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ORIGINAL RESEARCH

Frugivores flock, but do carnivores follow? Multi-trophic responses to masting in a tropical rainforest

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Abstract

Pulses of plant resources can influence the spatial aggregation and population dynamics of primary consumers, but the extent to which these effects cascade up the food chain to affect secondary consumers remains poorly understood. Mast fruiting events in Southeast Asian dipterocarp forests, for example, are known to impact a wide range of bird and mammal granivores, but it remains unclear whether the predators of these vertebrates are indirectly affected by seed production. Here, we assess bottom-up effects of masting on a suite of primary and secondary consumers in a tropical rainforest in Borneo, using structural equation models to characterize a network of frugivore/granivores and carnivores. The models were parameterized using 10 years of camera trap and seed availability data collected between 2013 and 2024, spanning two major masting events. These models also account for an outbreak of introduced disease (African swine fever) and the reduced abundance of human visitors in the forest during the COVID-19 pandemic. Dipterocarp seed availability was correlated with the intensity of local site use by omnivorous Malay civets (*Viverra tangalunga*) and bearded pigs (*Sus barbatus*), but not granivorous murid rodents or pheasants. Leopard cat site use was correlated with murid rodents, but not pheasants. These findings suggest that masting in this ecosystem is associated with site use intensity of some large-bodied primary consumers but not smaller granivores, and therefore did not percolate up the food web to influence the predators of these taxa, in contrast to research from temperate masting systems.

Keywords Bottom-up community regulation · Trophic dynamics · Granivory · Resource pulses · Food network · Boom-and-bust

Introduction

Episodic resource pulses, such as mast fruiting events, are important drivers of ecosystem dynamics, influencing species interactions and community structure across

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terrestrial systems (McShea 2000). Mast fruiting, or masting, refers to the synchronized and episodic production of large quantities of seeds or fruits by plant populations (Ashton et al. 1988). These events, driven by a combination of climatic variability (Holmgren et al. 2001), local disturbance regimes (Granados et al. 2019), and species-specific reproductive strategies (Kurten et al. 2017), can result in irregular fluctuations in fruit and seed availability across time and space, strongly influencing consumer populations. In particular, mast events often lead to pronounced increases in the abundance of some species, while resource scarcity during non-mast periods can lead to declines, producing characteristic boom–bust population dynamics (Ostfeld et al. 1996).

Primary consumers are notably responsive to masting events. For instance, in temperate forests, masting in oak (*Quercus* spp.) and beech (*Fagus* spp.) is associated with sharp increases in granivore populations, especially rodents (Ostfeld et al. 1996; Schnurr et al. 2002; Zwolak et al. 2018). In tropical Southeast Asia, the sporadic, supra-annual fruiting of the dominant dipterocarp trees, which typically reproduce at intervals of 2–10 years (Brearley et al. 2007), has similar effects on frugivores and granivores. These events temporarily increase the abundance and activity of a wide range of primary consumers in the tropics, including insects (Hosaka et al. 2014), rodents (Nakagawa et al. 2007a), terrestrial birds and pigs (Curran and Leighton 2000), and primates (Kanamori et al. 2017). In contrast, during non-mast periods in the tropics, reduced fruit availability can lead to food shortages, which cause starvation and emigration leading to declines in local abundance (Cosby et al. 2023; Wong et al. 2005).

The effects of masting may propagate through the food web, whereby increases in primary consumer abundance allow corresponding increases in secondary consumers—a bottom-up cascade (Selva et al. 2012). This has been demonstrated in temperate ecosystems (Ostfeld and Keesing 2000), where increased seed availability during mast years led to rodent population booms that supported elevated numbers of predators such as mustelids (Jensen et al. 2012) and raptors (Clotfelter et al. 2007). But whether similar bottom-up cascades from masting occur in hyperdiverse tropical systems remains unresolved. Given reported response of some primary consumers to masting, together with documented associations between frugivore–granivores and their carnivores (Chutipong et al. 2016; Nakagawa et al. 2007b; Petersen et al. 2019; Rajaratnam et al. 2007), such bottom-up cascades might be anticipated. But assessing cascades has been challenging because most studies on trophic interactions in tropical forests are based solely on pairwise associations, potentially missing broader network-level effects within complex species assemblages. Hence, assessing masting effects using a multi-trophic framework offers a promising approach to elucidating bottom-up cascades in tropical systems.

The widespread, but irregular mast fruiting of Southeast Asian dipterocarps has been described as "…perhaps the most spectacular phenomena in tropical biology" (Sakai 2002), but little is known about whether the masting cycles influence not just granivores, but also the predators of granivores. Unlogged rainforest canopy in the region is dominated by dipterocarp trees (Family: Dipterocarpaceae) (Newberry et al. 1992). In particular, the Southeast Asian island of Borneo experiences especially intense mast flowering events (Curran 1994), partly due to its exceptionally high concentration of dipterocarp species (Bartholomew et al. 2021). However, the high timber value of dipterocarps has driven extensive harvesting, leading to widespread population declines on the island. Furthermore, the island supports a diverse assemblage of wildlife that represents multiple trophic levels of consumers, including species of primary consumers such as rodents (Norhayati 2001), bearded pigs (*Sus barbatus*), mesocarnivores such as the leopard cat (*Prionailurus bengalensis*), and apex predators such as the Sunda clouded leopard (*Neofelis diardi*) (Marsh and Greer 1992). This condition was further shaped by two major recent events: the spread of African swine fever (ASF) in 2021, an introduced disease with near-complete fatality in Asian wild pigs, leading to the effective extirpation of the bearded pigs (Luskin et al. 2023) and the nationwide coronavirus-19 (COVID-19) lockdown in 2020 that lowered human presence in forested areas and therefore potentially altered wildlife habitat use (Burton et al. 2024). Together, this creates a unique context for examining how mast fruiting shapes multi-trophic interactions in a tropical rainforest.

We investigate whether the irregular mast fruiting events in a Southeast Asian rainforest trigger cascading effects that extend beyond primary consumers to influence secondary consumers such as carnivores. We examine how variation in dipterocarp seed availability influences site use intensity by both primary consumers (e.g., rodents, pigs, birds) and meso-predators (e.g., leopard cats, civets) in the rainforest of Sabah, Malaysia, located in the northern part of the island of Borneo using long-term camera trapping and fruit/seed survey data. Prior work in the region has shown that dipterocarp masting influences the abundance and spatial activity of many frugivores–granivores (Granados et al. 2019), and that spatiotemporal co-occurrence among some of these species is largely positive and strongest during mast years, suggesting that resource pulses influence associations between primary consumers (Williams et al. 2022). Here, we expand on these studies by using structural equation models (SEMs) to assess potential masting impacts on a multi-trophic network. We used 'piecewise' SEM, in which each hypothesized unidirectional causal relationship within the SEM is evaluated individually through its own component model, rather than assessing the entire structure simultaneously (Shipley 2000). This approach allows each trophic interaction to be interpreted individually, as in the typical pairwise association, but within the context of multi-trophic networks. Using this approach, we aim to determine whether the cascading effects of masting observed in temperate systems also occur across multiple trophic levels in a tropical forest.

Material and methods

Study system

We investigated the relationship between masting and animal activity in the rainforest of Ulu Segama–Malua in Sabah, Malaysian Borneo (Fig. 1). Two sites were studied: the Danum Valley Conservation Area (DVCA) (N 5.102°, E 117.688°), which is an unlogged forest, and the Malua Forest Reserve (MFR) (N 5.167°, E117.564°), which has been selectively logged several times, most recently in 2007 (Hector et al. 2011). Both locations were situated in lowland areas below 300 m above sea level.

Our study builds on a long-term dataset generated from annual surveys conducted between May and September each year from 2013 to 2024. This period includes major masting events in 2014 and 2019 when multiple dipterocarp species produced fruit in synchrony across the landscape. There were also more minor masting events in 2013, 2015, 2023, and 2024, when only a few dipterocarp species produced fruits and at small, localized scales. Year-by-year climate measurements (O'Brien et al. 2025) across survey months (see Online Resource 1) showed generally stable maximum temperatures of 29–34.5 °C, except in 2015, when a noticeable decline in temperatures during the survey period was observed. Meanwhile, total monthly rainfall typically exceeded 100 mm throughout the survey periods, except in July 2015.

Data collection

We collected data on wildlife presence using passive, motion-triggered camera traps deployed at permanent grids in the study site. A total of 46 camera trap stations were located in two separate grids within the Ulu Segama–Malua forest complex, each camera-trapping grid used a ~ 1 km camera spacing (see Fig. 1). Each camera was mounted on a tree approximately 30 cm above the ground and checked every 14 days to ensure functionality, including battery life and resistance to environmental damage. Each time a camera was triggered, it captured three consecutive photos with a 30-s delay before reactivating.

Fruit biomass was estimated from fallen fruit on the ground every 14 days at all operational camera trap stations. Fruit surveys have been conducted at the same plot using

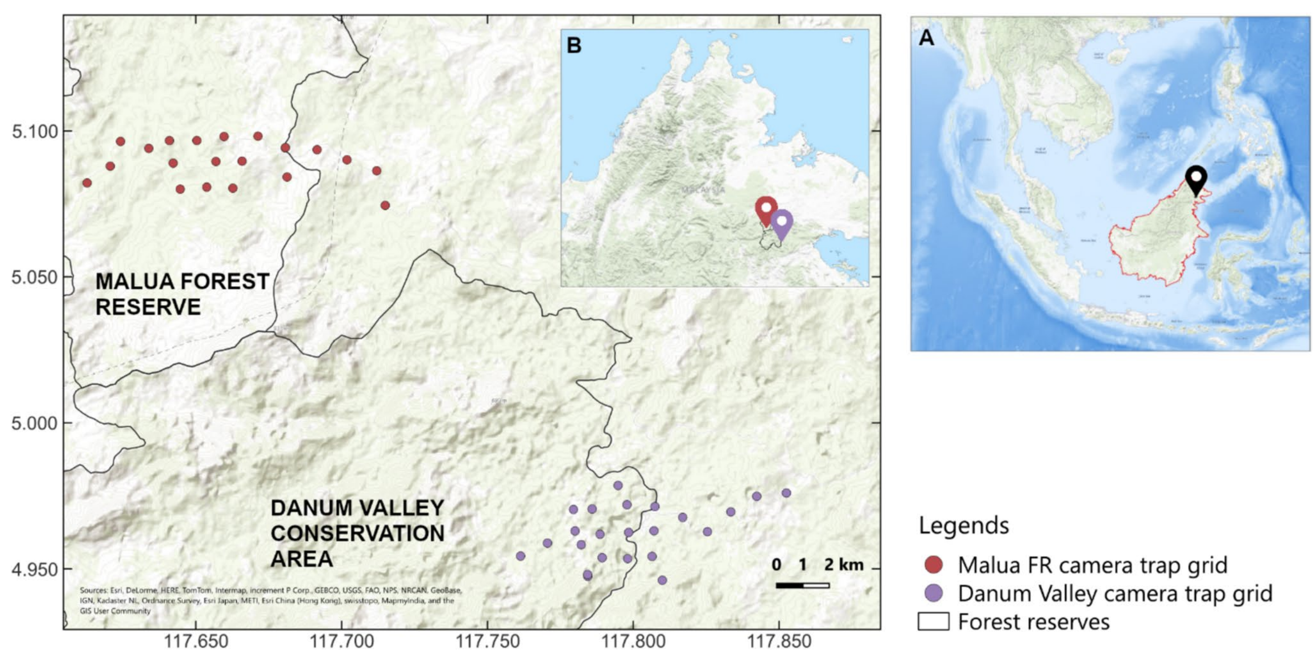

Fig. 1 Map of study sites in Sabah, Malaysia (inset: location of the grid within Borneo island [**A**]) showing 46 camera trap stations (and fruit survey plots) set in the Ulu Segama–Malua forest complex, within two forest reserves (inset: locations of the reserves in Sabah [**B**]): Malua Forest Reserve and Danum Valley Conservation Area, surveyed from 2013 to 2024. The camera trap stations were spaced 1 km apart from one another.

the same collection design from previous studies (Granados et al. 2019; Williams et al. 2022). Fallen fruits were collected from the ground within four 2-m radius circular plots, established around each camera trap station. One plot was established directly at the camera trap position, while the other three plots were placed 20 m away, forming a triangular array (see Online Resource 2). In total, this plot design covers an area of approximately 50 m^2. Fruits collected from these plots were identified to genus or family by trained botanists. Up to ten fruits of the same species were collected from the survey plots for drying and weighing; if more than ten pieces were found, the total number was estimated. We divided the total fruit mass for each group by the ground survey area (50.24 m^2), yielding an estimate of fruit biomass per unit area.

Camera trapping and fruit surveys were conducted annually from 2013 to 2024, except that there were no fruit surveys in 2016 due to limited resources and no camera or fruit surveys in 2017 due to logistical constraints. Additionally, in some years, certain stations were not surveyed due to accessibility issues; for example, the entire MFR grid was excluded in 2021 and 2022, while four camera trap stations in the MFR grid were not surveyed in 2023 and 2024 due to the collapse of the access road.

Fruit biomass data for 2013 were estimated as zero rather than derived from standardized field surveys. In that year, fruit monitoring was conducted using three 20×30 cm traps suspended from tree branches, before transitioning in subsequent years to the ground transects described above. Zero biomass estimation is justified by the following observations: first, none of the traps collected any dipterocarp fruits. Second, a published record (Kanamori et al. 2017) classified 2013 as a minor masting event year, but in recent years where similar minor masting occurred, dipterocarp biomass was either not recorded at the camera trap stations (year 2023) or was recorded as low or negligible (year 2024). Therefore, we assumed that while small, localized dipterocarp masting may have occurred in Danum Valley in 2013, no dipterocarp trees produced seeds at our camera trap stations.

Piecewise structural equation modeling

We modeled multi-trophic responses to masting using piecewise SEMs, with each node represented by a linear mixed-effects model. These nodes measure the correlation between species' site use intensity that could be driven by species interactions. We modeled daily photographic observations of animals as a measure of site use intensity rather than abundance. These observations do not distinguish between repeated visits by the same individual and visits by multiple individuals. To reduce temporal autocorrelation, multiple photographs of the same species recorded within 1 hour at a camera trap were treated as a single observation, and the number of individuals in each photograph was not recorded.

We analyzed daily associations among five animal groups: bearded pigs, pheasants (Phasianidae), Malay civets (*Viverra tangalunga*), murid rodents (Muridae), and leopard cats. Pheasants and murid rodents were grouped at the family level, because some individuals could not be identified to species and confamilials tend to have similar diet patterns. Bearded pigs, pheasants, and murid rodents, though omnivorous, were considered frugivore/granivores (hereafter 'frugivores') in our models due to their strong dietary use of fruits and seeds (Curran and Leighton 2000; Wells and Bagchi 2005); all three are classified as primary consumers in our trophic SEM analysis. Malay civets were considered both primary and secondary consumers because they consume both fruit and small animals (Colon and Sugau 2012). Leopard cats were classified as secondary consumers known to consume both murid rodents (Rajaratnam et al. 2007) and pheasants (Kamler et al. 2020). We also explored models that included clouded leopards as an apex predator, but these failed to converge due to low sample size.

We considered additional environmental factors that could shape or obscure bottom-up dynamics. The outbreak of ASF, which caused a regional collapse of bearded pig populations, was included as a binary predictor (1 for the 2021–2024 period, 0 for before 2021) for pig observations due to its potential to alter species interactions and resource competition. Meanwhile, the COVID-19 lockdown in 2020–2021 dramatically reduced human access to our study sites in comparison to the pre-lockdown period. This effect is included as a binary predictor (1 for the 2020–2021 period, 0 for others) influencing the observation of all five animal groups.

We used zero-inflated Poisson distributions for all variables to account for the large number of sampling units with no animal or fruit records, with camera trap stations as a random effect in all models. As our goal was to assess bottom-up effects, we depicted trophic associations with the influence going strictly from lower to higher trophic levels. For associations potentially involving competition between bearded pigs and Malay civets, we tested two separate models where pigs influenced civets and vice versa. We compared these models using AIC-based model selection. SEMs were fit using the *piecewiseSEM* package (Lefcheck 2015) in the R programming language (version 4.4.0) (R Core Team 2022).

Results

Camera trapping and dipterocarp records for 10 years

The total camera-trapping effort, calculated as the total number of photographic observations across 10 years, amounted to 19,390 observations (see Online Resource 3). This effort yielded 2970 independent observations of bearded pigs, 1763 of pheasants, 548 of murid rodents, 438 of Malay civets, 18 of leopard cats, and 9 of clouded leopards, with strong fluctuations in estimated site use intensity throughout the sampling periods (Online Resource 4). Our long-term camera trap data shows a dramatic drop in bearded pigs due to ASF, from 2967 observations from 2013 to 2020 to 3 observations from 2021 to 2024. Dipterocarp seeds fluctuated, with peaks during masting years (2014 and 2019) and none or low biomass outside of these years (Online Resource 5).

Bottom-up trophic associations with masting

The SEM with Malay civet site use affecting bearded pig site use outperformed the model with the influence going in the other direction (ΔAIC_c compared to the next-best model = 5.12; Online Resource 6, Online Resource 7) and was therefore the model we used for inference. In this model, dipterocarp seed availability was significantly related to bearded pig ($\beta = 0.0254$, $p < 0.01$) and Malay civet ($\beta = 0.0365$, $p < 0.01$; Table 1; Fig. 2) site use and displayed no significant relationship with murid rodents or pheasants. Bearded pig site use was significantly related to that of Malay civets ($\beta = 0.3542$, $p < 0.01$). Leopard cat site use was significantly related to that of murid rodents ($\beta = 1.0956$, $p < 0.05$; Table 1; Fig. 2), but not pheasants. Malay civet site use was unrelated to both rodents and pheasants.

Site use of bearded pigs and murid rodents was associated with COVID-induced changes in human use of the forest (Table 1, Online Resource 8). Bearded pig site use was strongly associated with ASF (Table 1, Online Resource 8). Based on this, we attempted a follow-up analysis where we built separate SEMs for pre- versus post-ASF years, to examine whether the loss of bearded pigs changed the structure of trophic dynamics of the system. The post-ASF model did not converge because of the limited data available.

Discussion

Our analysis suggests that dipterocarp seed availability in a Borneo rainforest influences site use intensity by some (but not all) primary consumers, and that these effects do not clearly translate to secondary consumers, as has been observed in some temperate systems. A key mechanism that may dampen bottom-up cascades is that rapid consumption of pulsed resources by highly abundant consumers could reduce food availability for other taxa. For example, rodents in Costa Rica limited access to seeds for larger mammals, thereby constraining population growth in the latter (DeMattia et al. 2004). This in turn reduced prey availability for predators that fed on the larger prey species. In our study system, bearded pigs likely consumed sufficient dipterocarp seeds to suppress responses in other granivores such as murid rodents (Curran and Webb 2000)—and while site use intensity by murids was related to that of predators, site use by bearded pigs was not. Bearded pigs are highly mobile and

Table 1 Result for the most parsimonious piecewise structural equation model's estimate for bottom-up model, with Malay civet affecting bearded pig site use

Trophic level	Response	Predictor	Estimate (β)	Std. estimate	Std. error	*P* value	
Primary consumers	Bearded pigs	Dipterocarp biomass	0.0254	0.0082	0.0030	< 0.0001	*
		ASF	− 5.9987	− 0.2322	0.5790	< 0.0001	*
		COVID-19 lockdown	− 0.6114	− 0.0191	0.0957	< 0.0001	*
		Malay civets	0.3542	0.0049	0.0838	< 0.0001	*
	Murid rodents	Dipterocarp biomass	0.0066	0.0047	0.0103	0.5186	
		COVID-19 lockdown	− 0.4394	− 0.0297	0.1494	0.0033	*
	Pheasants	Dipterocarp biomass	− 0.0092	− 0.0095	0.0117	0.4296	
		COVID-19 lockdown	− 0.1002	− 0.0114	0.0854	0.1801	
Secondary consumers	Malay civet	Dipterocarp biomass	0.0365	0.0209	0.0099	0.0002	*
		Pheasants	− 0.1449	− 0.0102	0.1526	0.3423	
		Murid rodents	− 0.0262	− 0.0007	0.2698	0.9227	
		COVID-19 lockdown	0.0759	0.0042	0.1471	0.6060	
	Leopard cat	Murid rodent	1.0956	0.0108	0.5356	0.0408	*
		Pheasants	0.0468	0.0011	0.4037	0.9077	
		COVID-19 lockdown	− 1.1617	− 0.0221	1.0326	0.2606	

ASF African swine fever, *COVID-19* coronavirus outbreak starting in 2019

*Denotes significance

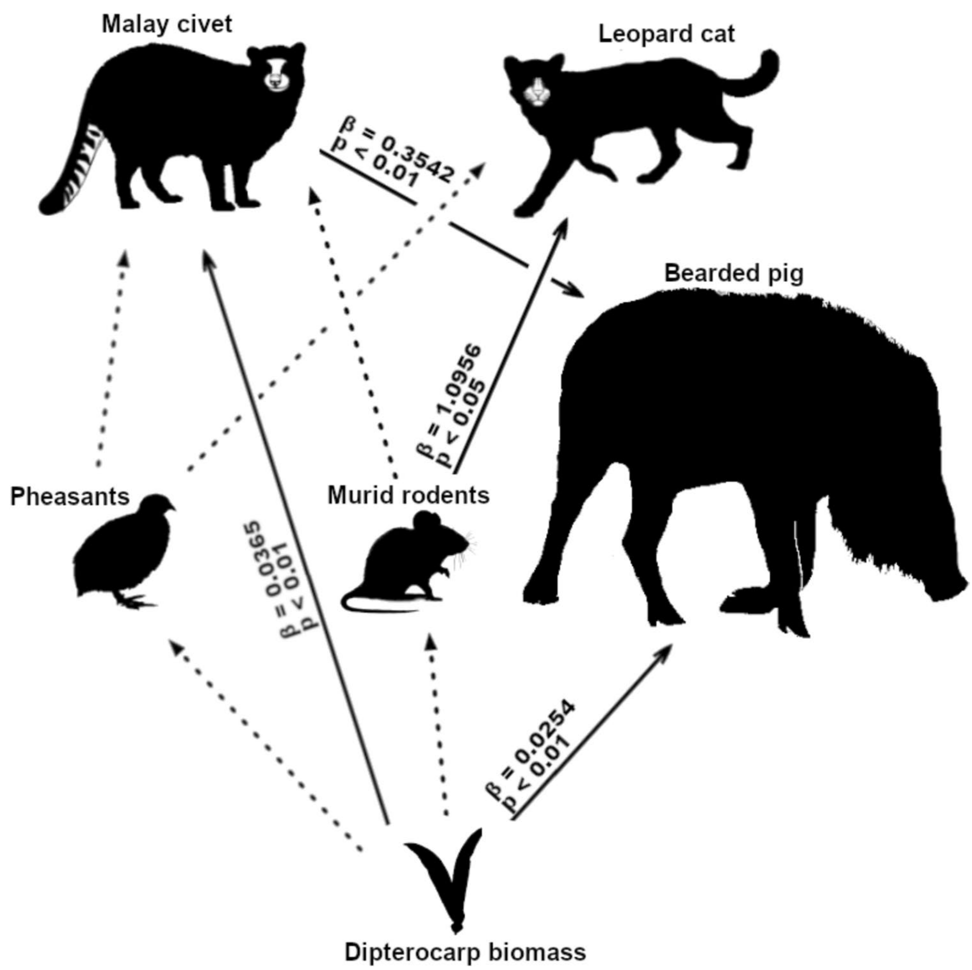

Fig. 2 A representative of the most parsimonious structural equation model for species associations in the tropical rainforest of Danum Valley, Sabah, Malaysia (Borneo). Trophic interaction is inferred from site use intensity for each of the species and the causal pathway is represented by arrows. Direction of the arrows indicates association, whereas species at the start of arrows are affecting the species at the end of the arrow. Solid and broken arrows represent significant and non-significant associations, respectively.

capable of tracking mast events across large distances, enabling them to remove vast quantities of seeds and undergo rapid population growth (Caldecott 1991; Hancock et al. 2005). At least until ASF appeared late in our study, this may have reduced access to mast resources for other granivorous species (Williams et al. 2021), which precludes population increases in smaller frugivores that would otherwise serve as prey for mesocarnivores such as leopard cats.

Consequently, mast production in some systems may be channeled primarily through one or a few dominant primary consumer species. The loss of such dominant consumers can then restructure trophic dynamics. For example, the extinction of the highly mobile and once-dominant passenger pigeon (*Ectopistes migratorius*) (Hung et al. 2014) in the temperate forests of eastern North America could have made mast resources available to a suite of less mobile species such as rodents and deer, amplifying bottom-up trophic cascades that were previously suppressed (Ellsworth and McComb 2003). This could explain why trophic cascades are now so pronounced in those systems: with reduced competition, less mobile granivores such as rodents and deer now have greater access to acorn and beech mast, allowing their populations to increase and providing an enhanced prey base for predators (Ostfeld and Keesing 2000). A comparable transition may be unfolding in our system with the recent ASF-related collapse of bearded pig populations. The loss of dominant bearded pigs may increase access to dipterocarp seeds for other granivores, potentially reshaping consumer-resource dynamics. As data to support complex modeling accumulate, future work will enable more robust assessments of such potential shifts in the trophic structure of the assemblage.

Alternatively, the differing responses to mast among primary consumers in our system may reflect the diversity of edible fruits available in tropical forests compared to temperate forests (Hanya and Aiba 2010). In temperate systems, mast fruiting typically involves one or two dominant genera, such as oaks or beeches (Cleavitt and Fahey 2017). In contrast, dipterocarp masting in equatorial Southeast Asia involves a much wider diversity of trees, including intra-annually fruiting dipterocarps and a wide variety of more regularly fruiting non-dipterocarps (Heideman 1989). This availability of alternative food sources could mean that generalist murid rodents and pheasants are not reliant on dipterocarp seeds (Granados et al. 2019), weakening the overall ecological importance of mast events. Rodents and pheasants could use other food sources such as figs (*Ficus* spp.) and invertebrates (Davison 1981; Sripho et al. 2024; Wells et al. 2009) more than dipterocarps, reducing their sensitivity to fluctuations in dipterocarp seed availability.

Interestingly, both SEMs revealed a positive association between Malay civets and bearded pigs, contrary to expectations if these species were primarily competing for dipterocarp seeds. Such positive associations may reflect facilitation between species sharing similar resources; for example, in Spanish Iberian forests, larger frugivorous ungulates can indirectly aid access to fruit by smaller frugivores, such as red foxes, by removing obstacles like thorns (Selwyn et al. 2020). However, we cannot provide mechanistic evidence for similar facilitation in this system from our model. Instead, the observed association may reflect shared responses to unmeasured environmental factors, leading to overlapping site use without implying direct interactions.

As with any ecological study, there are important caveats to our data and analyses. We did not collect data on other key consumers such as insects and fungi. As a result, we are not able to assess their ecological roles via direct competition for dipterocarp seeds (Williams et al. 2021) and through potentially supporting prey switching by omnivorous consumers. Insects can respond rapidly to mast events by exploiting increased fruit, flower, and nectar resources, thereby supporting a wide range of frugivorous, folivorous, and nectarivorous species (Chung et al. 2011; Corlett 2004; Sun et al. 2007). This insect community may in turn compete directly with vertebrate seed predators, potentially dampening their expected population responses to masting. Moreover, insects may serve as an alternative prey source for omnivorous and carnivorous species during periods of low fruit availability. For example, civets are known to increase insectivory when fruit is limited (Ribeiro et al. 2019; Zhou et al. 2008), and leopard cats opportunistically consume insects (Rajaratnam et al. 2007). With additional data, incorporating insect and fungal into future models would enhance our capacity to understand the many potential relationships between masting and consumer abundance.

Another limitation of our modeling approach is the potential underestimation of top-down control (Letourneau and Dyer 1998). Our analysis framework focused on bottom-up processes driven by seed availability but did not assess top-down forces that could influence the same consumers through predation by terrestrial apex predators (Mayhew et al. 2024). Yet, prior work in Borneo suggested that top-down control by apex predators such as clouded leopards appears rare (Brodie and Giordano 2012). Furthermore, in our study, clouded leopards were so infrequently detected that models including them failed to converge. This highlights that their ecological impacts may be weak at best due to inherent rarity. Nevertheless, future research with sufficient data to address both top-down and bottom-up pathways could help evaluate how predation and resource availability interact to shape community dynamics in tropical ecosystems.

Finally, our findings highlight the importance of considering tree phenology in managing tropical forests and wildlife. While masting events significantly influence site use intensity by primary consumers, their effects on higher trophic levels are less predictable due to ecological complexities such as predator–prey dynamics and interspecific competition. In light of the ASF-driven declines in bearded pig populations, future masting cycles may have different impacts on the dynamics of other frugivores in the system, potentially including cascading effects on forest regeneration and altered trophic interactions. Monitoring these changes will be important for assessing how changing patterns of seed predation (for example, driven by climate change) lead to long-term shifts in the composition of both trees and vertebrates. More broadly, our study underscores the need for long-term, multi-trophic level monitoring to capture the diverse influences on species associations and site use. By integrating phenological data into ecological monitoring and assessment, managers can develop more adaptive conservation strategies that account for the complexity of species interactions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-026-05867-9.

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Author contribution statement JFB originally conceived the idea; AS, AG, PJW, and JFB developed the methodology; AS, AG, PJW, CTT, and JFB conducted fieldwork; MAF and AYC provided field support and co-developed the methodology; AS and JFB performed statistical analyses; AS and JFB wrote the manuscript.

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Data availability Data is available upon request to AS.

Code availability Code is available upon request to AS.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study was conducted with permission from Danum Valley Management Committee (recent approval no: 2022/10, DVCA Project No: 561), Sabah Forestry Department (recent letter no: JPHTN/PPP/:EK100-24/1 JLD.7(5)), and Sabah Biodiversity Center (recent access license no: JKM/MBS.1000-2/2 JLD.16 (189)). Protocol for animal data collection is approved by the University of Montana Institutional Animal Care and Use Committee (IACUC) (022-23JBDBS-042723).

Informed consent Not applicable.

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