



What drives food security for wildlife in logged and intact forests of tropical Borneo?

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Abstract

Timber extraction is often cited as detrimental to wildlife ecology. Little information, however, in particular from the South-east Asian tropics, is available on how exactly logging affects wildlife food security. To address the gap, this paper presents the first high-resolution comparison of fruit production between logged and intact forests in lowland Borneo. In the period of 2004–2008, dry weight of fruit litter was assessed as a proxy for food security of wildlife. The pheno-phases of 1,054 trees in 14 sampling plots were monitored for 54 months. A total of 143,184 fruits from 50 tree families were collected from six sampling transects totalling 810 km in 34 months. Surprisingly, logged forest (mean = 23.3 kg ha⁻¹, SD = 48.9) produced more fruit litter than intact forest (mean = 16.7 kg ha⁻¹, SD = 23.3), although the difference is not significant based on Student's *t* test; $t(66) = 0.702$, $p = 0.485$. Pheno-phases could not be entirely explained by rainfall and temperature variables. Some evidence, however, indicates tree species composition, stand structure and sunlight exposure were likely determinants of flowering and fruit litter intensity. All things being equal, results imply selective logging if considerably practiced may increase food security for wildlife. The findings, however, should be interpreted with caution since tropical forest phenology and fruit productivity are also driven by a suite of small-scale edaphic attributes and large-scale spatio-temporal meteorological forcing. Although this research deals mainly with Borneo, the principles discussed and insights offered herein are valuable for furthering conversation around sustainable forestry in tropical Asia and elsewhere globally.

Keywords Frugivore · Fruit · Insolation · Meteorology · Phenology

Introduction

The Southeast Asia region is a mega-biodiversity hotspot (Mittermeier et al. 2011) with the highest proportion of endemic species globally (Myers et al. 2000). However, nearly 70% of lowland forests were lost to timber extraction and agriculture expansion (Harrison et al. 2020; Verma et al. 2020). Remnant wildlife population is now in a precarious position, and such vulnerability is exemplified in Borneo.

The tropical lowland forest of Borneo was intensively logged since the 1960s in the Malaysian Sabah/Sarawak and Indonesian Kalimantan, respectively (Collins et al. 1991; Appanah and Turnbull 1998). Generally, two logging approaches were applied, namely, clear felling and selective logging (Appanah and Turnbull 1998). In clear felling practice, all trees were removed, and bare landscapes were often readapted for industrial agriculture (e.g. oil palm and rubber plantations) (Wicke et al. 2011; Gaveau et al. 2016). Selective logging, on the other hand, removes a small percentage of trees in a single operation because most tree species have no commercial value (Appanah and Turnbull 1998).

Malaysia first practised the selective management system (SMS) in the late 1970s involving felling of all commercial species (> 45 cm dbh for non-dipterocarps; > 50 cm dbh for dipterocarps) in a system of 30-year harvest cycle (Appanah and Turnbull 1998). Inevitably, the SMS was replaced by polycyclic management system (PMS) which prescribed the removal of 12–15 trees ha⁻¹ (Appanah and Turnbull 1998). It was viewed as less destructive since dbh was no longer

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the felling threshold (i.e. not all large trees should be felled). The PMS approach typically yielded $90 \text{ m}^3 \text{ ha}^{-1}$ and $120 \text{ m}^3 \text{ ha}^{-1}$ in Sarawak and Sabah, respectively (Johns 1988; Meijaard et al. 2005). Nonetheless, although only 3% of the forest was processed with the PMS approach, studies found c. 50% portion of trees and canopy cover was lost and damaged directly or indirectly during and after the felling process (Johns 1988; Whitmore 1990; Saiful and Latiff 2014).

Although selective logging is often hailed as the answer for sustainable forestry, alarmingly, up to 41% of the unselected trees can be uprooted, crushed or suffer bark and canopy damages during the felling of selected trees (Pinard and Putz 1996). Bulldozers paths, skid trails and timber staging areas further damage the forest floor and disturb soil hydrology (Bryan et al. 2013; Tarigan et al. 2018). Whether clear felling or selective logging is deployed, it is easy to imagine how the overall forest ecology and food web vitality would be inevitably impaired. For example, if a disturbed forest is not able to sustain a reasonable level of fruit productivity after a logging exercise, frugivorous and omnivorous wildlife are likely reduced, thus offering less prey to carnivorous wildlife.

A key measure of forest vitality is fruit biomass per hectare (McCarty et al. 2002; Pessoa et al. 2017). All else being equal, forests that produce more fruit biomass are likely more valuable to wildlife. However, phenology in the tropical forest can be erratic. The lack of climatic seasonality in the tropics often gives a superficial notion that fruiting is continuous throughout the year. This is however not true. Mast flowering and fruiting in the tropical lowland forests are irregular and may occur at intervals of 2 to 10 years (Appanah 1985; Ashton et al. 1988; Azmy et al. 2016; Hosaka et al. 2017; Chechina and Hamann 2019), although a minority of tree species like those from the *Ficus* genus can reproduce several times annually. Past studies linked abiotic factors (e.g. rainfall, temperature) and biotic factors (e.g. pollinators, tree species physiology) for triggering synchronous flowering (e.g. Ng 1977; Ng 1981; van Schaik 1986; Wright and van Schaik 1994; Sakai et al. 2006; Satake et al. 2019; Ushio et al. 2020). Nonetheless, the relationship between forest fruit productivity, wildlife and these factors is still not resolutely clarified in Borneo. This raises a worrying prospect as climate change and socio-economic pressure are becoming more intense in the region. To be effective, the formulation of wildlife conservation actions needs better and more data from the field.

The objective was to clarify fruit productivity differences between selective logged and intact forests in the Danum Valley, Sabah, north Borneo. In this study, we revisited our archive and report the analysis of historical data collected during the period of 2004–2008. To drive the analysis, we asked (1) what are the levels of fruit litter productivity in logged and intact forest and (2) are phenological events

linked to rainfall and temperature? We hope that the data and findings would be valuable to researchers interested to begin or continue where we left off.

In the context of our work, wildlife is regarded as an array of terrestrial vertebrates, and frugivores are dominant vertebrates in tropical forests (Gautier-Hion et al. 1985; Kitamura et al. 2002). We however observed very few vertebrates in Borneo rely entirely on fruits for sustenance. This is expected as an obligate frugivore would most probably not survive the frequent low or non-fruiting periods. Thus, most vertebrates are partially frugivorous and will consume other food sources. Nonetheless, because flowers, seeds and fruits support other wildlife feeding guilds such as nectarivores, granivores, herbivores and omnivores and these animals in turn become food resources for carnivores in the food web, there is an a priori expectation that the phenology events and fruit litter are plausible proxies for providing an overall picture of wildlife food security.

Materials and methods

In general, two key overarching metrics were sampled during the study, namely, phenology events and fruit litter. The phenology metric was observed as an “above-ground” indicator (i.e. tree canopy), while the fruit litter metric was observed as an “on-ground” indicator (i.e. forest floor). For analysis of timber extraction effects on fruit productivity, we collected and compared data from two strata, namely, (1) logged forest and (2) intact forest. Since rainfall, temperature and El Niño–Southern Oscillation (ENSO) events were explicitly included in 73.4%, 19.3% and 1.4% of phenology studies, respectively (Mendoza et al. 2017), such climatic data were also collected and examined for determining their roles in regulating phenology and fruit litter of our study site.

Study site

Study site comprised Ulu Segama Forest Reserve (USFR) (logged forest stratum) and Danum Valley Conservation Area (DVCA) (intact forest stratum) located within the Sabah Foundation Forest Management Area ($9,730 \text{ km}^2$) in Sabah, north Borneo (Fig. 1). Lowland evergreen dipterocarp forest and lower montane forest comprise about 90% and 10% of the area, respectively (Marsh and Greer 1992). The lowland evergreen dipterocarp forest is characterized as a tropical forest dominated by trees of the Dipterocarpaceae family located in regions $< 500 \text{ m}$ above sea level (Slik et al. 2003; Wulffraat et al. 2016). However tree species diversity may vary strongly between locations, even when they were close together, and diversity patterns were more pronounced for genera than for families (Slik et al. 2003). Potts et al.

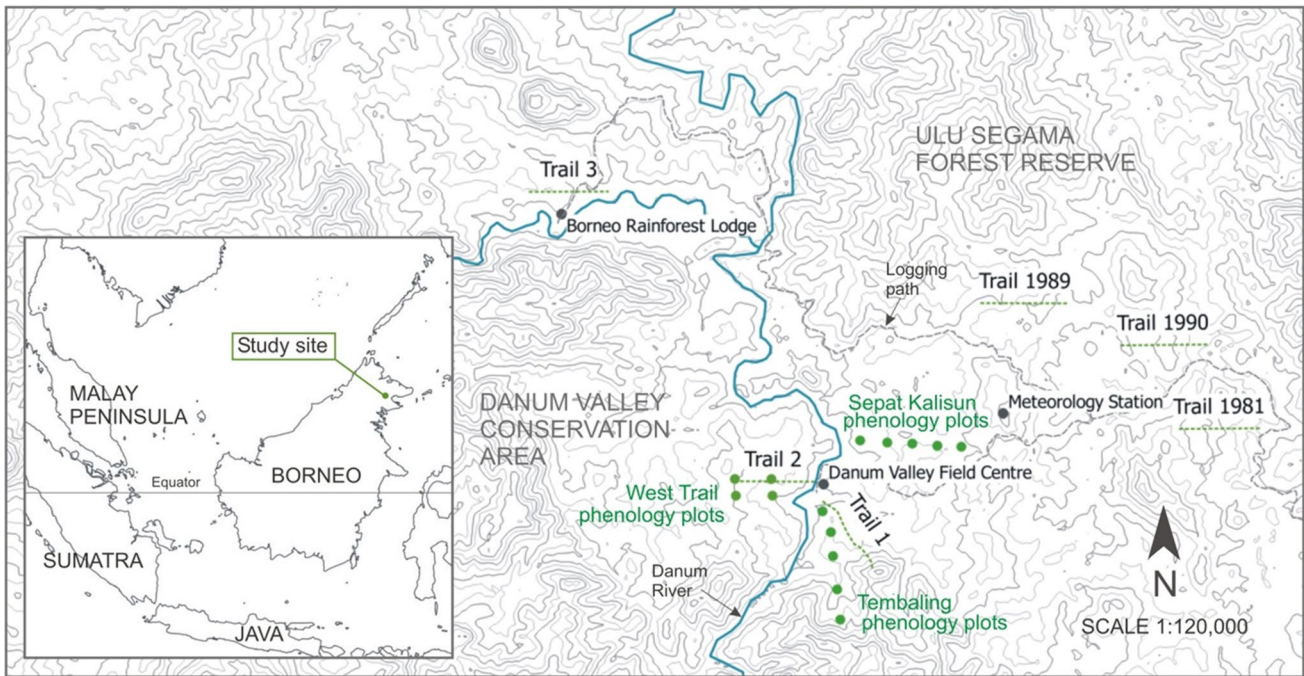


Fig. 1 Study site and the corresponding phenology and fruit litter sampling plots and transects, respectively. The sampling exercises in logged forest were carried out in Sepat Kalisun, Trail 1981, Trail

1989 and Trail 1990. In intact forest, the sampling exercises were deployed in West Trail, Tembaling, Trail 1, Trail 2 and Trail 3

(2002) reported that soil variables were largely responsible for floristic composition between sites in northern Borneo.

Historically, selective logging was carried out in the lowland evergreen dipterocarp forest of USFR, averaging at $118 \text{ m}^3/\text{ha}$ (range $73\text{--}166 \text{ m}^3 \text{ ha}^{-1}$; about 8 trees ha^{-1}) during the 1970–1990 period (Marsh and Greer 1992). Under a 60-year rotation system, trees of $> 60 \text{ cm}$ diameter at breast height (dbh) on lowlands with $< 20^\circ$ slope were selectively logged (Whitmore 1984; Marsh 1995). Berry et al. (2010) reported that up to 53% of above-ground biomass was lost as a result of selective logging in the study site.

Sampling design

Phenology

In this study, we consider phenology events and fruit litter (i.e. ripe fallen fruits, including fleshy and non-fleshy remnants) as primary proxies of forest vitality, productivity and carrying capacity since 82–90% of tropical forest tree species produce fruits (Willson et al. 1989; Hanya and Aiba 2010) that are likely passed on to the second trophic level consisting a large range of wildlife community (Dew 2005).

This study adopted the same sampling plots that were examined by Norhayati (2001) to enable phenology data from Norhayati (2001) to be integrated with data from this study. The sampling exercises were stratified into two sites,

namely, (1) logged forest and (2) intact forest. In logged forest stratum, the Sepat Kalisun phenology sampling plot was established. In intact forest stratum, the West Trail and Tembaling phenology sampling plots were instituted. In every plot, an area of 20 m width and 100 m length (0.2 hectare) was established, and the three plots were about 500 m apart (Fig. 1 and Table 1). All trees with $> 10 \text{ cm}$ dbh were marked, numbered and identified to species level, and pheno-phase sampling (i.e. flushing, flowering and fruiting) was carried out in the phenology sampling plots. Canopies of marked trees were visually monitored monthly for phenophases with binoculars as practiced in most studies (77%; Mendoza et al. 2017) from July 2004 to December 2008 (54 months).

Fruit litter

Similar to the pheno-phase sampling exercise, the fruit litter sampling transects were also stratified into two sites, namely, (1) logged forest and (2) intact forest; there were three such transects in logged forest and three in intact forest. In logged forest stratum, sampling transects were established in Trail 1981, Trail 1989 and Trail 1990. In the intact forest stratum, sampling transects were established in Tembaling (Trail 1), West Trail (Trail 2) and Borneo Rainforest Lodge (Trail 3). Each transect has an area of 0.7 m width and 2000 m length (0.14 hectare). Transects were at least 500 m apart,

Table 1 Sampling design

Metric	Phenology		Fruit litter	
	Logged forest	Intact forest	Logged forest	Intact forest
Name designation	Sepat Kalisun (<i>n</i> = 443 trees)	West Trail (<i>n</i> = 140 trees) Tembaling (<i>n</i> = 471 trees)	Trail 1981 Trail 1989 Trail 1990	Trail 1 Trail 2 Trail 3
Sampling plot/transect size	Plots of 20 m width and 100 m length (0.2 ha) were established at least 500 m apart		Transects of 0.7 m width and 2000 m length (0.14 ha) were established at least 500 m apart	
Sampling frequency	Monthly by three field assistants. Pheno-phase variables were manually observed by binoculars		Twice monthly by three field assistants. Fruit litter was manually collected by hand	
Sampling period	July 2004 to December 2008 (54 months)		April 2005 to January 2008 (34 months)	
Variable	Flushing, flowering and fruiting trees		Dry biomass of fruit litter	
Unit	% trees		g ha ⁻¹ or kg ha ⁻¹	

and distance markers were placed at 50-m interval in each transect (Fig. 1 and Table 1). The transects were cleared from leaf litter and debris after every fruit litter collection process to ensure fruit litter was visible in subsequent collections 2 weeks later. The bi-monthly sampling exercises were carried out from April 2005 to January 2008 (34 months). Transect in Trail 3 (intact forest stratum) however had to be abandoned from January 2007 onwards due to access difficulties; the path was damaged by flood. The shortcoming was not expected to affect the results since fruit litter data was normalized to the unit of g ha⁻¹ and not the number of transects sampled.

Variable description

Pheno-phases were categorized as follows: (1) flushing (emergence of young leaves), (2) flowering (emergence and development of inflorescence) and (3) fruiting (emergence and development of infructescence). Following Norhayati (2001) who first sampled the designated phenology plots described earlier, a marked tree was considered flushing, flowering or fruiting when its canopy has a coverage of > 4% emerging young leaves, inflorescence or infructescence, respectively. Correspondingly, the presence of flower buds, blooming flowers (anthesis) and opened flowers on the canopy was collectively considered as flowering. Data were recorded through visual estimation until all flushes, flowers and fruits ceased to exist in the canopy of marked trees. The methods and thresholds described followed Norhayati (2001) to ensure data collected in this study can be integrated with data collected by Norhayati (2001) to support a more comprehensive analysis.

The morphology of fruits and leaves on tree crowns was observed with binoculars (10×40 magnification) for species identification. Fresh leaves, fallen dry leaves and fruit litter were further scrutinized for taxonomic confirmation, and

tree species were identified by resident botanists in Danum Valley Field Centre (DVFC) with reference to the collection of DVFC herbarium and Sabah Forestry Department (Forest Research Centre, Sepilok).

A fruiting event was regarded as the period from the first observed ripe fruit to the time when almost all fruits (> 95%) had fallen. Following Ashton et al. (1988) and Numata et al. (2003), we defined 4–20% and > 20% of marked trees fruiting as minor and major mast fruiting events, respectively. All whole or decomposed fallen seeded structures with fleshy arils and non-fleshy remnants were categorized as “fruits”. Given our intent was to analyse food availability for wildlife, fleshy and tightly clustered inflorescences (i.e. syconium lined with tiny uniovulate flowers) of tree species such as those from the *Ficus* genus were also considered as “fruits” in an ecological sense.

Collected wet fruit litter was brought back to the laboratory for identification to species level, counted, weighed and dried in a laboratory oven at 80 °C for 48 h. Oven-dried fruit litter was weighed with an electronic scale sensitive to 0.01 g to obtain dry biomass weight. The wet and dry biomass variables were standardized to g ha⁻¹ or kg ha⁻¹ to enable comparison with other similar studies. We further defined a major fruiting event as a period when the dry biomass weight of fruit litter was > 2.5 kg ha⁻¹ month⁻¹.

Climatic data

The study site has a mean temperature of 26.7 °C and mean rainfall of 2,669 mm annually, which is typical of moist aseasonal tropical forest. Wide variations in monthly rainfall, however, may occur as the local climate is also partly driven by atmospheric movements influenced by monsoons or typhoons. Rainfall and temperature data (1985–2008) were obtained from a meteorological station operated by the Royal Society South East Asian Rainforest Research Project

in DVCA. Any month recording rainfall of < 100 mm was referred to as a drought month. The Oceanic Niño Index (ONI) was monitored to determine the effects of ENSO on the study site. El Niño conditions (i.e. anomalous warming) were expected to be prevalent when ONI is +0.5 or higher. In contrast, La Niña conditions were anticipated (i.e. anomalous cooling) when the ONI is –0.5 or lower (Deliège and Nicolay 2017). Monthly Oceanic Niño Index data were obtained from the Climate Prediction Center, National Oceanic and Atmospheric Administration (NOAA), US Department of Commerce (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

Statistical analyses

Statistical analyses were examined using functions provided in software IBM SPSS version 20. All linearity between variables was examined by Pearson's correlation test. The Student's *t* test was computed to determine differences in fruit litter productivity in logged and intact forests. We applied Ward's hierarchical clustering algorithm to determine the statistical similarity or Euclidean distance, between the trails of logged and intact forest. To detect potential bias due to temporal autocorrelation, the residual maximum likelihood (REML) method often used in forest phenology studies (e.g. Gleeson and Cullis 1987; Costa e Silva et al. 2019; Bogdziewicz et al. 2020; Gastauer et al. 2020) was applied with function provided in SPSS to account for variances of fixed from random effects. Statistical values with *p* value equal or lesser than 0.05 were considered significant. The Kaiser–Meyer–Olkin (KMO) and Bartlett's sphericity tests were also explored to determine whether factor analysis can be applied to explain variance maxima. KMO values of equal or greater than 0.5 were considered significant. Bartlett test *p* value equal or less than 0.05 was taken as significant. The Shapiro–Wilk test and Q–Q plot were applied to examine normality, and *p* values equal or greater than 0.05 were taken as the dataset was normally distributed.

Results

Pheno-phase correlations with rainfall and temperature data were mired by outliers when the Pearson linear correlation test was carried out; thus, statistical inferences could not be decisively applied. Similar problem was encountered by studies elsewhere, and the time series visualization method was commonly adopted to support result interpretation (e.g. Sakai et al. 1999; Numata et al. 2003; Hamann 2004; Polansky and Boesch 2013; Pires et al. 2018). Correspondingly, our results presented herein are mainly underpinned by time series illustration provided in Fig. 2.

Phenology

Across 14 sampling plots, we monitored and recorded pheno-phases of 1,054 trees in 54 months. Flushing, flowering and fruiting of various sporadic intensities occurred in logged and intact sampling plots throughout the years (Fig. 2). Comparatively, logged forest sampling plots recorded more percentage of flowering trees but fairly less percentage of fruiting trees during the study period. The West Trail (*n* = 140 trees; intact forest) had somewhat consistently recorded a higher percentage of fruiting trees although its sampling plots have the least trees as compared to Tembaling (*n* = 471; intact forest) and Sepat Kalisun (*n* = 443; logged forest). Data showed flowering occurrences were higher in logged forest but did not translate to higher fruiting occurrences when compared to intact forest (Fig. 2).

Fruit litter

A total length of 810 km was surveyed in six designated sampling transects throughout the sampling period of 34 months. We collected 143,184 fruits from 50 tree families with 176 and 113 trees identified to species and genus level, respectively. Trail 1990 (logged forest; 133.9 kg ha⁻¹) recorded the highest fruit litter followed by Trail 1989 (logged forest; 70.6 kg ha⁻¹) and Trail 2 (intact forest; 54.6 kg ha⁻¹). As mentioned earlier, Trail 3 (intact forest) was abandoned from January 2007 onwards due to access difficulty. With only 21 months' exercises, Trail 3 recorded a fairly high level of fruit litter at 60.3 kg ha⁻¹. Thus, Trail 3 fruit litter was expected to exceed the amount of Trail 1989, and all sampling transects in the intact forest if it were not abandoned.

All sampling transects recorded low fruit litter from January 2006 to January 2007 (Fig. 2; see C). Since our study focused on wildlife food security, this was taken as the worst-case scenario warranting critical attention. Alarmingly, the monthly average fruit litter was only 0.393 kg ha⁻¹ (SD = 0.366) and 0.241 kg ha⁻¹ (SD = 0.212) in logged and intact forests, respectively, during said period.

Although the stratum of logged forest produced more fruit litter (mean = 23.3 kg ha⁻¹, SD = 48.9) than intact forest (mean = 16.7 kg ha⁻¹, SD = 23.3), the Student's *t* test indicated that the mean difference is not significant; *t*(66) = 0.702, *p* = 0.485. This implied fruit litter amount in sampling transects of logged and intact forest did not demonstrate a stark dissimilarity. Also, the result could have been affected by outlier data recorded in 2005 and 2007 (Fig. 3). For unknown reason(s), trees in trail 1990 were exceptionally productive (55.5 kg ha⁻¹) in July 2005. Cluster analysis and resultant dendrogram showed some trails in logged, and intact forests were grouped together (Fig. 4).

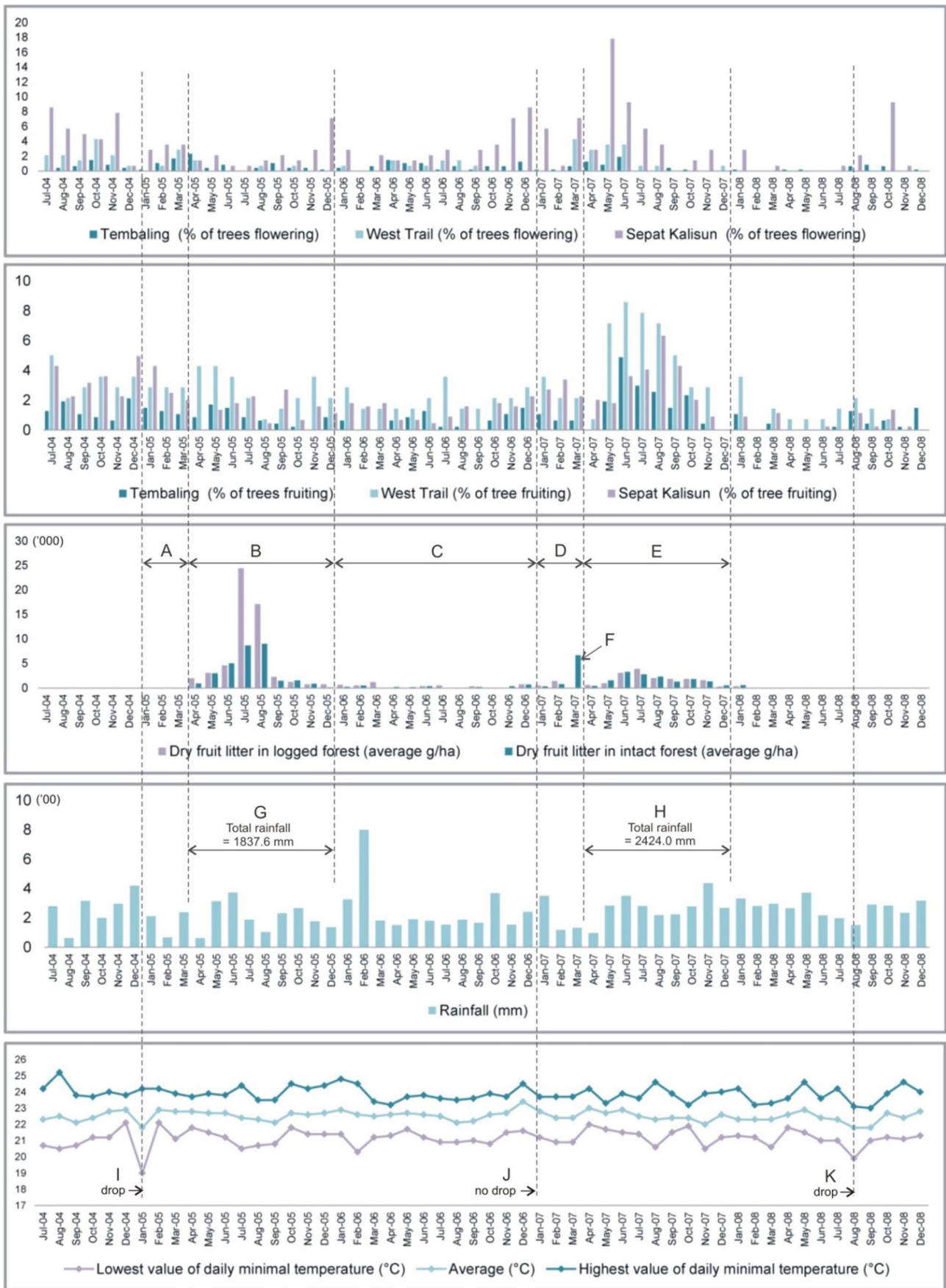


Fig. 2 Time series trend of all variables recorded in this study illustrated in matching sequence and direction

Two major fruit litter episodes were recorded during the period of April to December 2005 and April to December 2007 (Fig. 2; see B and E). During peak fruit litter in July 2005, the average fruit litter of logged forest (24.4 kg ha^{-1}) was about triple that of fruit litter in intact forest (8.6 kg ha^{-1}). Surprisingly, the period of April to December 2005 recorded a much higher level of fruit litter although the flowering and fruiting percentage of trees were not pronounced (Fig. 2; see B). In contrast, the flowering and fruiting percentage of trees was abnormally high during the period of April to December 2007, and yet, the resultant fruit litter was clearly lower (Fig. 2; see E).

In general, sampling transects in logged and intact forests demonstrated similar monthly fruit litter trend but not intensity. Relatively higher fruit litter was recorded in more sampling transects in logged forest (Trail 1981 mean = $0.9764 \text{ kg ha}^{-1}$; Trail 1989 mean = 2.077 kg ha^{-1} ; Trail 1990 mean = 3.941 kg ha^{-1}) than in intact forest (Trail 1 mean = $0.9578 \text{ kg ha}^{-1}$; Trail 2 mean = 1.606 kg ha^{-1} ; Trail 3 mean = 2.871 kg ha^{-1}). The trees in Trail 1990 were exceptionally productive (Fig. 3) (55.5 kg ha^{-1}) in July 2005.

An abnormal fruit litter surge occurred in March 2007 (Fig. 2; see F). Close examination showed the surge was contributed by 24 tennis ball sized fruits from a single *Diospyros macrophylla* tree (Ebenaceae) (total dry weight = 916 g) and a soccer ball sized fruit from a *Neesia syndandra* tree (Malvaceae) (dry weight = 755 g) collected from Trail 2 sampling transects in intact forest. Together, fruit litter from both trees totalled 1671 g or 94% of the total 1716 g fruit litter collected in Trail 2 during that particular sampling exercise. If fruit litter from the two trees were excluded, mean dry fruit litter of intact forest for March 2007 would be $< 2.5 \text{ kg ha}^{-1} \text{ month}^{-1}$. Consequently, we did not consider the surge in March 2007 as a major fruiting event.

Rainfall

During the study period, 2005 recorded the lowest annual rainfall (2,345.9 mm). The year was also the third driest year in the period of 1985–2009. In general, April and August were typically the driest months annually with mean rainfall of 142.0 mm (SD = 88.8) and 143.7 mm (SD = 62.7), respectively, compared to the mean monthly rainfall of 245.2 mm (SD = 118.3) during the study period. Based on Pearson's correlation test, the monthly rainfall frequency and intensity could not be statistically explained by ONI ($n = 288$, $R^2 = 0.0727$, $p = 0.27$) (Fig. 5), thus implying the ENSO cycle has no direct effect on the climate of the study site.

Flowering, flushing, fruiting and fruit litter dataset could not be statistically associated with rainfall and temperature

although values were additionally examined with a time lag of 1–5 months. When a REML analysis was further performed, we found no significant temporal autocorrelation between rainfall with flushing (Tembaling, $F = 0.000$, $p = 0.989$; West Trail, $F = 0.743$, $p = 0.394$; Sepat Kalisun, $F = 0.319$, $p = 0.575$), flowering (Tembaling, $F = 1.926$, $p = 0.172$; West Trail, $F = 0.482$, $p = 0.491$; Sepat Kalisun, $F = 0.023$, $p = 0.879$) and fruiting (Tembaling, $F = 0.036$, $p = 0.851$; West Trail, $F = 0.302$, $p = 0.586$; Sepat Kalisun, $F = 0.032$, $p = 0.858$). The pheno-phases of flushing, flowering and fruiting occurred throughout the year regardless of rainfall intensity. During two major fruit litter episodes in the period of April to December 2005 and April to December 2007, total rainfall was 1837.8 mm (Fig. 2; see G) and 2424.0 mm, respectively (Fig. 2; see H). Although rainfall difference was 586.2 mm, the mean fruit litter of logged forest was about triple that of fruit litter in intact forest as highlighted earlier. Although the results showed rainfall did not consistently drive flushing, flowering, fruiting and fruit litter, we however detected the occurrence of dry months (Fig. 2; see A and D) prior to major fruit litter episodes in the period of April to December 2005 and April to December 2007.

Temperature

The mean minimum temperature was $22.6 \text{ }^\circ\text{C}$, with only two values falling below $20 \text{ }^\circ\text{C}$ on 16–19 January 2005 ($19.0\text{--}19.9 \text{ }^\circ\text{C}$) (Fig. 2; see I) and 17 August 2008 ($19.9 \text{ }^\circ\text{C}$) (Fig. 2; see K). The temperature drops occurred at night time, and we observed the night sky was cloudless. Nonetheless, these markedly drops in temperature could not be associated with the triggering of flowering as shown in Fig. 2 (see I, J, K). Results suggest flowering tends to occur throughout the year in logged and intact forest regardless of fluctuation or sudden drop of temperature.

Discussions

Rainfall and temperature drops were previously suggested to trigger flowering in our region of study (Opler et al. 1976; Ashton et al. 1988; Appanah 1993; Sakai et al. 1999). Our results however could not support the studies mentioned but agree with a seminal study by Putz (1979, p. 13) who remarked that "... there are many exceptions" and "rainfall per se, or the lack of it, may not be the factor directly responsible for stimulating trees to flower". Also, results showed logged forest produced more fruit litter than intact forest—which was surprising. The findings were interesting and warrant deliberation as it challenges conventional notions, especially that intact forest is supposed to be ideal for wildlife.

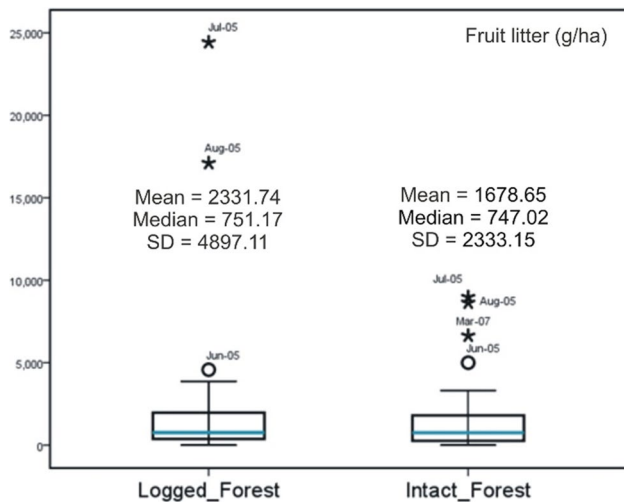


Fig. 3 Monthly fruit litter comparison (g ha^{-1}) of each forest stratum recorded during the study. Results showed monthly fruit litter was higher in logged forest, although the Student's t test indicated that the mean difference is not significant; $t(66)=0.702$, $p=0.485$

Although some studies agree with our findings since they found vertebrate richness was comparable or relatively higher in logged forests when compared to intact forest (e.g. Bernard et al. 2016; Roopsind et al. 2017), our analyses, however, should be interpreted with caution. We do not suggest logged forest is particularly favourable for wildlife food security, nor we are suggesting rainfall and temperature have absolutely no influence on tropical tree phenology. Consequently, we are now certain there are other proximate abiotic and biotic factors at play. Fruit productivity in aseasonal tropical forest is highly sensitive to a mix of factors (Kinnaird 1992; Appanah 1993; Numata et al. 2003). The

outcomes are expected to shift even with just a slight variance in one or two direct or indirect factors. In the following sections, we discuss the possible dynamisms that may have triggered or enhanced fruit productivity, in particular mast flowering and peak fruit litter episodes. The discourse is further integrated with previous research in our study site and elsewhere globally to suggest trends and identify gaps for future research.

Tree physical composition

As mentioned earlier, relatively more monthly fruit litter was recorded in logged forest (mean = 23.3 kg ha^{-1} , $\text{SD}=48.9$) than in intact forest (mean = 16.7 kg ha^{-1} , $\text{SD}=23.3$), although the difference is not significant; $t(66)=0.702$, $p=0.485$. We argue the phenomenon may be explained by tree scarcity resulting from selective logging practices in the study site. With less canopy crowding, we observed sunlight reached more parts of the logged forest canopy. We argue this may have contributed to higher percentage of flowering trees recorded in the pheno-phase sampling plots of logged forest. Following Calle et al. (2010), sunlight exposure is scientifically termed as insolation or incoming solar radiation. Many studies have attributed insolation, some using the term photoperiod, for triggering mast flowering in the aseasonal tropical forest (e.g. Ng 1977; Calle et al. 2010). Studies also show insolation increase explicitly supports higher levels of photosynthesis and carbohydrate production critically needed for the fruit production process (e.g. Greene et al. 2002; Ichie et al. 2013).

In the context of our study site, a possible explanation is, with less canopy crowding (i.e. as a result of selective logging), the overall canopy surface of each tree can receive

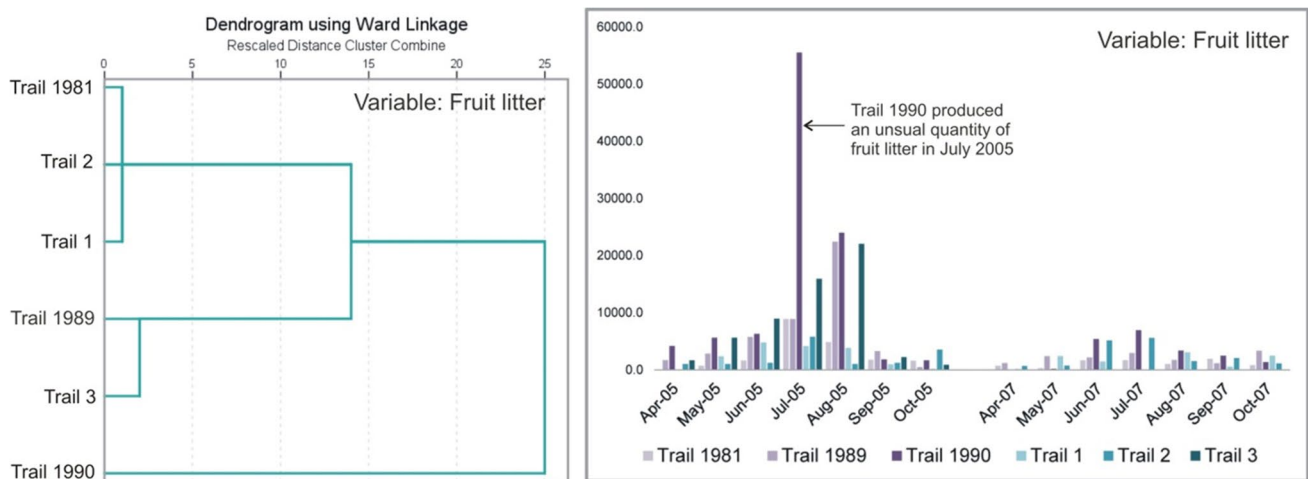


Fig. 4 Result of cluster analysis (left) showing the levels of fruit litter similarity and time series trend (right) of each sampling transect during major fruit litter of April to October period in 2005 and 2007,

respectively. Logged forest sampling transects are represented by Trail 1981, Trail 1989 and Trail 1990; intact forest sampling transects are represented by Trail 1, Trail 2 and Trail 3

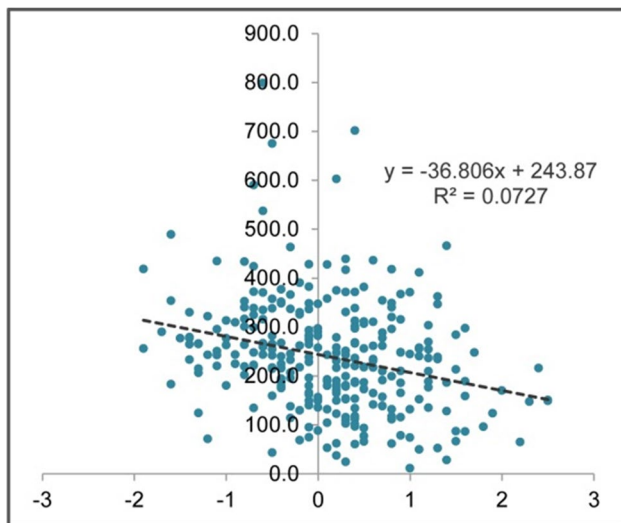


Fig. 5 The correlation between rainfall (mm) and ONI was poor based on data recorded in the period of 1985–2011 (26 years)

higher exposure of insolation. This may have resulted in higher flowering and fruiting intensity. Along similar lines, the measure of rainfall may actually be a useful proxy—although not robust enough for statistical inferences. Widespread stormy cloud coverage could shield off sunlight from the forest canopy, and this may be more frequent in certain periods of the year. We shall discuss the cloud coverage factor in greater detail in section “[Insolation](#)”.

Tree species variation

Tropical forests in Borneo, of course, are a complex mix of tree age and species with a wide spectrum of physical and biological characteristics. As outlined earlier, there were 140 and 471 trees in pheno-phase sampling plots of West Trail and Tembaling Trail, respectively. There were more trees in Tembaling Trail although both localities were in the same stable and intact forest stratum. Also, our results showed trails in the same stratum did not record fruit litter of same intensity. In March 2007, two trees (*Diospyros macrophylla* and *Neesia synandra*) contributed 94% of the fruit litter dry weight in Trail 2 during non-fruiting period. Our data implies tree species diversity and fruit production were highly heterogenous and patchy. Such species disparity was also reported in our study area by Norhayati (2001) and other parts of Borneo (Slik et al. 2002; Howlett and Davidson 2003; Brearley et al. 2004).

The fruit litter levels recorded in logged and intact forest of our study site may have been influenced by tree species variation caused by timber extraction practices. Larger tree species were typically targeted during timber extraction exercises. If small tree species happened to produce the most fruit litter, logging practices may have systematically caused higher food

production. The notion was first raised by Hanya et al. (2005) who also found forest food production in logged and naturally regenerated forest which was higher than intact forest. They found small tree species that produced more fruits had become dominant after the selective logging exercise in their study site. This was compounded by more sunlight that enhanced the flowering and fruiting capacity of small tree species when the large tree species were fell. These are plausible factors worth investigating in the future.

Many studies also linked tree species variation in the forest with small-scale disturbances, topography, climatic forcing and soil fertility (e.g. Phillips et al. 1994; Givnish 1999; Onyekwelu et al. 2008; Silva-Flores et al. 2014; Khaine et al. 2018). But the studies often fail to explain, as in our case, why two particular trees in Trail 2 were present among many other species. They did not seem to be a part of a larger cluster of *D. macrophylla* or *N. synandra* since no other similar species were observed within the vicinity. What causes such heterogeneity? We speculate wildlife diversity present in the forest may also be a factor.

Fruit adaptations, namely, colour, chemistry and morphology, are often hypothesized as an adaptation of plant–animal seed–disperser interactions and mutualism (Kitamura et al. 2002; Voigt et al. 2004; Hodgkison et al. 2013; Muñoz et al. 2017). In the tropical forest, 50–75% of tree species bear fruits that are adapted for consumption by vertebrates (Howe and Smallwood 1982). In our study site, Hanya et al. (2020) investigated the foraging behaviours of five primate species and found each species has varying spatial segregation in their horizontal and vertical movements. It is therefore fair to expect foraging behaviour, movement distance and abundance of a wide range of vertebrates to have a delicate effect on tree species dispersal over temporal and spatial scale. Large vertebrates tend to select large fruits, but their population are usually small and prone to extinction from habitat degradation or loss (Kitamura et al. 2002). The quantity of dispersal services for large fruit tree species may likely be less. On the other hand, small fruits are consumed by a wider range of vertebrates, some with aerial capacity (e.g. bats and birds). Trees species with small fruits are likely more prevalent in the forest. Since each vertebrate species has unique foraging behaviour and perhaps predator avoidance strategy, it may disperse seeds in a certain location but not in another, though in the same forest stratum. When such process is further compounded by vertebrates of various sizes and movement dynamism, it will create a complex distribution pattern of seedlings in the forest over time.

Climatic factors

Rainfall

Our results showed phenology event of flushing, flowering, fruiting and fruit litter could not be explained solely or in part by temperature, ONI and rainfall factors. This is not unusual since some studies elsewhere had also showed rainfall and temperature fluxes are not decisive factors in triggering flowering and fruiting in tropical ecosystems (e.g. Kallarackal and Roby 2012; Polansky and Boesch 2013; Harrison et al. 2016). Further placing our results into a broader context, we integrated our data with data from previous research in the study site and encountered some interesting observations (Fig. 6). Although the time series trend could not explicitly show any stable correlation between fruiting episodes and climatic forcing, we could somewhat detect some sporadic conditions that may implicate rainfall.

Malayan sun bears (*Helarctos malayanus*) and bearded pigs (*Sus barbatus*) in various stages of emaciation and starvation were detected from August 1999 to September 2000 (Wong et al. 2005). The period was interestingly accompanied by unusual prolonged drop of ONI (anomalous cooling period) accompanied by consistent high rainfall (Fig. 6). During the 1999–2000 famine detected by Wong et al. (2005), rainfall was consistently high. Such condition was also observed in our study as the low fruit litter

period coincided with consistent high rainfall period from January 2006 to January 2007 (Fig. 2; see C); the monthly average fruit litter was only 0.393 kg ha^{-1} ($\text{SD} = 0.366$) and 0.241 kg ha^{-1} ($\text{SD} = 0.212$) in logged and intact forests, respectively. In the context of wildlife food security, this is alarming and could be the worst-case scenario. In contrast, during major fruit litter period, the climate was punctuated by numerous months of low rainfall (Fig. 2; see G). Our data showed both logged and intact forest were capable of flowering and fruiting throughout the year, regardless of rainfall and temperature fluctuation. Nonetheless, only one major fruit litter and minor fruit litter episodes were recorded. Fruit litter was generally low in other periods of time.

From field observation, we have an a priori reason to deduce that rainfall over an extended period may be detrimental to fruit productivity in tropical forests. Heavy or consistent rainfall causes flowers to drop and result in poor or no fruit set. Fruit buds may also drop prematurely in the same manner. Notably, major fruiting episodes tend to occur at 4–11 years interval in our study site (Fig. 6). However, this may not result in actual fruit litter production. As illustrated in Fig. 2 (see B), low trees flowering percentage can successfully produce high levels of fruit litter.

A total of 111 dipterocarps were reportedly dead from snapping and uprooting after an extreme rainfall event in July 2006 in Kabili-Sepilok Forest Reserve, about 100 km from our study site (Margrove et al. 2015). It would not be

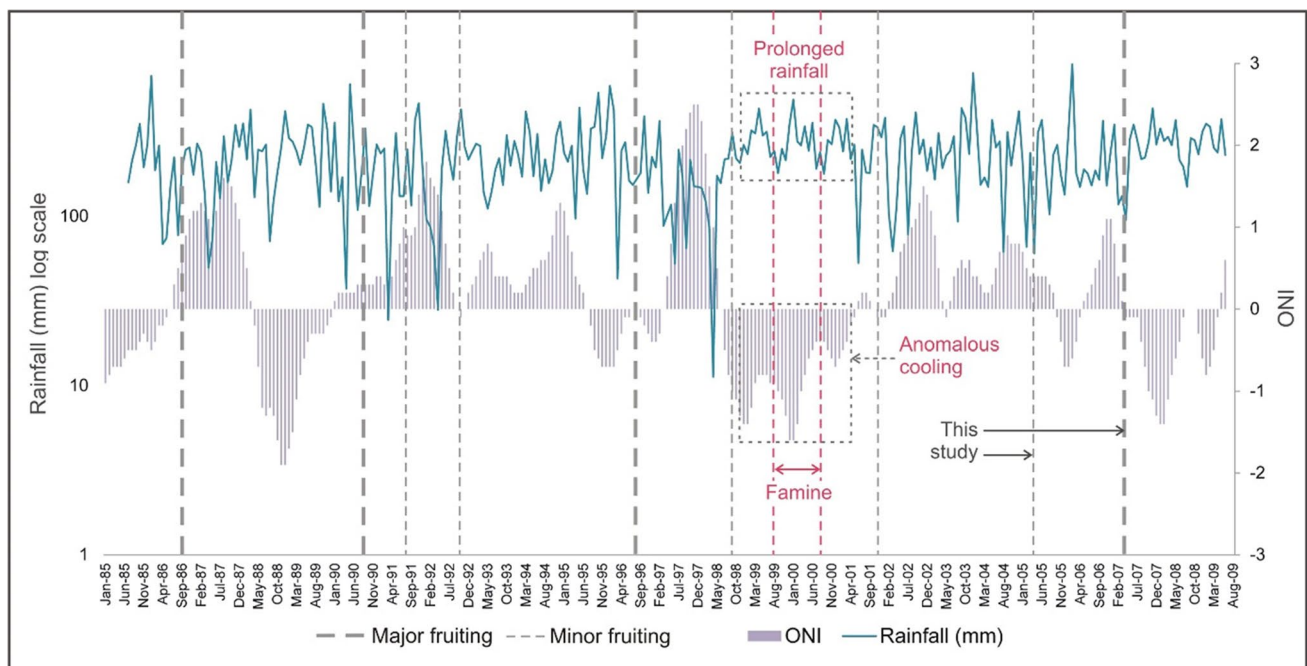


Fig. 6 Time series illustration showing correlation between fruiting and climatic metrics cannot be significantly established when data from this study was consolidated with previous studies (Zakaria 1994; Heydon and Bulloh 1997; Norhayati 2001; Wong et al. 2005).

However, visuals from illustration show prolonged rainfall, possibly induced by anomalous cooling of La Niña, may have reduced fruit litter drastically from August 1999 to September 2000 and caused the famine described by Wong et al. (2005)

surprising if similar incident can occur in our study site, thus affecting fruit litter productivity. On these grounds, although rainfall could not be link to phenology events, we argue that rainfall is a valuable metric after all. Prolonged and sporadic extreme rainfall disrupts fruit setting processes, and this is not a favourable condition in the context of fruit productivity. Crucially, dry periods are imperative to support fruit production in the tropical forest of Borneo. We also speculate excessive rainfall may disturb pollination processes. These concerns should be explored by future research.

Insolation

Day length and temperature do not differ much in regions close to the equator. There are occurrences of insolation cycles, however, in the equatorial regions due to tilt and elliptic orbit of the earth around the sun. Therefore, daily insolation received by the forest canopy is also variable according to different time of the year. In our study site located in the equatorial region, equinoxes occur in March and September resulting in a bimodal cycle of insolation annually. Insolation maxima occur when the sun passes directly overhead during these months and reduces during solstices. The bimodal cycle would gradually combine at latitudes further from the equator. Insolation that reaches

the forest canopy is dependent on length of daytime, and this may be different in the tropical and temperate regions according to season. Also, insolation is determined by sunlight angle striking the forest canopy. Since there is very little change in length of daytime in the tropical region, we argue synchronous flowering, or sometimes termed as mast flowering (Fig. 7), in our study site may be triggered by sunlight angle. But what about the bimodal cycle of insolation that occurs annually? Shouldn't there be two prominent flowering events annually?

Such enigma exemplifies the complexity of tropical ecosystem and brings us back to the subject of cloud coverage pointed out earlier in section "**Tree physical composition**". Insolation reaching forest canopy may be substantially reduced when cloud cover is widespread during the monsoon season. Additionally, on average, c. 20 tropical typhoons of various intensities pass by the northern region of our study site throughout the year (United Nation Office for Disaster Risk Reduction (2019)), and vortex they produce can draw heavy clouds and rain to north Borneo (Ng et al. 2019). Further to this, despite its fairly small land size, the north Borneo region does not typically experience a homogenous rainfall pattern. The analysis of dataset from 2006 to 2015 suggests there are six groupings with dissimilar rainfall trends in north Borneo (Ng et al. 2019),

Fig. 7 Synchronous flowering event (A photo credit, Mohd. Aminur Faiz Suis of Forest Research Center, Sabah Forestry Department) and examples of fruit litter (B and C), including fleshy and non-fleshy remnants, collected during the study



and pheno-phase disparity is likely between two small neighbouring regions over relatively small distances. This is expected as north Borneo is flanked by the South China Sea, Sulu Sea and Celebes Sea. Intra-seasonal and inter-decadal meteorological forcing and interaction among them would certainly shape the amount of cloud coverage over north Borneo. Other climatic forcing includes the Indo-Australian monsoon system, Madden–Julian Oscillation (MJO), ENSO, Indian Ocean Dipole (IOD) and the Borneo vortex phenomenon (Manton et al. 2001; Juneng and Tangang 2005; Zheng et al. 2010; Xavier et al. 2014). As such, cloud cover over Borneo is highly influenced by the dynamics of episodic and sporadic meteorological forcing. Correspondingly, insolation can vary wildly and therefore affecting the consistency of flowering and fruiting events.

Limitations and future research

Biological and edaphic factors can generally influence fruit litter production. In our study, we did not investigate pollinator efficacy, or discern between male and female flowering trees, or analyse ages and species of trees (i.e. older or certain species of trees may produce more fruits). Although evidence from Wich et al. (2011) tells us that forest fruit productivity is generally higher in Sumatra than Borneo and soil fertility is likely the cause, we did not investigate soil quality of the study site. Borchert et al. (2005) also inform us that tropical phenology may be determined by water stress during dry season and varies widely with soil water storage ability. Research that clarifies such dynamics should be pursued. For broader perspectives, we also did not examine how wildlife persists during fruit scarcity bottleneck periods and what is the significance of asynchronous tree species such as figs in offering fallback food during the bottlenecks. We are curious to know—do climatic cues affect asynchronous tree species, even marginally?

Nonetheless, given mentioned caveats and that the phenology and fruit litter variables included in our study were fairly robust and commonly applied in other studies (Mendoza et al. 2017), we are confident the results accurately reflect relative fruits productivity of the sampling sites. We urge researchers to explore limitations highlighted in future studies. Additionally, Mendoza et al. (2017) reported only 3.2% of phenology studies, however, had included insolation data collection and analysis. This shows the insolation factor is relatively under-studied globally, much less in our region. In the advent of anthropogenic climate change, the flux and intensity of insolation are expected to shift. Will such alteration affect wildlife food security in the upcoming decades? We urge future research to focus on such concerns.

Conclusion

Study outcome underscores the profound effects of logging practices on wildlife food security. Contrary to the notion that intact forest is ideal for wildlife, our results imply food security was better in selectively logged forest. However, the findings should not be disseminated without being framed with caution. Tree species variation and physical structure in logged and intact forests may have played various circumstantial roles in creating the dissimilarity. Sustainable forestry initiatives should therefore consider fruit productivity patterns of tree species before selecting or excluding them for felling operations. We provide evidence that rainfall, ONI and temperature variances have no direct statistical linearity with phenology events and fruit productivity. Prolonged and excessive rainfall, however, is suggested to be detrimental for fruit setting. There are yet unidentified factors that drive phenology events, and we propose cloud cover intensity that affects insolation may be the unifying denominator.

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We dedicate this paper to field assistant Teck-Chai Koh who met with a fatal accident during this study. We lost a great ecologist and wonderful friend. Teck-Chai will forever remain in our memories and we shall honour him by continuing his passion of tropical ecology research.

Author contribution STW conceived the idea and methodology; STW led the field data collection exercises; STW and KCKN analysed the data and produced the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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