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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Food availability alters community co-occurrence patterns at fine spatiotemporal scales in a tropical masting system

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Abstract

Patterns of co-occurrence among species can help reveal the structure and assembly of ecological communities. However, studies have been limited by measuring co-occurrence in either space or time but not both simultaneously. This is especially problematic in systems such as masting forests where resources are highly variable, meaning that spatial use and co-occurrence patterns can change on fine spatiotemporal scales. We develop an analytical framework for assessing species co-occurrence at fine spatial and temporal scales simultaneously and apply these models to a camera trapping dataset from Borneo. We sought to determine how substantial variation in food availability across space and time affects co-occurrence among terrestrial vertebrates. We detect many significant, mostly positive, co-occurrence patterns among species, but almost entirely in unlogged forest and during dipterocarp mast years. The most strongly co-occurring pair of species, bearded pig (*Sus barbatus*) and sambar (*Rusa unicolor*), only positively co-occur in areas and years when fruit is locally abundant. Species occurrences in logged forest and non-mast years are mostly random with respect to other species. This suggests that frugivore–granivore species positively co-occur when resources are plentiful (i.e., large trees are present and fruiting), likely because they use the same resources; these patterns disappear when food availability is lower. Our approach demonstrates the utility of measuring co-occurrence in space and time together and highlights the importance of resource abundance for driving the co-occurrence structure of communities. Furthermore, our method could be broadly applied to other systems to assess fine-scale spatiotemporal patterns across a range of taxa.

Keywords Frugivory · Logging · Resource pulse · Southeast Asia · *Sus barbatus*

Introduction

Ecologists have long tried to interpret patterns of species co-occurrence to understand ecological processes more fully. Diamond (1975) famously described checkerboard distribution patterns where related pairs of species never co-occurred on small islands, which he attributed to competitive exclusion, though these interpretations were highly contentious (Connor and Simberloff 1979; Harvey et al. 1983; Strong et al. 1984). Decades later, spatial co-occurrence patterns are still widely used to infer ecological processes such as species interactions (Beaudrot et al. 2013; Araújo and Rozenfeld 2014; Davis et al. 2018). While changes in co-occurrence across time or environmental gradients may help

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elucidate drivers of community change (Bar-Massada and Belmaker 2017; Holt 2020), the use of spatial co-occurrence patterns to infer interactions may be unfounded (Freilich et al. 2018; Blanchet et al. 2020). There are several reasons for this, including the role of environmental preferences in determining species occurrences, the role of indirect effects and multi-species interactions in driving co-occurrence patterns, and the effects of asymmetrical interactions (Blanchet et al. 2020).

Interpretations of co-occurrence patterns usually implicitly assume that co-occurrence is constant through time, whereas substantial evidence suggests that ecological dynamics change over time with resource availability (Ostfeld and Keesing 2000; Stapp and Polis 2003; Greenville et al. 2014). For example, when prey is scarce, dingoes (*Canis familiaris dingo*) strongly suppress non-native mesopredator populations, but the effect is weaker when prey are abundant (Greenville et al. 2014). On islands in Mexico, deer mice (*Peromyscus maniculatus*) exclude pocket mice (*Chaetodipus rudinoris*) when resources are low, but both species are able to co-exist when resources are abundant following El Niño-driven resource pulses (Stapp and Polis 2003). A static perspective of co-occurrence misses the important role of resource variability.

Mast fruiting—the synchronous production of fruit on a supra-annual cycle—provides an excellent example of how resource variability can affect community dynamics. In eastern North America, for example, episodic fruit production increases consumer populations (Ostfeld et al. 1996), generating cascading impacts throughout the food web (Ostfeld and Keesing 2000; Kelly et al. 2008). Spatiotemporal variability in resource availability is particularly acute in equatorial Southeast Asia, where forests are characterized by irregular, supra-annual mast-fruiting events (Sakai 2002). Trees in the dominant family Dipterocarpaceae, along with many others, synchronize fruit production across large spatial extents (Sakai 2002). Fluctuating fruit and seed availability drives the movement patterns of several arboreal and volant species in these forests, including long-tailed parakeets (*Psittacula longicauda*) and orangutans (*Pongo pygmaeus*) (Curran and Leighton 2000; Marshall et al. 2021). On the ground, bearded pigs (*Sus barbatus*) respond strongly to masting cycles (Curran and Leighton 2000). Masting is a cue for reproduction in bearded pigs and their populations often explode following masting events (Caldecott et al. 1993; Hancock et al. 2005). Huge groups of pigs may move across the landscape tracking resource pulses (Caldecott et al. 1993) and devouring a substantial proportion of fallen fruit in a given area (Curran and Leighton 2000). But while bearded pigs clearly respond behaviorally and demographically to mast availability (Wong et al. 2005), and their diets overlap with those of arboreal species such as gibbons (Marshall et al. 2009), it remains unclear whether other terrestrial frugivorous and granivorous species use the same mast resources as bearded pigs (Granados et al. 2019), and it remains unclear how differences in resource availability may alter co-occurrence among these species.

Fruit and seed resources are ephemeral and temporally variable, so co-occurrence methods that do not include a temporal dimension may not detect how these resources affect ecological processes. There are many metrics that quantify spatial associations among species (Keil et al. 2021). These metrics can compare whether species co-occurrence (e.g., Gotelli and Mccabe 2002; Veech 2013) or co-abundance (e.g., Brodie et al. 2017) differs from what would be expected by chance. Multispecies occupancy models account for imperfect detection and can model co-occurrence as a function of environmental variables (Rota et al. 2016), but these models assume that occupancy is temporally fixed within sampling seasons. In nature, however, occupancy could fluctuate as a function of changing resource availability and the recent presence of sympatric species, which could not be captured in a temporally fixed occupancy framework. Temporal co-occurrence is commonly assessed by comparing the overlap in daily activity patterns of species (Ridout and Linkie 2008), but this method does not evaluate whether species co-occur simultaneously at the same sites.

A fine-scale spatiotemporal approach is necessary to determine, not just whether species occur in the same space or are active at the same time of day, but also whether species occur in the same space at the same time. For example, Swanson et al. (2016) found that even though broad-scale temporal activity patterns and spatial distributions did not differ between lions (*Panthera leo*) and cheetahs (*Actinonyx jubatus*), cheetahs were never detected within 12 h of lions at camera traps, suggesting strong behavioral avoidance at fine spatiotemporal scales. This example highlights how a fine-scale spatiotemporal approach can detect significant patterns that would not be detected using spatial or temporal co-occurrence alone.

Fine-scale spatiotemporal co-occurrence addresses several limitations of spatial-only co-occurrence analyses. First, spatial co-occurrence only identifies whether species use the same sites, which may be due to shared habitat preferences. Spatiotemporal co-occurrence, on the other hand, identifies whether species use those same sites at the same time. Thus, even when spatial use overlaps, spatiotemporal co-occurrence can identify temporal partitioning, avoidance, or positive spatiotemporal association. Second, while indirect interactions can complicate the interpretation of spatial co-occurrence patterns, the narrower scope of a fine spatial and temporal scale reduces the chance that observed patterns between focal species are indirectly caused by interactions with non-focal animal species. Third, a fine-scale spatiotemporal approach allows for asymmetrical associations, such as cheetahs avoiding lions but lions not responding to cheetahs

(Swanson et al. 2016). While some spatial-only methods allow for asymmetrical associations (e.g., Rota et al. 2016), most do not.

In assessing fine-scale spatiotemporal co-occurrence patterns, we want to know whether, after detecting one species, we are more or less likely to detect a different species. This type of analysis relies on time-to-event data—the time differences between detections of the two species. However, the analytical tools to interpret such patterns from time-to-event data are underdeveloped. One method has been to group sightings into bins, such as grouping all sightings of species A that occurred 0–12 h after sightings of species B (Swanson et al. 2016; Cusack et al. 2017). This approach, however, treats bins as independent, which they are not, and sets the division points between bins (and therefore the widths of the bins) arbitrarily. Another method compares the median time that species A was detected after species B against a null expectation (Karanth et al. 2017), but using the median value alone does not incorporate variance in the time differences.

Here, we develop a novel spatiotemporal co-occurrence framework to assess species co-occurrence in high- and low-resource situations in a masting ecosystem. We study a suite of vertebrate species in Malaysian Borneo where fruit resource availability is highly variable across years, due to mast-fruiting cycles, and across space, where the removal of large trees in selectively logged forests greatly reduces forest-wide fruit production. We develop a novel time-to-event model to analyze the temporal delay between detections of one species and subsequent observations of another, allowing us to measure how species co-occurred with each other at fine spatial and temporal scales. Specifically, our objectives are to (1) assess whether spatiotemporal co-occurrence patterns change under different resource conditions, (2) determine whether these patterns are consistent with broad shared use of resources, as predicted by studies in temperate masting ecosystems, and (3) compare the inference generated from our novel spatiotemporal approach with that from more typical spatial-only and temporal-only co-occurrence analyses.

Methods

Study system and camera trapping

We conducted our research at two sites in Sabah, Malaysian Borneo: (1) Danum Valley Conservation Area (DVCA; N 5.102°, E 117.688°), a lowland dipterocarp forest that has never experienced industrial logging or permanent settlement (Marsh and Greer 1992), and (2) Malua Forest Reserve (MFR), 25 km north of Danum Valley. The two sites had similar tropical moist forest habitat, but MFR was selectively logged in the 1980s and again in 2003–2007, with most of the large dipterocarp trees removed (Reynolds et al. 2011).

Forests in this region are characterized by irregular, supra-annual mast-fruiting patterns (Sakai 2002). Many plant taxa participate in mast-fruiting events, but members of Dipterocarpaceae adhere particularly strictly to mast-fruiting cycles, producing very little to no fruit between masts (Sakai 2002). Before we began our study, the most recent masting event in our system was in 2010 (Granados et al. 2019). During the years of our study, which ran from 2013 to 2016 and 2018 to 2020, masts occurred in 2014,

Table 1 Distribution of fruit resources in Danum Valley Conservation Area (DVCA; unlogged) and Malua Forest Reserve (MFR; logged)

	Mast years (2014, 2015, 2019)		Non-mast years (2018, 2020)	
	DVCA (unlogged)	MFR (logged)	DVCA (unlogged)	MFR (logged)
Total fruit				
Mean ± SE (g m^{-2})	2.72 ± 0.41	1.22 ± 0.19	0.04 ± 0.02	0.01 ± < 0.01
Median (g m^{-2})	0.24	0.14	0	0
CV	3.22	2.97	8.45	4.18
Dipterocarp fruit				
Mean ± SE (g m^{-2})	1.65 ± 0.30	0.35 ± 0.11	0 ± 0	0 ± 0
Median (g m^{-2})	0.03	0.00	0	0
CV	3.92	5.69	NA	NA
Non-dipterocarp fruit				
Mean ± SE (g m^{-2})	1.07 ± 0.22	0.87 ± 0.16	0.04 ± 0.02	0.01 ± < 0.01
Median (g m^{-2})	0.06	0.07	0	0
CV	4.40	3.43	8.45	4.18

These data are calculated from ground surveys conducted in 2014–2015 and 2018–2020. Overall fruit production was higher and more variable in the unlogged forest

2015, and 2019. There was no mast in 2017, the year in which we did not collect data.

Fruit availability in this system is strongly determined by masting cycles and history of logging. Very little fruit is produced in non-mast years compared to mast years, making mast versus non-mast a useful proxy for resource availability (see Table 1). Selective logging in dipterocarp forests affects resource availability in several important ways. First, logging reduces fruit production by removing many of the large, reproductive adult trees (Curran et al. 1999). Second, selective logging of large dipterocarps can also reduce non-dipterocarp fruit availability, particularly for strangler figs (*Ficus* spp.) and lianas that are destroyed when the large trees upon which they grow are removed; many of these are critical food sources for rainforest vertebrates (Johns 1988; Lambert 1991; Hardus et al. 2012; Dillis et al. 2015). Third, logging can make fruit production more spatially homogeneous if the removal of large canopy trees leads to fruit being produced in smaller but more evenly distributed patches (Table 1).

Of the many at least partly frugivorous and granivorous vertebrates in our system, the most important consumer of dipterocarp mast may be the bearded pig (*Sus barbatus*). Bearded pigs are thought to track dipterocarp masts on large spatial scales and to have their reproduction and population dynamics entrained to masting cycles (Caldecott et al. 1993; Curran and Leighton 2000; Hancock et al. 2005; Wong et al. 2005). Predation of dipterocarp seeds has also been documented by murid rodents, Bornean crested fireback pheasant (*Lophura ignita*), long-tailed macaque (*Macaca fascicularis*), and pig-tailed macaque (*Macaca nemestrina*) (Curran and Leighton 2000). Other vertebrate granivores and frugivores in our system include the sun bear (*Helarctos malayanus*), civets (Viverridae), great argus pheasant (*Argusianus argus*), sambar deer (*Rusa unicolor*), muntjac deer (*Muntiacus* spp.), chevrotains (*Tragulus* spp.), and porcupines (*Hystrix brachyura*, *H. crassispinis*, and *Trichys fasciculata*) (Meijaard et al. 2005; Corlett 2017).

To monitor these animals, we attached Reconyx HC500 cameras to trees in DVCA and MFR, with one camera per 1 km grid cell (Granados et al. 2019) following the Tropical Ecology, Assessment and Monitoring (TEAM) protocol (Rovero and Ahumada 2017). Cameras were deployed from May or June through September of each year. Our total sampling effort varied across years, from 1073 camera days in 2016 to 3997 camera days in 2015. There were 22 camera stations in DVCA (unlogged study area) and 20 stations in MFR (logged).

Spatiotemporal co-occurrence analysis

We developed an extension of time-to-event models to analyze the time delay between detections of any two species at the same camera station. Time-to-event models analyze the time differences between events, such as the time between the beginning of a study and the death of an organism, or in this case the time between the detection of one species and the detection of another. Time-to-event models have been widely used in ecology to study mortality (Landes et al. 2020), estimate detectability and occurrence (Bornand et al. 2014), and estimate abundance of unmarked animals from camera trap data (Moeller et al. 2018). This is the first application of time-to-event models to co-occurrence patterns. We grouped detections of each species into independent events. If the time between two detections of the same species at the same camera was less than 1 h (Tobler et al. 2008; Granados et al. 2019), we considered these detections part of the same event. We identified the period of time that each camera was continuously active; "periods" ended when cameras either malfunctioned or were retrieved at the end of the field season. Because we replaced malfunctioning cameras, some camera locations had multiple periods within a single year. In 2019, a great argus established a display site in front of one of our cameras resulting in thousands of photos of that individual, so we removed these periods from analyses that included this species.

To identify spatiotemporal co-occurrence patterns, we designated an "inducer" species and a "responder" species. We analyzed each given pair of species twice, once where one was the inducer and the other was the responder and then vice versa. We analyzed patterns of responder detections subsequent to inducer detections, but did not assume that the two species were directly interacting (e.g., via interference competition or facilitation). For example, positive spatiotemporal co-occurrence could be driven by use of the same ephemeral resources rather than facilitation per se. For each instance that the responder was detected after an inducer in the same period, we calculated the time difference between the end of the most recent inducer event and the beginning of the responder event. A single inducer event could be followed by multiple responder events. The list of these time differences was our "observed" dataset.

To calculate the null distribution of detections expected if there was no pattern between responder and inducer, we calculated the durations of time between all sequential inducer events and the duration of time between the last inducer event and the end of the period—i.e., all of the times when it would have been possible to detect the responder. We then randomly selected times within those durations to simulate 50,000 responder detections. For each simulated responder detection, we calculated the time difference between the end of the most recent inducer event and the simulated detection. This list of these time differences was our "expected" dataset.

We fit truncated Weibull distributions (Fig. S1) to the observed and expected data. The Weibull distribution is determined by two parameters: the scale parameter λ and the shape parameter k. When $k = 1$, the Weibull distribution is equivalent to an exponential distribution. If inducer and responder detections were random, responder detections as a function of time-since-inducer would fit an exponential distribution. The value of k identifies deviations in shape from the exponential distribution (Fig. S1). If $k < 1$, more detections appeared early before leveling off. In this case, the responder would be positively co-occurring with the inducer, often appearing soon after the inducer was detected. If $k > 1$, few detections appeared initially, but detections increased later before declining again. In this case, the responder would be negatively co-occurring with the inducer, appearing less often soon after the inducer was detected, then appearing more frequently after time had passed, and finally approximating the exponential detection curve after the effect of the inducer had worn off. Our null model assumes that responder detections are random with respect to the inducer, but the distribution of inducer detections determines the shape of the Weibull distribution. Thus, the value of k for the expected curve may differ from 1 if inducer detections are not randomly distributed throughout time. For example, a social species may lead to more short time differences between detections. Therefore, we compared the k values of observed curves to the k values of the expected curves rather than to an exponential curve with $k = 1$. To detect co-occurrence patterns on a biologically relevant timescale, we truncated our data at 14 days, because, based on fruiting periods, fruit availability will have changed considerably after 2 weeks. We assume that after 14 days, it would be so long since the inducer had been present that the exact time since the inducer had been at the site would not affect responder presence. Using a truncated curve, we fit a continuous Weibull distribution but only based on datapoints with a time difference < 14 days.

We compared the truncated Weibull curves of our observed and expected data to test whether the responder showed significant co-occurrence patterns in response to the inducer. We used a likelihood ratio test to determine whether considered observed and expected curves were significantly different from each other. Bonferroni corrections are not suitable for spatial co-occurrence data, because they are often too conservative and assume that tests are independent (Gotelli and Ulrich 2010), so instead we controlled for multiple tests with the Benjamini and Yekutieli (2001) false discovery rate method, using the false discovery rate at $\alpha = 0.05$. The Benjamini and Yekutieli method allows for dependency among tests by modifying the significance threshold sequentially, such that the strongest effects are subject to the lowest threshold and weaker effects are subject to higher thresholds. This results in a less-conservative false discovery rate than a Bonferroni correction while still rejecting weak effects.

Our model accounts for imperfect detection by comparing the conditional distribution of time-since-inducer given our observations of the responder against a null expectation based on our actual detections of the inducer. Imperfect detection of the inducer species would change the null curve, giving longer expected times-since-inducer than truth. However, our model makes inference only to the relationship between the observed and expected time-since-inducer curves, which would only be biased if the detection probability of the responder species were dependent on observations of the inducer species. In other words, there would need to be some mechanical or biological reason for photographs of the responder species to be consistently missed (even though the responder was present) due to the recent presence of the inducer species.

Rather than using the median time-since-inducer or another summary statistic, our approach accounts for the variance and overall distribution of time differences between inducer and responder detections. In doing so, it allows for appropriate inference dependent on sample size. Sample size (number of detections of the responder species after the inducer species) does not affect the shape of the observed curve, but a smaller sample size does increase the uncertainty around the parameter estimates of the fitted curve. An observed curve with a small sample size is less likely to be detected as significantly different than the expected curve. In addition to testing for statistical significance, we also assessed biological significance by measuring the percent change in k between the expected and observed curves (Δk). The higher the magnitude of Δk, the higher the effect size and the more likely that a significant difference between expected and observed curves reflects an ecologically meaningful co-occurrence pattern.

We conducted pairwise tests among the nine most commonly detected medium- and large-bodied (> 1 kg) species in the system: chevrotain, bearded pig, yellow muntjac (*Muntiacus atherodes*), pig-tailed macaque, sambar, fireback pheasant, great argus, Malay civet (*Viverra tangalunga*), and banded civet (*Hemigalus derbyanus*). We chose these nine, because all pairwise comparisons among them had sufficient sample size for analysis; that is, regardless of which species were designated inducer and responder, there were at least 50 independent observations of the responder detected within 14 days of the inducer. Also, fruit makes up a significant portion of the diet for all nine species except for banded civet (Meijaard et al. 2005). Of these species, pig-tailed macaque is the most frugivorous, followed by chevrotain and yellow muntjac which also consume other plant parts. Both pheasant species consume fruits and insects. Bearded pig and Malay civet are omnivorous, while banded civet is strictly carnivorous. Sambar is mainly herbivorous but consumes fallen fruit. See Table S1 for further diet information. For each inducer–responder pair, we simulated an expected dataset, fit truncated Weibull curves to the observed and expected datasets, and compared the observed and expected curves to calculate a P value and Δk. We tested all pairwise combinations, including switching inducer and responder designations among species within each pair.

To assess the role of resources in driving species co-occurrence, we repeated our pairwise analyses on subsets of the overall dataset. Specifically, we analyzed data from mast years only, non-mast years only, unlogged forest only (DVCA), and logged forest only (MFR). We did not have large enough sample sizes for most species to explore factorial combinations of mast/non-mast and unlogged/logged. For bearded pigs and sambar, however, which showed the strongest and most consistent co-occurrence patterns, we did analyze mast years in unlogged forest, non-mast years in unlogged forest, mast years in logged forest, and non-mast years in logged forest.

Assessment of co-occurrence in response to measured fruit availability

In 2014–2015 and 2018–2020, we conducted ground surveys to assess the amount of fruit available at each camera station. We visited cameras every 2–3 weeks and searched for fruit in a 2 m radius circle around the camera, as well as in three additional 2 m radius circles located 20 m in different directions from the camera (Granados et al. 2019). Fruit traps suspended from branches, with polyvinyl chloride frames and plastic mesh, were also set up in 2013–2015 (Granados et al. 2019). Fruit collected was brought to the nearby field station, identified by an experienced botanist, dried, and weighed. From the ground surveys, we calculated the total fruit biomass available per unit area.

To investigate the influence of fruit resources on species co-occurrence, we first used logistic regression to determine whether fruit availability predicted the likelihood of detecting a given species. Our response variable was whether or not a species was detected on a given day at a given camera station (binary). For each of our nine focal species, we compared eight models varying in predictor variables: (1) total fruit (percentile rank), (2) dipterocarp fruit (percentile rank), (3) non-dipterocarp fruit (percentile rank), (4) forest type (binary: logged or unlogged), (5) total fruit × forest type, (6) dipterocarp fruit × forest type, (7) non-dipterocarp fruit × forest type, and (8) intercept-only. We identified the model with the lowest AIC as the best fit (See Table S2). Because of extremely low fruit availability in non-mast years, we only included data from the three mast years. The distribution of fruit had a very long tail and many zero values, so we used the percentile rank of fruit biomass (g m^{-2}) for our fruit covariates, based on the fruit biomass calculated for all surveys in the 3 mast years. For each day at each camera station, if the day fell within 7 days before or after a fruit survey, we assigned the values from that survey as fruit data for that day. If a day at a given station was more than 7 days before or after a fruit survey, we did not include this day in our analysis.

We then used logistic regression to investigate co-occurrence between sambar and bearded pigs. For sambar, we took the model with the lowest AIC for that species and added bearded pig as a binary covariate (whether or not pigs were detected at that camera station on the same day) as well as an interaction between bearded pig and whichever fruit variable was included in the model. Likewise, for bearded pigs, we took the pig model with the lowest AIC and added sambar (binary) and an interaction between sambar and whichever fruit variable. This analysis allowed us to determine whether detection of sambar or pigs predicted detection of the other, and whether these patterns of co-occurrence differed according to resource availability.

Comparison with spatial and temporal co-occurrence analyses

We assessed how the inference generated from our spatiotemporal model compared to that generated by a more typical, spatial-only model. Specifically, we analyzed our camera trap dataset with a probabilistic pairwise method of measuring spatial co-occurrence (Veech 2013), using the cooccur package version 1.3 (Griffith et al. 2016) in R version 3.5.1 (R Core Team 2018) with the same nine species as in our spatiotemporal analysis. Our sampling unit was each camera station in each year. Again, we controlled for multiple tests using the Benjamini–Yekutieli (2001) procedure with a false discovery rate of $\alpha = 0.05$.

We also assessed how our spatiotemporal model analyses compared to a temporal-only overlap method. We used the overlap package (version 0.3.2) (Ridout and Linkie 2008) in R to estimate the coefficient of overlap (Δ) for sambar and bearded pigs, generating 10,000 bootstrapping iterations to calculate 95% confidence intervals. We chose this pair of species, because they had the strongest and most consistent co-occurrence patterns in our spatiotemporal analysis. Values for Δ range from 0 (complete segregation) to 1 (complete overlap). We estimated Δ for sambar and pigs for mast years, non-mast years, logged forest, unlogged forest, and for all years and sites combined. Of the several estimators described by Ridout and Linkie to estimate Δ, we used $\hat{\Delta}_4$ as recommended in the *overlap* package, because all sample sizes were greater than 50 (Ridout and Linkie 2008).

Results

Fruit resources were far more abundant in mast years than in non-mast years, and no dipterocarp fruit was detected in non-mast years (Table 1). Fruit availability was higher in unlogged forest than in logged forest for both mast years

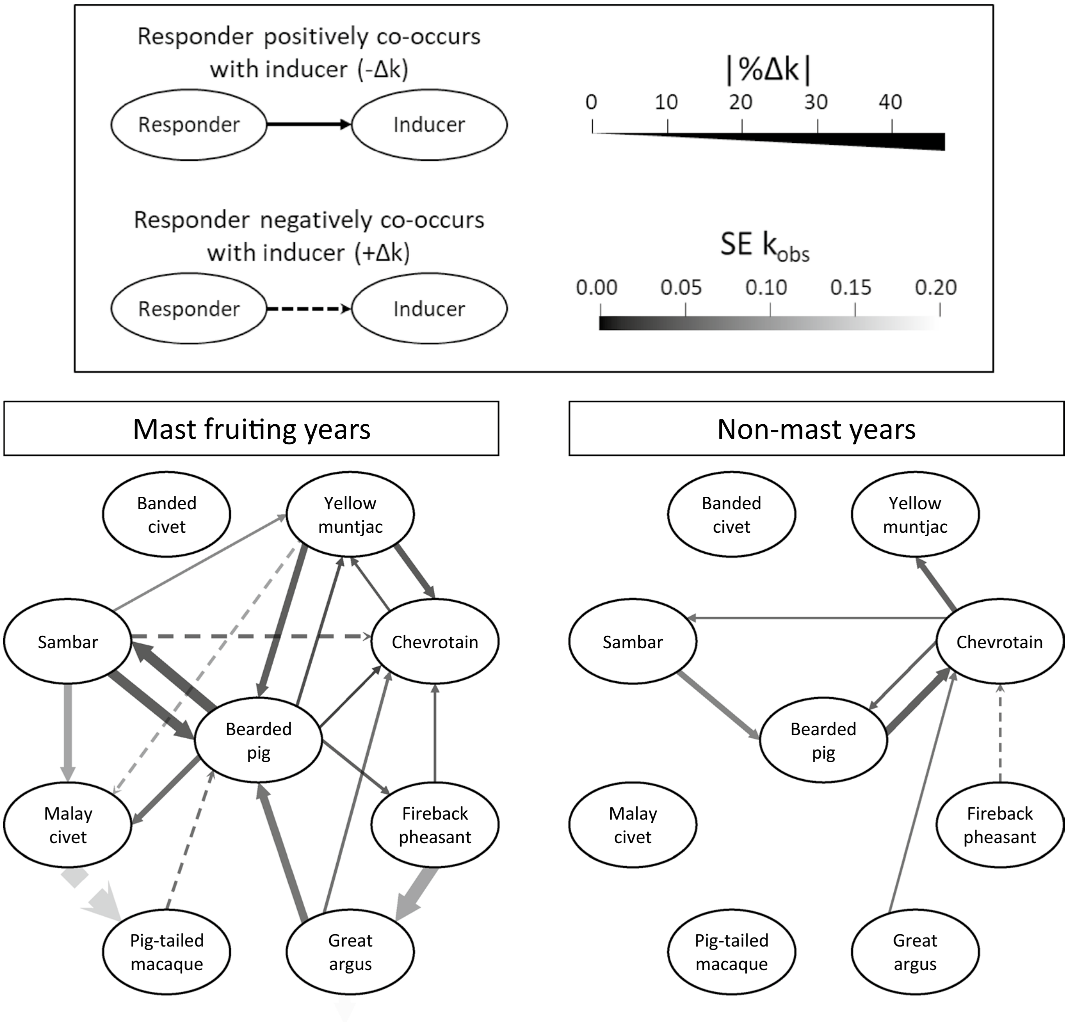

Fig. 1 Species co-occurrence patterns significant following the Benjamini–Yekutieli (2001) procedure. Arrows point from responder to inducer species. Solid and dashed arrows show positive (co-occurrence; negative Δ*k*) and negative (avoidance; positive Δ*k*) co-occurrence, respectively. Line thickness represents magnitude of Δ*k*; color represents standard error of estimate for observed *k*

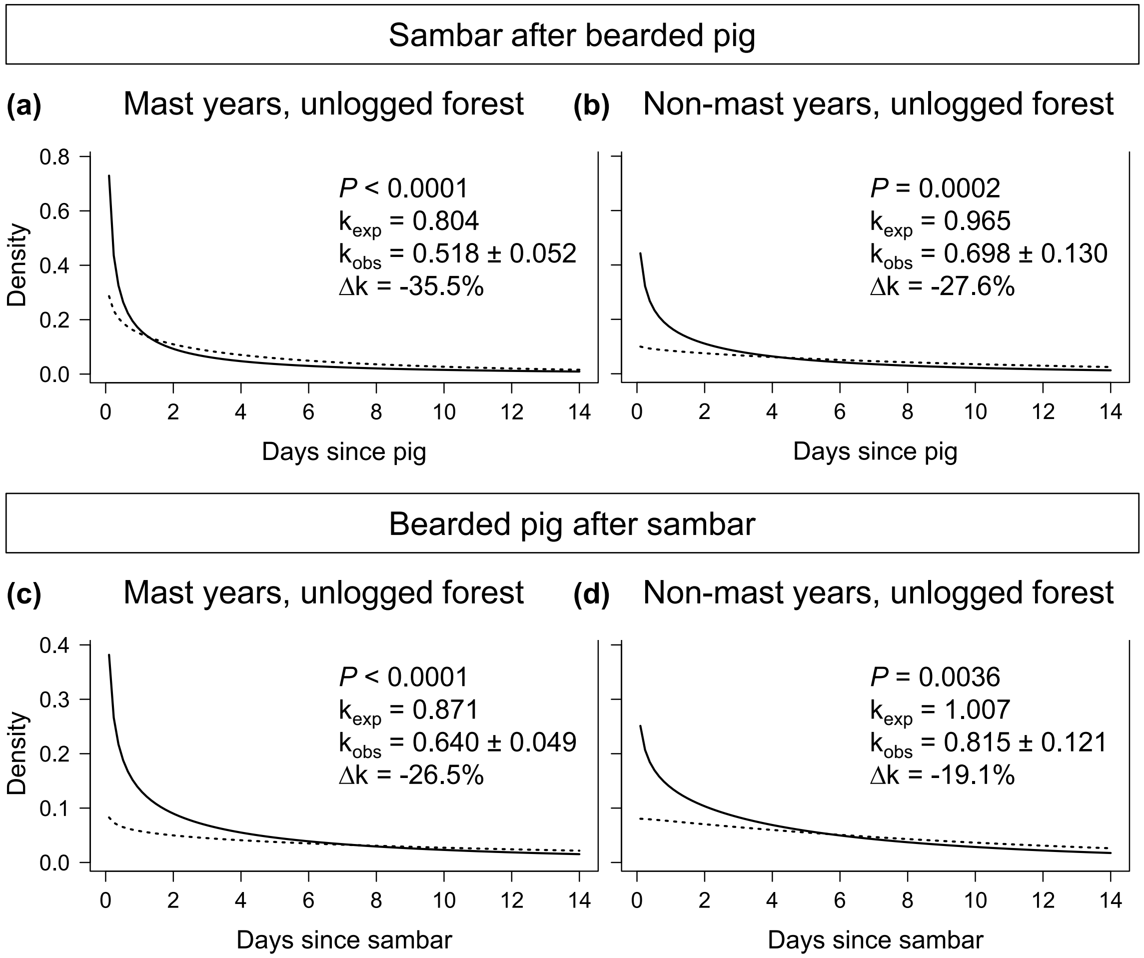

Fig. 2 Co-occurrence patterns between sambar and bearded pigs in unlogged forest, all of which are significant using the Benjamini–Yekutieli (2001) procedure with a false discovery rate of $\alpha = 0.05$. Dotted and solid lines show expected curves and observed curves, respectively. The two species positively co-occurred in unlogged forest in both mast and non-mast years, but co-occurrence was stronger in mast years

(2.72 ± 0.41 g m^{-2} vs. 1.22 ± 0.19 g m^{-2}, respectively) and non-mast years (0.04 ± 0.02 g m^{-2} vs. $0.01 \pm < 0.01$ g m^{-2}, respectively; Table 1). Total fruit resources and non-dipterocarp fruit resources were less evenly distributed at camera trap stations in unlogged forest than in logged forest (Table 1).

Using our spatiotemporal model, we found many more significant interspecific co-occurrence patterns in mast years and in unlogged forest than in non-mast years or logged forest (Fig. 1). Considering only significant patterns with a relatively high effect size ($|\Delta k| > 5\%$), we found 15 significant co-occurrence patterns in mast years and 16 in unlogged forest, with four in non-mast years and one in logged forest (Fig. S2). In all cases except in logged forest, positive co-occurrence was more common than negative, and the negative co-occurrence patterns in logged forest were very weak (Fig. 1). The only negative co-occurrence pattern with $|\Delta k| > 10\%$ was between Malay civets and pig-tailed macaques in mast years ($P = 0.0002$, $\Delta k = 44.0\%$, Fig. 1), but the standard error for the observed k was high ($k_{\text{obs}} = 1.41 \pm 0.16$), indicating that the curve did not fit the data well. Sambar, yellow muntjac, and fireback pheasant all positively co-occurred with bearded pigs in mast years (Fig. 1). Banded civet, the only non-frugivorous species of the nine (Table S1), was the only species to show no significant co-occurrence with other species.

Sambar and bearded pigs stood out for their strong, consistent, and bidirectional co-occurrence patterns. Sambar and pigs positively co-occurred in mast years in unlogged forest (sambar arriving after pigs, $P < 0.0001$, $\Delta k = -35.5\%$, Fig. 2a; pigs after sambar, $P < 0.0001$, $\Delta k = -26.5\%$, Fig. 2c). Sambar and pigs also positively co-occurred in non-mast years in unlogged forest, but the patterns were not as strong as in mast years (sambar after pigs, $P = 0.0002$, $\Delta k = -27.6\%$, Fig. 2b; pigs after sambar, $P = 0.0036$, $\Delta k = -19.1\%$, Fig. 2d). In logged forest, sambar weakly

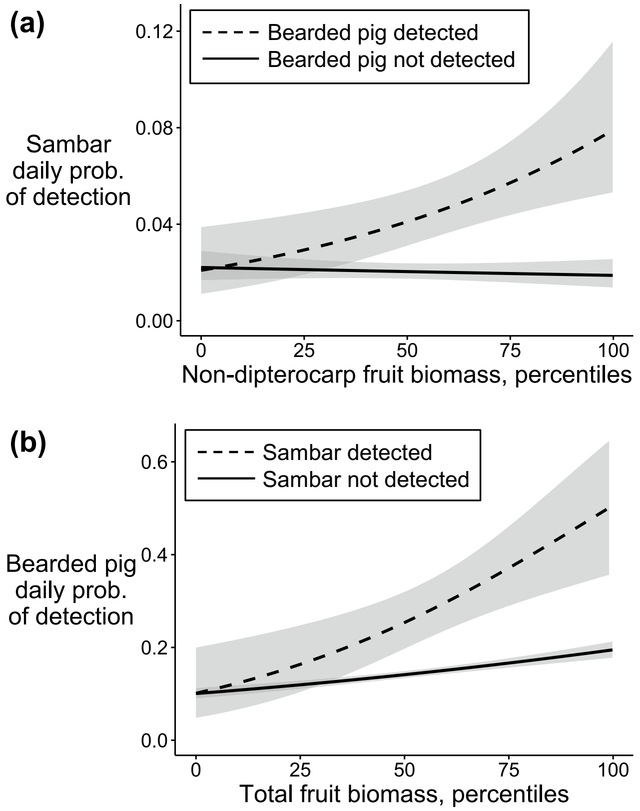

Fig. 3 Logistic regression showing responses of sambar and bearded pigs to fruit availability when the other species was or was not also detected on that day. Fruit variables are the percentile rank of total or non-dipterocarp fruit biomass, calculated from all fruit surveys conducted in the 3 mast years. Daily probability of detection is the probability that the species was detected on any given day at any given camera station. The shaded bands show standard errors. Detections of bearded pigs and sambar predicted detections of the other species, but only when fruit abundance was high (bearded pig × non-dipterocarp fruit: $\beta = 1.55 \pm 0.53$, $P = 0.004$; sambar × total fruit: $\beta = 1.44 \pm 0.65$, $P = 0.027$)

negatively co-occurred with pigs in mast years ($P = 0.0010$, $\Delta k = 6.8\%$), but otherwise there were no significant co-occurrence patterns between sambar and pigs (Fig. S3).

Total fruit biomass was correlated with bearded pig detections (logistic regression: $\beta = 0.81 \pm 0.010$, $P < 0.001$), and non-dipterocarp fruit biomass was correlated with sambar detections ($\beta = 0.88 \pm 0.32$, $P = 0.005$; Table S2). Detections of bearded pigs predicted detections of sambar, but only when non-dipterocarp fruit availability was high (bearded pig × non-dipterocarp fruit: $\beta = 1.55 \pm 0.53$, $P = 0.004$; Fig. 3a, Table S3). Detections of sambar predicted detections of bearded pigs but only when total fruit availability was high (sambar × total fruit: $\beta = 1.44 \pm 0.65$, $P = 0.027$; Fig. 3b, Table S3).

The spatial-only and temporal-only pairwise co-occurrence analyses showed different co-occurrence patterns than our spatiotemporal approach. The spatial-only model detected a significant pattern between sambar and bearded pigs (Fig. 4, $P = 0.00055$), which emerged strongly in our spatiotemporal model, but also included several significant co-occurrence patterns with banded civet (Fig. 4), which in our spatiotemporal analysis had none (Fig. 1). Sambar and bearded pigs showed relatively high temporal overlap ($\widehat{\Delta} = 0.61$; 95% CI: 0.57–0.65), though sambar tended to be more nocturnal and bearded pigs more diurnal (Fig. S4). Temporal overlap was slightly higher in mast years ($\widehat{\Delta} = 0.65$) than in non-mast years ($\widehat{\Delta} = 0.52$) but did not differ between logged ($\widehat{\Delta} = 0.62$) and unlogged forest ($\widehat{\Delta} = 0.60$; Fig. S4).

Discussion

Resource availability strongly influences animal behavior and species interactions, in turn affecting patterns of species co-occurrence; but assessing the spatial and temporal aspects of co-occurrence separately is problematic in systems where resources are fluctuating and ephemeral. Using a novel spatiotemporal approach, we found that species co-occurrence was strongly influenced by resource availability, measured directly using fruit counts and also indirectly using masting and logging as proxies. We detected many more significant co-occurrence patterns in mast years and in unlogged forest, where fruit was locally abundant, than in non-mast years and logged forest, where fruit was much less abundant. These differences are robust given the large effect sizes and relatively small differences in sample sizes among forest types and years (Table S4). Positive spatiotemporal co-occurrence suggests that frugivore–granivore species are using the same ephemeral resources when such resources are abundant. That is, the species are visiting the same places at the same times, because they are feeding on the same plant fruits and seeds, though they may or may not be actively following each other (i.e., our results should not be taken as indicative of interactions such as competition or facilitation; also see Blanchet et al. 2020). Indeed, sambar and bearded pigs only positively co-occurred with each other when local fruit biomass was high, so either they only follow each other when there is sufficient fruit or they are independently attracted to the same resources.

The abundance of strong species co-occurrence patterns that we observed in mast years may reflect greater diet overlap (consistent with decreased interspecific competition), as observed in other studies. Deer mice (*Peromyscus maniculatus*) in Mexico, for example, shifted their diets following El Niño-driven resource pulses and were able to co-exist with pocket mice (*Chaetodipus rudinoris*), but as resources declined pocket mice excluded deer mice (Stapp and Polis 2003). This is consistent with predictions from optimal foraging theory that the strength of competition is inversely

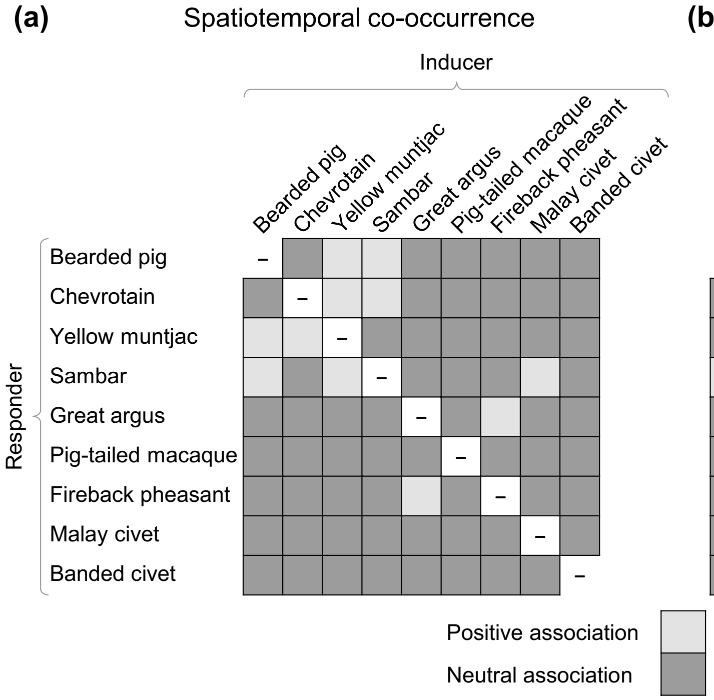

Fig. 4 Community co-occurrence patterns based on **a** spatiotemporal co-occurrence, following the methods described in the main text, with all cameras from all years, only showing $|\Delta k| > 5\%$ to eliminate very weak effects, and **b** spatial co-occurrence only, following the methods of Veech (2013), with each camera in each year a separate sampling unit. Only statistically significant co-occurrence patterns are shown, using the Benjamini–Yekutieli (2001) procedure with a false discovery rate of $\alpha = 0.05$

proportional to resource availability (Pyke et al. 1977). In our study, although we did not have detailed diet information for the vertebrate species, the positive co-occurrence patterns suggest that species may have shifted their diets to consume the same mast resources, while such shared resource use may not have been possible when resources were less abundant. Bearded pigs are known to have strong behavioral and demographic responses to mast-fruiting (Curran and Leighton 2000; Wong et al. 2005; Granados et al. 2019), but there has been little evidence of such responses in other terrestrial vertebrates. Though we did not measure demographic responses, our results suggest that masting may drive behavioral responses throughout the community, influencing multiple vertebrate species such as sambar, yellow muntjac, and fireback pheasants, which all positively co-occurred with bearded pigs at sites and in years when dipterocarp fruit was abundant.

Strong species co-occurrence patterns were less prevalent in the logged forest, also consistent with differences in the abundance and distribution of resources. There are, of course, numerous biotic and abiotic differences between logged and unlogged tropical rainforest. However, we note that the logged forest in our study, where large dipterocarp trees have been selectively removed, had much lower fruit abundance than the unlogged forest in mast years, and even in non-mast years, fruit was less abundant and more evenly distributed spatially. Meanwhile, with the exception of great argus and possibly yellow muntjac, the relative abundance of vertebrate species did not differ strongly between the logged and unlogged sites (Granados et al. 2016, 2019; Table S4). When resource patches occur at high densities, consumers can partition their use of patches; but when patches occur at low densities, consumers are more likely to aggregate at the same resources (Symington 1988). In social primates, for example, individuals may form larger groups when resources are patchy but split off into smaller groups when resources are more evenly distributed so as to reduce intraspecific competition (Vasudev et al. 2008). The lack of large, clumped resource patches in the logged forest could explain why we did not see species co-occurring at the same locations at the same times. Consumers may also shift their diets to reduce diet overlap with other species, given that fruit resources are less abundant in the logged forest and thus able to support fewer consumers.

Our results suggest that accounting for both space and time in the assessment of co-occurrence can reveal important patterns not detected by other methods. The positive co-occurrence patterns that we found in our spatiotemporal analysis were not detected or were much weaker in the spatial-only and temporal-only analyses. The spatial-only analysis also detected many significant patterns with the non-frugivorous banded civet, likely due to shared habitat preferences, but our spatiotemporal analysis found no such patterns. In a system like ours, where most species are widespread throughout the study area, a spatial-only approach is not particularly useful. Our spatiotemporal approach, though, provided a fine-scale analysis of not just whether species occurred in the same location, but whether they occurred in the same location at the same time period (or shortly thereafter). This allowed us to disentangle broad-scale habitat preferences from behavioral responses to either another species or to a shared ephemeral resource. Thus, differences in co-occurrence patterns between logged and unlogged forest were likely not driven by differential responses to logging among species but instead by the influence of fine-scale resource availability. One disadvantage of our spatiotemporal model is that it does not have the statistical power to detect co-occurrence patterns involving rare species. This is an issue, however, with any such analysis.

Comparing co-occurrence patterns under different conditions could help elucidate how anthropogenic pressures affect ecological dynamics (Keil et al. 2021). Across Southeast Asia, habitat loss and hunting have dramatically altered the species composition of tropical forests, likely changing co-occurrence patterns. Habitat loss and changes in land use have not only reduced populations of some species, but they have also altered diets and behaviors. In forest fragments bordering oil palm plantations, wild pig populations are sustained by the abundant year-round supply of oil palm fruit (Love et al. 2017), which can lead to population booms (Ickes 2001). The hyperabundance of pigs can lead to forest degradation (Luskin et al. 2017), but it is unclear how such hyperabundance affects the mast response of pigs, or whether pig hyperabundance could influence the mast response of other species by exhausting available resources. Our methods could be used to address these questions. In the short term, though, bearded pig populations have declined steeply due to African swine fever (ASF) (Luskin et al. 2021). In 2021, there were confirmed reports of ASF cases and mass deaths among bearded pigs in Sabah (Kurz et al. 2021). Our results suggest that, in the absence of bearded pigs, other terrestrial species will consume mast resources and may even benefit from the lack of competition with pigs. African swine fever provides an unfortunate but fascinating natural experiment to understand how the selective removal of one important species may alter co-occurrence and other community patterns. More broadly, our approach can be used to understand how changes in species composition might affect co-occurrence patterns within communities.

Our spatiotemporal model could be broadly applied across other systems. One considerable advantage of our spatiotemporal model is that it allows for asymmetrical co-occurrence patterns, whereby the association of one species to another is different than the reciprocal association. This approach may be particularly useful in studies of carnivore co-existence, where sympatric species often co-exist in dominant-subordinate hierarchies (Elbroch and Kusler 2018), or in studies of predator–prey interactions (Swanson et al. 2016). Our analysis could detect patterns where the subordinate species avoids the dominant one (negative co-occurrence), but the dominant does not respond to the subordinate (no pattern) (e.g., Swanson et al. 2016; Karanth et al. 2017), or patterns where the prey avoids the predator (negative co-occurrence), but the predator tracks the prey (positive co-occurrence) (e.g., Swanson et al. 2016). Our time-to-event model could also be used to study the arrival of frugivores at fruiting trees. When fruits become available on a tree, multiple species converge to consume the resources, and these species may facilitate one another by making resources accessible to other species or by advertising the resource location (Olupot et al. 1998; Prasad and Sukumar 2010). If resource availability were known, our spatiotemporal analysis could determine whether frugivorous species converge on shared resources (bidirectional positive co-occurrence), whether some species trail behind other species (unidirectional positive associations), or whether frugivorous species track resources independently of other consumer species (no significant co-occurrence patterns).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-022-05252-2.

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Author contribution statement PJW and JFB conceived of the study. PJW and AG led the fieldwork. JFB secured funding. JFB, HB, and RCO assisted with fieldwork logistics. PJW and AKM developed the analyses. PJW wrote the initial manuscript, which was edited by JFB and reviewed by all authors.

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Availability of data and materials Data are publicly available online at https://github.com/pwilliams0/spatiotemporal-association, https://doi.org/10.5281/zenodo.6582111.

Code availability The code for our spatiotemporal co-occurrence analysis is publicly available online at https://github.com/pwilliams0/spatiotemporal-association, https://doi.org/10.5281/zenodo.6582111.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics approval Ethics approval was not required for this study as it did not involve any human subjects or direct contact with any animals.

Consent to participate Not applicable.

Consent for publication Not applicable.

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