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ORIGINAL RESEARCH

# Arboreal camera trapping: a reliable tool to monitor plant-frugivore interactions in the trees on large scales

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## Abstract

Although arboreal camera trapping is a growing field, it has rarely been used for monitoring plant-frugivore interactions in the trees. Frugivore foraging behavior generally occurs in trees, hence arboreal camera trapping can be a potentially useful tool for frugivory research. We developed a camera trap sampling method to monitor plant-frugivore interactions during mature fruiting periods. We used this method to monitor 318 individuals (camera sites) of 18 fleshy-fruit plant species on 22 subtropical land-bridge islands in the Thousand Island Lake, China. We recorded a total of at least 52 frugivorous animals, including a ground-foraging bird species (*Lophura nycthemera*) and several mammals with foraging behaviors in the trees. We also recorded 4399 independent interaction events, including 275 unique plant-bird interactions. We proposed a framework to classify interaction types and performed a sampling completeness test. We found that a sampling strategy that covered approximately a third of the fruit maturation period when most fruits were ripe was sufficient to sample plant-frugivore interactions. Our results demonstrated that our sampling method with camera transects is reliable to monitor plant-frugivore interactions in a fragmented landscape. This study helps to lay the methodological foundation for building networks of plant-frugivore interactions with arboreal camera trapping on large spatial/temporal scales. As a non-invasive, labor-saving, and largely unbiased sampling method, the field application of arboreal camera trapping in different regions can advance the technology of biodiversity monitoring and lead to more accurate biodiversity inventories in arboreal environments.

## Introduction

The use of infrared camera trapping technology has expanded quickly in recent decades, and it has rapidly become a standard tool for wildlife monitoring (Cutler & Swann, 1999; O'Connell et al., 2011). Camera traps can remotely record endothermic animals (e.g., birds and mammals) day and night. Compared with traditional survey methods, camera trapping is relatively non-invasive and cost-effective (Silveira et al., 2003). This technology is thus widely used to evaluate species richness (Tobler et al., 2008a), estimate population densities (Karanth & Nichols, 1998), record animal behavior (Rowcliffe et al., 2014), and study occupancy modeling (e.g., Kéry & Royle, 2016; MacKenzie et al., 2017; O'Brien et al., 2011; Tobler et al., 2008b) in recent decades. Although camera trapping is widely used in wildlife monitoring worldwide, it generally targets ground-dwelling vertebrates (Kays et al., 2020; Steenweg et al., 2017). However, with increasing interest in arboreal habitats (Burton et al., 2015; Nakamura et al., 2017), researchers have begun to develop arboreal camera trapping methods (e.g. Gregory et al., 2014; Whitworth et al., 2016; Zhu et al., 2021). The potential of this application to monitor associations between arboreal fauna and plants has been demonstrated but minimally reported (but see Laughlin et al., 2020).

Arboreal animal communities provide essential ecosystem services, such as seed dispersal, which is an important component of mutualistic interactions (Bascompte & Jordano, 2014). Seed dispersers (or frugivorous animals) help maintain forest regeneration (Howe & Smallwood, 1982; Kays & Allison, 2001), and can affect germination and forest dynamics (Wang & Smith, 2002). Although the importance of frugivory and seed dispersal by animals has been widely recognized in ecology, it is challenging to record species interactions in the treetops in the field (Jordano, 2016). Several methods have been used to survey plant-frugivore interactions. The most commonly used method is direct observation (Cordeiro & Howe, 2003). Researchers have also collected defecated seeds (Vizentin-Bugoni et al., 2019) to identify species consumed, as well as used molecular techniques to identify plant species in droppings (González-Varo et al., 2014). However, these methods cannot be employed at large scales due to the high labor and/or financial costs.

Another restriction on sampling plant-frugivore interactions is that most of these mutualistic interactions occur in the treetops. To solve that problem, arboreal camera trapping has been applied to examine the visits of frugivores in target tree species (Rivas-Romero & Soto-Shoender, 2015). For example, using cameras, Amico and Aizen (2000) demonstrated that nocturnal mammals were highly efficient dispersers of mistletoe seeds. However, studies of plant-frugivore interactions with arboreal camera traps have generally been restricted to relatively small spatiotemporal scales, using few cameras or focusing on a single plant or animal species. For example, Amico and Aizen (2000) used just two cameras for 90 days; Jayasekara et al. (2007) used one camera for each of 15 plant species; Rivas-Romero and Soto-Shoender (2015) used eight cameras and studied only *Oreopanax echinops*; and Carpenter et al. (2018) used eight cameras on only *Elaeocarpus dentatus*. To our knowledge, although the technical advantages of using camera trapping to monitor arboreal species have been introduced previously (Laughlin et al., 2017; Whitworth et al., 2016), there are still few studies designed to monitor species interactions in arboreal environments on a large spatial scale with arboreal camera trapping (but see Zhu et al., 2021).

In the present study, we used arboreal camera traps to document plant-frugivore interactions, on subtropical reservoir islands formed by the building of a dam. Because frugivores would be expected to be attracted to fleshy fruits and visit sampling sites regularly during the fruiting period, we expected arboreal camera trapping to be an appropriate method to record frugivore species at monitoring sites with high food densities (Olson et al., 2012). We set camera traps in trees along line transects on 22 subtropical land-bridge islands, with a total of 318 camera sites. The main objective of this study was to test the feasibility of arboreal camera trapping on fragmented land-bridge islands to record frugivores and their behaviors.

We also tested a sampling method with camera transects and a new framework to calibrate and grade the probabilities of various kinds of plant-frugivore interactions. Finally, we evaluated sampling completeness of frugivores and determined the necessary sampling effort to take a relatively complete frugivore inventory on an island.

By evaluating the efficiencies of arboreal camera trapping, we aimed to test whether this method is a reliable tool to record plant-frugivore interactions in fragmented landscapes, such as on the reservoir islands in this study. We also planned to improve sampling strategies according to local conditions and fruiting periods. Based on Gregory et al. (2014), we provided recommendations on the installation and maintenance of arboreal cameras to improve sampling efficiency for use in studies within similar environments.

## Materials and Methods

### Study area

This study was conducted in the Thousand Island Lake, an artificial reservoir located at Chun'an County of Zhejiang Province, eastern China (29°22"–29°50" N, 118°34"–119°15" E; Fig. S1). The lake was formed by the construction of the Xin'anjiang Dam in 1959, and contains 1078 islands with an area greater than 0.25 ha at the high-water mark (108 m, Si et al., 2014b; Fig. S2). The local climate is typical subtropical monsoon. Currently, 88.5% of the land area on the islands is covered with secondary forest, and most of the forest (~90%) is dominated by *Pinus massoniana*, with many broad-leafed plants in the sub-canopy and understory (Liu et al., 2020), including many fleshy-fruit plants (e.g., *Vaccinium carlesii*, *Lindera glauca*, and *Smilax davidiana*).

### Fruiting tree sampling

We set line transects across the mountain ridges to cover as many habitat types as possible on each island. As the forests on study islands are secondary, the line transects in this study cover the main habitat types, including broad-leaved forests, coniferous-broad mixed forests, and shrubs with some fruiting trees. The line transects were 20 meters wide, and the total length of line transects on each island was roughly proportional to the logarithm of the island area (Zhu et al., 2021). We then monitored the transects for fruiting plant species. We identified all plants and the fruiting period of all target fleshy-fruit plants during our study based on *Flora of Zhejiang* (Flora of Zhejiang Editorial Committee 1993) (Table S2; Zhu et al., 2021).

From June to December 2019, we monitored the transects on the study islands twice a month and searched for individual fleshy-fruited trees. Transects covered both the edges and the interior of the islands (Fig. 1A), so that we could record a relatively complete plant-frugivore assemblage for each island (Menke et al., 2012). Upon finding a fruiting tree (Fig. 1B), we immediately set up infrared cameras to monitor frugivory (Fig. 1C). If there were many individuals of the same tree species within a transect, we selected the individual tree with the most abundant fruits within a radius of 20 m. Hence arboreal cameras for the same species were separated by at least 20 m along transect lines to reduce the oversampling.

## Camera placement

Passive infrared camera traps (LTL Acorn 6210MC infrared digital cameras) were used to assess the presence or absence and record the relative frequency of plant-frugivore interactions by monitoring trees with high fruit densities. We used a ladder to climb trees adjacent to the target trees and placed cameras facing areas with plentiful fruits (Fig. 1C). We placed infrared cameras to monitor the fruits immediately prior to ripening and removed

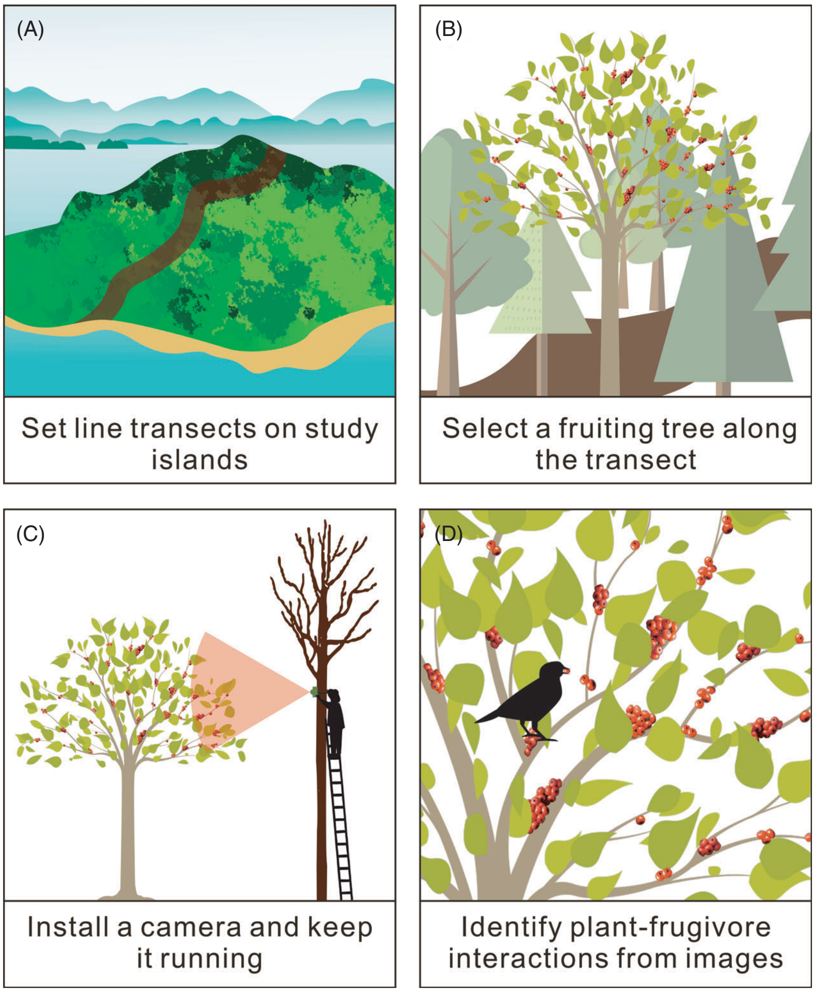


**Figure 1.** Illustration of the placement of arboreal cameras along line transects on an island: (A) set a line transect from the edge and the interior of a study island, (B) select a tree along the transect with abundant fruits, (C) install a camera on the trunk or branch of a tree that is nearby to the target tree, and set the camera face to the target tree in an area of high fruit density (the red area indicates the area detected by the camera sensor), and (D) identify plant-frugivore interactions (i.e., the moment of bird foraging) from camera trap images. See more details in Table S1.

 

them when fruits were close to dropping from the tree. Therefore, sampling effort for different focal tree species was roughly proportional to the duration of their fruit maturation periods. Once all cameras were retrieved from the field, we examined all photos and videos in the lab that contained frugivore species (Fig. 1D).

A total of 318 camera trapping sites were established on 22 islands from June 2019 to February 2020. Prior to field trials, we conducted a pilot study by setting camera traps to monitor trees (*Symplocos stellaris*) in early June 2019. When considering the trade-off between a large monitoring area within the camera's field of view (i.e., setting the camera farther from the target tree) and the resolution of the images taken for identification purposes (i.e., setting the camera closer to the target tree), we found the camera performed best when placed approximately two meters from the fruit clusters (Zhu et al., 2021). After we selected an individual target tree, we chose a specific position for arboreal camera placement to optimize the viewing angle (Ortmann & Johnson, 2021).

Each camera was adjusted to face north or south to the extent possible, to reduce overexposure and unwanted triggering events induced by the sunrise and sunset. We placed the cameras in either an adjacent tree or on solid branches of the target tree directly, depending on where there was the least movement of the camera by the wind. The cameras were set at ≤8 m in height depending on fruit densities and the requirement of optimizing the camera sensor range. We removed dead branches and withered leaves and clipped branches without fruits within the view of the camera to further avoid unwanted triggering events by vegetation (Gregory et al., 2014; Si et al., 2014a).

The sensitivity of the camera was set to high or medium, with a delay of 10 s between triggers. We set cameras to take three photographs plus one 10-s video per trigger. Each camera was equipped with 12 batteries and 32 GB memory cards. Cameras were activated to function 24 h per day, 7 days a week. We checked the cameras every two weeks to change the memory cards and batteries. If necessary, the camera angle was adjusted to face the area of maximum fruit density during every routine check.

## Data collection and the classification of interaction types

All image data were checked independently by at least two people. We defined an independent interaction event (IIE) as consecutive photographs of the same plant-frugivore interaction taken more than 5 min apart (Snow & Snow, 1988), which was similar to other definitions used in wildlife research (e.g., O'Brien et al., 2003).

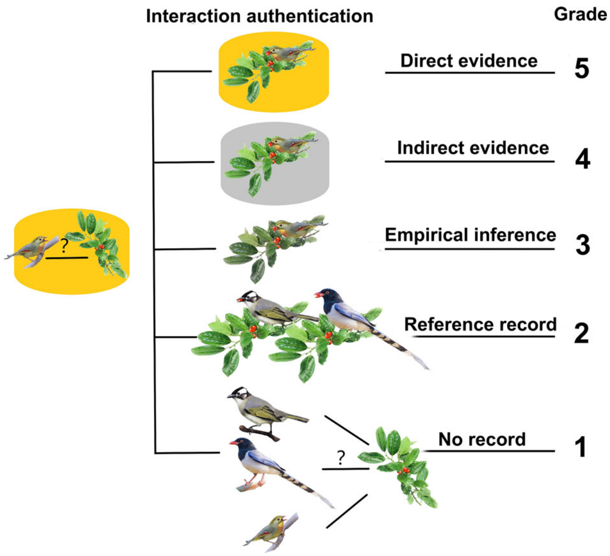


**Figure 2.** The probability of potential interactions: Grade 5—Direct evidence; Grade 4—Highly probable interaction; Grade 3—Probable interaction; Grade 2—Possible interaction; Grade 1—Unlikely interaction. Grades 5 and 4 are identified by photos or videos (see Fig. 3); Grade 3 is identified by interactions with closely related species occurring in the study area; Grade 2 is identified by a reference record from the literature. Image background color indicates occurrence on a focal island (yellow) or non-focal island (gray).

We classified an independent detection either as a foraging or a non-foraging event. The probability of a potential interaction occurring on a focal island (local area) was categorized into a five-level confidence ranking from high (5) to low (1) (Fig. 2):

1 Grade 5 (direct evidence): Frugivore foraging on fruits (hereafter 'an interaction event') was recorded by a camera on a focal island (see Fig. 3).
2 Grade 4 (indirect evidence): An interaction event was not recorded by any cameras on a focal island but was recorded by cameras on other islands.
3 Grade 3 (empirical inference): Interaction events were not recorded in any cameras on the islands (focal or non), but interactions that included closely related species (i.e., species in the same family or genus) were recorded.
4 Grade 2 (reference record): Interaction events were not recorded by any camera on the islands, but the potential interactions were recorded in the literature; the fruits of monitored plants could be dispersed by frugivores according to the literature, and the recorded bird species in the images were frugivorous.
5 Grade 1 (no record): Interaction events were neither recorded by cameras on the islands, nor were there references in the literature; the recorded species in the images were not known to be frugivorous.

 


**Figure 3.** Examples of frugivory recorded by arboreal camera traps: (A) *Pycnonotus sinensis* and *Symplocos paniculate*, (B) *Phoenicurus auroreus* and *Symplocos paniculate*, (C) *Ixos mcclellandii* and *Symplocos stellaris*, and (D) *Spizixos semitorques* and *Symplocos paniculate*. Similar photos or videos were identified as direct evidence or indirect evidence (i.e., Grades 5 and 4 as shown in Fig. 2).

## Sampling completeness test

To test the sampling completeness of our monitoring method for recording plant-frugivore interactions, we selected two common fleshy-fruit plants (*Symplocos stellaris* and *Eurya muricata*). These two plant species belong to different genera, so their fruiting seasons are largely nonsynchronous (July to August for *S. stellaris* and August to October for *E. muricata*). From July to October, there were almost no other species with overlapped fruiting periods along the camera transect where these two species were studied (Table S2). Thus, the interference of species interactions caused by other fruiting species could be minimized during this sampling period.

We set a 400-m camera transect to sample plant-frugivore interactions on an island with abundant *S. stellaris* and *E. muricata*. Along the transect, we selected the fruiting *S. stellaris* and *E. muricata* trees with the largest fruit quantities as our monitoring trees. The distance between conspecific target trees was ≥20 m (Table S1). Following this sampling method, we selected five individual trees of each species along the transect (Fig. S3).

From July 2 to August 1 and August 19 to October 20, 2019, we sampled plant-frugivore interactions in *S. stellaris* and *E. muricata*, respectively, setting five cameras for each species. We defined valid sampling days as the period from the day of camera installation until the point at which nearly all fruits had fallen or been consumed. We recorded 30 valid sampling days for *S. stellaris* (July 2 to August 1) and 53 days for *E. muricata* (August 19 to October 20). We thus monitored frugivorous birds that visited *S. stellaris* and *E. muricata* during the valid sampling days. Based on the categories of probability of plant-frugivore interaction types defined in Figure 2, we conservatively selected independent interaction events (IIEs) in Grades 4 and 5 for analyses.

For both tree species, we tested the sampling completeness of plant-frugivore interactions by plotting a species accumulation curve using the Chao 2 estimator of asymptotic species richness. Completeness of sampling was inferred by reaching the asymptote before sampling completion (Nielsen & Bascompte, 2007). The Chao 2 estimator is a non-parametric estimator based on the proportion of unique detections (species detected in only one sample day) relative to duplicates (species detected in two sample days) (Chao, 1984). We chose the Chao 2 estimator because it can provide the least biased estimator for small sample sizes (Chao et al., 2009), and it performs better than other methods for the estimation of species richness (Walther & Moore, 2005).

We ran Chao 2 estimation using EstimateS 9.1.0, and the species accumulation curves were made using the function "*specaccum*" in R package "vegan" (Colwell, 2013; Oksanen et al., 2019). We then fitted the relationship between the cumulative number of independent interaction events and sampling days by a logistic regression model.

# Results

## Overview of recorded interaction events

We recorded 4399 independent interaction events (IIEs), including 275 unique plant-bird interactions, from 1 490 556 photos and videos over 12 140 camera trapping days by monitoring 318 trees. The average number of monitoring days (i.e., the period from initial fruit ripening to dropping) for each tree was 54 days, ranging from 17 to 87 days (Table S3). Among the trees monitored, we recorded 18 fleshy-fruit plant species that were seed-dispersed by frugivorous birds. These bird-dispersed plants include broad-leaved dominant species such as *Vaccinium carlesii* and common liana species such as *Smilax china*. Birds accounted for 78.88% of all IIEs (Table S3).

We identified 49 presumed frugivorous bird species in all IIEs, including canopy omnivores (e.g., *Pycnonotus sinensis* and *Hemixos castanonotus*), canopy insectivores (e.g., *Zosterops japonicus*), and understory omnivores (e.g., *Alcippe hueti*) (Table S3). We further classified foraging behaviors of frugivores into swallowing, pecking, or carrying when the information in the images was available. Unexpectedly, a ground-foraging bird species, *Lophura nycthemera* (Phasianidae), was also recorded foraging in a tree during the day. The majority of the photographs only contained a single species, either in single-species groups or as solitary individuals, but there were more than 300 photographs recording avian mixed-species flocks foraging in the same fruiting tree (e.g., *Leiothrix lutea* with *A. hueti*; Fig. S4).

Besides frugivorous birds, in 21.12% of IIEs we recorded mammals foraging in the trees, and 99% of mammal IIEs were of rodents (Muridae). However, it was not easy to identify rodents to species because of the insufficient characters in the grayscale photos—16.85% of the images were taken during low-light times when rodents are most active (cameras take grayscale photos in low-light). For the images with identifiable mammals, the most commonly recorded species was *Niviventer confucianus* (Zeng et al., 2021), and *Callosciurus erythraeus* was also recorded feeding on ripened fruits of *S. stellaris* and *E. muricata*. In addition, several bat species and arboreal nocturnal predators (e.g., *Paguma larvata*) were recorded, though we cannot confirm whether they participated in seed dispersal.

## Sampling completeness

After 30 sampling days, we recorded seven frugivorous bird species in *S. stellaris* in the five cameras and after 53 sampling days, 11 frugivorous bird species in *E. muricata* in the five cameras (Table S4). For *S. stellaris*, each of the five cameras recorded at least five species. The understory omnivore *L. lutea* occurred in all five of the *S. stellaris* cameras as well as the common canopy insectivore *Z. japonicus*, which alone accounted for 66.9% of total IIEs. For *E. muricata*, ground-foraging *L. nycthemera* was recorded in five IIEs from two of the five cameras, while *Z. japonicus* and canopy omnivore *H. castanonotus* occurred in all five cameras.

The species accumulation curves of frugivore species richness for both tree species gradually reached an asymptote after 20 sample days, roughly equal to the richness estimated with the Chao 2 method (i.e., 7.00 and 10.79 species; see Table S5).

To record all frugivorous bird species for *S. stellaris* ($n$ = 7), we needed 10 sampling days, which was approximately a third of the fruit maturation periods (33.3%, $n$ = 30 days). For *E. muricata*, 21 sampling days were required to record all frugivorous bird species ($n$ = 11), representing 39.6% of the entire fruiting season ($n$ = 53 days) (Table 1). Logistic regression curves have a good fit to the cumulative relationships, and both reached an asymptote ($K$ value) (Fig. 5).

# Discussion

## Sampling frugivory using arboreal camera traps

Arboreal camera trapping aimed at baited feeding platforms has been used to document arboreal species and their feeding behaviors (Olson et al., 2012), and it can be a valuable method to develop frugivore inventories, especially for cryptic and nocturnal species (Rivas-Romero & Soto-Shoender, 2015). In our study, we advanced the application a step further by targeting trees with high fruit densities to effectively document frugivory. We found this method to be reliable, cost-effective, and non-invasive to record plant-frugivore interactions in difficult-to-access arboreal environments.

 

**Table 1.** The number of sampling days, independent interaction events (IIEs) of birds, observed richness of frugivorous bird species ($S_O$), the estimated richness using the Chao 2 estimator ($S_E \pm$ SD), and sampling days necessary to detect various proportions of the frugivorous bird community that visited *Symplocos stellaris* and *Eurya muricata*.

| | | | | | Sampling days that need to detect proportions of the frugivorous bird richness | |
|---|---|---|---|---|---|---|
| Monitored trees | Sampling days | IIEs of birds | $S_O$ | $S_E \pm$ SD | 80% | 100% |
| *Symplocos stellaris* | 30 | 271 | 7 | 7 ± 0.14 | 3 | 10 |
| *Eurya muricata* | 53 | 209 | 11 | 11 ± 0.16 | 10 | 21 |

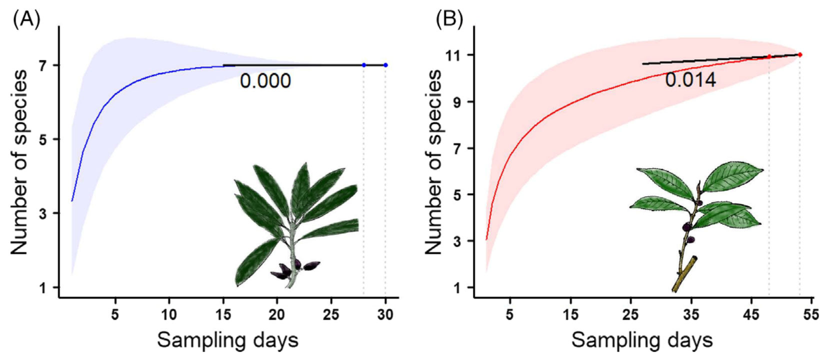


**Figure 4.** The rarefaction curves for the number of sampling days by the five cameras (temporal sampling effort) and the number of frugivorous bird species for: (A) *Symplocos stellaris* and (B) *Eurya muricata*. The area between the two points indicates the last 10% of the rarefaction curves. Black lines and numbers indicate the slopes. Shaded areas indicate the 95% confidence intervals.

We found arboreal camera trapping was also useful for documenting various foraging behaviors in detail, such as specific fruit removal processes. Different behaviors could lead to contrasting functional outcomes of species interactions (Simmons et al., 2018). In contrast to direct observations from observers on the ground, with cameras, foraging records are clearly identifiable and less disputable. We can easily use photos and videos to classify animal behaviors into different categories, such as swallowing entire fruits, pecking pulps, or simply visiting. In addition, we captured other arboreal behaviors on videos. For example, we found that mixed-species bird flocks led by nuclear species (e.g., *A. hueti*; Fig. S4) often fed on fruits in the same tree. The image data taken by arboreal camera traps will promote research on ecological processes and functions mediated by these different behaviors.

Another benefit of this method was our ability to record activity patterns of cryptic and nocturnal species in the arboreal ecosystem (Zhu et al., 2021). From our monitoring, *L. nycthemera* is a potential seed disperser for many fleshy-fruit plant species, while previously, foraging records only occurred on the ground (Corlett, 2017; Sankamethawee et al., 2011). It is possible that the foraging niche of *L. nycthemera* may have expanded in this study because of the low availability of feeding resources on small islands. It could also be possible that this is the first record of the arboreal foraging behavior of *L. nycthemera*. Nocturnal mammals (Muridae and *Paguma larvata*) were also recorded by arboreal camera traps at night. One of our videos indicated fruit removal in the tree and potential seed dispersal on the ground in Muridae (Video S1), with an individual recorded carrying fruits in its mouth at night. Further investigation of this point could clarify the functional role of Muridae as potential seed dispersers in island ecosystems (Zeng et al., 2019).

## Sampling strategies according to fruit production and fruiting periods

Arboreal camera trapping could be expanded to monitor various phenological stages of target trees (e.g., Ganesh & Devy, 2006). Here, we effectively recorded plant-frugivore interactions during the fruit maturation periods (Fig. 4). In our study, we found the number of foraging individuals increased as fruit ripening proceeded. Accordingly, animals began to reduce their visits when the number of fruits decreased (Fig. 5). This phenomenon provides useful practical guidance for similar studies in other areas: trees with high fruit production (i.e., large fruit crop size) are more attractive to frugivores (Palacio & Ordano,

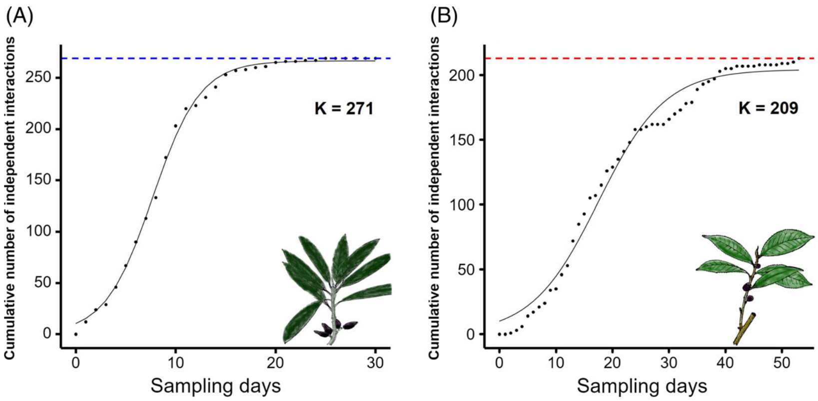


**Figure 5.** Cumulative independent interaction events (IIEs) over the course of sampling and the fitted curve using logistic regression. Dashed horizontal lines illustrate the number of IIEs at the asymptote: (A) *Symplocos stellaris*, $K = 271$, $R^2 = 0.9976$, $P < 0.001$ and (B) *Eurya muricata*, $K = 209$, $R^2 = 0.9854$, $P < 0.001$. $K$ = the number of independent interaction events.

2018). In our study, we selected the individuals with the most abundant fruits within a radius of 20 m if there were multiple individuals of the same tree species along the transect. This method can avoid unnecessary workloads and reduce oversampling effectively, while can also effectively record plant-frugivore interactions.

Our results suggest that after monitoring approximately a third of the fruit maturation periods, a complete frugivorous species inventory was achieved for *S. stellaris,* while around four more days were necessary for *E. muricata* to achieve sampling completeness (Table 1). Furthermore, our sampling began when just a small proportion of fruits were ripe (Period 1 in Fig. S5) and ended when the majority of the fruits were consumed or had fallen (after Period 3 in Fig. S5). Based on Figure 5 and processes of fruits removal, we suggested that it could be a sufficient strategy to focus sampling efforts between the period when the number of ripe fruits increases rapidly (Period 2 in Fig. S5) and the period when almost all fruits were ripened but some fruits were falling and consumed (Period 3 in Fig. S5). When there were enough individual trees to be monitored, an appropriate sampling period was necessary to achieve sampling completeness. For example, one can enhance camera replacement frequency and increase sampling efforts (i.e., add more cameras to monitor different fruiting individuals) in the camera transect during these periods as preferred sampling strategies. In this way, sampling can be maximized and more fruiting individuals can be monitored.

## Methodological advantages in the fragmented landscape

Monitoring trees with abundant fruits selectively along camera transects can provide robust documentation of frugivores in the patch (i.e., in our case, different islands). Arboreal camera trapping has the potential to effectively monitor plant-frugivore interactions over larger areas in the landscape (Bowler et al., 2017). This method also permits monitoring of the entire fruiting periods of several plant species simultaneously. Therefore, the method allows the study of spatial patterns and temporal dynamics of the same ecological processes even when they vary spatiotemporally. In a complex habitat, like in different patches with low-connectivity, camera-trap sampling is fairly time-saving and labor-efficient. Because our study was conducted in an artificial island archipelago, our method might be the preferred option because traveling among islands is costly, and camera traps on different islands can record animal-plant interactions remotely simultaneously.

## Limitations and solutions

Although our method has successfully recorded plant-frugivore interactions, there were some problems that caused failure in some cameras. In our study, arboreal cameras malfunctioned or did not successfully monitor the target for various reasons, including internal camera failure ($n = 3$, where n is the number of damaged cameras), damage and movement by rodents (gnawing fixed straps, $n = 2$; e.g., Gregory et al, 2015), wind causing camera movement (lens covered by leaves, $n = 2$), and the camera falling out of the tree ($n = 1$). In a number of cases ($n = 19$) memory cards were filled due to triggers by non-target stimuli, a common challenge in both arboreal and terrestrial camera trapping (Gregory et al., 2014); hence, the cameras were checked every two weeks to minimize data loss. In our study, 98.1% of all photographic events (97.8% as a contrast in Gregory et al., 2014) were of non-target stimuli. We found that most problems could be identified and solved at the first routine check. Here, we provide two suggestions for combating arboreal camera malfunctions: (i) removing leaves from in front of the camera and making sure the fruits are clear in view when installing and maintaining cameras and (ii) checking camera sites routinely and reinstalling the cameras at sites with problems. Fortunately, Gregory et al. (2014) have provided a trouble-shooting guide for camera placement and programming. If a camera was set in a proper position and no fatal problems occurred (e.g., in malfunction, or destroyed by animals), it was possible to monitor the entire fruiting period of the targeted tree.

One challenge of camera trapping in arboreal habitats is the installation of cameras at heights due to limited accessibility. On subtropical reservoir islands in our study, many fleshy-fruit plants were in the sub-canopy and understory. The maximum height at which our cameras were placed was eight meters. Besides climbing trees with hands and feet, using a collapsible ladder was a straightforward and reliable climbing technique in this specific habitat (Fig. 1C). Alternative access methods, such as rope-based methods, could be useful for climbing to higher vertical stratifications, for example, in tropic areas (Anderson et al., 2015).

Another disadvantage of camera trapping is the time-consuming manual review of images. We screened more than two million photographs taken by more than 300 cameras for this study. The burden of manual review may limit the large-scale use of camera traps for further studies. The development of artificial intelligence (AI) technology used to identify species in photos from camera traps could potentially solve this problem (Norouzzadeh et al., 2018; Yousif et al., 2019). However, the background in arboreal camera trap photos is not always static, due to the unavoidable movement of cameras by wind. Another challenge is that most bird species are relatively small in body size in comparison to medium or large-bodied mammals, for which the cameras are designed. For this reason, they may not always be detected by the cameras or even the image reviewers (Ortmann & Johnson, 2021). Nevertheless, camera trapping is still cost-effective and preferred in studies in circumstances similar to ours. With the development of deep learning systems (Norouzzadeh et al., 2018), we believe more effective methods will overcome the challenge of image identifications. Additionally, harnessing the collective effort of citizen scientists can contribute to reducing the time for information extraction (Hsing et al., 2018; Willi et al., 2019).

## Future directions in sampling methods for plant-frugivore interactions

Many studies have used only direct observation to record frugivory events (Albrecht et al., 2013; Snow & Snow, 1988). However, an observer cannot directly observe a target tree continuously over a fruiting season without breaks, and being basically an invasive survey method, direct observation may cause some cryptic species to avoid visiting the target tree. This can largely limit the sampling of frugivores in arboreal environments and impede our comprehensive understanding of arboreal frugivores and seed dispersers.

Sampling schemes that mix methods allow for more robust identification of plant-frugivore interactions. For example, in one study, camera trapping was an effective complementary sampling method to record interactions of inconspicuous and nocturnal animals (Timóteo et al., 2018). However, estimates of interaction frequencies may be confounded, due to sampling bias caused by different methodologies (Schleuning et al., 2014).

Camera trapping has been used to record frugivory at ground level in combination with direct observations at arboreal level (Acevedo-Quintero et al., 2020; Li et al., 2020). However, this methodological combination may result in underestimates of cryptic and nocturnal species in the arboreal habitats. Perhaps a sampling method that combines camera trapping both at ground and arboreal level is a viable solution (Tongkok et al., 2020), because it has the potential to detect all species (Moore et al., 2020).

In tropical forests, communities of frugivores and their interactions with plants differ along vertical gradients (Schleuning et al., 2011; Thiel et al., 2021). The height of plants could affect the sampling of plant-frugivore interactions and IIEs, especially for plant species with varying heights and for bird species with multiple foraging strata (e.g., understory, midstory, or canopy). Setting arboreal camera traps at different forest strata will allow sampling of plant-frugivore interactions at specific vertical stratifications simultaneously. Ecological research on the nature of plant-frugivore interactions across the vertical gradient will be facilitated through use of arboreal camera trapping, and long-term monitoring programs at larger temporal-spatial scales can be performed.

Photographs and videos can miss momentary plant-animal interactions, which may not reflect actual frugivory events. For example, we defined an independent detection as a non-foraging event if the frugivory moment was not captured. To develop a high-quality frugivory inventory, we proposed a new framework to categorize plant-frugivore interactions (Fig. 2), which is applicable in fragmented landscapes like the land-bridge islands reservoir in this study.

An unbiased frugivory or seed-dispersal database will inform conclusions on related ecological processes and improve our understanding of the functions of plant- frugivore mutualisms. Such a database will also allow us to understand the roles of various frugivore species in maintaining community structure and ecosystem services in the face of ecosystem change. Consequently, an appropriate sampling method with the matched theoretical framework is needed when we evaluate complex interactions between multiple species. Camera trapping has the potential to be that sampling method.

# Conclusions

Our proposed sampling method with the matched theoretical framework for plant-frugivore interactions has established a strong basis for our ongoing study on seed-dispersal networks in a fragmented landscape. Our approach may facilitate ecological studies of frugivory and seed dispersal, especially on large-spatial scales. Nevertheless, arboreal camera trapping is still a new technology relative to ground camera trapping, and some fine-tuning is still needed for the method to reach its full potential.

Our work suggests the following three conclusions:

1 Arboreal camera trapping is a non-invasive, labor-efficient, and relatively unbiased sampling method to record plant-frugivore interactions in difficult-to-access arboreal environments. It therefore provides an avenue to better assess animal activities above the ground in future wildlife research.
2 Based on our sampling completeness test, arboreal camera trapping can sufficiently record species richness in plant-frugivore interactions through sampling of approximately a third of the fruit maturation periods for a plant species, especially when cameras are placed during Periods 2 and 3 (Fig. S5).
3 We suggest using a combination of setting cameras at arboreal and ground level to optimize sampling, and we foresee this combined method to be a methodological trend for future wildlife monitoring. This combined sampling protocol can be integrated into a standardized monitoring platform to build a multi-scale camera network for biodiversity research.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1**. Description of methods used to set line transects and place arboreal cameras in Figure 1.
**Table S2**. Fleshy-fruit plant species that suggest frugivory by frugivorous birds so far in lake region of the Thousand Island Lake.
**Table S3**. Main results for species monitored by arboreal camera traps in lake region of the Thousand Island Lake from June 2019 to February 2020.
**Table S4**. Monitoring results for *Symplocos stellaris* and *Eurya muricata* respectively on the experimental island after 30 and 53 sampling days.
**Table S5**. Statistical estimation of species richness for sampling frugivorous birds of *Symplocos stellaris* and *Eurya muricata*.
**Figure S1**. The 22 study islands of the Thousand Island Lake in Zhejiang Province, eastern China.
**Figure S2**. Landscape of the Thousand Island Lake.
**Figure S3**. The distribution of target trees on the experimental island.
**Figure S4**. An example of avian mixed-species flocks (i.e., *Leiothrix lutea* with *Alcippe hueti*).
**Figure S5**. An example of the different periods of tree fruiting during the sampling period.
**Video S1**. Original video file with Muridae taking fruits.

 