

Beyond mast-fruiting events: Community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types

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Most empirical and theoretical work on the reproductive behavior of Bornean rainforests has focused on supra-annual mast fruiting (SMF). Here, we emphasize that the complexity of plant reproductive behavior, from the landscape to the individual plant, does not end with SMF events. During these inter-mast intervals, no annual pattern was detected and reproductive activity was not correlated among the seven forest types. A substantial proportion of large stems never reproduced during the 5.5 year observation period. Montane and peat swamp forests did not participate in SMF events and the fraction of participating individuals varied substantially among forest types. These patterns have major consequences for Bornean frugivorous fauna. Conservation efforts must protect a full suite of forest types, particularly ‘keystone’ habitats.

Keywords: ENSO, keystone forest type, lianas, phenology, phylogenetic diversity, tropical woody climbers.

THE spectacular phenomenon of supra-annual mast-fruiting (SMF), also commonly referred to as general flowering (GF), in the Malesian rainforests has long been a major topic of discussion among tropical botanists^{1,2}. These regional SMF events are fairly well documented, as the results from several long-term studies have become available recently^{3–10}. Here, we report the results of 67 months of continuous observation of woody plant reproductive behavior in a single watershed on the western coast of the island of Borneo, West Kalimantan, Indonesia¹¹. Our study is unique as it represents a landscape perspective on the forest community, including simultaneous observations of all large woody plants growing in seven contiguous rain forest types across major elevation, soil, and drainage gradients. This comprehensive landscape level approach places the observed SMF events within a

rich context for further ecological and evolutionary study. Additionally, because the availability of fruit resources is a major factor in determining vertebrate carrying capacities, we also discuss the implications of these results for the conservation of viable habitat for frugivores.

In this paper, we summarize the major features of the SMF events with respect to forest type, diversity and growth form¹¹. We also consider the significance of plant reproduction occurring outside SMF events, a topic given little attention by botanists and ecologists working in South-east Asia. Additionally, we contemplate the time scale of our dataset and its pertinence to understanding the evolution and maintenance of SMF events, and their relationship to historical variation in ENSO cycles. Finally, we discuss the importance of landscape-scale asynchrony in fruit production for the ecology and conservation of populations of rainforest vertebrates.

Study site and methods

The Cabang Panti Research Station (CPRS) in the Gunung Palung National Park (GPNP) was established to examine a broad diversity of plant–animal interactions across the major forest types present on the island of Borneo. Detailed site description is provided elsewhere^{5,12,13}. A major component of this research program was the creation of a network of 126 small (0.1–0.2 ha) permanent vegetation plots distributed along the major axes of environmental variation. This approach to vegetation plot design^{14,15} provides an effective means of assessing the distribution of woody plants at the community level^{12,13,16}, particularly given the inherent spatial autocorrelation in species distribution observed in single large plots¹⁷ and the difficulty in selecting a site which is representative of a landscape or region.

Our research station is situated on the western slopes of a small coastal mountain range, reaching 1100 m eleva-

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tion. Because of its proximity to the coast, elevational zonation of vegetation types are generally compressed¹⁸ so that the upper ridges are covered with stunted mossy cloud forest formations. This small mountain complex is geographically isolated from the large central Bornean Schwaner range. Genetic variation sampled from stone oak (*Lithocarpus*) trees¹⁹ and Muridae rodents²⁰ suggests the forests have been historically isolated for some time. While the park has experienced some habitat disturbance after the period of this study²¹, the faunal populations remain largely intact, ensuring that seed dispersal mechanisms are still ecologically viable²².

The CPRS contains a majority of the forest types present on Borneo within its 15 km² area. Here, we distinguished seven distinctive types, based upon elevation, soils and drainage. 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, due to 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 between 300 and 700 m elevation. *Montane* forests are found on the steep slopes and ridges above 700 m elevation. Detailed descriptions of these forest types and their soils have been provided elsewhere^{16,23}. The number of plots established in each forest type varied considerably, with at least two hectares sampled in all but the montane forest (Table 1). A total of 7288 stems were observed during this study, composed mostly of trees.

We observed plant reproductive behavior between March 1986 and September 1991 for a total of 67 months. We defined successful reproduction as the production of ripe fruit with mature seed. We monitored reproductive be-

havior of all woody plants rooted within each plot by visually scanning the plant using binoculars and the ground underneath the canopy for the presence of mature seed and ripe fruit. This technique may be prone to some underestimation of reproductive activity, particularly for smaller woody climbers growing in tall canopy trees. To reduce this potential source of error, assistants were well-trained and we are confident only smaller events, involving a relatively small fraction of an individual's canopy possibly were missed.

Suprannual mast fruiting events

Two intensive fruiting events, with a four-fold increase in reproduction, were observed in five of the forest types (Figure 1 a), excluding the montane and peat swamp forests¹¹. These events were tightly synchronized, each spanning two or three months, and involved a substantial portion of the overall taxonomic and phylogenetic diversity of the woody plant community. The two highest levels of reproduction observed occurred in the first months of 1991 with roughly 8–10% of the forest fruiting. Just two months later, fruiting was back down to normal 'background' levels (generally <3% of total stems). This level of synchronization across virtually the entire angio-

Table 1. Sample areas and number of individuals observed for reproductive behavior for each growth form across the different forest types. Sample areas for small trees (14.5–24.5 cm DBH) were nested within these plots and the total is shown after the forward slash. Total number of individuals observed is listed for each plant form within each forest type is listed. Totals are shown for forest types and plant forms

Type	Area	Figs	Climbers	Trees	Total
MO	0.7	0	21	298	319
UG	2.1	18	138	843	999
LG	2.9	22	136	941	1099
LS	4.2	38	334	1152	1524
AB	3.0	47	185	788	1020
FS	2.7	31	374	895	1300
PS	2.4	16	269	742	1027
Total	18.0/12.6	172	1457	5659	7288

MO = Montane; UG = Upland Granite; LG = Lowland Granite; LS = Lowland Sandstone; AB = Alluvial Bench; FS = Freshwater Swamp; PS = Peat Swamp.

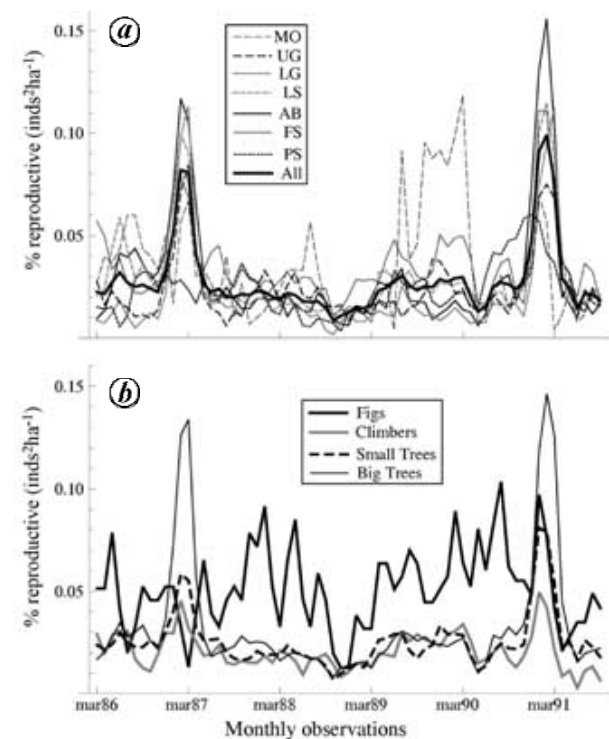


Figure 1. Community level patterns of reproduction over 67 months in a Bornean rainforest: **a**, Forest type. **b**, Growth form. Percentage of stems reproducing per hectare is shown. All forest types are depicted with a thick black line. Codes for forest types are given below Table 1.

Table 2. Taxonomic groups found to be SMF specialists in their reproduction. 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 symbol#. 'Obs in SMF' indicates the number of individuals observed fruiting during SMF events. 'Ratio' indicates the ratio of observed to expected fruitings in SMF events. Significance levels indicated are *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. SMF specialization was determined by nonparametric rank tests of observed against expected values

Taxa	Obs in SMF	Ratio	Taxa	Obs in SMF	Ratio
Anacardiaceae			<i>Shorea pauciflora</i>	8***	8.0
<i>Gluta</i>	9***	3.5	<i>Shorea pinanga</i>	11***	7.2
Annonaceae			<i>Shorea quadrinervis</i> [#]	30***	7.8
<i>Polyalthia</i> [#]	35	1.3	Ebenaceae		
Apocynaceae			<i>Diospyros</i>	17***	2.8
<i>Willughbeia</i> [#]	20***	2.4	Euphorbiaceae		
Burseraceae			<i>Neoscortechinia</i>	10***	6.2
<i>Dacryodes</i> [#]	13***	4.3	<i>Pimelodendron griffithianum</i>	9*	2.6
Chrysobalanaceae			Fabaceae		
<i>Licania</i>	2**	1.8	<i>Koompassia</i>	4***	3.1
Clusiaceae			Fagaceae		
<i>Calophyllum</i> [#]	58	1.4	<i>Castanopsis</i>	8***	4.8
Connaraceae			Icacinaceae		
<i>Rourea</i> [#]	12	1.4	<i>Stemonurus</i>	14***	2.5
Cornaceae			Meliaceae		
<i>Mastixia</i>	4***	2.8	<i>Lansium</i>	4***	2.7
Dilleniaceae			Moraceae		
<i>Dillenia</i>	7***	3.7	<i>Artocarpus</i>	9*	1.9
Dipterocarpaceae			Myristicaceae		
<i>Dipterocarpus</i> [#]	100***	16.3	<i>Gymnacranthera</i>	14*	2.0
<i>Dipterocarpus stellatus</i> [#]	9***	7.8	Myrtaceae		
<i>Dipterocarpus step</i> [#]	6***	5.2	<i>Syzygium</i>	62*	1.9
<i>Dipterocarpus sublamellata</i>	52***	9.5	Olacaceae		
<i>Hopea</i>	22***	11.1	<i>Ochanostachys amentacea</i>	31***	5.8
<i>Shorea</i> [#]	186***	11.5	<i>Strombosia ceylanica</i>	30*	2.2
<i>Shorea coriacea</i>	9***	5.7	Sapindaceae		
<i>Shorea crassa</i>	11**	2.3	<i>Nephelium</i>	9***	5.4
<i>Shorea hopeifolia</i>	11***	5.3	Sapotaceae		
<i>Shorea johorensis</i> [#]	8***	6.7	<i>Planchonella</i>	3**	1.8
<i>Shorea leprosula</i>	4***	3.7	Simaroubaceae		
<i>Shorea longisperma</i>	4***	2.9	<i>Ailanthus</i>	4*	2.1
<i>Shorea parvifolia</i>	10***	6.0	Unknown		
<i>Shorea parvistipulata</i> [#]	16***	8.4	Unknown	277***	3.3

sperm 'Tree of Life' present in the community is truly remarkable and highlights the extreme variability in fruit availability over extended periods in these forests.

A wide range of taxa were found to be SMF specialists in their reproductive behavior (Table 2)¹¹. At the family level, the Dipterocarpaceae were the most extreme specialists, with the type genus, *Dipterocarpus*, exhibiting the highest ratio (16.3:1) of observed to expected fruiting in the SMF events. Some variability did exist within the dipterocarps as not all individuals restricted their reproduction to the SMF events⁵. The level of significance for *Shorea crassa*, for example, was low and the ratio of observed to expected fruiting (2.3:1) is substantially lower than for any other species in the genus. Several other taxa in other families were also extreme SMF specialists, including *Neoscortechinia* spp. (Euphorbiaceae) and *Ochanostachys amentacea* (Olacaceae). The species in two of the most diverse genera at the study site, *Diospyros* (Ebanaceae) and *Syzygium* (Myrtaceae)¹³, com-

prised 23 and 54 species respectively, were also found to be SMF specialists, suggesting that the evolution of the behavior occurred prior to the diversification of the two groups. Overall, 27 genera in 24 families significantly restricted their reproduction to SMF events, representing at least 80% of phylogenetic diversity within the community. Current measures are probably underestimates because the proportion of unidentified individuals increased during the SMF events, suggesting that several rarely seen and poorly known taxa are also SMF specialists.

While large trees were the main drivers of the SMF events, the other two growth forms (woody climbers and hemi-epiphytic figs) did not participate (Figure 1 b). The only climbing plants found to significantly restrict their reproduction to the SMF events were species in the genus *Willughbeia* (Apocynaceae) (Table 2). While fruiting of woody climbers was slightly elevated during SMF events, the increase was not significant¹¹. Fruiting behavior in figs was completely aseasonal, but the percentage of fruiting

individuals in the community was generally two-fold greater than that of other growth forms (5% fig individuals vs <2% tree and climber individuals).

Landscape patterns of plant reproduction

The strength of the SMF events varied considerably among forest types. The lowland sandstone, lowland granite and alluvial bench forest types demonstrated up to five fold increases in reproductive levels during these events. The upland granite forest participated in both events, although at substantially lower levels than the former types, while the freshwater swamp forest exhibited a significant increase in reproduction during only the second SMF event. The montane forest was unique as a single event occurred in late 1989-early 1990, outside of either community-wide SMF event. This singular event was sustained for almost seven months and indicates that these plants are responding to different environmental signals and/or evolutionary forces. The peat swamp forest exhibited virtually no seasonality, although a substantial amount of variation existed in reproduction levels. While the SMF events demonstrate a dramatic level of synchronization at the community level among the large trees, few other significant seasonal or annual patterns were obvious either among forest types or plant growth forms. When the SMF events are excluded, temporal patterns of reproductive activity were strongly correlated between only the alluvial bench and lowland sandstone forest types. This correlation is not surprising as the two forest types are similar in overall species composition¹³. Overall, reproductive behavior of woody plants in different forest types is not synchronized outside of the SMF events.

Fruiting productivity, as measured by the amount of reproductive basal area observed each month, varied considerably through time and among both forest types and growth forms (Figure 2). Woody climbers were most productive in the lowland sandstone forest type and variability was low (mean = $82.7 \text{ cm}^2 \text{ ha}^{-1}$, SD = 54.7), although few periods of high productivity spanned more than three consecutive months. Productivity, and its variability, among woody climbers was slightly lower in the freshwater swamp forest type, but climbers in this forest type were the most productive for eight months, beginning in early 1987, which was generally a period of low productivity at the landscape level. Thus, fruits produced by woody climbers may serve as key 'fallback foods' for frugivores, sustaining them through periods of low overall food availability.

While mean monthly productivity of the upland granite forest ($1.24 \text{ m}^2 \text{ ha}^{-1}$) was not as large as the lowland sandstone and alluvial bench forests (1.66 and $1.39 \text{ m}^2 \text{ ha}^{-1}$, respectively), the upland granite did have the highest average rank in reproductive productivity due to its low variability. The upland granite was the most productive forest

type for two periods of over five months each. The peat swamp forest was also the most productive for extended periods of time, including one episode in 1990 which lasted eight months. As peaks in fruit production are often asynchronous across forest types, many frugivores travel between forest types to maximize their caloric intake. The interpretation of 'productivity' in these analyses represents total fruiting productivity, including all types of fruits. Frugivores, particularly specialists, do not consider all available fruits equally, but strongly prefer certain types or are excluded by chemistry and morphology from others^{24,25}. For example, a significant portion of the steady productivity in the upland granite forests is due to the ecologically dominant species of the genus *Calophyllum* (Clusiaceae), which produce fruits that are predominantly consumed and dispersed by small bats.

Beyond mast-fruiting

Most of the empirical and theoretical discussion about the phenology of Southeast Asian rainforests has focused on supra-annual mast fruiting or general flowering. While this behavior does involve a significant proportion of the

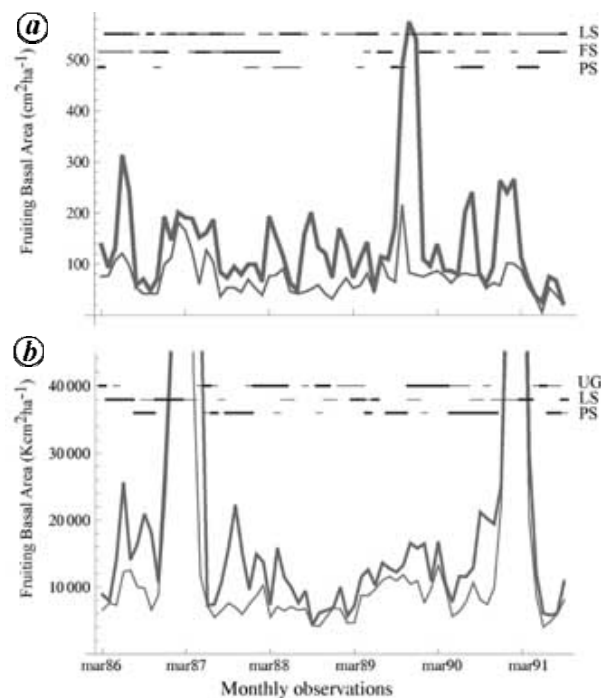


Figure 2. Maximum reproductive productivity by growth form and forest type. *a*, Woody climbers. *b*, Trees. The thick line indicates the most productive forest type while the thin line indicates the second most productive. The three most productive forest types are (*a*) LS = Lowland sandstone, FS = Freshwater swamp, PS = Peat swamp; (*b*) UG = Upland granite, LS = Lowland sandstone and PS = Peat swamp. The temporal sequence of dominant productivity is shown along the top of each graph: most productive (thick black squares) and second most productive (small gray squares).

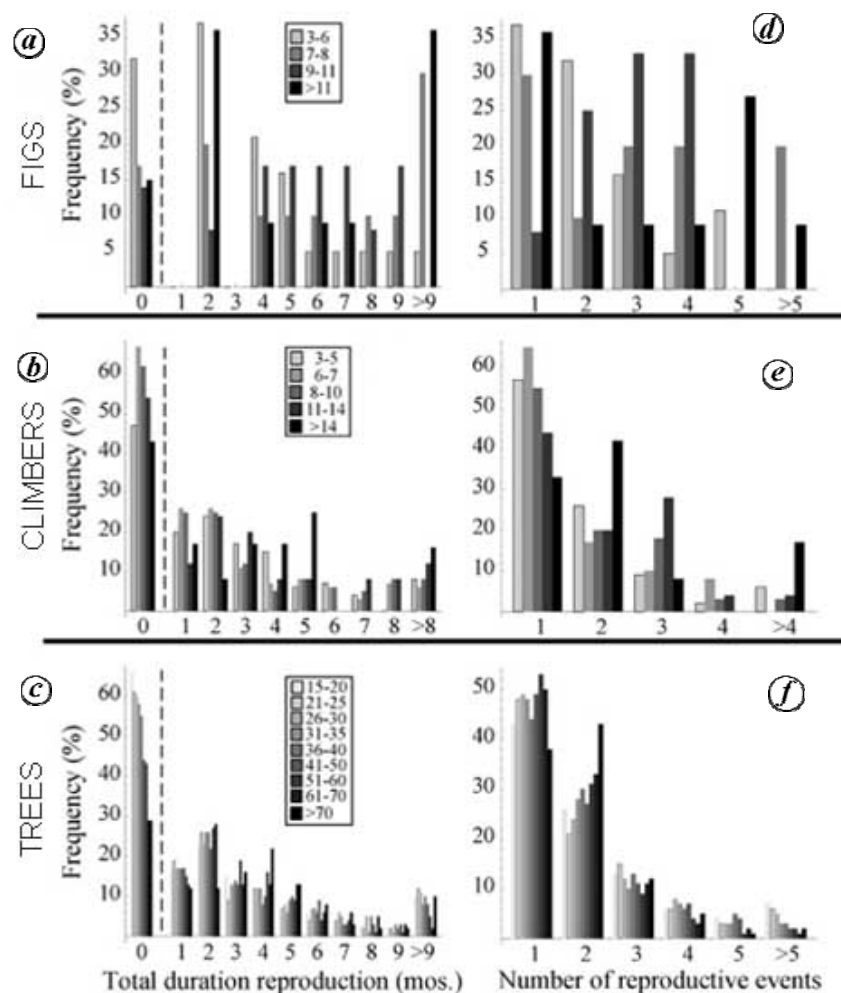


Figure 3. Fruiting duration and frequency by plant form and stem size. *a-c*, Total duration of fruiting, measured by the number of months observed fruiting. Legend indicates stem diameter classes. In each figure, the leftmost column represents the proportion of non-reproductive stems. *d-f*, Number of reproductive events per stem.

woody plant community and plays a major role in shaping species composition and ecosystem structure, the complexity of plant reproductive behavior is not completely defined by the SMF events. While SMF specialization is found in most clades of the angiosperm supertree, a substantial amount of species diversity within these clades did not limit their reproduction to SMF events. The lack of synchrony in reproductive behavior among the forest types is particularly compelling, as it may indicate that there are no consistent environmental signals to synchronize reproduction other than major global events, such as the ENSO cycle. Additionally, there may be advantages to reproducing outside of the SMF events, particularly if seed predation is not a strong selective force. These advantages would include greatly reduced competition for seed dispersal and specialist pollinators. Seedlings would also experience less density-dependent selection²⁶. To

test these assertions, more detailed data and analyses are necessary in order to understand population level synchrony within taxa. Obviously, some level of synchrony among the members of a population is required for successful outcrossing.

Interesting patterns can be found by examining the total duration of reproduction during the study across different size classes of the three plant forms (Figure 3). First, while a majority of fig individuals did reproduce, a substantial portion of woody climbers (>60% for 6–7 cm DBH stems) and trees (>50% for stems less than 30 cm DBH) were non-reproductive throughout the observation period. Secondly, larger stems were generally reproductive for greater total duration than smaller stems for all growth forms. For figs and climbers, this trend was caused by more frequent fruiting of larger individuals compared to smaller individuals (Figure 3 *d-e*). For trees, on the other hand, most large

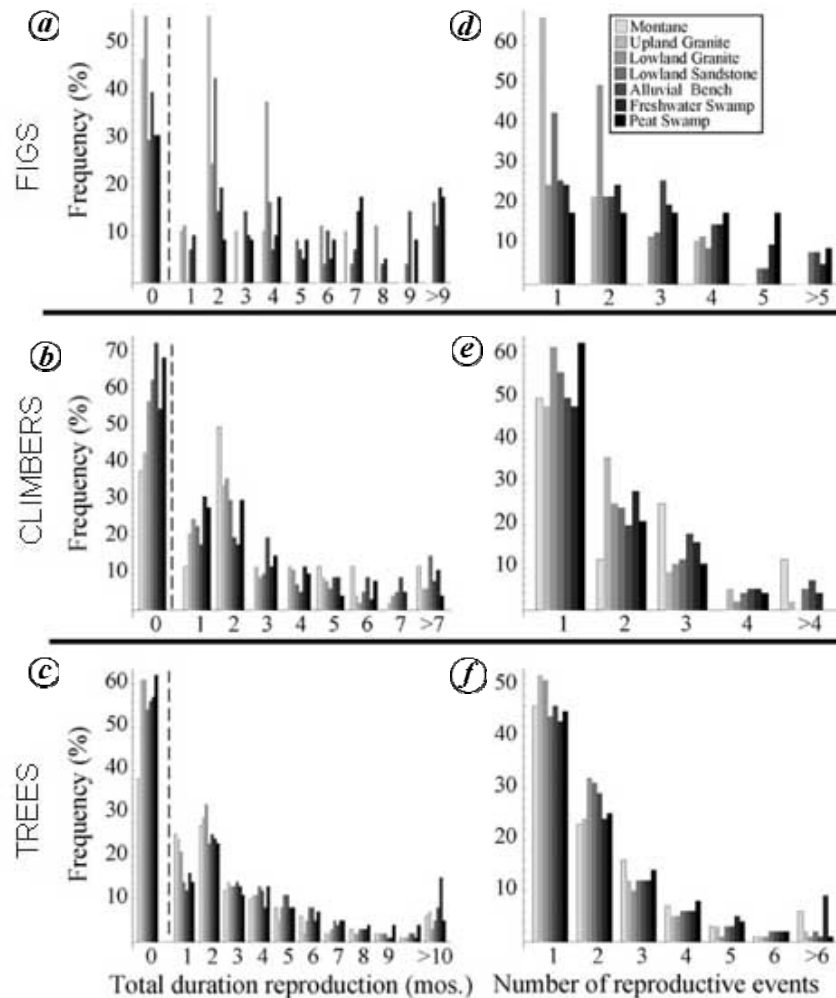


Figure 4. Duration and frequency of fruiting by plant form and forest type. *a–c*, Total duration of fruiting, measured by the number of months observed fruiting. The leftmost column in each figure represents the proportion of non-reproductive stems. Percentages for each fruiting duration are calculated relative to reproductive individuals only. *d–f*, Number of reproductive events.

individuals fruited only twice while individuals that fruited three or more times were generally smaller individuals (Figure 3*f*).

Differences in duration and frequency of fruiting were also found among forest types (Figure 4). For figs, individuals in the upland forests did not fruit for more than four months in generally fewer than three fruiting episodes. For climbers, fruiting duration and frequency varied considerably with no apparent trend in relation to size. Among forest types, little difference was detected among trees, although the freshwater and peat swamp forests did have a relatively high proportion of individuals that fruited for nine months or more, across five or more fruiting events.

While most theoretical discussions about woody plant reproductive behavior has focused on the evolution of SMF behavior, several of the theories about ultimate proc-

esses are still applicable to non-participants in SMF events, particularly the resource matching hypothesis²⁷ and the pollination enhancement hypothesis²⁸. Depending on the proximate cues used by these individuals to initiate reproduction, the trends discussed above would agree well with the idea that larger individuals, with greater leaf area, presumably more direct incident sunlight, and a larger vascular system, would accumulate resources more rapidly and could fruit more frequently or for longer periods of time during each event. Other strategies for reducing the impact of seed predation, such as toxic secondary compounds or massive mechanical protection, may allow some taxa to produce fewer, but highly expensive, fruits and thus have the advantage of attracting dispersers. Again, more detailed data and analyses are required to directly address this issue.

Defining 'long-term'

Our study represents one of the longest continuous records of tropical woody plant reproductive behavior and the only long-term simultaneous data for an entire community across numerous forest types and growth forms. Nevertheless, caution must be exercised in interpreting the evolutionary and ecological implications of the observed patterns. This interpretation depends a great deal on how one defines 'long-term' dynamics. To develop an approximation of the proportion of an individual plant's lifetime reproductive effort, our observations represent that old-growth trees live, on average, for 300 years. While determining the age of tropical trees remains problematic, various approaches have provided estimates which range between 200 and 1400 years for old-growth species, with an average of ~300 years^{29–31}. Assuming individual trees require a century to attain full reproductive maturity, individuals would enjoy roughly 200 years of reproductive activity. Given an average interval of three years between SMF events, individuals of the Dipterocarpaceae, for example, could participate in over sixty SMF events. Given the variance in lifespan for trees, some individuals may participate in substantially more events. We observed two SMF events over a five and half year period. Our observations obviously represent brief portion of a healthy tree's reproductive activity.

The relatively large fraction of individual plants that remained non-reproductive throughout the study period (Figures 3 and 4 a–c), particularly among trees, also emphasizes the limitations of our observations. Even among large trees (DBH >50 cm DBH), most of which can be safely considered as mature adults, nearly 30% of the individuals observed never reproduced during the observation period. This is a substantial proportion of large individuals that did not respond to any environmental cue and bypassed opportunities for reproduction for nearly six years. The fraction of woody climbers which remained non-reproductive was also quite high, reaching nearly 70% for stems between 6 and 7 cm DBH. Given the difficulty of observing fruiting events in some climbers, this measure may be an over-estimate of sterility.

The functional definition of 'long-term' not only hinges on the life history strategies of the organism, but also on the consistency and predictability of the selective forces. The evolutionary dynamics of old-growth rainforest trees, given their potential for extremely long life spans with an increasing capacity for reproduction with size, will obviously occur on a time scale beyond any vertebrate species. Recent models suggest that, given a typical biogeographic setting for rainforest trees and a number of assumptions about gene flow and phenotypic variability, rapid speciation can occur within 50 K generations³², which for generation times of 50 years equals 2.5 million years. The frequency and strength of the ENSO cycle, the most likely proximate cue for current SMF behavior, has

probably varied considerably over this time period³³. Recent reviews have also indicated that 'ecologically significant evolutionary change' can occur over very short periods of time³⁴, but the ability of an organism to respond and modify its behavior must be closely linked to its life history strategies. Most examples of rapid ecological and evolutionary change are of short-lived organisms, particularly annual plants³⁵. The pace of these changes cannot be simply extrapolated for long-lived organisms, with overlapping generations.

Given that substantial periods of time are required for speciation and the amount of climatic and even geological change that has occurred in the Southeast Asia region, the evolution of reproductive behavior in these organisms has probably been a multivariate process and cannot be explained by a single selective force. It is doubtful that a single selective force has even dominated the evolutionary dynamics leading to these SMF events. None of the evolutionary processes proposed for the evolution of SMF behavior are mutually exclusive, but are more likely to have been synergistic and reinforcing through the millions of years necessary for these communities to evolve such complex behavior across such a wide range of lineages. It is also important to bear in mind that a different process may have been responsible for the evolution of the behavior than the current observed process maintaining the behavior.

Implications for conservation of vertebrate populations

Given the great deal of variance in fruit availability, particularly in any one forest type, frugivores and omnivores experience extended periods of food shortage, forcing most to migrate between forest types^{5,36}. Gibbons (*Hylobates albobarbis*) are territorial and non-migratory animals and their population densities at CPRS were largely determined by fig stem densities²⁵. Throughout the study period, figs maintained a much higher level of reproductive behavior (averaging 5% of stems) than other growth forms, further supporting the critical role that figs play as a 'keystone' fruit resource in Bornean forests³⁷.

The lack of woody plant reproductive synchrony among the different forest types likely contributes to the maintenance of resident consumer populations, as they move locally and follow fruit availability or shift to less preferred food sources^{24,38,39}. The landscape level sampling approach employed in this study highlights the need for resource managers to consider the diversity of forest types within management units, particularly for migratory frugivorous vertebrates. Certain 'keystone' forest types (e.g., swamps and montane regions) may be critical for animal populations during periods of low plant reproductive behavior in the low to mid-elevation dipterocarp forests^{5,11,40,41}. Landscape integrity is especially critical to conserve these

Bornean ecosystems and thus, adequate geographic planning in these supra-annual mast fruiting forests is essential to facilitate the migration among a diversity of forest types due to the high variability and asynchrony of fruit availability.

Conclusions

Long-term studies are critical to understand the reproductive behavior of tropical trees and how this behavior affects the frugivorous and nectivorous animal populations who depend on such resource availability. Our results further support the importance of supra-annual mast fruiting in the Southeast Asian forests, but we also highlight the great variability among plant growth forms and major forest types for this behavior. Additionally, we stress the importance of research on non-participants in SMF behavior – given the alternative evolutionary strategies they pursue and their importance as keystone resources for animals – as they comprise a majority of the stems in the forest and taxonomic diversity within it. While our ability to interpret ecological behavior and evolutionary dynamics of these long-lived woody plants may be limited, these ‘long-term’ studies are a key element in the monitoring of future change in these behaviors, as they are affected by both global climate change and human-mediated disturbance of natural forest landscapes.

Because SMF events across Malaysia are probably regulated by El Niño Southern Oscillation (ENSO) cycles^{2,6}, future global climate change may shift these ENSO cycles⁴², altering the synchrony of reproduction at the community level, with potentially diverse and interactive effects on both the fauna and flora⁴³. Additionally, if droughts become more intense and prolonged with global climate change, critical populations of pollinators may be adversely affected causing a decline in the outcrossing ability of the woody plants, crop production and poor regeneration^{7,44,45}.

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ACKNOWLEDGEMENTS. We thank the Government of Indonesia for the privilege to conduct scientific research in West Kalimantan, particularly the Indonesian Institute of Sciences/LIPI-PPPB and the Indonesian Parks and Conservation/PHPA-Kalbar. A full list of financial sponsors of this work is provided in Cannon *et al.*¹¹. We thank the research assistants from several countries who participated in this work.