

LETTER

Long-term reproductive behaviour of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): suprannual synchrony, temporal productivity and fruiting diversity

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Abstract

For 68 months, we observed the reproductive behaviour of 7288 woody plants (172 figs, 1457 climbers and 5659 trees) spanning major soil and elevational gradients. Two 2–3 month community-wide supra-annual fruiting events were synchronized across five forest types, coinciding with ENSO events. At least 27 genera in 24 families restricted their reproduction to these events, which involved a substantial proportion of tree diversity (> 80% of phylogenetic diversity). During these events, mean reproductive levels (8.5%) represented an almost four-fold increase compared with other months. These patterns indicate a strong behavioural advantage to this unusual reproductive behaviour. Montane forest experienced a single, separate fruiting peak while the peat swamp forest did not participate. Excluding these events, no temporal reproductive pattern was detectible, at either the landscape or forest type. These phenological patterns have major implications for the conservation of frugivore communities, with montane and swamp forests acting as ‘keystone’ forests.

Keywords

Keystone forest type, liana, mast fruiting, phenology, phylogenetic diversity, tropical trees.

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INTRODUCTION

The seasonality and intensity of woody plant reproduction varies considerably between equatorial tropical forests on a continental scale (Bawa 1983; Appanah 1993; van Schaik *et al.* 1993; Sakai 2001; Primack & Cortlett 2005). South-East Asian tree communities in Sundaland (Myers *et al.* 2000; Olson & Dinerstein 2002) are renowned for exhibiting community-wide supra-annual mast fruiting (Appanah 1993; Sakai *et al.* 1999; Kudo & Suzuki 2004), especially among the dominant canopy trees in the

Dipterocarpaceae (Janzen 1974; Ashton *et al.* 1988; Curran *et al.* 1999; Curran & Leighton 2000; Curran & Webb 2000; Maycock *et al.* 2005). Several non-mutually exclusive mechanisms have been proposed to explain the evolution and maintenance of this behaviour (Janzen 1974; Kelly 1994; Isagi *et al.* 1997; Kelly & Sork 2002; Iwasa & Satake 2004; Ichie *et al.* 2005; Sakai *et al.* 2006). In Bornean forests, these brief and infrequent pulses of fruits and seeds have a major impact on vertebrate population dynamics (Leighton & Leighton 1983; Ostfeld & Keesing 2000).

At the community level, previous studies of plant reproductive behaviour in the aseasonal Malaysian forests have been limited to a single forest type. Here, we examine the reproductive behaviour of terrestrial woody plants across a broad range of elevation, soil types and drainage conditions over a 68 month period within a single 15 km² watershed in the Gunung Palung National Park (GPNP), West Kalimantan, Indonesia. Our observations included woody climbers, which are fundamental to understanding the dynamics of the entire community (Schnitzer & Bongers 2002), and figs (*Ficus*:Moraceae), known to be a 'keystone' resources for many vertebrates (Leighton & Leighton 1983; Lambert & Marshall 1991; O'Brien *et al.* 1998; Harrison 2003).

The GPNP watershed (15 km²) provides an ideal research site to examine reproductive behaviour of woody plants at both the alpha and beta levels of community diversity. Firstly, major regional climatic cues are largely controlled among the observed individuals. Secondly, soils vary as much as 16-fold in available phosphorus, allowing direct comparisons between sites with substantial differences in nutrient availability (Paoli *et al.* 2005, 2006; Paoli & Curran 2007). Most importantly, the landscape pool of plant lineages is quite large and interaction across forest type boundaries is extensive. This juxtaposition of different forest types at a small geographic scales has been effective approach at understanding tree distributional patterns (Curran *et al.* 1999; Webb & Peart 2000; Cannon & Leighton 2004; Paoli *et al.* 2006).

The current analysis addresses several fundamental questions. To what degree are supra-annual mast fruiting (SMF) events synchronized across forest types and plant growth forms? What level of synchrony is detectable outside of SMF events? How diverse are the plant groups that restrict their reproduction to these events? Which forest types are most productive, in terms of total reproductive stem basal area?

METHODS

Study site

The Gunung Palung National Park (GPNP, 90 000 ha West Kalimantan, Indonesia: 1°15'S, 110°10'E) contains most major Bornean forest types. The 15 km² study site within GPNP spans a single large watershed. Detailed site descriptions have been provided previously (Curran & Leighton 2000; Cannon & Leighton 2004; Paoli *et al.* 2006). Seven distinctive forest types are recognized in this study. Poorly drained lowland sites include peat swamps with considerable humic accumulation and freshwater swamps with nutrient-poor gleyic soils. Freshwater swamp forests undergo seasonal patterns of flooding because of large rain

events and poor drainage. Alluvial bench forests are scattered along the lower reaches of the main river system. These deposits are recent in origin and are a mixture of parent rock material. Lowland sandstone and lowland granite forests are found below 300 m elevation on well-drained sites. Upland granite forests are found generally above 300 but below 700 m elevation. Montane forests are found on the steep slopes and ridges above 700 m elevation. GPNP is a coastal mountain complex, influenced by the *Massenerhebung* effect, creating compressed vegetational zonation (Grubb 1977).

Plant reproductive behaviour

Dimensions and locations of the 126 vegetation plots, mostly 0.1 ha in size, were similar to Cannon & Leighton (2004), but included more plots (Table S1). Sample areas vary among the seven forest types, with the largest sampling area available for the lowland sandstone and the smallest in the montane forest. We distinguished four plant growth forms: woody climbers, figs, small trees (14.5–24.5 cm DBH) and big trees (> 24.5 cm DBH). We broadly construed *Ficus* spp. (Moraceae) as a 'growth form', because of their unique hemi-epiphytic strategy and their widely recognized position as an asynchronously fruiting 'keystone' resource for many animals (Leighton & Leighton 1983; Terborgh 1986; Lambert & Marshall 1991; O'Brien *et al.* 1998; Shanahan *et al.* 2001; Marshall & Leighton 2006). Small trees were sampled using a nested design, within the larger sample areas for figs, climbers and large trees. All woody plants rooted within the plot area were measured and observed.

Plant reproductive behaviour in this study was observed between February 1986 and September 1991 for a total of 68 months. 'Reproduction' was defined as the production of ripe fruit with mature seed. Reproductive behaviour of all woody plants rooted within each plot was monitored by visually scanning the plant using binoculars and the ground underneath the canopy for the presence of mature seed or ripe fruit.

Statistical analysis

All analyses are standardized on a per hectare basis (Table S1). Individual plants were characterized as being either 'sterile' or 'reproductive' each month, based upon the presence of mature seed or ripe fruit. The temporal pattern of reproductive behaviour was examined at the level of the entire study site, among growth forms and among forest types. Observed values were compared with expected values for each group of individuals. 'Expected values' for each group were generated by randomizing reproductive behaviour (the dependent value) against an individual's

attributes, e.g., forest type, growth form (the independent variables). Partial analyses for each group were performed by randomizing those individuals found in a specific forest type or a particular growth form. A sufficient number of randomizations were performed until a normal distribution of 'expected' values was obtained, usually 100 times. Randomizations were limited to prevent the complete removal of the monthly variance among reproductive values, which occurs when randomizations are performed thousands of times. The significance of the observed value was determined by comparing it to the distribution of 'expected' values, using standard non-parametric techniques (Manly 1997).

After examining the preliminary results, definitions for 'mast' or supra-annual mast fruiting (SMF) and 'background' or aseasonal fruiting (AF) fruiting periods were developed using finite mixture theory (Strait *et al.* 1996). Finite mixture theory simply evaluates the probability that a population of values is best described by a single distribution, given a mean and standard deviation, or a known 'mixture' of two or more distributions, each with a distinct mean and standard deviation. This approach provides an effective and objective method for classifying the observed reproductive behaviour as being a SMF or AF period. After classifying the months into one of the seasons, subsequent tests of reproductive behaviour were performed separately for the two seasons.

Taxonomic and phylogenetic diversity

Taxonomic identity of slightly > 60% of the 'morpho-species' was determined to the genus level by several of the authors. A smaller subset of plants was identified to the species level. Individuals of unknown taxonomic identity were predominantly small trees and woody climbers. A supertree of phylogenetic diversity at the genus level was generated using Phylocom (Webb & Donoghue 2005). To avoid biases in phylogenetic resolution, all phylogenetic structure in the supertree was collapsed at the family level.

Two measures of diversity were generated: taxonomic and phylogenetic. 'Expectations' for taxonomic diversity were generated by randomizing generic names while phylogenetic diversity was examined using the matrix representation of the supertree. Phylogenetic diversity was measured as the mean pair-wise phylogenetic distances between each individual observed fruiting during a particular month, by counting the number of nodes separating the two individuals. The percentage of unknowns was controlled during randomizations. Randomizations were limited to reproductive individuals. All analyses were written in Mathematica 5.2 (Wolfram 1998) by CHC and can be provided upon request.

Forest type productivity

Forest structural data was gathered in a much larger sample area (Tables S2 and S3; see Marshall 2004). Plot locations were chosen so that samples were randomly distributed within each forest type. Total sample area for woody climbers (> 4.5 cm DBH), large trees (> 34.5 cm DBH) and hemi-epiphytic figs (> 4.5 cm DBH) was 5 ha while small trees (14.5–34.5 cm DBH) were sampled in half the area. Hemi-epiphytic figs and climbers had to be rooted within the sample area.

Fruit productivity for each forest type was then calculated by multiplying the number of fruiting individuals each month with the mean basal area per hectare for each size class of trees and climbers. Results were then combined to obtain total 'fruiting basal area per hectare' for each month. The mean, standard deviation and maximum value were calculated across the entire observation period for each forest type. To determine the relative productivity among forest types, the relative rank of fruit productivity was calculated for each month and an average rank across for each forest type was obtained for the entire observation period.

RESULTS

Community-level behaviour

During the 68 months of continuous monitoring of reproductive behaviour across the seven forest types and three growth forms, two brief episodes were identified as 'supra-annual mast fruiting' or SMF events (Fig. 1). During AF months, no annual or biannual pattern of reproduction was detected (Fig. S1). The two SMF events were separated by nearly 4 years, each lasting only 2 or 3 months. The second mast event (January–March 1991) lasted 3 months and, on average, fruiting levels were higher than in the first monitored mast event (February–March 1987). Average reproductive levels during SMF events (8.5%) represent an almost fourfold increase in comparison to AF months. One period of significantly low reproductive activity (< 1.6% fruiting) lasted for 7 months, from September 1988 to March 1989. Only 1.0% of monitored individuals fruited in October 1988.

Both taxonomic and phylogenetic measures of diversity were less than expected during SMF events (Fig. 1c–d). Trends between the two measures generally agreed, although the correlation between the two varied in interesting ways. During AF months, reproductive individuals were generally more diverse than expected, particularly given phylodiversity in the 8 months with *c.* 3% reproduction. Although all SMF months were significantly less diverse given taxonomic measures, one SMF month (the

second highest level of reproduction observed) was not significantly less diverse given phylogenetic measures. Interestingly, the expectations for phylogenetic diversity are relatively invariant to sample size, indicating that the central tendency of average phylogenetic distance between two individuals is stable for small sample sizes.

The decline in diversity during SMF events is largely because of the reproductive behaviour of the ecologically dominant Dipterocarpaceae (Table S4). The genus *Vatica* was the only genus, which did not completely restrict its reproduction to SMF events, while the genera *Dipterocarpus*, *Shorea* and *Hopea* exhibited the highest ratio of observed to expected number of individuals fruiting within the masting events (16.3, 11.5 and 11.1, respectively) of any taxonomic group. All species of *Dipterocarpus* significantly restricted their reproduction to SMF events, while five of sixteen *Shorea* species were more variable in their reproductive behaviour (Table S4). These results agree well with more detailed results published previously (Curran *et al.* 1999; Curran & Leighton 2000; Curran & Webb 2000).

While the Dipterocarpaceae dominated SMF events, a wide diversity of other taxa participated as well. It is important to consider that the overall diversity contributed by the Dipterocarpaceae is relatively small. This family is represented by only four genera in our data, but all SMF events involved at least 60 and as many as 90 genera. Given phylogenetic diversity, the contribution of the Dipterocarpaceae is obviously quite small (Fig. S2). Several species rich genera significantly restricted their reproduction to SMF events, including *Diospyros* and *Syzygium*, two of the most diverse genera at the study site (Cannon & Leighton 2004). Overall, at least 27 genera in 24 families were determined to significantly restrict their reproduction to SMF events. These taxa include a number of small genera, including *Neoscortechinia* (*Euphorbiaceae*), *Ochanostachys* (*Olaceae*) and *Nephelium* (*Sapindaceae*), which have the highest ratio of reproductive events within SMF events versus outside, other than the Dipterocarpaceae. Other diverse and strictly SMF genera include *Lansium* (*Meliaceae*), *Artocarpus* (*Moraceae*) and *Castanopsis* (*Fagaceae*). Additionally, the percentage of unknown individuals that fruited during the SMF events was greater than expected, indicating that several taxa, which are rarely seen and poorly known at the study site, are SMF taxa and our current estimates for diversity during SMF events are clearly underestimates. *Willughbeia* spp. (*Apocynaceae*) was the only group of climbing plants which restricted, rather weakly, its behaviour to the SMF events. A few genera had significantly elevated levels of reproduction during the months immediately preceding or following the SMF events without being strict SMF taxa: *Polyalthia* (*Annonaceae*), *Calophyllum* (*Clusiaceae*), including a genus of climbers, *Rourea* (*Connaraceae*; see Table S4). A single species in the genus *Cyathocalyx* (*Annon.*) significantly

avoided the SMF events in its reproductive behaviour. These results are similar to those found using conventional statistical analyses (Marshall 2004).

Reproductive behaviour by growth form

Fruiting behaviour varied substantially among growth forms (Fig. 2) and the SMF events were most apparent within the tree community, being most sharply evident among large (> 24.5 cm DBH) trees (Fig. 2). *Ficus* (*Moraceae*) were clearly aseasonal in their reproduction (Fig. 2a,e), with absolutely no difference between the models assuming one or two seasons. Throughout the study period, figs also maintained a much higher level of reproductive behaviour (averaging 5% of stems) than other growth forms. The woody climber community did participate weakly in the SMF events, although the likelihood ratio of the mixed model of reproduction assuming two seasons to a single model with a single season is only marginally significant (Fig. 2b,f). Woody climbers also produced the most sustained period of significantly increased reproduction (averaging 3.5% of stems) for any plant form or forest type during the latter half of 1989 into 1990, for a period of 10 months.

When a single model for reproductive behaviour is assumed among trees, a majority of the observations are significantly below expectations, with only 1.1% of trees were fruiting at the lowest point. But, when large and small trees are separated in the analysis and two seasonal patterns are assumed (SMF and AF), then only a small number of low reproductive periods were observed (Fig. 2). Both large and small trees exhibited SMF behaviour, although reproduction levels during SMF events among small trees was substantially lower than among large trees and the first SMF event in 1987 was less pronounced than the second SMF event (Fig. 2). During the peak of second mast event, nearly 15% of the large trees, across all forest types, were reproductive (Fig. 2).

Taxonomic and phylogenetic diversity among woody climbers were roughly near expectations, although a few months of high reproductive activity were significantly less diverse in terms of phylogenetic diversity than expected (Fig. 3). While taxonomic diversity was low among climbers, the phylogenetic diversity is substantially greater among these plants than either small or large trees. The relationship between diversity of reproductive individuals and overall reproductive activity among small trees did not show a substantially negative trend, as it does among large trees (Fig. 3). Diversity among reproductive small trees was generally lower than expectations, particularly for the phylogenetic measure, suggesting that these small trees have a greater level of synchrony within closely related taxa. The phylogenetic measures for diversity among large trees show a strong negative correlation with overall reproductive

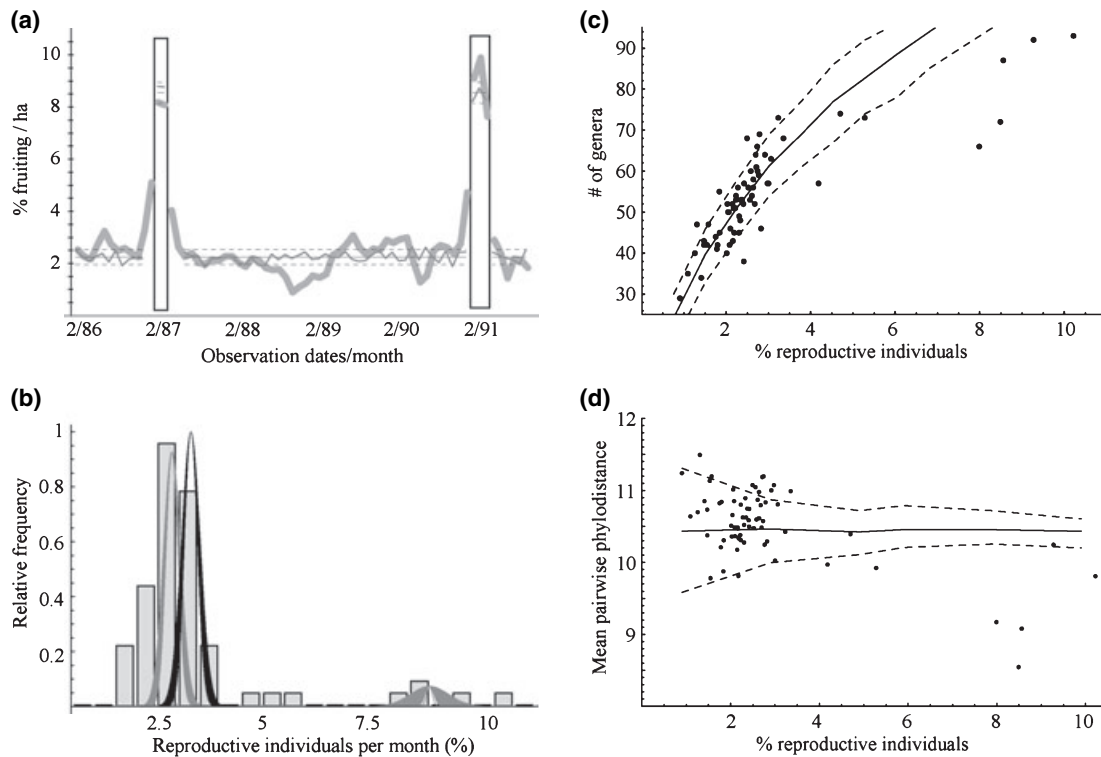


Figure 1 Community level patterns of reproduction over 68 months in a Bornean rainforest for all plants across all forest types. (a) Monthly levels of reproduction. Percentage of stems reproducing per hectare is shown. Average number of stems observed each month = 4832 (min = 4152, max = 5018). Observed levels of reproduction are shown by thick grey line. The expected mean level of reproduction, across the entire observation period, is shown by the solid black line while 95% confidence limits are shown by the dashed black lines. The thin grey line illustrates a single replicate of fruiting behaviour, given temporal stochasticity. For statistical analysis, the two SMF events were separated from the rest of the observation period. These SMF events are shown in the black boxes. (b) Frequency distribution of community-wide levels of reproduction for all plants across all forest types. The bar chart in the background represents the observed levels of reproduction by month. The black curves indicate the expected distributions from ten random reproductive patterns, chosen to represent the range of standard deviation values, given all months. The grey curves indicate the two expected distributions, given the assumption of two seasons: 'SMF' and 'background' reproduction. (c) Taxonomic diversity at the genus level, in relation to percentage of stems fruiting. Each point indicates 1 month. Mean and 95% confidence limits are shown, as in (a, d). Phylogenetic diversity measured by pairwise nodal distance between reproductive individuals. Observed diversity values are shown by black dots in relation to percent reproductive stems each month, the expected mean diversity is shown by the solid red line, 95% confidence limits are shown by the dashed red lines and maximum and minimum values are shown by thin purple lines for randomizations.

behaviour. Again, it is important to note that these diversity levels are still much greater than would be expected if only the Dipterocarpaceae participated (Fig. S2).

Reproductive behaviour by forest type

The two SMF events were apparent in five forest types, excluding only the montane and peat swamp forests (Fig. 4). Levels of participation in the SMF events varied substantially across forest types, with the alluvial bench demonstrating the greatest increase in reproduction (Fig. 4e,l) while both the upper granite (300–700 m a.s.l.) and freshwater swamp forests only weakly participated (Fig. 4b,f,i,m). While the montane (> 700 m a.s.l.) and peat swamp forests

did not participate in the general mast events, each forest type did exhibit sustained periods of higher than average reproduction. Beginning in mid-1989, the montane forest exhibited a 6-month period of elevated reproduction (Fig. 4a,h), which correlated weakly with a similar and simultaneous episode in the freshwater swamp. In the peat swamp, the reproductive peak preceded and overlapped with the second SMF event (Fig. 4g). However, the mixture model results did not significantly differ between the single and two season models. This lack of significance is due to the complete absence of the first SMF event in the peat swamp. When the plant communities are analyzed separately among forest types, the three 'mid-season' months noted for the entire community largely disappear. In the lowland

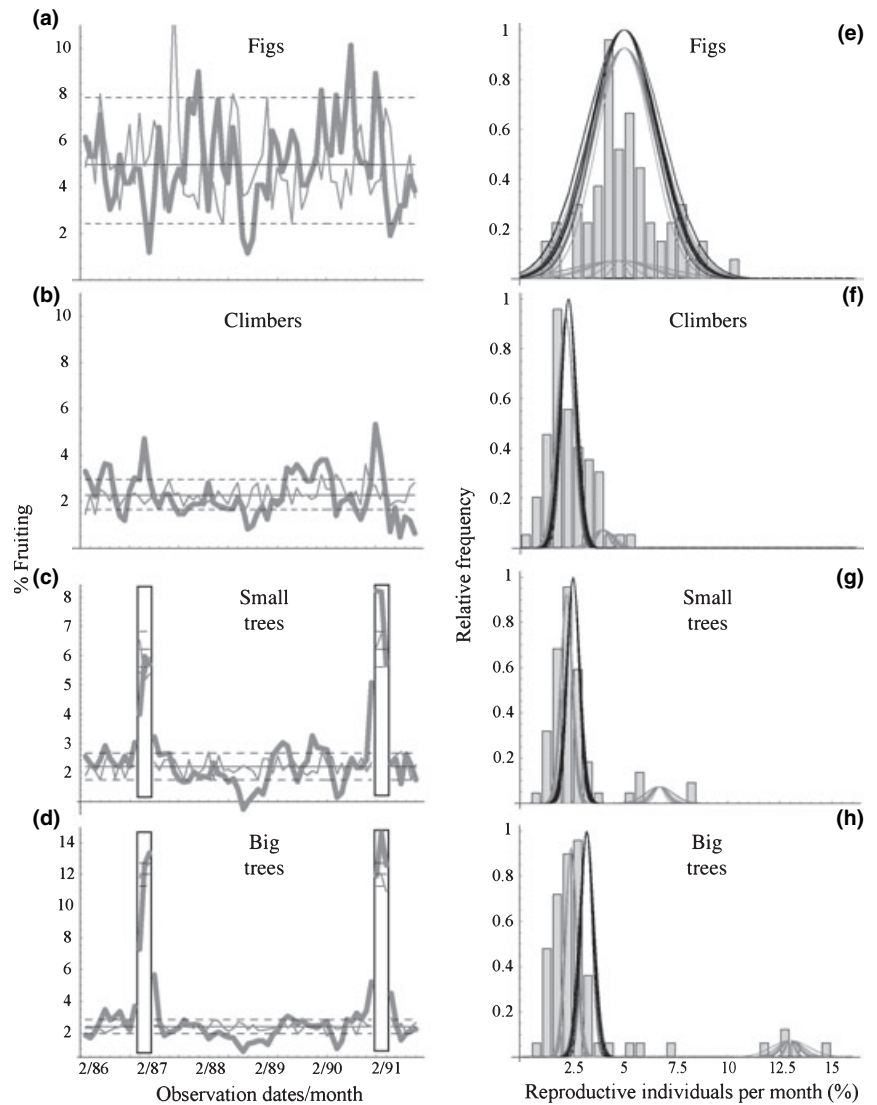


Figure 2 Fruiting behaviour over 68 months in a Bornean rainforest for different plant forms. (a) Figs: average number of stems observed each month = 116 (min = 93, max = 121); (b) Woody climbers: average number of stems observed each month = 951 (min = 847, max = 991); (c) Small trees (14.5–24.5 cm DBH); (d) Large trees (> 24.5 cm DBH). Observed values are shown in thick grey line. The average level of fruiting expected across all months is indicated by the solid black line while 95% confidence limits are shown by the dashed black lines. The thin grey line illustrates a single replicate of random fruiting behaviour. (e) Frequency distribution of fig reproductive levels by month. (f) Frequency distribution of woody climber reproductive levels by month. (g) Frequency distribution of small tree reproductive levels by month. (h) Frequency distribution of small tree reproductive levels by month. Barcharts illustrate observed levels of reproduction. Black curves assume a single season, grey curves assume a mixed model with two seasons.

sandstone and alluvial bench, two ‘mid-season’ months are apparent. This pattern suggests that the ‘mid-season’ period may largely be due to slight differences in the timing of reproduction among the forest types. Lowland granite has the lowest AF level (slightly > 2%), while SMF levels (12%) were among the highest (Fig. 4c,j).

Both in absolute terms and in the correlation with reproduction levels, forest types differed significantly in the patterns of taxonomic and phylogenetic diversity relative to reproductive levels (Fig. 5). Montane forest had the lowest levels of expected taxonomic diversity (Fig. 5a) while the lowland sandstone had the highest (Fig. 5d). The general expected level of phylogenetic diversity was similar across all forest types, indicating that while species numbers may be lower in the montane forest, these taxa come from a diverse set of lineages. Few forest types exhibited negative trends

between taxonomic diversity and increasing reproductive levels, primarily the lowland sandstone and peat swamp. This pattern was most pronounced in the peat swamp, where almost all months with > 5% reproduction fell significantly below expectations (Fig. 5g). Phylogenetic diversity in each forest type was consistently below expectations, except in the montane and lowland granite (Fig. 5h,j). Declines in phylogenetic diversity with increasing reproductive participation were only weakly apparent in most forest types (Fig. 5).

The correlation of reproductive levels across forest types was quite strong when the SMF events were included (Table 1). Reproduction across all plants in the three well-drained lowland forest types (lowland granite, lowland sandstone and alluvial bench) were strongly correlated while the upper and lowland granite forests were also tightly

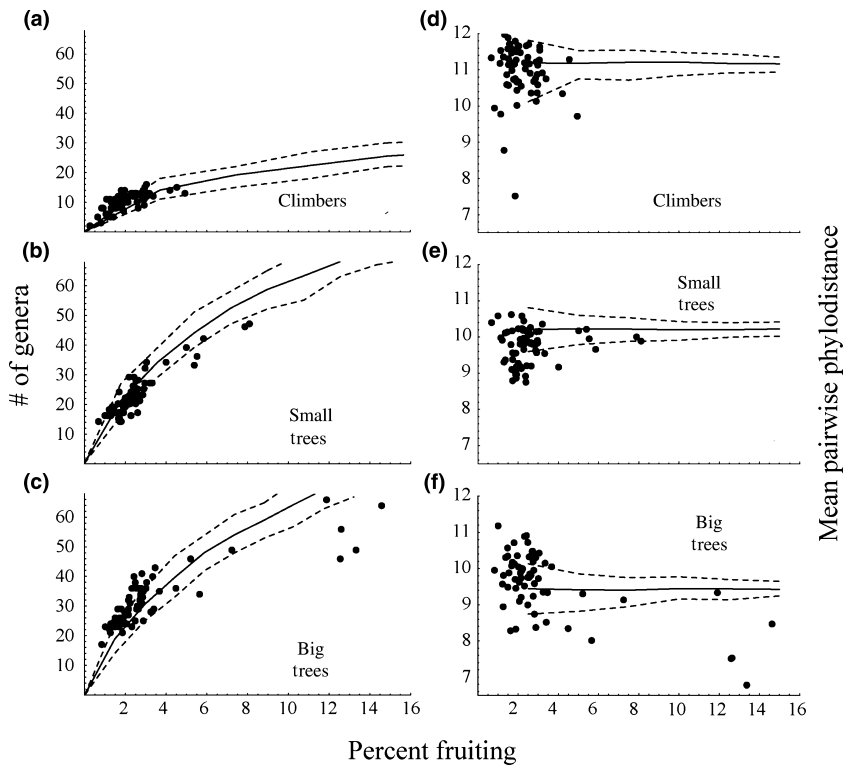


Figure 3 Taxonomic and phylogenetic diversity of reproductive stems per month for different plant forms. (a–c) taxonomic diversity at the genus level. (d–e) phylogenetic diversity measured by pairwise nodal distance between reproductive stems. Figure shows plots of climbers (a, d), small trees (b, e) and large trees (c, f). Observed diversity values are shown by black dots in relation to percent reproductive stems each month, the expected mean diversity is shown by the solid black line and 95% confidence limits are shown by the dashed black lines.

correlated as was documented independently for the Dipterocarpaceae (Curran *et al.* 1999). This temporal synchrony in reproduction vanishes when the SMF events are removed from the analysis (Table 1). This lack of synchrony during AF periods matches the lack of an annual pattern in reproduction (see Fig. S2). Only the lowland sandstone and alluvial bench remain significantly correlated while AF reproduction is slightly correlated between the montane and freshwater swamp forests.

These forest types differ significantly in structure, both for trees and climbers (Tables S2 and S3). Size class structure and stem densities are typical for their respective forest types (Curran & Leighton 2000; Paoli *et al.* 2005, 2006). Stem density and basal area of trees is greatest on granite derived soils, with a predominance of larger trees found in the lowland areas and an increasing abundance of small trees in the uplands. Montane forests also have a significantly greater basal area than expectations because of very high densities of the smallest two sizes classes of tree, with large trees being virtually absent. The significantly low density of small trees in the lowland sandstone is offset by a significantly high density of large trees. Swamp forests, on peat soils and in freshwater gleyic areas, generally contain lower densities of stems in all size classes.

Across the forest types, the general trends among liana communities are inversely related to tree stem density and basal area measurements. Both swamp forests have the

highest densities and basal areas of lianas, particularly in the freshwater swamp where densities are significantly greater for all size classes and overall basal area is twice the average across the entire landscape. The alluvial bench is remarkable in having the highest density of the largest lianas, more than twice the landscape average. Intermediate sized lianas are predominant in the lowland sandstone forests, although again the total basal area is only slightly greater than average. In the two upland forests, climber densities prevalence drop dramatically, as all size classes are underrepresented. The large climber community was largely absent in the montane forest.

Among trees, the alluvial bench had the highest average amount of reproductive productivity, as measured by stem basal area (Table 2). Freshwater swamp and lowland sandstone forests were slightly less productive while upland granite and montane forests were substantially less productive. Because of the strong SMF events in the well-drained lowland forest types, variability in productivity was highest in the alluvial bench and lowland sandstone forests as well. During one SMF event, the alluvial bench had over $7 \text{ m}^2 \text{ ha}^{-1}$ fruiting, which is substantially greater than all other forest types. In terms of relative rank, the freshwater swamp forest was the most consistently reproductive forest while the lowland granite was the least productive. Among climbers, the upland and lowland granite were the most productive, but because of the SMF behaviour of lowland

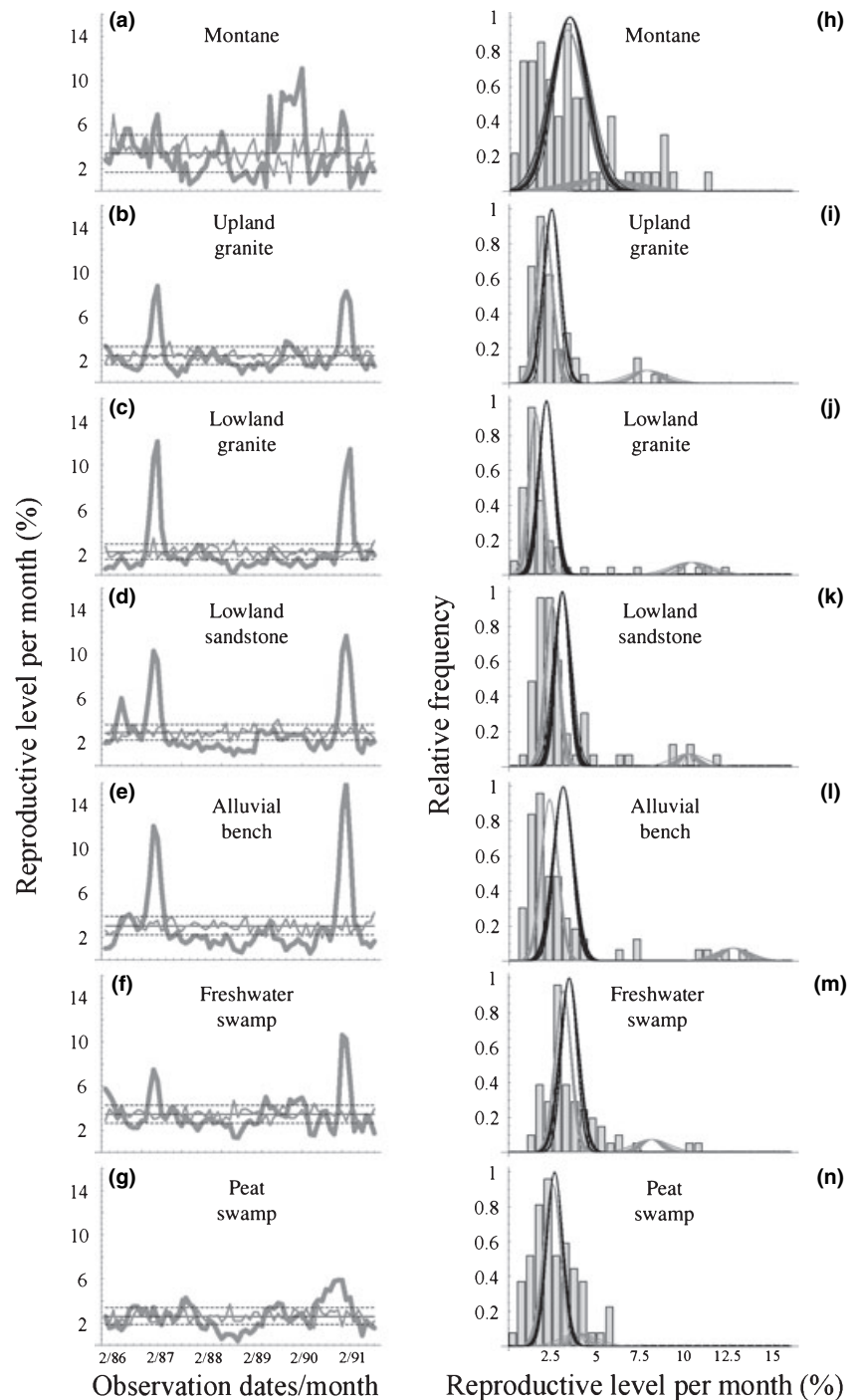


Figure 4 Fruiting behaviour over 68 months in a Bornean rainforest for different forest types. (a) montane (mean $N \text{ month}^{-1} = 283$, min = 266, max = 301); (b) upper granite (mean $N \text{ month}^{-1} = 640$, min = 504, max = 678); (c) lower granite (mean $N \text{ month}^{-1} = 673$, min = 572, max = 696); (d) lower sandstone (mean $N \text{ month}^{-1} = 1023$, min = 911, max = 1049); (e) alluvial bench (mean $N \text{ month}^{-1} = 646$, min = 578, max = 671); (f) freshwater swamp (mean $N \text{ month}^{-1} = 870$, min = 676, max = 922); and (g) peat swamp (mean $N \text{ month}^{-1} = 688$, min = 610, max = 701). Observed values are shown in thick grey line. The average level of fruiting expected across all months is indicated by the solid black line while 95% confidence limits are shown by the dashed black lines. The thin grey line illustrates a single replicate of random fruiting behaviour. Frequency distribution of reproductive levels by month follow: (h) montane; (i) upper granite; (j) lower granite; (k) lower sandstone; (l) alluvial bench; (m) freshwater swamp; and (n) peat swamp. Barcharts illustrate observed levels of reproduction. Black curves assume a single season, grey curves assume a mixed model with two seasons.

granite climbers (Fig. S3), variability in reproductive productivity is quite high. In the lowland sandstone, climbers were the most consistently reproductive, ranking substantially higher than all other forest types across the observation period. This high relative rank is largely due to the very

low variability in reproductive productivity as the mean and maximum productivity values for the lowland sandstone are quite low. The freshwater swamp climber community was the second most consistently reproductive of the seven forest types examined.

Table 1 Regression values of reproductive levels by month between each forest type

	MO	UG	LG	LS	AB	FS	PS
MO		0.09	0.02	0.09	0.05	0.18	0.03
UG	0.12		0.81**	0.74**	0.73**	0.59**	0.08
LG	0.01	0.02		0.77**	0.80**	0.47*	0.08
LS	0.13	0.01	0.02		0.90**	0.64**	0.10
AB	0.01	0.02	0.11	0.40**		0.59**	0.19
FS	0.22*	0.08	0.01	0.09	0.00		0.10
PS	0.02	0.00	0.03	0.03	0.14	0.01	

Values above the grey diagonal include the two mast events, while values below exclude those events. Significant regression values are * $P < 0.05$; ** $P < 0.01$.

Individual behaviour

Over 7288 individuals were monitored for 68 months, including 172 figs, 1457 lianas and 5659 trees (see Table S1). More than half of these plants (4054 or 56%) were sterile during the observation period, including 66 figs, 824 lianas and 3164 trees. Fig individuals were much more likely to fruit during the course of our observations than other growth forms: with only 38% sterile individuals, while both lianas and trees were right at expectations (57% and 56% sterile, respectively). Of the remaining 3234 reproductive individuals, an average of 2.2 fruiting events was observed with an average total fruiting time of 4.4 months or < 10% of the observation period. One individual of an understory *Baccaurea* sp. (Euphorbiaceae) fruited almost continuously for a total of 44 months. The number of fruiting events by individuals followed a binomial distribution, with the mode of the distribution at zero and a maximum of 16 separate reproductive episodes observed in a single individual.

More than half of the reproductive individuals (1654 or 51%) participated in at least one SMF event. Less than 10% of reproductive individuals can be considered strictly 'masting', as only 320 individuals completely restricted their reproductive behaviour to the five SMF months. By extending the SMF events period by a single month, both pre- and post-peak, the total mast fruiting individuals increased twofold to 768 individuals. Most of this increase occurred among trees. Fully 25% of tree individuals fruited within this extended mast period, but at no other time in the observation period. For all individuals with fruiting restricted to the expanded mast window, slightly more than a quarter (199) fruited in both mast events.

Among the forest types, the percentage of reproductive individuals varied relatively little from the general pattern except in the montane forests, where 64% of all individuals did produce fruit during the observation period. The

lowland granite and peat swamp had the lowest rates of reproduction (40% and 41%, respectively) while the freshwater swamp had the highest rate (47%) among the remaining forest types. The average fruiting duration for individuals in different forest types varied from 5.1 months in the freshwater swamp down to 3.5, 3.7 and 3.7 months in the lower granite, montane and upper granite, respectively.

DISCUSSION

Supra-annual mast fruiting events

In this study, the SMF events were synchronized across several different forest types in a single watershed and a substantial proportion of the community level taxonomic and phylogenetic woody tree diversity participated (60–70% of total genera and at least 80% of total supertree breadth). The events were most pronounced in the alluvial bench and lowland sandstone forests, tapering off both upslope and in poorly drained lowland conditions. Synchronized SMF events were not apparent in the montane and nutrient-poor peat-swamp forests. The occurrence of a single and separate mast fruiting event in the montane forest may represent an independent evolution of the behaviour. This montane forest event was sustained for a longer period of time and exhibited little reduction in diversity with increasing levels of reproduction.

The Dipterocarpaceae were the most extreme in their specialization on SMF behaviour, with three speciose genera (*Dipterocarpus*, *Hopea* and *Shorea*) having the greatest ratio of observed to expected reproductive events confined to these brief periods. Yet, a wide diversity of taxa significantly restricted their reproduction to SMF events as well, including several other unrelated speciose genera (*Dacryodes*:Burseraceae, *Diospyros*:Ebenaceae, *Artocarpus*:Moraceae and *Syzygium*:Myrtaceae). The negative relationship between taxonomic and phylogenetic diversity with level of reproductive behaviour is strongly apparent at the community level while it largely disappears within a single forest type. This pattern occurs because the taxa participating in the SMF events are similar across forest types. However, within forest types, diversity during SMF events was not or only slightly reduced, in comparison to expectations, suggesting that most clades of the woody plant supertree are participating. In the montane forest, phylogenetic diversity measures did not decline with increasing levels of reproduction, despite the low overall community diversity relative to other forest types.

Among trees, larger individuals were clearly the major drivers of the SMF events, as smaller individuals (14.5–24.5 cm DBH) rarely reached half their intensity. The majority of woody climbers did not participate and only a weak event appears to have occurred in the lowland granite

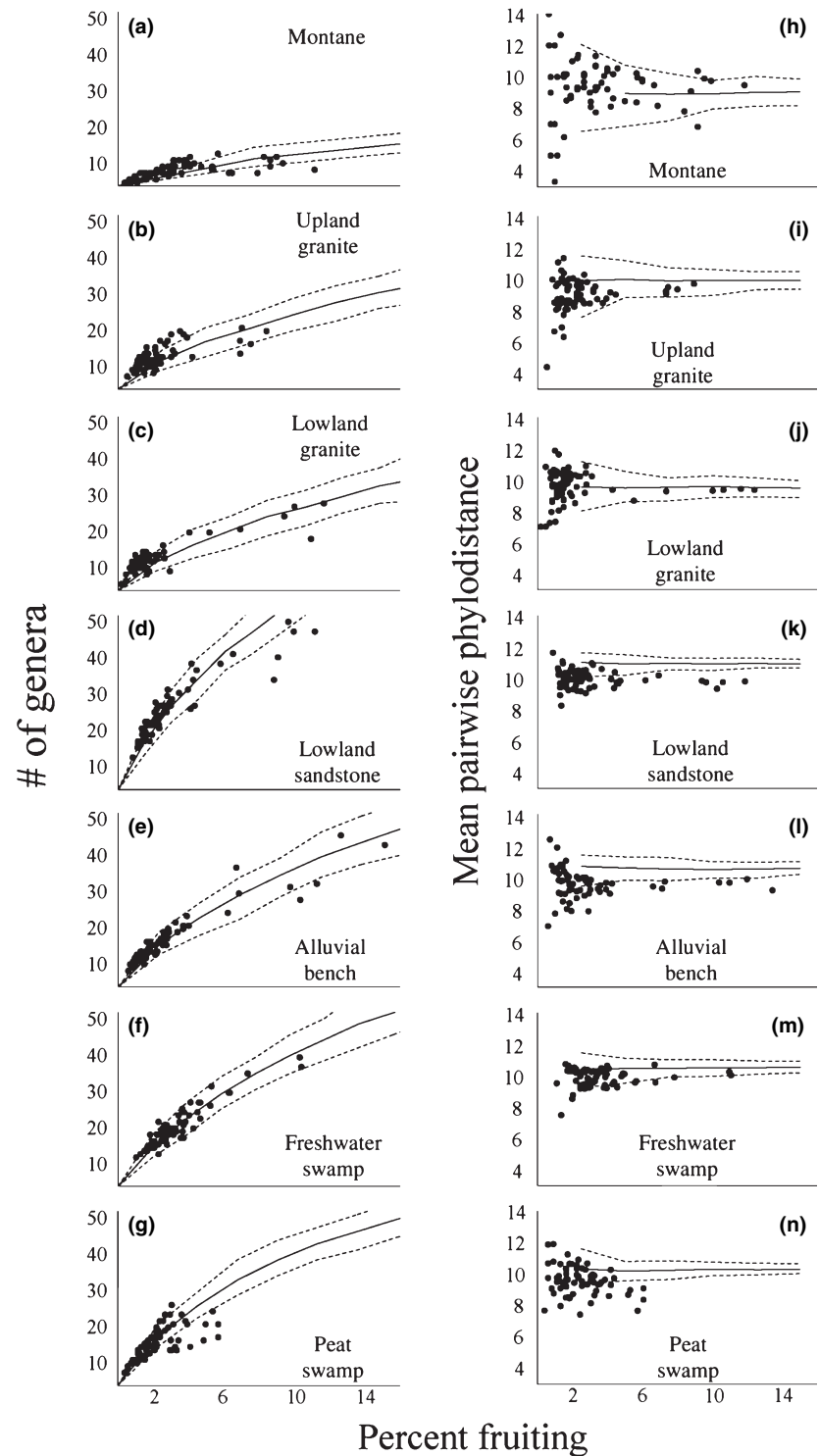


Figure 5 Taxonomic and phylogenetic diversity of reproductive stems per month for different forest types. (a–g) Taxonomic diversity at the genus level. (h–n) Phylogenetic diversity measured by pairwise nodal distance between reproductive stems. Observed diversity values are shown by black dots in relation to percent reproductive stems each month, the expected mean diversity is shown by the solid black line and 95% confidence limits are shown by the dashed black lines. Letters correspond to habitat types as in Figure 4.

climber community (Fig. S3c). The bias in this behaviour towards large trees, seems to indicate that the selection pressure has not been experienced equally by the two growth forms.

Aseasonal fruiting

Outside of the SMF events, few, if any, apparent reproductive cycles emerged (Table 2 and Fig. S1). Overall, the

Table 2 Reproductive productivity of forest types for trees and climbers

	Trees (m ² ha ⁻¹)				Climbers (cm ² ha ⁻¹)			
	Mean	SD	Max	Rank	Mean	SD	Max	Rank
MO	0.65	0.50	2.15	4.94	10.82	13.21	53.86	<i>6.18</i>
UG	1.24	1.17	6.77	3.04	61.31	112.23	573.72	4.55
LG	1.21	2.51	15.86	<i>5.14</i>	23.51	22.79	87.48	5.27
LS	1.66	2.69	12.13	3.47	82.74	54.72	313.22	2.26
AB	1.39	2.29	12.53	3.99	44.78	60.31	267.30	4.40
FS	0.99	0.81	4.43	3.72	79.99	45.90	212.35	2.40
PS	0.97	0.58	2.28	3.69	59.19	55.50	242.49	3.78

Productivity is expressed by basal area of reproductive individuals during each month of observation. Mean, standard deviation and maximum values are shown for each forest type in the first three columns for each growth form. Rank is the average rank of productivity among all forest types for each month of observation. Lower ranks indicate higher relative productivity. Bold-faced rank values indicate the most productive type, italicized values indicate least productive.

community displays a relatively constant background fruiting level of *c.* 2.5% of the stems (Fig. 1). Figs reproduce at a much higher rate than the rest of the community (Fig. 2), providing further evidence of their keystone role (Leighton & Leighton 1983). Lowland granite forest had the lowest AF levels, with average reproduction slightly < 2% of stems (Fig. 4j) while the upper montane and freshwater swamp both have substantially higher rates of constant reproduction than other forest types (Fig. 4h,m). Phylogenetic diversity at AF levels was generally lower than expectations among small trees while the converse held for large trees. A reduction in phylogenetic diversity at lower levels of reproduction indicates a certain amount of taxonomic synchrony while the converse indicates that individuals may actually be staggering their reproduction. Another interesting and important aspect of phylogenetic diversity is its invariance to sample size, indicating that phylogenetic measures not only capture a more relevant aspect of 'diversity' than taxonomic measures, but also serve as a more robust descriptor than taxonomic diversity *per se*.

More than a third of the trees (> 40 cm DBH) never fruited during the observation period (444 of a total of 1162 individuals). No obvious bias was detected in the forest type distribution of these non-reproductive individuals. Among legumes, the three most common large tree genera possessed the smallest fraction of sterile individuals (out 33 trees of *Sindora*, *Koompassia* and *Parkia* only 1 was sterile). Because the ratio of fruiting to sterile unknown taxa is the same for all trees, we can eliminate potentially undetected cryptic and rare species among these sterile individuals. Other taxa in which most individuals were reproductive are *Diospyros*, *Shorea*, *Iringia*:Simaroubaceae, *Dipterocarpus* and *Ochanostachys*:Olacaceae. Several genera had ratios greater than one (more sterile trees than fruiting), including *Calophyllum*:Clusiaceae, *Atuna*:Chrysobalanaceae and *Beilschmedia*:Lauraceae.

Across the observation period, reproductive productivity of trees (e.g. basal area fruiting per hectare; Table 2), varied considerably across forest types. The two most productive types, alluvial bench and freshwater swamp forests, achieved this distinction in very different ways. Alluvial bench forest was massively reproductive during the SMF events, indicated by both the large standard deviation and maximum values, while the freshwater swamp was more consistently reproductive. Peat-swamp displayed the most consistent reproductive productivity of all forest types. Woody climber productivity was highly variable across forest types, with productivity varying almost three-fold.

Conservation implications

Given the brief 2–3 month duration of SMF events and low levels of plant reproduction during long *c.* 4 year AF periods, the vertebrate community of frugivores and omnivores in these forests experience chronic food shortages (Curran & Leighton 2000; Wong *et al.* 2005). The complete lack of synchrony among plants in different forest types during AF periods likely contributes to the maintenance of resident consumer populations, as they move locally and follow fruit availability or shift to less preferred food sources (Leighton & Leighton 1983; Leighton 1993; Fredriksson *et al.* 2006). Freshwater swamp forest appears distinctive among the forest types studied, as it maintained generally high and consistent levels of productivity and only weakly participated in the SMF events. Our results highlight the need for a diversity of forest types within management units for certain vertebrates, particularly potential 'keystone' forest types (e.g. swamps and montane regions) that are critical for some animal populations during periods of low plant reproductive behaviour in the low to mid-elevation dipterocarp forests.

Synchronization of SMF events across Malaysia is likely regulated by environmental cues, particularly prolonged droughts and their associated effects, caused by the El-Niño Southern Oscillation (ENSO) cycle (Ashton *et al.* 1988; Curran *et al.* 1999). While the ENSO cycle currently repeats roughly 2–3 times a decade, this pattern has potentially changed on a relatively short historical time scale. Paleoclimate simulations indicate that the cycle may have been more frequent and weaker during much of the Last Glacial Cycle (Bush 2007). This would mean that the current supra-annual nature of the SMF events would have been less apparent roughly 10 Ka and that forest productivity may have been more evenly distributed through time. Additionally, ENSO cycles are likely to shift due to global climate change (Trenberth & Hoar 1997) and the observed synchrony may be disrupted or altered in various ways resulting in cascading effects on both frugivores and plant regeneration. Given the synergies of land use and global climate change in South-East Asia, future changes in the cycle could unravel the synchronization of the behaviour (Sherry *et al.* 2007). Current evidence suggests that the more frequent and intense droughts now occurring might cause reproductive miscues and frequent but unsuccessful fruiting events (Harrison 2000; Maycock *et al.* 2005; Sakai *et al.* 2006). The predictability and intensity of the probable cue for SMF reproductive behaviour in the Bornean forests, both historically and in the future, is a key component maintaining both this unusual reproductive behaviour among woody plants within and across forest types but the current animal populations, which depend upon fruit and seed production by these plants.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Annual reproductive behaviour of all woody plants. Monthly observations are plotted for each year of the percentage of the reproductive stems. Each year is indicated by a different type of line, as shown in the legend.

Figure S2 The relationship between percentage of reproductive stems and their overall phylogenetic diversity among large trees (> 24.5 cm DBH). The lines and black dots are identical to Figure 7. The grey dots indicate the average phylodiversity measured among reproductive stems of the Dipterocarpaceae.

Figure S3 Fruiting patterns over 68 months in a Bornean rainforest for two plant forms in each forest type. The column of figures represents woody climbers and the second column represents all trees. Forest types are in the same order as in Figure 8. (a, h) montane; (b, i) upper granite; (c, j) lower granite; (d, k) lower sandstone; (e, l) alluvial bench; (f, m) freshwater swamp; and (g, n) peat swamp. Observed values are shown in thick green line. The average level of fruiting expected across all months is indicated by the solid red line while 95% confidence limits are shown by the dashed red lines. The inner thin purple line illustrates a single random fruiting behaviour, while the two outer thin purple lines indicate the maximum and minimum of all randomizations.

Table S1 Sample areas and number of individuals observed for reproductive behaviour for each growth form across the different forest types. Sample areas for figs, climbers and big trees (> 24.5 cm DBH) are identical while sample areas for small trees (14.5–24.5 cm DBH) were generally smaller. Total number of individuals observed for each plant form within each forest type is listed with stem density per hectare. Totals for forest types and plant forms are shown. Type labels are: MO, Montane; UG, Upland Granite; LG, Lowland Granite; LS, Lowland Sandstone; AB, Alluvial Bench; FS, Freshwater Swamp and PS, Peat Swamp.

Table S2 Structural differences of tree communities among forest types. Values are in stem density per hectare. Basal Area (BA) values are $\text{m}^2 \text{ha}^{-1}$. Forest types are indicated as follows: PS, peat swamp; FS, freshwater swamp; AB, alluvial bench; LS, lowland sandstone; LG, lowland granite; UG, upland granite and MO, montane. Bold values are greater than expected, italicized values are less than expected. (* $P < 0.95$, ** $P < 0.99$, *** $P < 0.999$).

Table S3 Structural differences of liana communities among forest types. Values are in stem density per hectare. Basal Area (BA) values are $\text{m}^2 \text{ha}^{-1}$. Forest type types are indicated as follows: PS = peat swamp, FS = freshwater swamp, AB = alluvial bench, LS = lowland sandstone, LG = lowland granite, UG = upland granite, MO = montane. Bold values are greater than expected; italicized values are less than expected. (* $P < 0.95$, ** $P < 0.99$, *** $P < 0.999$).

Table S4 Taxonomic groups that significantly restricted their reproductive behaviour to the SMF events. Genera are organized by family and species by genus. Taxa with significantly elevated levels of reproduction during the months immediately preceding or following the SMF events are indicated by the following symbol #. 'Diversity' indicates the number of species (including evenness) reported in Cannon & Leighton (2004). 'Obs in SMF' indicates the number of individuals observed fruiting during SMF events. 'Ratio' indicates the ratio of observed to expected observations in SMF events. Significance levels are * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Significance was determined by nonparametric rank tests of observed against expected values.

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