating up to 300 m from the forest edge. The extremely high mortality recorded in burned areas might also be a cumulative effect of several severe ENSO events over the last decades, each of which probably has caused elevated mortality, resulting in a more open canopy and higher water stress during subsequent droughts. The fact that annual mortality rates in unburned forest were elevated for 2 years post-ENSO, could indicate that, with an increased rate of ENSO events, such prolonged elevated mortality rates will also be occurring on a more frequent basis. If forests in these drought prone areas experience mortality rates of 6–7% every 15 years for extended periods of time, recruitment might not balance mortality and significant changes in forest structure could occur even without any direct human influence.

Conclusions

Large changes in vegetation structure and environmental conditions in burned forests, coupled with a significant decrease in fruit resources important in the diet of sun bears, have caused a significant reduction of suitable habitat for this bear species in fire-affected areas. The slow regeneration of these burned areas will probably influence re-colonization by bears, even if they have been able to maintain large enough population numbers within the burned forest matrix and adjacent unburned forest areas. Little is known about the ability of sun bears to exploit new pioneer fruit resources which have sprouted since the fires. The most dominant pioneer genus (*Macaranga*) has dehiscent fruits with small arillate seeds primarily attractive to birds (Davies and Ashton 1999; Slik et al. 2000), and has not (yet) been encountered in the sun bear diet.

The damage due to fires in primary forest has far surpassed that encountered in logged-over areas (Woods 1989; Slik et al. 2002). Unburned logged-over areas might have higher potential for biodiversity conservation than primary forest that has burned once, although long-term monitoring of floral regeneration patterns and wildlife diversity and abundance in burned areas needs to be carried out in order to determine the future value of such forest for conservation. The massive spatial scale of these fire disturbances and the relatively short timespan during which they have affected vast areas (usually 2–3 months of fires) is a new and worrying phenomenon. With the increase in the frequency and severity of ENSO (Timmermann et al. 1999), the future of these burned over forests looks grim as regeneration will only take place if no further fires affect these areas, whereas repeated fire damage is common (Cochrane et al. 1999; Siegert et al. 2001). These factors, aggravated by low fire prevention activities and a lack of law enforcement in the region, call for highly increased conservation efforts in these drought prone rainforest areas if productive sun bear habitat is to be retained.

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Appendix List of the how many of the	he 1997–1998 f he 1997–1998 f 0.4 ha plots (9	t genera/species of ire. A " $$ " indicates of plots in burned an	that that the	 <10 cm L ie genus/s ots in unl 	pecie	encour s was er ed edge	forest) the genu	e plots, a "0" indic s/species was enco	ad burned (Dr) veg ates it was absent. I buntered	Number	c of plots (u	indic	ates in
Genus	Species	Family	UBF- edge	No. of plots	BF	No. of plots	Genus	Species	Family	UBF- edge	No. of plots	BF	No. of plots
Aglaia	spec.	Meliaceae	~	7	0	0	Glochidion	spec.	Euphorbiaceae	N	2	0	
Alangium	ridleyi	Alangiaceae	~	б	~	1	llex	cymosa	Aquifolicaeae	~	1	~	1
Artocarpus	anisophyllus	Moraceae	7	6	7	3	Irvingia	malayana	Simaroubaceae	~	1	~	4
Artocarpus	dadah	Moraceae	7	1	0	0	Lansium	domesticum	Meliaceae	~	1	~	1
Artocarpus	integer	Moraceae	~	3	$\overline{}$	1	Lansium	spec.	Meliaceae	>	1	0	0
Artocarpus	lanceifolius	Moraceae	~	2	0	0	Lithocarpus	gracilis	Fagaceae	~	1	0	0
Artocarpus	nitidus	Moraceae	~	3	0	0	Lithocarpus	spp.	Fagaceae	~	8	~	2
Artocarpus	spp.	Moraceae	~	4	~	2	Litsea	firma	Lauraceae	>	4	0	0
Baccaurea	bracteata	Euphorbiaceae	~	Э	0	0	Litsea	spp.	Lauraceae	~	7	0	0
Baccaurea	macrocarpa	Euphorbiaceae	~	9	0	0	Madhuca	kingiana	Sapotaceae	~	9	~	4
Baccaurea	spec.	Euphorbiaceae	~	8	~	2	Magnolia	lasia	Magnoliaceae	~	2	0	0
Baccaurea	stipulata	Euphorbiaceae	~	1	0	0	Mangifera	macrocarpa	Anacardiaceae	~	1	0	0
Borassodendron	borneensis	Palmae	~	7	~	8	Mangifera	spp.	Anacardiaceae	~	1	~	-
Canarium	spp.	Burseraceae	~	4	0	0	Monocarpia	kalimantanensis	Annonaceae	~	7	0	0
Crypteronia	spec.	Crypteroniaceae	~	7	~	1	Nephelium	spec.	Sapindaeae	~	5	~	1
Cryptocarya	spec.	Lauraceae	~	e	0	0	Ochanostachys	amentaceae	Olacaeae	~	6	~	2
Dacryodes	costata	Burseraceae	~	3	~	1	Oncosperma	horridum	Palmae	>	9	0	0
Dacryodes	rostrata	Burseraceae	~	7	~	1	Palaquium	spp.	Sapotaceae	>	6	~	ŝ
Dacryodes	rugosa	Burseraceae	~	2	~	1	Polyalthia	lateriflora	Annonaceae	0	0	>	_
Dacryodes	spec.	Burseraceae	~	5	~	4	Polyalthia	laterifolia	Annonaceae	~	7	0.	C
Dialium	indum	Ceasalpiniaceae	7	4	0	0	Polyalthia	rumphü	Annonaceae	7	б	~	_
Dialium	platysepalum	Ceasalpiniaceae	~	1	0	0	Polyalthia	spec.	Annonaceae	~	5	~	0
Dialium	spec.	Ceasalpiniaceae	~	4	0.	0	Polydocarpus	spec.	Palmae	~	б	>	0
Diospyros	borneensis	Ebenaceae	7	9	~	4	Prunus	volgens	Rosaceae	7	9	0.	C
Diospyros	cf buxifolia	Ebenaceae	0	0	~	-	Pternandra	spec.	Melastomataceae	7	8	~	2
Diospyros	spec.	Ebenaceae	7	7	~	4	Quercus	spp.	Fagaceae	7	7	0	0
Durio	dulcis	Bombacaceae	2	-	7	, ,	Sandoricum	spp.	Meliaceae	~	ς,	0	0
Durio	graveolens	Bombacaceae	~	, ,	0	0	Santiria	cf apiculata	Burseraceae	~-	,	0-	<u> </u>
Durio Durio	kutejensis ovlevanus	Bombacaceae Bombacaceae	~ ~	- "	- 	o -	Santiria Santiria	spp. tomentosa	Burseraceae Burseraceae	~ ~	οv	~ ~	
2	and and and			5		4					2	,	,

Appendix cor	ntinued												
Genus	Species	Family	UBF- edge	No. of plots	BF	No. of plots	Genus	Species	Family	UBF- edge	No. of plots	BF	No. of plots
Dysoxylum Eugenia Eugenia Ficus Garcinia Garcinia	spec. spec. tawahense spp. spp.	Meliaceae Myrtaceae Moraceae Guttiferae Guttiferae	<pre>< < <</pre>	00004 4	20220 Z	$\begin{array}{ccc} 1 \\ 1 \\ 0 \\ 0 \\ 0 \\ \end{array}$	<i>Syzygium</i> <i>Tetramerista</i> <i>Xerospermum</i> Unburned edge J species Burned plots: 37	spp. <i>glabra</i> spec. plots: 66 species	Myrtaceae Tetrameristaceae Sapindaeae	707	9 1	055	۲ 2 2 0

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