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The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia

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ABSTRACT. Long-term data on flower and fruit production of the forest community in two lowland tropical rain forests in north-western Sumatra are presented. The proportion of years with mast fruiting was found to be similar to that found elsewhere in Malesia. However, masting at the two sites, 70 km apart, did not coincide, and showed no correlation with the El Niño–Southern Oscillation phenomenon (ENSO). Comparisons with other sites in Malesia suggest a general waning of ENSO's impact toward western Malesia. Spatial variation at various scales in the timing of masting events was noted in Sumatra and elsewhere. This suggests that additional factors to ENSO play a role in determining forest-level mast fruiting, and we hypothesize that frugivorous animals have the opportunity to track mast fruiting. It is hypothesized that asynchrony between nearby areas in masting increases toward the western edge of Malesia.

KEY WORDS: animal migrations, El Niño, Malesia, mast fruiting, phenology, Sumatra

INTRODUCTION

The Malesian dipterocarps are well known to show marked peaks in flower and fruit production on a supra-annual basis (Appanah 1985, Ashton 1989, Curran *et al.* 1999, Wood 1956, Wycherley 1973), a phenomenon known as masting. Masting at the level of species or families occurs in other tropical areas (Africa: e.g. Newbery *et al.* 1998; Central and South America: e.g. Wheelwright 1986) and the temperate zone (Silvertown 1980). Herrera *et al.* (1998) concluded from a meta-analysis of many studies that masting was not a parsimonious

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concept because reproductive output tends not to show strict bimodality at the species level. However, they did not include plants from Malesia, for which several convincing demonstrations of dramatic interannual variability exist (see above).

In many Malesian forests, masting is not limited to dipterocarps alone, but is displayed by many tree species, producing remarkable interannual variability at the community level (Corlett 1990, Leighton & Leighton 1983, Medway 1972, van Schaik 1986). This phenomenon is thought to be limited to Malesia (Janzen 1974), and is of great significance for frugivorous animals (Knott 1998, van Schaik & van Noordwijk 1985). However, species vary predictably in the degree to which they show masting (van Schaik 1986), and thus community-level masting is more pronounced in some habitats than in others. Hence, recognising community-level masting is to some extent arbitrary.

Masting events in the tropics tend to be associated with periods of increased irradiation (Newbery *et al.* 1998, Ng 1977, 1981, van Schaik 1986, Wycherley 1973), drier than normal weather conditions (van Schaik 1986, Wood 1956), and sharp drops in night-time temperatures (Ashton *et al.* 1988, Newbery *et al.* 1998, Wycherley 1973). The latter factor is actually thought to trigger the onset of mast flowering, at least in dipterocarps (Ashton *et al.* 1988, Yasuda *et al.* 1999). Ashton *et al.* (1988) suggested a link between low night-time temperatures, and hence subsequent mast flowering, and the El Niño–Southern Oscillation (ENSO) phenomenon (but see Yasuda *et al.* 1999).

There is spatial variation in the occurrence of dipterocarp masting in Borneo (Ashton *et al.* 1988) and West Malaysia (Burgess 1972, Yap & Chan 1990). Ashton *et al.* (1988) argue that the effect of ENSO on masting was strongest on the eastern sides of the Malesian land masses (see also Yasuda *et al.* 1999). This spatial variation suggests that additional, probably more local, factors affect masting as well, in addition to the more global effects of ENSO.

In this paper, we present long-term phenology data for two mast-fruiting lowland forest communities in north-western Sumatra: Ketambe and Suaq Balimbing. For this westernmost part of Malesia, we assess the rate of masting (both qualitatively and quantitatively), coincidence with ENSO, and geographic coincidence. We then compare these findings to the rest of Malesia. Finally, we briefly discuss the possible implications for animal movements.

METHODS

Phenological data were collected in two study areas (Ketambe and Suaq Balimbing) with a similar climate (C. van Schaik, unpubl. data) in the Gunung Leuser National Park, northern Sumatra, Indonesia. Ketambe is located in a rift valley inside the Barisan mountain range, whereas Suaq Balimbing is located on the western coastal plane, some 70 km to the south-west, separated by mountains to over 2000 m asl.

Ketambe (3°41′N, 97°39′E) is located in the upper Alas valley at an altitude

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of 350–500 m asl. This study area mainly consists of primary rain forest and was described in detail by Rijksen (1978) and van Schaik & Mirmanto (1985). Shorter-term phenological studies were done by van Schaik (1986), Palombit (1992) and Sterck (1995). The phenological records used here do not include the forests on the lowest riverine terraces which do not show masting (van Schaik 1986).

Suaq Balimbing (3°04′N, 97°26′E) is located in the western coastal plain, and consists of a variety of floodplain and hill forest habitats. The phenological records used here refer to the hill forest, starting at 5 m asl, the only habitat at this site to display masting (C. van Schaik, unpubl. data).

Phenological records for Ketambe are a mix of fruit-trail data and tree plot-based data. Between March 1980 and January 1988, ripe fruits were counted on the ground on a trail of 4.6 km. Whenever ripe fruits were found the patch from which the fruits came was recorded and counted as one ripe fruit source. From these data the monthly number of ripe fruit sources per kilometre trail were calculated and used in the analyses. Ripe fruit trail data showed a very good correspondence with phenological data based on monitoring of ripe fruit production (monthly presence or absence of ripe fruits in each individual tree) of individual trees in vegetation plots during both the 1980–1983 (van Schaik 1986 for details) and the 1986–1988 periods (Spearman r = 0.7, P = 0.02, n = 17). Although between March 1980 and February 1984 the presence or absence of ripe fruits for trees in vegetation plots were also recorded (van Schaik 1986), we used fruit-trail data for the period from March 1980 until August 1986 for the analyses, because this was a long continuous data set. Since September 1986, around 420 trees above a girth at breast height (GBH) of 39 cm in 17 vegetation plots have been monitored on a monthly basis. Details of species composition of these vegetation plots have been published by Palombit (1992). For flowers, plot-based data (monthly presence or absence of flowers in each individual tree) were used for March 1980–February 1984 as well as for the period of September 1988–December 1998. Because of the different methods and different researchers, we combined the various data sets by standardizing within each data set (March 1980–February 1984, March 1984–January 1988 (used until August 1986), September 1986–August 1988, September 1988–March 1993, April 1993–December 1998). We standardized the data by computing the z-scores for each datapoint within a data set. For ripe fruits we were able to make an almost complete data set for the 1980–1998 period (except for 6 mo in 1983 and 1984 when no data on phenology were collected), whereas for flowers there was a gap from March 1983 until September 1988.

In Suaq Balimbing 500 plot-based trees above a GBH of 30 cm have been monitored monthly since February 1994 and monthly presence/absence data for flowers and ripe fruits on each tree was used here. Two experienced observers collected the phenology data, and an inter-observer reliability test showed a very good correspondence (C. van Schaik, unpubl. data).

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At Ketambe (as at some other sites: see Ashton *et al.* 1988), masting is not an all-or-nothing event, and a mast needs to be identified. We defined a mast year as one in which the ripe fruit scores were higher than 1.96 standard deviations above the mean, corresponding to a value reached in less than 5% of observations. Because masting creates a bimodal frequency distribution of fruit or flower availability scores, the risk of spurious masting peaks in smaller data sets in which no masting actually occurred, is fairly low. Moreover, where checks with general impressions of animal researchers for years with unusual heavy flowering and fruiting at the Ketambe and Suaq sites could be made, their impressions of masting years agreed with the above criterion for masting. For other sites or areas used in the comparison, we relied on the assessments of the original researchers for the occurrence of a masting event. In light of the good agreement between researchers' impressions and the quantitative assessment of masting, we assume that the assessments of masting by other researchers at other sites are a reliable indicator of masting.

We defined an El Niño–Southern Oscillation event as the period in which the NINO3-anomaly of the seasonally corrected expected sea surface temperatures in the Eastern Pacific exceeded + 0.5. This definition differs slightly from Ashton *et al.* 1988 who used the Southern Oscillation index instead of sea surface temperatures. We preferred the NINO3-anomaly because measures based on sea surface temperatures correspond well to the state of the tropical ocean-atmospheric system (Latif *et al.* 1998, Shukla 1998). For masting to be associated with ENSO, the ENSO had to occur during the period of the major flower induction (December to June for West Malaysia and Sumatra; June to December for the other areas (van Schaik 1996).

RESULTS

Incidence of masting at Ketambe and Suaq Balimbing

For Ketambe mass flowering, defined as standard scores of over 1.96 SD, occurred in 1981, 1992, 1997 and 1998 (Figure 1a; however, note that no flowering data were available for March 1983 to September 1988). Mast fruiting occurred in 1981, 1984, 1988, 1992, 1995 and 1998. During 1981, 1988 and 1992, the mast came in a double peak a few months apart, whereas single peaks were reached in the three other years (Figure 1b).

The rate of mass flowering at Ketambe was 0.31 for the years 1980–1998. In combination with earlier mast fruiting records from this site (van Schaik 1986), there are eight mast fruiting events in the 28 y of records (1971–1998), a rate of 0.29. One masting event was observed in 5 y of observations at Suaq Balimbing. These findings indicate that rates of mast fruiting in Sumatra are very similar to those found elsewhere in the region (Table 1).

The difference between the rates of mass flowering and mast fruiting are probably due to massive fruit failure or high fruit set and ripening. The 1997 mass flowering at Ketambe did not result in an unambiguous fruit peak of 1.96

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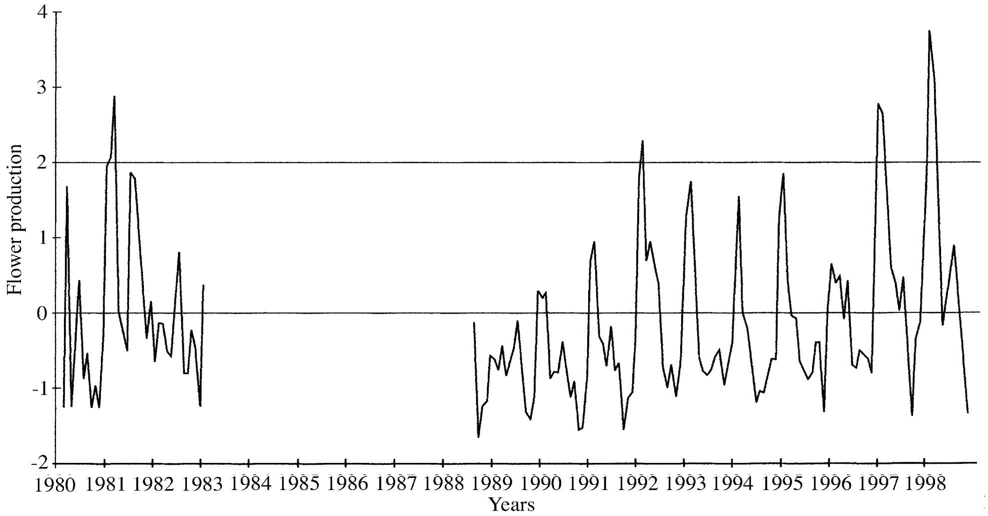
(a) Flowering



(b) Fruiting

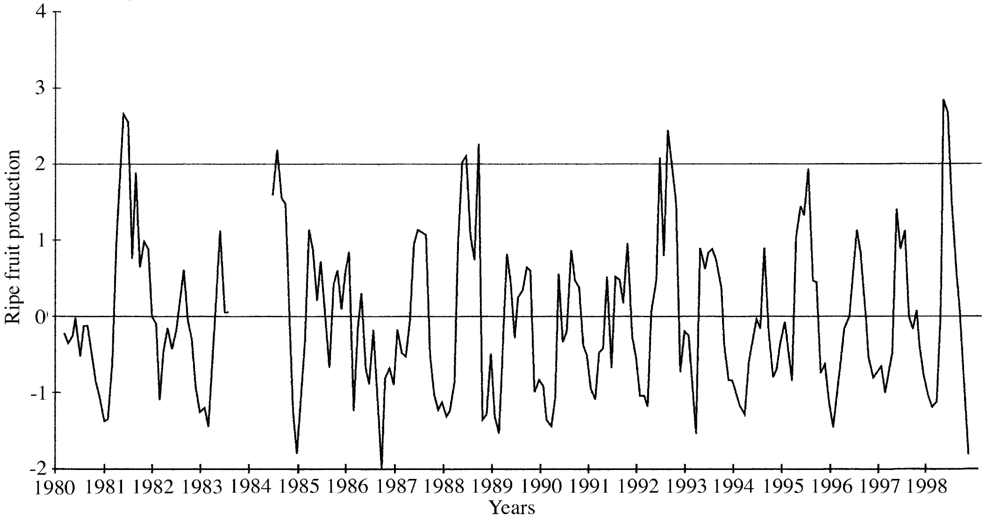


Figure 1. Standardized (z) scores for (a) flower production, and (b) ripe fruit production in Ketambe. Bars for the years indicate the first month of that year.

SD above the mean. This might possibly be due to this year having annual rainfall well above average (mean: 3288 mm (n = 20 y); 1997: 3744 mm). In 1995 (a very dry year: 2827 mm), however, flowering was not found to be unusually heavy, but fruiting was, suggesting very high fruit set and subsequent ripening. Overall, years with mast fruiting at Ketambe were not significantly drier than years without (mean = 3113 mm [n = 5] vs. mean = 3346 [n = 15]: t_{18} = 1.19 ns). In contrast, the one mast year at Suaq Balimbing was the driest year of the five on record (3067 mm vs. mean of 3439 mm for the non-mast years).

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Table 1. Rate of mast fruiting in various areas and sites in Malesia.

Area and sites	Number of years recorded	Probability of masting[1]	Source
East Borneo	34	0.21	Ashton *et al.* (1988)
West Borneo, Kuching	34	0.24	Ashton *et al.* (1988)
West Borneo, Pontianak	20	0.20	Peters (1996)
West Borneo, Gunung Palung	13	0.31	Curran *et al.* (1999)
East Peninsular Malesia	34	0.18	Ashton *et al.* (1988)
West Peninsular Malaysia	38	0.16	Ashton *et al.* (1988)
West Peninsular Malaysia, Ulu Gombak	7	0.29	Medway (1972)
Singapore	4	0.25	Corlett (1990)
Western Sumatra, Ketambe	28	0.29	This study, van Schaik (1986)
Western Sumatra, Suaq Balimbing	5	0.20	This study

[1] Masting probabilities were calculated by dividing mast fruiting years by the number of observed years.

A comparison between Ketambe and Suaq Balimbing is possible for the period 1994–1998 (Figures 2a and 2b). Mass flowering occurred twice at Ketambe, in 1997 and 1998, but only once in Suaq Balimbing, in 1997. At Ketambe, mast fruiting occurred twice, in 1995 and 1998, whereas it occurred only once at Suaq Balimbing, in 1997. Although the period for comparison between the two sites is relatively short it is of interest that these two sites, while only 70 km apart, show non-coincident mast fruiting.

Geography of masting and ENSO

Various exploratory analyses of standardized flowering scores for the 11 y at Ketambe (cf. Figure 1b) yielded no firm relationship with the temperature anomalies (NINO3 measure): neither time-lag (of 1–11 mo) Pearson correlations nor examination of threshold effects showed a consistent effect on flowering. This suggests that ENSO has little or no impact on mass flowering at this site. A similar analysis failed to yield an ENSO impact on flowering levels for two data sets from western Peninsular Malaysia (community-level flowering for Ulu Gombak: Medway 1972; dipterocarp flowering in Kepong: Ng 1981). Thus, the available data on flowering in western Malesia shows no clear impact of ENSO on masting.

Table 2 provides a compilation of ENSO events and of mast fruiting records for the period since 1950, based on Ashton *et al.* (1988) and a variety of additional sources. This compilation allows us to examine whether ENSO during the major period of flower induction influences the probability of mass flowering or mast fruiting over a wider geographic area (cf. Ashton *et al.* 1988, Wycherley 1973). Note that the records had to be rescaled according to the timing of the peak flowering period, which varies in different parts of the Malesian region (van Schaik 1996). Thus, records of mast fruiting early in the calendar year (as in Borneo and eastern Peninsular Malaysia) have been placed in the previous calendar year (cf. Ashton *et al.* 1988). We assume that the three sets of records of dipterocarp flowering (see Table 2) accurately reflect mast fruiting, i.e. that no massive crop failure occurred.

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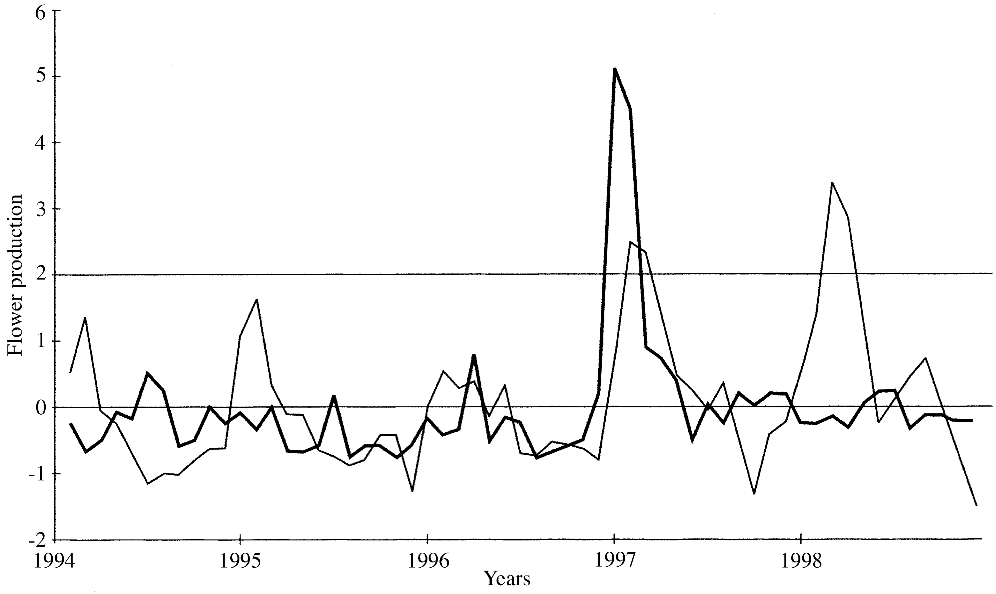
(a) Flowering



(b) Fruiting

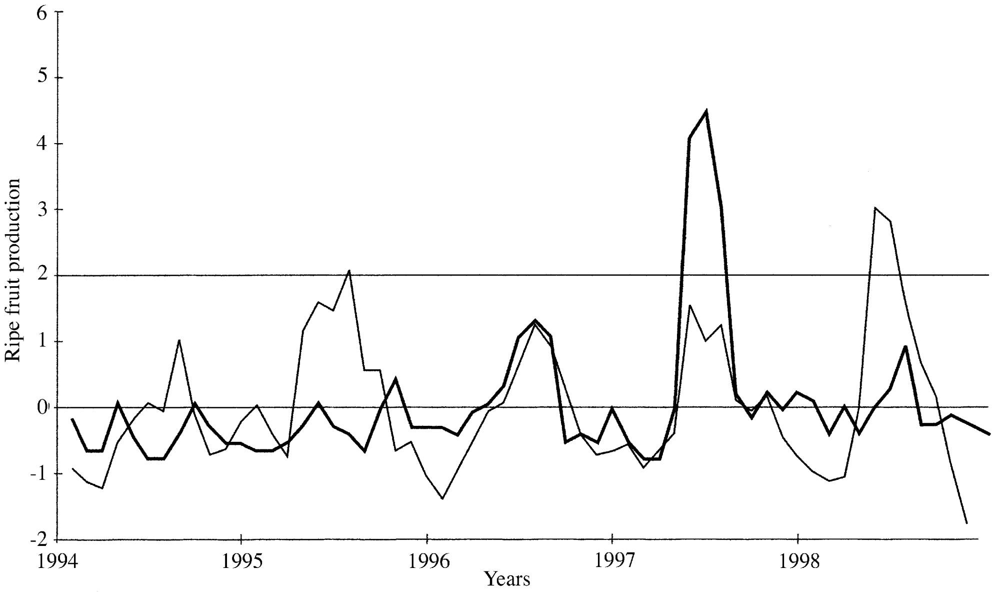


Figure 2. Standardized (z) scores for (a) flower production, and (b) ripe fruit production at Ketambe (thin line) and Suaq Balimbing (thick line). Bars for the years indicate the first month of that year.

In Table 3 the mast fruiting probabilities from the data in Table 2 are shown for the eastern and western parts of the three major landmasses in relation to ENSO periods (Table 3). While both eastern and western Borneo and eastern Peninsular Malaysia show a significant increase in the likelihood of mast

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Table 2. ENSO periods and the occurrence of mast fruiting in several Malesian study sites for 1950–1998[1].

Study sites Sources[2]		East Borneo 1	East Borneo Kutai 2	West Borneo Kuching 1	West Borneo Pontianak 3	West Borneo Gunung Palung 4	East Peninsular Malaysia 1	West Peninsular Malaysia 5	West Peninsular Malaysia 1	Singapore 6	North Sumatra Suaq Balimbing 7	North Sumatra Ketambe 7, 8
Years	ENSO periods (months)	Dipterocarps flowers	Forest community fruits	Illipe nut harvests	Illipe nut harvests	Dipterocarps fruits	Dipterocarps flowers	Forest community flowers and fruits	Dipterocarps flowers	Forest community flowers and fruits	Forest community flowers and fruits	Forest community flowers and fruits
1950			—		—	—		—		—	—	—
1951	7–12	M	—		—	—	M	—		—	—	—
1952	1–2	m	—		—	—		—		—	—	—
1953	1–11		—	M	—	—	M	—		—	—	—
1954		m	—		—	—		—		—	—	—
1955		M	—		—	—	m	—	m	—	—	—
1956			—		—	—		—		—	—	—
1957	4–12		—	m	—	—	M	—	M	—	—	—
1958	1–3	M	—	M	—	—		—	M	—	—	—
1959		m	—		—	—		—		—	—	—
1960		m	—		—	—	m	—		—	—	—
1961			—	m	—	—		—		—	—	—
1962			—		—	—		—		—	—	—
1963	7–12	m	—		—	—	m	M	m	—	—	—
1964	1		—		—	—				—	—	—
1965	5–12		—	m	—	—				—	—	—
1966	1–2		—		—	—				—	—	—
1967		m	—	M	—	—				—	—	—
1968	7, 10–12	M	—		m	—	M	M	M	—	—	—
1969	1–6, 8–12		—	M		—				—	—	—

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1970	1		—			—		—		—	—	—
1971			—			—		—		—	—	
1972	4–12	m	—	M	M	—		—		—	—	M
1973	1–3	m	—			—		—		—	—	
1974			—			—		—		—	—	
1975			—		M	—		—		—	—	
1976	6–12	M	—	M	m	—	M	—	M	—	—	
1977	1–3, 10–11	m	M			—		—		—	—	
1978	1					—		—		—	—	
1979	6, 9–12		—	M		—		—		—	—	M
1980	1, 6, 12		—	m		—		—		—	—	
1981	12	M	—	M	m	—		—	M	—	—	M
1982	1, 5–12		—	m	M	—	M	—		—	—	
1983	1–9	M	—			—		—	m	—	—	
1984		—	—	—		—	—	—			—	M
1985		—	—	—		—	—	—			—	
1986	9–12	—	—	—	M		—	—			—	
1987	1–12	—	—	—		M	—	—	M	M	—	
1988	1	—	—	—	—		—	—	—	—	—	M
1989		—	—	—	—		—	—	—	—	—	
1990	4–5	—	—	—	—		—	—	—	—	—	
1991	5–8, 10–12	—	—	—	—	M	—	—	—	—	—	
1992	1–6	—	—	—	—		—	—	—	—	—	M
1993	3–6, 10	—	—	—	—		—	—	—	—	—	
1994	11–12	—	—	—	—		—	—	—	—		
1995	1–2	—	—	—	—	M	—	—	—	—		M
1996		—	—	—	—		—	—	—	—		
1997	5–12	—	—	—	—		—	—	—	—	M	
1998	1–5	—	—	—	—	M	—	—	—	—		M

[1]Major mast (M) minor mast (m) follow Ashton *et al.* (1988). —, data not available.

[2]1. Ashton *et al.* (1988); 2. Leighton & Leighton (1983); 3. Peters (1996); 4. Curran *et al.* (1999); 5. Medway (1972); 6. Corlett (1990); 7. This study; 8. van Schaik (1986).

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fruiting following ENSO events, the sites in north-western Sumatra and western Peninsular Malaysia show no significant effect (Table 3), confirming the more detailed analyses of flowering in western Malesia. Small masting events (indicated by m in Table 2, as defined by Ashton *et al.* 1988) were ignored for this analysis, but including them does not affect the overall pattern reported in Table 3.

The compilation of masting (Table 2) also provides several opportunities for comparison of the coincidence of mast fruiting among adjacent sites or areas. We already noted the lack of coincidence of masting events between Ketambe and Suaq Balimbing. Table 2 shows that only a single pair of sites or areas shows a good association of mast years (the short series for Singapore and the dipterocarp data for western Peninsular Malaysia). Thus, although the three data sets for western Peninsular Malaysia show a good correspondence, several geographically near areas do not show perfect coincidence of mast years. Indeed, if we calculate the associations between mast years among the areas or sites with at least 20 y of records, we find only two associations to be significant at the $P = 0.003$ level (as required by the Bonferroni criterion): Ketambe vs. western Borneo, and western Peninsular Malaysia vs. eastern Peninsular Malaysia. This indicates that although ENSO has influence on the timing of masting in general local variation in the exact moment of masting is substantial.

DISCUSSION

Masting and the ENSO phenomenon

Masting probabilities in Sumatra were found to be equal to those found throughout Malesia. However, the influence of ENSO periods on masting seems weakened in western Peninsular Malaysia and Sumatra, regardless of whether we defined masting qualitatively or used the quantitative flowering index. Overall, however, we obtained a stronger relationship between masting and ENSO periods than Ashton *et al.* (1988) for Malaysia and Borneo, probably

Table 3. Probabilities of mast fruiting (P [M]) in several Southeast Asian areas in relation to the occurrence of ENSO conditions during the major flower induction period.

Region	P [M] following ENSO[1]	P [M] following non-ENSO[1]	Chance of mast after ENSO[2]	
			χ^2	P
Eastern Borneo	0.40 (15)	0.10 (20)	4.38	0.04
Eastern Peninsular Malaysia	0.40 (15)	0.00 (19)	9.23	0.002
Western Borneo	0.36 (33)	0.12 (34)	5.57	0.02
Western Peninsular Malaysia	0.21 (24)	0.12 (25)	0.70	n.s.
Western Sumatra	0.33 (21)	0.17 (12)	1.07	n.s.

[1] Between brackets are the number of observation years.

[2] It is calculated whether the chance of masting after an ENSO is different than after a non-ENSO year.

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in part because we used a different measure (NINO3-anomaly instead of Southern Oscillation index), and in part because we could use data from more sites than Ashton *et al.* (1988). Ashton *et al.* (1988) had predicted that the ENSO effects would be strongest on the eastern side of landmasses, but found only partial support for this idea. In the present study, no clear effect of position relative to mountain ranges was found for Borneo, but a clear difference is apparent in Peninsular Malaysia, consistent with the findings of Yasuda *et al.* (1999). Because no phenological data are available for eastern parts of Sumatra, we cannot determine whether the absence of ENSO's effects on masting in north-western Sumatra are due to the geographic position in Malesia, or due to the shielding effect of the Bukit Barisan mountain range running the length of Sumatra.

Overall, these findings are most consistent with a general waning of ENSO's impact toward western Malesia, especially in areas shielded by mountain ranges. The same trend is apparent in the distribution of the recent forest fires during a long and severe ENSO (May 1997–May 1998): large areas of both western and eastern Borneo were destroyed, whereas in Sumatra they were concentrated in the south-eastern part of the island (map in Simons 1998; western Malaysia was not subject to conversion of forest to agricultural land through burning). Rainfall data for several sites in Sumatra and Borneo (State Ministry for Environment Republic of Indonesia report 1998) also indicate that the 1997 ENSO had little effect in North Sumatra. Total annual rainfall for 1997 in northern Sumatra was hardly affected (93% of normal annual rainfall), but was reduced at least as much in South Sumatra (56%) as in parts of Indonesian Borneo (East: 71%; West 61%).

Masting is a phenomenon that results from an interaction between the external stimuli (meteorological factors) and the internal state of the plants, which is largely a function of the time elapsed since the previous masting event (Janzen 1974, Sork *et al.* 1993, van Schaik 1986). The western Sumatran sites do not deviate from the rest of Malesia in this respect: mast years are often drier, and hence sunnier, than average, but clearly not always (as expected when internal state is important; cf. van Schaik 1986). In contrast, the main difference between north-western Sumatra and the more eastern parts of Malesia is that the stronger ENSO effects on weather in the East may overwhelm local variation in weather and produce a stronger linking of masting to ENSO (but see Walsh 1996).

Strong ENSO impacts on weather should also increase the synchronisation of masts over larger areas. Thus, one could expect a faster decline in masting synchrony with distance between two sites for Sumatra than elsewhere in Malesia. At present, there is not enough evidence to evaluate this hypothesis. But consistent with this suggestion are data from Curran *et al.* (1999), who report masting synchrony over a large area in West Kalimantan (where ENSO's influence is strong) and our data showing the lack of masting synchrony

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between nearby Ketambe and Suaq Balimbing (where ENSO's influence is weak).

Masting coincidence and animal movements

Forest landscapes in north-western Sumatra show habitat and distance effects in the timing of seasonal fruit peaks (Djojosudharmo & van Schaik 1992, van Schaik 1986, S. Wich *et al.*, unpubl. data), as elsewhere in the (more seasonal) tropics (Loiselle & Blake 1991, Terborgh 1983). Many tropical frugivores are known to make seasonal movements of limited scale, thus lengthening the season of abundance (Leighton & Leighton 1983). In both Ketambe and Suaq Balimbing, we have noted large fluctuations in local abundance over relatively short periods of time for hornbills (especially *Aceros* spp. and *Rhyticeros* spp.) and fruit bats (*Pteropus vampyrus*), suggesting long-range movements of these animals. Smaller-scale movements are known for wild pigs (*Sus scrofa*: C. van Schaik, unpubl. data) and orang utans (*Pongo pygmaeus*: te Boekhorst *et al.* 1990, S. Wich *et al.*, unpubl. data).

Once animals make such movements, we hypothesize that they can also benefit from masting asynchrony. The comparison between Ketambe and Suaq Balimbing shows that even on a small spatial scale (around 70 km) masting events do not necessarily occur in the same year. A similar lack of synchrony was found on larger spatial scales in other parts of Malesia. Even minor imperfections in synchrony might make it profitable for animals to move around in search of masting events. Thus, we hypothesize that many of the long-distance movements may also concern the tracking of masting events. In Borneo, bearded pigs (*Sus barbatus*) are known to cover large distances to track dipterocarp masts (Dove 1993, MacKinnon *et al.* 1996). Bearded pigs used to be plentiful in south-eastern Sumatra, but are absent from northern Sumatra (van Strien 1996), perhaps because short-range masting asynchrony allows the wild pig to track masts as well and thus outcompete bearded pigs. The scale of movements of hornbills, pigeons and fruit bats in northern Sumatra suggests that many of them may also concern tracking of asynchronous masts. The presence on Sumatra of birds banded in West Malaysia suggests that these movements are not limited to single land masses (Wells 1988). Since the Malacca straits is less than 50 km wide near Malacca, such distances are modest compared to those covered within land masses. A more detailed study of movements of tagged individuals of nomadic frugivores in northern Sumatra is urgently needed to test this hypothesis.

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