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Five decades of observations reveal regional features of synchronised masting across Southeast Asia

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Five decades of observations reveal regional features of synchronized masting across Southeast Asia

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Abstract

Southeast Asia's dominant rainforest tree species act in reproductive unison every two to ten years to flood forests with seeds, a phenomenon called masting. Until now, masting has been documented mainly at the site scale with no consistent unit of comparison. While individual trees within a site synchronise reproduction, it remains unclear if sites across the region also synchronise, and whether all sites participate in regional masting events. Here, we compile the first regional dataset of masting events for Southeast Asia through collaboration with ecologists, botanists, conservation scientists, and a literature review. We use the 5,853 site-months of observation from 26 sites across five decades to define masting states using a novel statistical thresholding approach. We show that Southeast Asian masts cluster in time forming discrete regional masting periods separated by years of quiescence, and that site onset timing varies in antiphase across the equator. Masting is therefore a regional phenomenon, but still varies geographically, suggesting large scale triggers with geographic and local climate interactions. Masting is therefore a regional phenomenon, not a set of independent events, and can be studied as such. Our dataset can be used to answer a plethora of scientific questions and inform conservation actions in one of Earth's most important regions for biodiversity and carbon cycling.

Introduction

General flowering and mast fruiting is a widely recognized tree reproductive phenomenon in Southeast Asia, where tree communities flower and fruit in large volumes after multi-year inactivity. The phenomenon is a critical event in a rainforest's nutrient and energy cycling process, creating long periods (2-10 years) of scarcity followed by brief feast periods for fauna populations from weevils to sun bears (Medway 1972, Curran and Leighton 2000, Wong et al. 2005, Fredriksson et al. 2006, Hosaka et al. 2011). However, it remains unclear whether masting is a site-level occurrence or a landscape-scale event. Previous literature has considered masts to be regional, as studies point to shared large-scale triggers, but this has not been directly assess with region-wide analysis. Are tree communities reproducing in synchrony across thousands of kilometers, or do tree communities mast independently, coinciding only by chance? Without a standard definition of what constitutes a mast-level reproductive event, comprehensive regional datasets of masting, or empirical assessment of mast synchrony across sites, it is not possible to determine if masting is truly the landscape scale phenomenon that we consider it to be.

Significant gaps in our understanding of masting events is a major barrier to analysing the broader ecological processes that masting underpins, and the species that rely on this reproductive strategy. Dipterocarpaceae dominate Southeast Asian forests and include 201 single-country endemic species, 84% of which are threatened (Khoo et al. 2023). Malaysia and Indonesia have the highest Dipterocarpaceae diversity in the world: 260 of the 535 known species are found in Borneo alone (Khoo et al. 2023). The main threats to dipterocarps are land use change and land conversion for industrial agriculture (Khoo et al. 2023). They are under further threat in the region as climate change may alter the climatic triggers – such as El Niño Southern Oscillation events – they depend on to trigger reproductive events (Yasuda et al. 1999, Wich and Van Schaik 2000, Williamson and Ickes 2002, Numata et al. 2003, Sakai et al. 2006, Brearley et al. 2007, Satake et al. 2019, Bogdziewicz et al. 2024), and potentially decouple plant-pollinator relationships (Memmott et al. 2007). Such alterations, as has been documented in other biomes, could lead to significant biodiversity loss (Peng et al. 2025) or reduce the effectiveness of masting as a reproductive strategy (Bogdziewicz et al. 2020). Understanding the predictors, spatial scale, and frequency of masting can contribute to conservation action by improving timing for seed sourcing for native tree planting, strategic application of invasive species management (Hallworth et al. 2024), timing fauna species monitoring or supplemental feeding, and predicting tree communities' response to future climate scenarios (Pearse et al. 2021, Numata et al. 2022). However, studies vary widely on how they define the phenomenon, as flower and seed volume can be highly variable, and there is no singular definition of what amount of reproduction constitutes a mast (LaMontagne and Boutin 2009, Bogdziewicz et al. 2023, Kelly 2023).

While masting events are gregarious and highly visible, they are hard to define in terms of community participation, magnitude, or intensity (Bogdziewicz et al. 2023, Qiu et al. 2023). Studies often focus on a single site or single masting event measured as a proportion of individual tree participation (Brearley et al. 2007, Numata et al. 2012), species participation (Sun et al. 2007), or basal area participation (Curran and Leighton 2000) in reproduction (Lieb et al. 2026). There is no agreed upon statistical method to define a mast across all sites, as sites differ substantially in their community composition and baseline reproductive rates. Meaningfully comparing masting across sites and landscapes requires a statistically supported definition of masting and how the proportion of trees participating in reproductive activity at any given time rises to a sufficient magnitude to count as a masting event. Without a standard definition of what constitutes a mast-level reproductive event, comprehensive regional datasets of masting, or empirical assessment of mast synchrony across sites, it is not possible to determine if masting is truly the landscape scale phenomenon that we consider it to be.

Flowering and mast fruiting phenomena are widely studied at various spatial scales in temperate biomes; however, nearly all community-wide masting research in Southeast Asia has been conducted at the site level (Lieb et al. 2026). Further, a handful of closely monitored study sites

throughout the region are the basis for the vast majority of phenology research in SEA, namely Gunung Palung National Park (Cannon et al. 2007, Knott et al. 2021), Pasoh Forest Reserve (Sun et al. 2007, Chen et al. 2018), Forest Research Institute Malaysia (FRIM) (Numata et al. 2022), and Lambir Hills National Park (Sakai 2025). These sites have generated a wealth of robust phenological and associated meteorological data, spanning temporal scales sufficient to capture the long-term dynamics of masting (Lieb et al. 2026). Despite the richness of these datasets, no systematic compilation or synthesis exists across sites, even though ecological processes such as masting operate at scales far beyond any single site. Without integration, we risk missing critical insights into how these processes respond to environmental change, and how they in turn shape forest dynamics, biodiversity, and ecosystem resilience at a regional scale. With ever-increasing threats of climate change and land conversion, having an integrated regional dataset of these events will also enhance our ability to detect the subtle but significant impacts of altered climatic responses from trees in the world's most biodiverse ecosystem.

Here, we provide two advents to the research of Southeast Asian masting phenomenon: we present the first ever regional scale dataset of masting events spanning 50 years and 26 sites across the region; and we devise a new method to statistically define masting with a dynamic threshold assessment that can be applied across sites and account for background reproductive levels of tree communities (Box 1). We use this synthesised dataset to 1) assess to what degree sites have sychronised flowering onset, 2) test for seasonality in onset timing (if masting sites have a typical season) and 3) seek geographical differences in onset.

In doing so, we establish the foundational framework needed to understand one of the most ecologically consequential and least understood reproductive phenomenon on Earth, with profound implications for the conservation of Southeast Asia's biodiversity, the countless species that depend on mast fruiting events for survival, and our ability to predict how these forests will respond to an increasingly variable climate.

Box 1: Harmonious threshold setting in long-term phenology datasets

Thresholding methods

For brevity we report here the thresholding approach for one site (Lambir Hills National Park). Each site threshold is reported in Table 1 of Supplemental Materials ("threshold used" column).

The dataset from Lambir Hills National Park (Sakai 2025) originally included 171,008 observations of individual trees based on monthly census from April 1993 to February 2011. After subsetting this data to include only Dipterocarpaceae species (to limit the background noise of species that are not strictly masting), we had 61,998 observations. We calculated the proportion of trees participating in flowering and fruiting each month. We used the *diptest* package in R to test for multi-modality, which

supported the alternative hypothesis that the data were at least bimodal. We used the *mclust* package in R to fit a two component Gaussian Mixture Models (GMMs) to flowering and fruiting proportions separately.

We visualised the density of proportions values for flowering and fruiting separately to confirm bimodality, and placed a line (red) at the calculated threshold (Figures 1a and 1b). We repeated this approach for all long-term datasets provided to us that included data on proportions of trees participating in reproduction at a minimum of monthly temporal resolution.

Thresholding results

For our example site (Lambir Hills National Park), Hartigan's test showed that both flowering and fruiting were likely to be multimodal and so we applied the GMM approach to determine the threshold between background reproduction and masting. This yielded thresholds of 7.4% for flowering and 9.6% for fruiting, which correctly split the two distributions based on visual assessment (Figure 2a and 2b). To check the performance of the mixture model threshold, we compared the masting events as defined by the GMM with widely accepted observed masting events at Lambir Hills National Park based on literature (Sakai et al. 2006, Ushio et al. 2020, Miura et al. 2023)(Figure 1c). This showed generally matched outcomes, where events considered by human observers to be masts aligned with predicted masts based on the GMM.

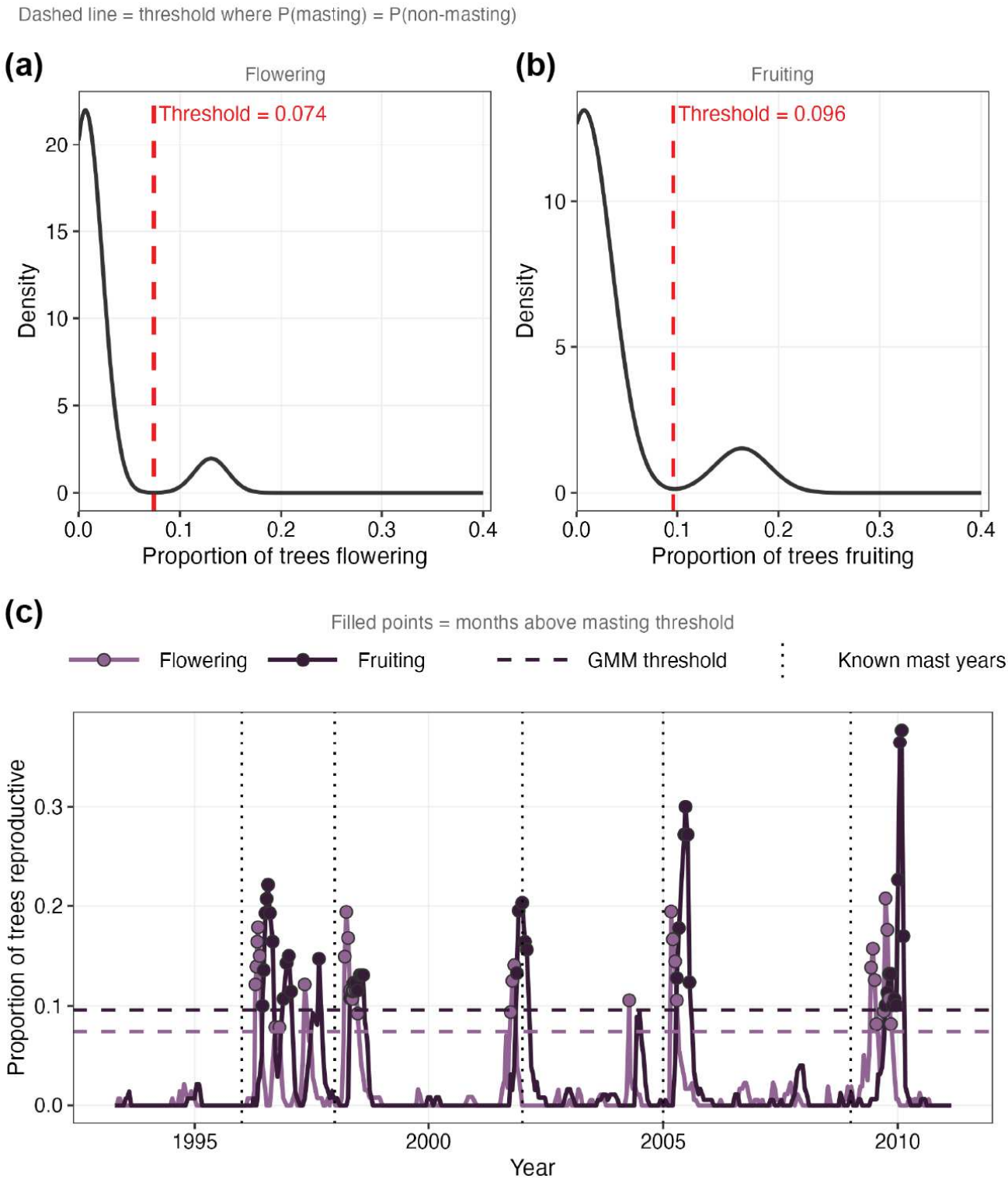


Figure 1: Results from Gaussian mixture model for Lambir Hills National Park, and proportions of individual Dipterocarpaceae trees flowering and fruiting from 1993 to 2011, based on monthly censuses. Panels a and b (Lambir Hills GMM threshold deviation) show the

density of proportions of reproduction in the dataset, the black line is the fitted two-component Gaussian mixture model density, with red vertical lines showing the GMM-derived threshold. Panel c shows the proportion of trees reproductive per month; vertical dotted lines represent confirmed and widely accepted general flowering and masting events at Lambir Hills National Park. Horizontal dotted lines indicate the thresholds for flowering and fruiting derived from Gaussian mixture models. Circular points show months that pass this model-derived masting threshold.

Results

Data integration results and dataset summary

Our data integration approach yielded 1,621 site-month instances from the literature review synthesis (20 sites), 1,343 instances from expert elicitation (8 sites), and 2,889 instances from seven long-term monitoring datasets (7 sites) (Figure 2b). Many sites had data from more than one source (data summary table available through Data Availability). This totals 5,853 rows of mast site-month instances from 26 unique sites, covering October 1972 to January 2026 (Figure 2a), though with significant patchiness and uneven sampling. Across the dataset, 323 flowering and 346 fruiting site-months were recorded, representing 109 and 105 discrete onsets respectively. A summary table with details of sites and datasets is provided (see in Data Availability).

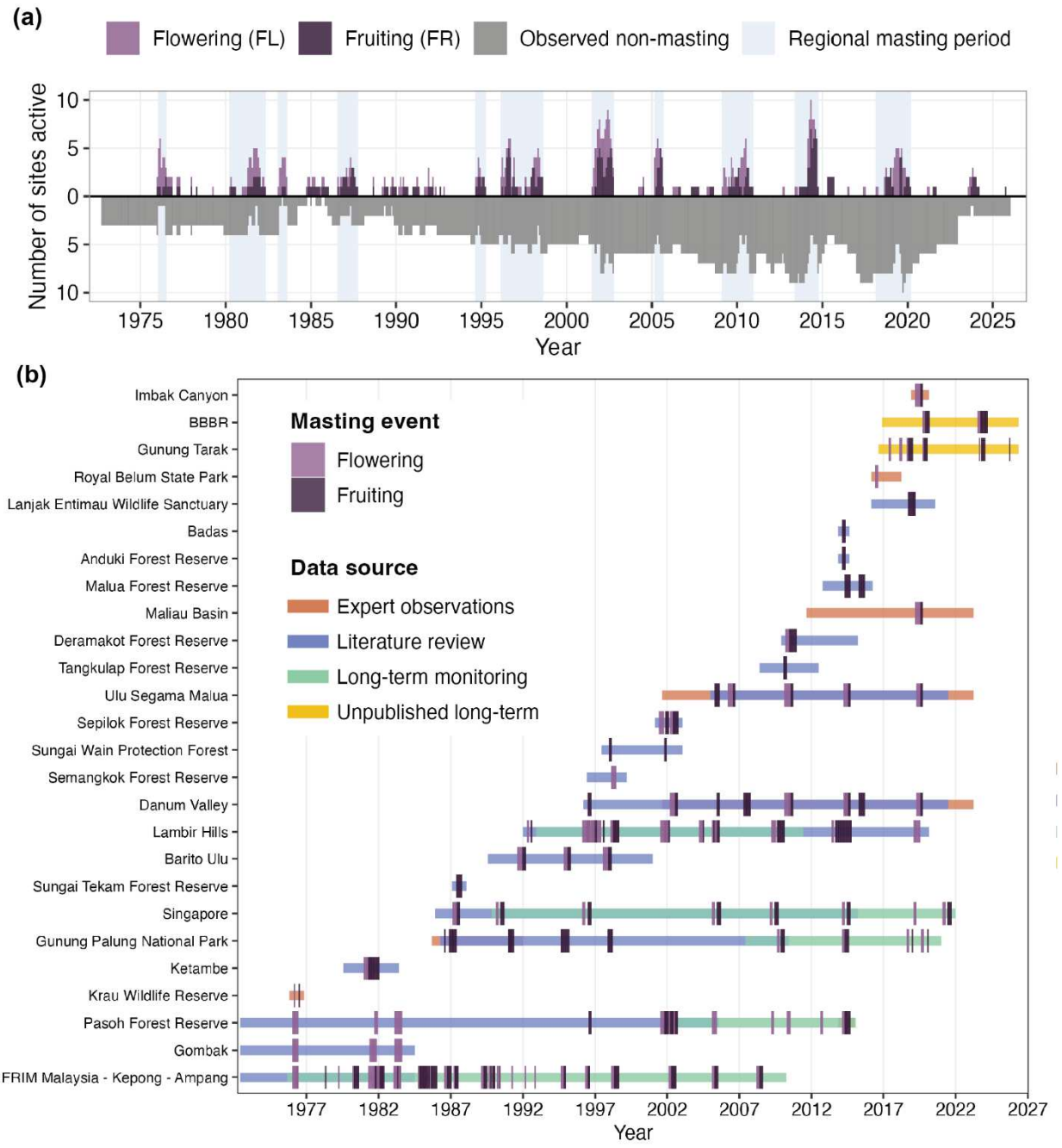
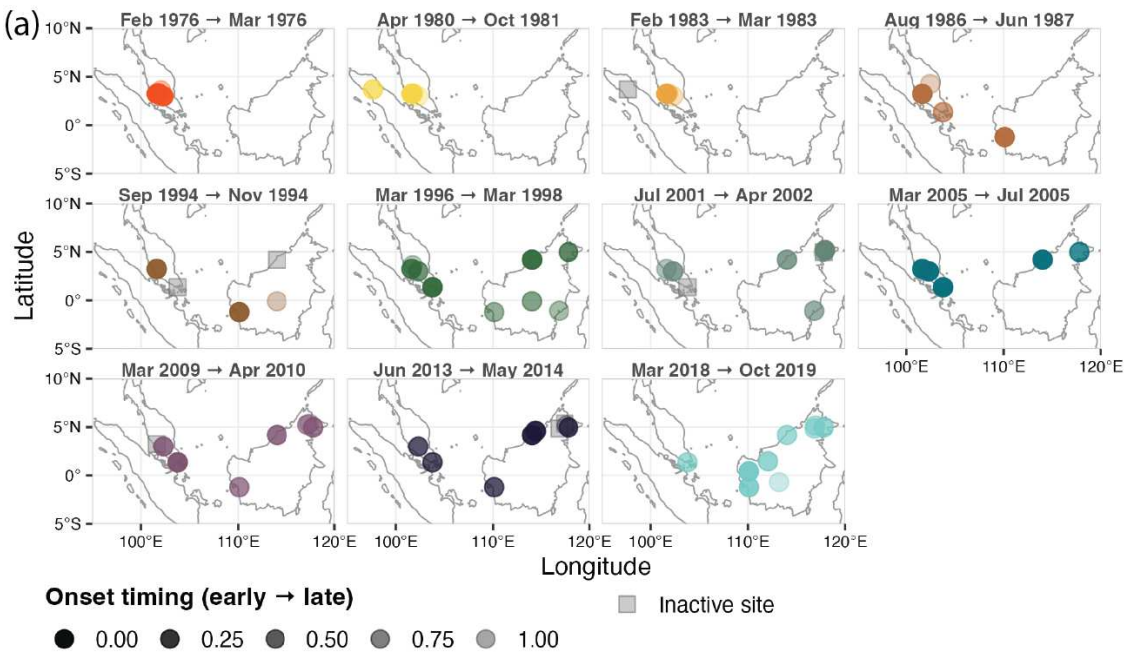


Figure 2: Temporal coverage on site observations for masting events. Data sources combine expert observations, events mentioned in literature, published long-term datasets, and private long-term datasets specifically provided for analysis. Abbreviation 'BBBR' is Bukit Baka Bukit Raya National Park. Panel **a** shows monthly counts of sites exhibiting general flowering (light purple) and mast fruiting (dark purple) across Southeast Asia, 1972–2026. Numbers on the lower half of the y-axis (grey bars) show the number of sites observed but not masting in each month. Shaded boxes indicate identified regional masting periods, defined as consecutive months of activity at ≥3 sites, separated by gaps of ≥6 months with no masting recorded at any site. Panel **b** shows each site and data coverage over time, color coded for the data type.


(a)
Feb 1976 → Mar 1976
Apr 1980 → Oct 1981
Feb 1983 → Mar 1983
Aug 1986 → Jun 1987
Sep 1994 → Nov 1994
Mar 1996 → Mar 1998
Jul 2001 → Apr 2002
Mar 2005 → Jul 2005
Mar 2009 → Apr 2010
Jun 2013 → May 2014
Mar 2018 → Oct 2019
10°N
5°N
0°
5°S
100°E
110°E
120°E
Latitude
Longitude
Onset timing (early → late)
0.00
0.25
0.50
0.75
1.00
Inactive site

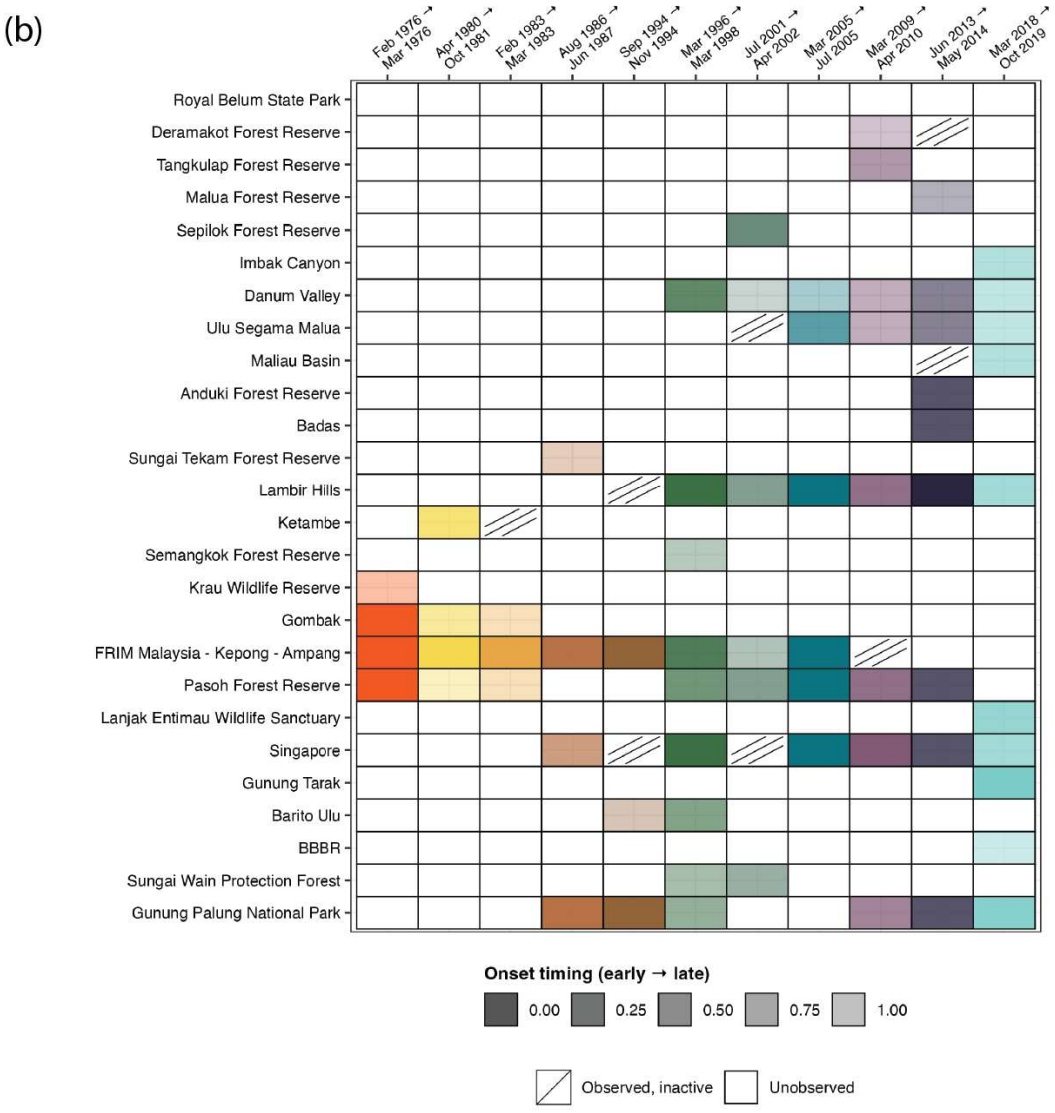

(b)
Feb 1976 → Mar 1976
Apr 1980 → Oct 1981
Feb 1983 → Mar 1983
Aug 1986 → Jun 1987
Sep 1994 → Nov 1994
Mar 1996 → Mar 1998
Jul 2001 → Apr 2002
Mar 2005 → Jul 2005
Mar 2009 → Apr 2010
Jun 2013 → May 2014
Mar 2018 → Oct 2019
Royal Belum State Park
Deramakot Forest Reserve
Tangkulap Forest Reserve
Malua Forest Reserve
Sepilok Forest Reserve
Imbak Canyon
Danum Valley
Ulu Segama Malua
Maliau Basin
Anduki Forest Reserve
Badas
Sungai Tekam Forest Reserve
Lambir Hills
Ketambe
Semangkok Forest Reserve
Krau Wildlife Reserve
Gombak
FRIM Malaysia - Kepong - Ampang
Pasoh Forest Reserve
Lanjak Entimau Wildlife Sanctuary
Singapore
Gunung Tarak
Barito Ulu
BBBR
Sungai Wain Protection Forest
Gunung Palung National Park
Onset timing (early → late)
0.00
0.25
0.50
0.75
1.00
Observed, inactive
Unobserved

Figure 3: **Representing general flowering and mast fruiting events across Southeast Asia.** Panel **a** shows maps of Southeast Asia showing onset of flowering timing by site within each regional masting period (regional masting periods correspond to the shaded areas in Figure 2a). Each map shows a different time when clusters of masting events occur, either synchronously or in close temporal proximity, forming distinct masting periods. Opacity of the point indicates an earlier date of onset of flowering per masting period. Panel **b** represents sites in order of latitude (North to South) and reflects the flowering onset activity represented in the corresponding maps. Darker shaded colors indicate that site onset masting earlier in the masting period, with lighter colors indicating they onset later. Diagonal lined cells indicate when a site was observed during a masting period, but it did not participate. Blank cells indicate that a site was unobserved during that masting period.

Masting is supra-annually seasonal, but in antiphase

Our thresholding of active and quiet periods, including all masting events in the dataset, yielded 11 masting periods between 1972 and 2025 (Figure 2a, Figure 3b). and their spatial distribution (Figure 3a). Across the integrated dataset, 109 flowering and 105 fruiting onset events were identified between 1976 and 2025 (Figure 3). Onset months were significantly non-uniformly distributed for both flowering (Rayleigh's test: $r = 0.42$, $p < 0.001$) and fruiting ($r = 0.18$, $p = 0.019$), indicating that although masting does not occur annually, reproduction shows a consistent tendency to begin during particular months when it does occur. The concentration statistic was more than twice as strong for flowering as for fruiting, indicating that flowering onset is far more tightly timed than fruiting onset across the region.

Both flowering and fruiting onset distributions were significantly non-unimodal across twelve calendar months (Hartigans' dip test: flowering $D = 0.105$, $p < 0.001$; fruiting $D = 0.080$, $p < 0.001$). Flowering onset formed two distinct clusters: a primary concentration in March and April with 62 of 109 events, a trough in July with two events, and a secondary concentration between August and October with 27 events. Fruiting onset was likewise non-unimodal though less pronounced. These differences in flowering time were explained by latitude: sites north of 1° N and sites at or south of this latitude each showed strong and highly significant seasonality in onset timing, but with mean onset approximately five months apart (Table 1). Northern sites showed mean flowering onset in March–April and mean fruiting onset in June–July, while southern and equatorial sites showed mean flowering onset in September and mean fruiting onset in December–January (Figure 4). Within each group, the interval between mean flowering and mean fruiting onset was approximately three months, estimated independently in each group and consistent with typical flowering-to-fruiting development times in dipterocarps.

Onset distributions differed significantly between the northern and southern groups for both flowering (Watson's two-sample test: $U^2 = 0.497$, $p < 0.001$) and fruiting ($U^2 = 1.154$, $p < 0.001$). This latitudinal offset accounts for the non-unimodal statistics reported above: these two seasonal

signals in approximate antiphase largely cancel out when analysed ungrouped, producing an apparent absence of regional seasonality where instead two opposing seasonal patterns exist.

The pattern was robust regardless of the dividing latitude; we tested boundaries at 0°, 0.5°, and 1° each produced similar results in direction and significance (Table 1). Even when excluding Gunung Palung National Park, the site contributing the largest number of southern onset events, the southern pattern persisted for both flowering (n = 10, r = 0.60, p = 0.024) and fruiting (n = 11, r = 0.78, p < 0.001).

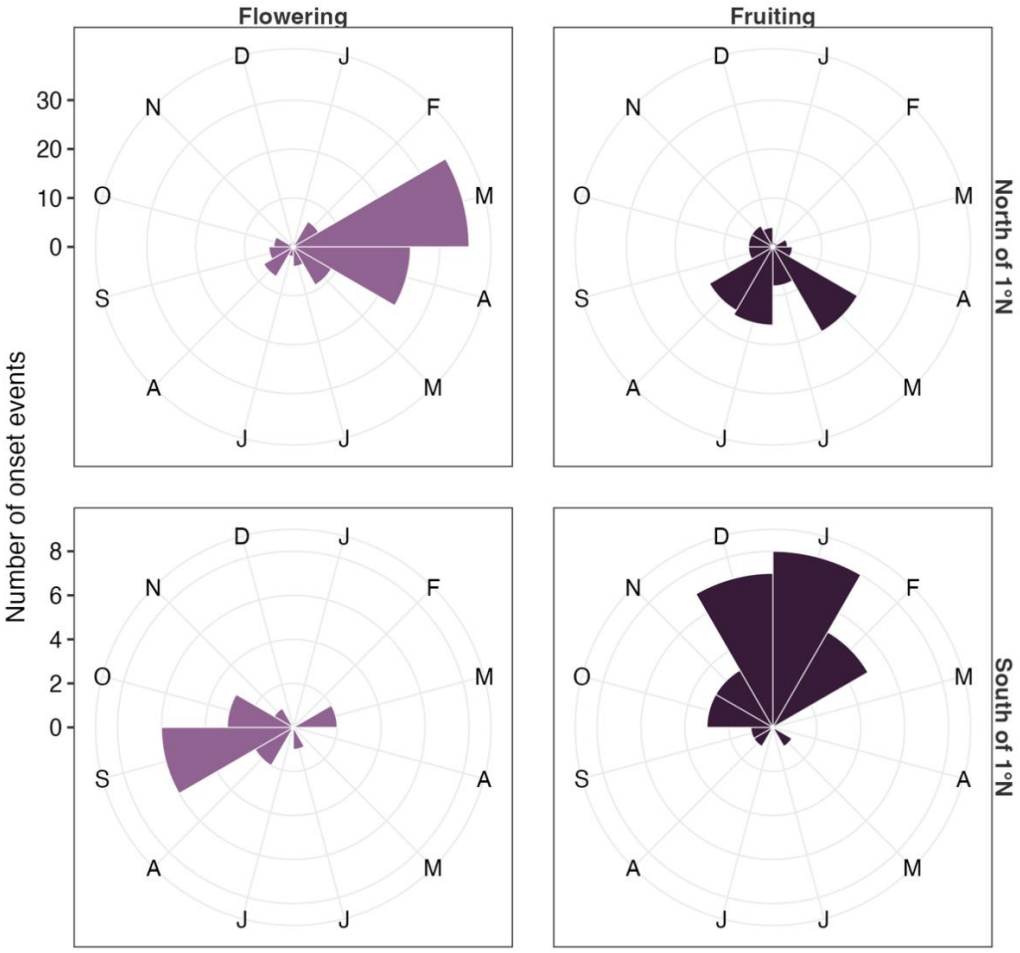


Figure 4: Seasonal distribution of general flowering and mast fruiting onset months, north and south of 1° N. Each wedge shows the number of onset events in that calendar month, across all sites and years (1976–2025). Upper panels show sites north above 1° N; lower panels show sites at or south of 1° N. The northern group shows approximately opposite seasonal onset compared to the southern group. Sample sizes and circular statistics are given in Table 1. Note that radial axis scales differ between panels.

Table 1. Seasonality of masting onset north and south of 1° N. Rayleigh's test for circular uniformity. r is the mean resultant length, ranging from 0 (onsets are distributed evenly through the year) to 1 (all onsets fall in the same month). Onset is recorded at monthly resolution; mean onset month is given to one decimal place and interpreted as falling within or between the named months. Onset distributions differed significantly between groups for both flowering (Watson's two-sample test: $U^2 = 0.497$, $p < 0.001$) and fruiting ($U^2 = 1.154$, $p < 0.001$).

Group	Phenophase	n	r	p	Mean onset month
North of 1° N	Flowering	99	0.56	< 0.001	3.8 (Mar–Apr)
North of 1° N	Fruiting	87	0.45	< 0.001	6.7 (Jun–Jul)
South of 1° N	Flowering	15	0.59	0.004	9.1 (Sep)
South of 1° N	Fruiting	29	0.67	< 0.001	0.3 (Dec–Jan)

Sites mast together more often than expected by chance

After limiting data to sites with at least 3 years of continuous data, 15 sites were available for temporal overlap analysis. Our mixed-effects logistic regression with site as a random effect showed that the number of other sites masting within a ±3 month window was a significantly positive predictor of masting at a focal site (n = 2,475 site-months, 15 sites, OR = 1.66, 95% CI: 1.53–1.79, $p < 0.001$), indicating significant cross-site temporal overlap of masting events across Southeast Asia (Supplemental Materials 1). Based on the OR result of 1.66, the likelihood of a focal site also masting increased by 66% when there is another site masting in close temporal proximity. The results are highly significant ($p < 0.001$), indicating that sites mast together much more than is expected by chance. The observed proportion of masting site-months increased consistently with the number of co-masting sites (0–6 sites), except for the highest category (n = 7 co-masting sites, n = 3 observations). This is most likely because there were too few samples for this number of sites. The results were robust to the minimum coverage threshold; a sensitivity analysis comparing 2-, 3-, and 5-year thresholds produced consistent results (Supplementary Table 2), as did widening the co-masting window from ±3 to ±6 months (Supplementary Table 3).

Discussion

Through collaboration with a broad community of ecologists, botanists, and conservation scientists, and a systematic review of published literature, we compiled the first harmonised regional dataset of general flowering and mast fruiting events for Southeast Asia. Southeast Asia is among the world's most important regions for biodiversity and carbon cycling and a key

setting for observing the effects of climate change. It is also home to the most extreme masting phenomena on Earth (Ashton et al. 1988, Sakai 2002), yet researchers have, unit now, been documented masting almost entirely at the scale of individual sites, with no consistent unit of comparison between them. By integrating 5,853 site-months of observation from 26 sites across five decades, and applying a common thresholding approach to define masting states, we show that masting events cluster significantly in time across the region, forming discrete regional masting periods separated by years of regional quiescence. Masting in Southeast Asia is therefore a regional phenomenon, not a set of independent local events, and can be studied as such.

Although masting does not occur annually in equatorial Southeast Asia, it shows a clear tendency to begin in particular months. Analysed across all sites, this tendency appeared weak, particularly for fruiting ($r = 0.18$). However, when sites are split by 1° N latitude, both groups demonstrate strong antiphase seasonality: sites north of 1° N begin flowering around March and April and fruiting around June and July, while sites at or south of the equator begin flowering around September and fruiting around December and January. The two groups are separated by approximately five months, and their onset distributions differ significantly. Within each group, the interval between mean flowering and mean fruiting onset is approximately three months, consistent with expected development times and estimated independently in each group.

The divide corresponds roughly to the equator, bisecting Borneo, but we cannot determine from these data alone whether latitude itself is the determinant variable. Effects from the Intertropical Convergence Zone could also explain this split in onset timing (An et al. 2015, Terasaki Hart et al. 2025), introducing variability in rainfall, although this has not yet been explored in relation to masting. A range of geographic and climatic differences between northern and southern Borneo also all covary with latitude group. Additional sites below 1° N latitude would help us better understand the difference in seasonal behavior of masting dipterocarp forests in Southeast Asia and to see if this pattern holds true across a wider Southern hemisphere latitudinal gradient. Modeling with climate and abiotic covariates could also help to disentangle shifts in seasonality based on geographic locations.

Aggregating across the 15 sites with sufficient continuous coverage, we found that the number of other sites masting within a ±3 month window was a significant positive predictor of masting at a focal site. Based on this, we identified 11 regional masting periods between 1972 and 2025 (Figure 3a,b), each typically one to two years long and separated by intervals of little or no site-level masting. Importantly, these regional periods are staggered, not simultaneous. Sites within a masting period do not necessarily begin reproducing in the same month, but within a window narrow enough to constitute a coherent regional event. Our regional results are broadly consistent with what has been reported at individual long-term sites, which is itself an important validation: the masting events our Gaussian mixture model identified at Lambir Hills correspond closely to

those independently recognised in the literature for that site (Sakai et al. 2006, Ushio et al. 2020, Miura et al. 2023).

The spatial extent of general flowering and mast fruiting has been described since at least the 1980s, with events characterised as spanning hundreds to thousands of kilometres of contiguous forest (Appanah 1985, Curran et al. 1999, Sakai 2002), and their proposed triggers (ENSO-associated drought and cool temperatures) span regional scales (Curran et al. 1999, Wich and Van Schaik 2000, Williamson and Ickes 2002, Numata et al. 2003, Satake et al. 2019). Yet almost all research on the phenomenon has been conducted at individual sites of less than one square kilometre, producing a mismatch between the scale at which masting is thought to occur and the scale at which it has been measured (Lieb et al. 2026). The assertion that masting is a regional phenomenon has therefore rested on the plausibility of a shared trigger rather than on any direct test of whether masting at one site coincides with masting elsewhere. We test and demonstrate this by showing that the number of co-masting sites within a three-month window significantly predicts masting at a focal site: for each additional co-masting site, the odds of a focal site masting increase by 66% (OR = 1.66, 95% CI 1.53–1.79).

Comparison between Southeast Asian phenology and temperate systems provides useful context: in European beech (*Fagus sylvatica*), masting synchrony shows distance decay but remains significant across the continent, explained by spatial synchrony in the weather cues driving reproduction rather than by proximity between populations (Bogdziewicz et al. 2021). The regional clustering we document spans a comparable spatial extent, and our results are consistent with a similar mechanism: a shared climatic driver acting across the region rather than a process dependent on proximity between sites. The taxonomic breadth and temporal structure spanning many co-occurring Dipterocarpaceae species distinguishes Southeast Asia, expressed as discrete supra-annual community-wide events separated by multi-year intervals of reproductive quiescence, rather than as between-years variation in intensity of otherwise annual reproduction.

One persistent barrier to synthesis in this field has been the lack of an agreed definition of what proportion of reproductive participation constitutes a mast (Medway 1972, Appanah 1985, Brearley et al. 2007, Bogdziewicz et al. 2024). By deriving thresholds statistically from each site's own distribution, rather than imposing a single fixed cutoff, we accommodate differences in community composition and baseline reproductive rate between sites while retaining comparability. This approach is transferable to any site with monthly individual tree reproduction participation data, and we encourage application to datasets not yet included here. Further, the analytical framework used in this study is highly transferable beyond Southeast Asian tree phenology. The problem we confronted (multiple datasets, collected under different protocols, reporting reproduction at different intensities and with different baselines, requiring a common unit) is the same challenge for most large-scale phenological synthesis. Indeed, phenomena with broad-ranging triggers and influences, like climate anomalies, are likely to cross site-level boundaries and require multi-dataset analysis. The combination of a bimodality

test, a mixture-model-derived threshold, and a fallback percentile threshold where bimodality is unclear, is applicable to other mast systems and to any multi-source phenology compilation facing the same comparability challenges.

Our results can inform a variety of restoration and conservation actions in the region. Dipterocarp seeds are recalcitrant and cannot be stored, so planting material is bounded entirely by the timing of mast fruiting, and collection is currently planned reactively as masts are noticed locally (Kettle et al. 2010, Kettle et al. 2011, Pearse et al. 2021). Knowing that masting periods are regional, staggered, and separated by intervals of quiescence allows collection effort and nursery capacity to be staged across sites in advance. With over 60% of Southeast Asian dipterocarp species threatened (Khoo et al. 2023), improving seed capture during the brief windows when it is possible has direct conservation value. This dataset can be used to estimate masting occurrence across time and space and make the timing of conservation actions more effective. Additionally, masting drives population dynamics across a wide range of consumers (Curran and Leighton 2000, Wong et al. 2005, Fredriksson et al. 2006, Hallworth et al. 2024). By analysing past masting events, we can enhance fauna population modeling with food resource availability metrics derived from modeled masting events across the region.

The patterns we describe apply most directly to lowland everwet dipterocarp forests and should not be extended without care. Seasonal mainland Southeast Asia, montane forest, peat swamp, and non-dipterocarp-dominated systems all have different reproductive dynamics (Cannon et al. 2007). The lack of bimodality in Gunung Palung's reproductive participation, even after removing montane and swamp forest, is a useful illustration of the boundary: not every forest in the region separates cleanly into masting and non-masting states.

Our analysis is potentially limited by the fact that our dataset is spatially uneven in ways that constrain generalisation within the region; Borneo, Peninsular Malaysia, and Singapore are well represented, while Sumatra contributed only a single site with distinctly reported onset months, and there are no other sites on outlying islands elsewhere in Sundaland. The regional masting periods we identify are therefore best understood as periods of synchrony across the well-sampled part of the region, and their extent into the wider Sunda and Wallacean archipelago remains unknown. Additional sites and data can readily be integrated into the dataset when they become available. Beyond this, masting events are not perfectly discrete phenomena, and our binarisation of masting and non-masting states imposes an artificial structure on the data. For macroecological purposes this is a necessary trade-off for for comparing sites across a 4.5 million square kilometre region using data collected by many people under many protocols over five decades. Intensity, magnitude, and community participation metrics are lost in the process, so questions depending on them cannot be addressed here.

The latitudinal divide we report is also limited by number of sites and distribution: all four sites south of 1° N lie in Indonesian Kalimantan, within 1.2° of the equator. Latitude therefore cannot

be distinguished from country, or other geographic and climatic differences between northern and southern Borneo. Records from two independent monitoring programmes, rather than a single source, support the southern group signal; however, the southern group includes only 15 flowering onset events compared to 99 flowering onsets in the northern group. Sites further south, and additional sites elsewhere in Indonesia and Malaysia, would be needed to determine whether the antiphase pattern continues beyond the tight equatorial band. Considering the gaps and sampling bias of the dataset, coverage could be improved by more outreach to non-English-speaking organisations and researchers, drawing on repository data such as GBIF and iDigBio, and developing a citizen science pipeline through platforms such as iNaturalist (Webb and Maycock 2022). Herbarium collections are a particularly underused resource in this respect. Dozens of Southeast Asian herbaria hold millions of dated specimens, with duplicates distributed globally, forming a spatial and temporal archive of plant reproductive events that extends well beyond the reach of any systematic monitoring programme (Miller-Rushing et al. 2006). Herbarium-based phenology is now well established across temperate and Arctic systems, but remains rarely applied in the wet tropics (Willis et al. 2017) and has never been used to study general flowering and mast fruiting(Park et al. 2023). The central constraint is that each specimen is a single snapshot subject to spatial and collector bias, so rare, short-lived mast events are captured only opportunistically and at more accessible locations (Daru et al. 2018). As digitisation expands, the accumulated record may become dense enough to detect regional reproductive pulses retrospectively, extending the spatial and temporal reach of this kind of analysis.

This newly synthesised dataset enables direct testing of climatic triggers at the scale at which they operate. El Niño Southern Oscillation and regional drops in rainfall and low nighttime temperature have all been proposed as masting cues on the basis of correlations at individual sites (Wich and Van Schaik 2000, Numata et al. 2003, Satake et al. 2019). Researchers have studied the relationship between such anomalies and the onset of masting at some sites in Southeast Asia, but much remains unknown about intra-annual seasonality for these events, the true spatial extent of these events, or what other factors are stimulating or moderating masting. The Indian Ocean Dipole, and variation across the Intertropical Convergence Zone could also be viable climate anomalies cueing, limiting, or moderating masting events that have yet to be explored. With regional mast mapping, we can also test site-level covariates proposed as moderators of masting behaviour, including distance to coastline, soil fertility, soil type, elevation, and forest type.

One of our findings are similar to those of (Chechina and Hamann 2019) in terms of different sites exhibiting different likely onset month based on geographic location, although they considered their sites as Southern and Western vs. Northern and Eastern, whereas we identified a latitudinal divide. (Chechina and Hamann 2019) also note that masting throughout the northern and eastern monitoring sites were more weakly associated with El Niño periods than other sites.

A valuable next step is to investigate factors that may alter the regional effect of El Niño across sites, perhaps explained by other climate anomalies.

The regional scale also supports spatial modelling of resource availability beyond monitored sites. Better predictions of food resource availability are a major missing link in fauna population models that rarely incorporate masting at present (Lieb et al. 2026). Important next steps will be to develop a regional metric to represent time-since-resource-event that could be integrated into species distribution models and used to predict animal distributions based on food availability. Ultimately, the potential for this new dataset to be used in ecological modeling and management applications is vast; with a dynamic thresholding method it is easily combined with new data and can be applied to myriad topics that thus far have not adequately integrated this critical function of tree communities.

Methods

Data integration from different sources

We used data from a recent literature review, long-term datasets both procured from literature and provided by co-authors, and expert observational contributions to construct a region-scale (covering sites from -1.22 to 5.78 latitude) summary dataset of masting events. For all datasets, flowering and fruiting events were recorded separately. We subset long-term datasets were to Dipterocarpaceae species only to limit background reproduction data noise from species that are not strictly masting, and in the absence of an existing comprehensive summary of masting and non-masting species at each site. Other data include community-wide rather than species-specific observations, and because Dipterocarps dominate all sites, we consider this analysis roughly representative of community masting.

We summarised all datasets into flowering, fruiting, and non-masting site-month states in the following ways:

Literature review

Prior work (Lieb et al. 2026) analysed 150 peer-reviewed scientific articles on tree reproductive phenology in Southeast Asia, yielding 47 that specifically mentioned masting events or provided data. We manually extracted mast events from these articles where details were available, including masting onset and conclusion months and the study's observation period.

Long-term datasets (raw tree sample data)

We handled long-term data of individual tree reproduction from monitoring sites and other study areas differently from author-reported masting events in the literature. We identified long-term datasets through a systematic literature review (Lieb et al. 2026) or via suggestions by experts and co-authors. Some unpublished raw datasets were provided by organisations or individuals in the form of data summaries of masting events, or full datasets of individual trees at study sites. We downloaded long-term datasets from published work or they were provided by co-authors or other collaborators if they were not already publicly available. These datasets all included some form of monthly individual-tree participation in reproductive activity, reported as a proportion. This 'individual tree participation in reproductivity proportion' is the number of trees in a plot that are reproductive, divided by the total number of trees in that plot, and represents the magnitude of the reproductive event. We standardised these datasets by: 1) subsetting to Dipterocarpaceae to reduce data noise from participating trees, 2) applying our thresholding method to define when each site is considered to be in a masting condition (Box 1), and 3) classing each site-month as mast-level flowering, mast-level fruiting, non-masting, or NA/missing (times when the site was not observed and we cannot be sure a masting event was occurring or not).

Expert observations

We requested input from a broad network of tropical ecology researchers who are familiar with at least one Southeast Asian study site. Either through filling out a site-level reporting datasheet (Supplementary Materials 4) or in follow-up conversations, experts provided monthly observational information about when they witnessed flowering or fruiting levels that they believed constituted masting. Experts were encouraged to use their personal notes, unpublished datasets, and their conversations with their colleagues to increase their confidence that the site-month observations they reported were accurate. Expert elicitation did not include proportion of tree participation in reproduction, so no thresholding tests were used. (Datasets are listed per site in the Site Summary table in the Data Availability section.)

Defining a masting event

While a binary definition of masting has been criticised (Bogdziewicz et al. 2024), for the purposes of collating varied datasets across large areas, and dealing with local variability of background reproduction, thresholding, and peak productivity, it was necessary for this analysis to condense data of tree participation proportions into mast/non-mast categories (Box 1). When drawing observations of masting from literature, we assumed authors' and observers' determinations of what constituted a mast to be correct. We did not re-analyse the proportion of tree participation in reproductivity data from the literature, as this data was often not reported or available. If a study reported an event to be at the level of masting, we assumed this to be true.

For long-term datasets that included plot trees' participation in reproduction, we quantified the proportion of monitored dipterocarp individuals that were flowering or fruiting for each census month. To identify a threshold for general flowering or mast fruiting events, we first tested for bimodality (indicating non-masting and masting states) with Hartigan's dip test (Hartigan and Hartigan 1985, Maechler 2024). This test compares the distribution of a dataset to the best-fitting unimodal distribution, and measures if the dataset significantly differs, or has more "dips", from the unimodal distribution. We then modelled the distribution of these proportions using a two-component Gaussian Mixture Model (GMM), which assumes that observations are from a mixture of two normal distributions representing low reproductive states (low proportions of tree participation in reproduction) and high reproductive states (high proportion of tree participation in reproduction). The GMM estimates the mean, variance, and mixing proportion of each component via maximum likelihood. To define the masting threshold, we identified the proportion value where the posterior probability of belonging to the high-participation group and low participation group were equal (when both = 0.5). This is equivalent to the weighted intersection point between the two fitted distributions. Months in which the proportion of reproducing individuals exceeded this threshold were classified as masting months.

One out of five available long-term datasets (Gunung Palung National Park) did not show significant bimodality (Hartigan's dip test $p > 0.05$), even after removing montane forests that are unlikely to exhibit masting, indicating that the proportion of reproducing individuals did not separate cleanly into low- and high-reproductive states. In this case, the GMM intersection threshold was considered unreliable, so we applied a conservative threshold at the 95th percentile of the observed proportion distribution, retaining only months with unusually high reproductive participation as masting events.

Analysis

We grouped sites if they were within 5km of each other. Reported masting months were only included if they identified a specified onset and ending month, rather than singular random months of observed masting.

Characterising regional periods of masting

To characterise masting activity across the whole region, we counted how many sites were actively masting each month in the dataset. Consecutive months of activity were grouped into regional masting periods, separated by gaps of six or more months with no recorded masting at any site. We selected this threshold based on the observed distribution of quiet period lengths in

the data, which showed a natural break between short within-event gaps (1–2 months) and longer between-event gaps. We retained periods when at least three sites were simultaneously active as regional masting periods.

Testing seasonality in timing of flowering and fruiting

We compiled all flowering and fruiting onset months (data were eliminated if it was unclear whether a month was an actual onset month or a singular month of observation with no event start and end documented, such as a peak flowering month). We treated onset months as angular data – where monthly data is described as sections of a circle instead of linearly – to represent the circularity of calendar months (e.g. December is adjacent to January, rather than being at opposite ends of a line). Onset months are recorded at monthly resolution, so circular means are reported to one decimal place and interpreted as falling within a month or between two adjacent months, not as a within-month date.

We first used Rayleigh's test for circular uniformity to determine whether onset months were uniformly distributed throughout the year or concentrated around certain months, testing flowering and fruiting separately across all sites (Mardia and Jupp 2000, Agostinelli and Lund 2023). We then tested both phenophases for multimodality using Hartigan's dip test (Maechler 2024), which compares the observed distribution to the best-fitting unimodal distribution. Both flowering and fruiting phenophases departed significantly from unimodality, so we did not treat a single regional mean as describing either distribution. Considering this multimodality of the data, we grouped sites geographically to determine which sites form different modes in the data. Based on this initial test of circular uniformity, we found two modes in onset timing, indicating two distinct concentrations of onset month. Therefore, we sought to determine if latitude could explain the divide in sites' onset timing: we split sites into a northern group (latitude $\geq 1°$ N) and a southern group (latitude $< 1°$ N), and repeated Rayleigh's test separately within each group (North and South) and phenophase (flowering and fruiting). We chose 1° N degree after sensitivity testing.

We assessed the sensitivity of the latitudinal grouping (northern and southern hemisphere groups) in three ways: by repeating the analysis with the dividing latitude set to 0°, 0.5°, and 1°; by excluding the site contributing the largest number of southern onset events (Gunung Palung National Park); and by calculating circular statistics separately for each administrative area with at least eight onset events, which tests the pattern without reference to any latitudinal grouping.

We report the mean resultant length (r), which ranges from 0 when onsets are distributed evenly around the year to 1 when all onsets fall in the same month, alongside the circular mean onset month. We then used Watson's two-sample test of homogeneity, a non-parametric test for circular data, to determine whether onset distributions differed between the two groups (Watson

1961, Agostinelli and Lund 2023). Rayleigh's test establishes whether a group is seasonal, and Watson's test establishes whether two groups are seasonal at different times.

Testing for temporal overlap across years with a mixed-effects logistic regression

We tested whether masting events were occurring at the same time across sites using a temporal overlap analysis analysis. We selected sites that had at least three years of continuous data and included observation periods outside of masting events (data included "none" events). We selected three years, a more liberal cutoff than for the frequency analysis, because three-year spans of data collection could still include a masting event with sufficient non-masting observation periods. To test the implications of this temporal subsetting on our results, we ran a sensitivity analysis using 2- and 5-year data-span thresholds. For each site-month, we counted the number of other sites masting within a +/- 3 month window. We selected this window because we expect masting events to be close in time but not perfectly synchronous. We fitted a mixed-effects logistic regression (using the *glmer* package in R), with masting as the response variable (is_masting = 0 or 1) and the number of other sites masting within 3 months (n_co_masting) as a fixed effect. We included site as a random effect to control for differences in mast frequency at different sites. We compared this to the null model using likelihood ratio testing. A similar method has been used to assess the spatiotemporal clustering of crime events (Briz-Redón 2024), but to our knowledge has not yet been applied to an ecological application.

Data availability

The Github repository for the paper is available to the public and includes:

- A data summary of all sites and their sources used to construct our region-wide dataset
- The summarised data of all general flowering and mast fruiting observations included in this study
- R code for the analysis included in this paper
- Metadata and readme information

Available at: https://github.com/ZoeLieb1/sea-masting-phenology.git

Artificial intelligence use statement

A chat-based large language model (Anthropic Claude, Sonnet 5) was used to generate R code for data cleaning, processing, and analysis. A human trained in R coding was always engaged with prompting, reading, checking, and revising R code, and revising and editing all outputs from this code.

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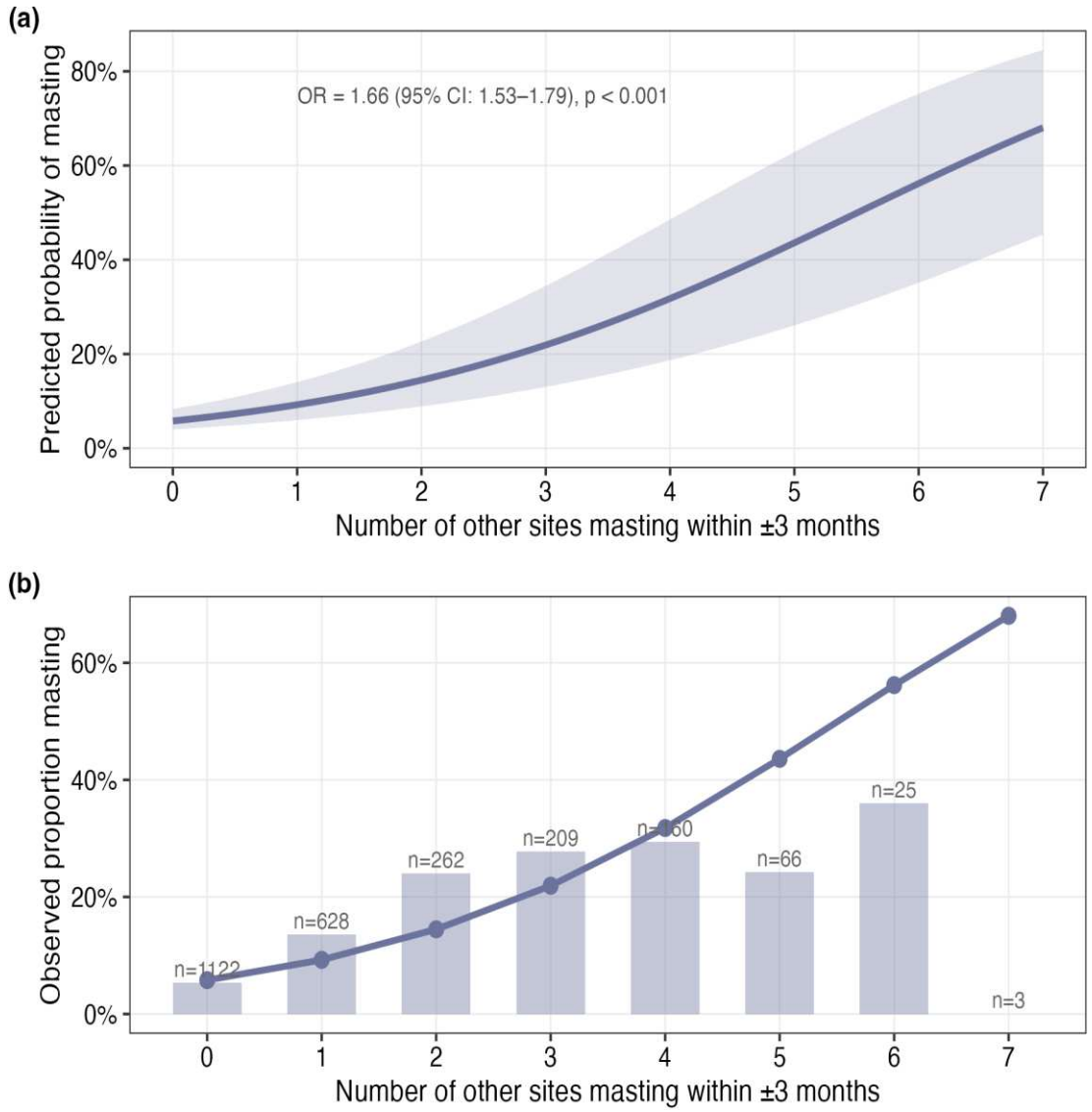
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Supplemental Materials



Supplementary Figure 1: Temporal clustering of masting events across Southeast Asia, tested using a mixed-effects logistic regression with site as a random effect (n = 2,475 site-months, 15 sites). The predictor variable is the number of other sites masting within a ±3 month window of each focal site-month. Panel a: model-predicted probability of masting as a function of the number of co-masting sites, with 95% confidence interval (shaded). Panel b: observed proportion of site-months that were masting at each level of the predictor (bars), with model-predicted probabilities overlaid (line and points). Sample sizes (n) above bars indicate the number of site-months at each predictor value. The n = 3 observation at 7 co-masting sites should be interpreted cautiously due to small sample size.

Supplemental Table 2: Sensitivity test for selecting data coverage threshold in clustering analysis.

Minimum coverage threshold (years)	Sites included (n)	Site-months (n)	Odds ratio	95% CI	χ^2 (df = 1)	p-value
2	15	2475	1.659	1.534–1.795	167.75	2.30E-38
3	15	2475	1.659	1.534–1.795	167.75	2.30E-38
5	11	2291	1.763	1.605–1.936	144.63	2.60E-33

Supplementary Table 3. Sensitivity of cross-site clustering to co-masting window width.

Window	n site-months	OR	95% CI	p
± 3 months	2,475	1.66	1.53–1.79	< 0.001
± 6 months	2,475	1.49	1.39–1.60	< 0.001

Results were also robust to the width of the co-masting window. Widening the window from ±3 to ±6 months reduced rather than increased the effect (OR = 1.49, 95% CI: 1.39–1.60, p < 0.001), indicating that co-masting sites cluster within a narrower interval than the seasonal offset between northern and southern sites, and that the ±3 month window does not under-detect synchrony across that offset.

Given Name: **Surname:**

Affliation for publication:

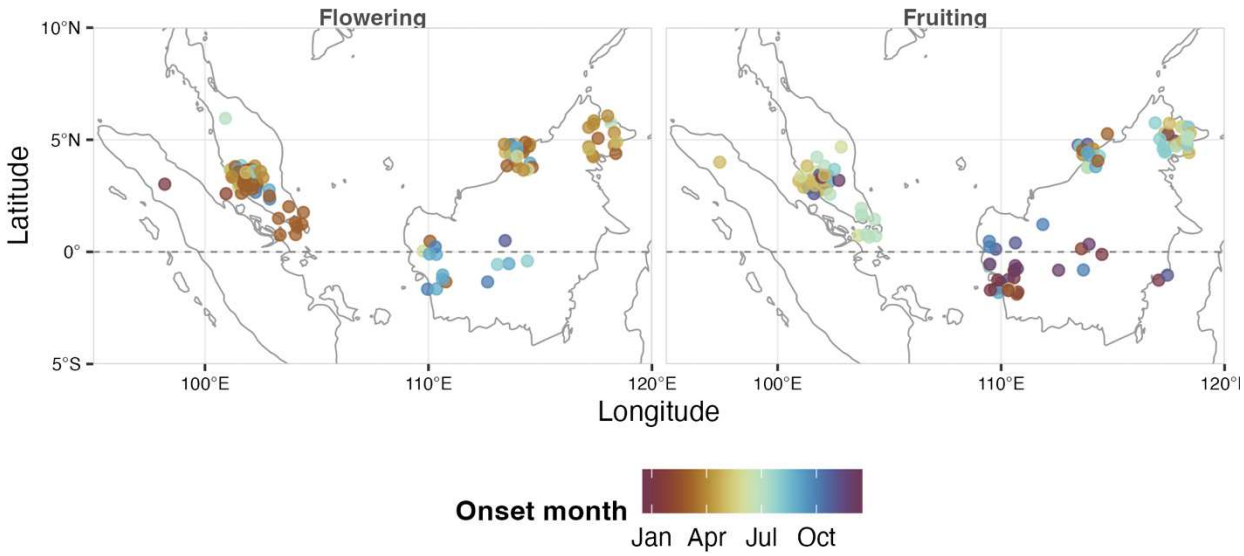
Email address:

LEGEND :		**Instuctions:**
NA	No info	Fill in cells with legend categories for the month and year you are aware of conditions in the area.
0	No GF	
GF1	Small/weak general flowering	
GF2	medium GF	*Put NA for years when you have no knowledge of the area.
GF3	biggest GF I have seen	
F1	small/weak mast fruiting	
F2	mediu MF	
F3	biggest GF I have seen	

Location	
Example	Pasoh Forest Reserve, Malaysia
Lat / Long (optional)	
Example	2.981638, 102.313045
Notes	
	Anything else you want to share about the observations you are providing for this site?

	Q1			Q2			Q3			Q4		
	Jan	Feb	March	April	May	June	July	August	September	Oct	Nov	Dec
1981												
1982												
1983												
1984												
1985												
1986												
1987												
1988												
1989												

Supplementary Figure 4: Example of a blank datasheet for an contributor to report their personal knowledge of a masting event at a specific site.



843
844 **Supplemental Figure 5:** Maps showing the onset timing of flowering and fruiting events in
845 Southeast Asia, illustrating the contrast between onset timing at sites above and below 1° N.
846
847
848