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Composition of frugivores of *Baccaurea ramiflora* (Phyllanthaceae) and effects of environmental factors on frugivory in two tropical forests of China and Thailand

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ABSTRACT

Frugivory and seed dispersal are key processes that shape both plant and animal communities, they are important in the maintenance and regeneration of forest ecosystems while threatened by environmental changes. This study investigated the frugivores and environmental factors affecting animal visitation and fruit consumption of the evergreen tree *Baccaurea ramiflora* (Lour.) in Chinese (Xishuangbanna) and Thai (Mo Singto) tropical forest plots. The two plots differ in their mammal faunas, with more large species (Asian elephant, white-handed gibbon, bears) surviving on the Mo Singto plot. We asked whether these differences could resulted in different seed dispersal patterns on the two plots. Nine individual trees were selected in each plot to record arboreal and ground frugivores of *B. ramiflora* using camera traps. A total of 27 frugivore species were captured from both forest plots, 15 species in Xishuangbanna and 22 in Mo Singto, with ten species shared in both plots. The major frugivores of *B. ramiflora* in Xishuangbanna were all pre-dispersal seed predators with little contribution to seed dispersal, including Palla's squirrel (*Callosciurus erythraeus*), red-cheeked squirrel (*Dremomys rufigenis*) and black giant squirrel (*Ratufa bicolor*). Meanwhile, the major frugivores in Mo Singto were two effective seed dispersers pig-tailed macaque (*Macaca leonina*) and white-handed gibbon (*Hylobates lar*), and seed

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predator black giant squirrel (*Ratufa bicolor*). The diversity and body size of frugivores in the Xishuangbanna plot were relatively small compared with those in Mo Singto plot. Small-bodied frugivores showed higher activity in Xishuangbanna plot whereas relatively larger frugivores were most active in the Mo Singto plot. The environmental factor that consistently influenced frugivore activity (visitation and consumption of *B. ramiflora* fruits) was fruit abundance. Ground cover was also a predictor for average visit length and fruit consumption of frugivores. Frugivores visitation rate was higher in Xishuangbanna while average visit length and consumption rates were higher in Mo Singto. The defaunation of large body-size frugivores in Xishuangbanna could have been a result of habitat loss and higher hunting pressure. This may lead to shorter dispersal distances for large-seeded plants, restricting their ability to move across changing landscapes, and threatening their chances of survival over the long term.
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1. Introduction

Frugivory and seed dispersal are two linked processes that shape animal and plant communities (Corlett, 1998; 2017). However, we still lack basic data on dispersal of tropical plant species needed to answer preliminary questions such as (1) How many and what types of animals feed on the plant species? (2) Which species are important or essential predators/dispersers of the seeds? (3) Which species are seed predators or otherwise reduce survival? and (4) How strongly do particular frugivores depend on the plant's fruits during its fruiting period? Answering these questions will help us understand how frugivory and seed dispersal affect the maintenance and regeneration of forest ecosystems (Bascompte and Jordano, 2006; Côrtes and Uriarte, 2013; Chanthorn et al., 2018). Understanding patterns of frugivory and seed dispersal in different circumstances will allow us to address a range of critical conservation problems in preserving plant and animal communities in the Anthropocene (Fritz and Purvis, 2010; Campos-Arceiz and Blake, 2011).

Frugivory and seed dispersal are threatened by environmental changes such as habitat loss, fragmentation, and modification through reduction in species richness and abundance of dispersal agents (McConkey and O'Farrill, 2015; Howe, 2016; Neuschulz et al., 2016; Chang et al., 2019). Altered seed dispersal patterns due to environmental changes could lead to changes in community composition or even species extinction (Corlett, 2007; Vanthomme et al., 2010; Walther, 2010). Another change that will influence seed dispersal patterns is defaunation of large and medium-sized vertebrates (Dirzo et al., 2014). Defaunation modifies frugivore composition which then affects frugivory and seed dispersal patterns, which may ultimately decrease forest capacity to store carbon (Chanthorn et al., 2019). This is of considerable concern, particularly for large-seeded plant species, as smaller vertebrates are often unable to replace the seed dispersal services provided by larger species. The loss of large-bodied dispersal agents which can carry seeds for longer distances may reduce chances of seeds reaching suitable micro-sites and affect gene flow within and between populations (Wenny, 2001; Bacles et al., 2006).

Previous studies on frugivory and seed dispersal have relied on direct observations and fruit-fall traps (Howe, 1980; Dennis and Westcott, 2006). However, the presence of human observers and traps may deter some large frugivores from feeding sites, and may also result in bias against detection of some types of frugivores (Prasad et al., 2010; Jayasekara et al., 2003) such as terrestrial and nocturnal species. One alternative and now widely used method for the study of frugivory is camera trapping (Trolliet et al., 2014). Camera traps eliminate the need for observers to record observations *in situ*, and enable observation of animals that are highly sensitive to human presence, and nocturnal animals (O'Brien and Kinnaird, 2008; Trolliet et al., 2014). Camera traps are not without problems, however; they can be damaged or stolen by hunters or poachers, and some animals have been known to interfere with or move the cameras (Newey et al., 2015; Caravaggi et al., 2017). Moreover, cameras do not capture the behavior of small species as well as larger species (Caravaggi et al., 2017). Nevertheless, camera trapping has become the method of choice in studies of frugivory as it offers more advantages than disadvantages over direct observation.

In this study, camera trapping was used to determine frugivores and potential seed dispersers of a large-seeded tree species, *Baccaurea ramiflora* (Phyllanthaceae). We firstly compared frugivore composition and attempted to determine the effects of several environmental factors on visitation of frugivores to *B. ramiflora* between two large tropical forest dynamics plots (FDPs). The Xishuangbanna FDP (hereafter XSBN FDP) is in Yunnan, southwestern China, 7° north of the Mo Singto FDP (hereafter MS FDP) in Khao Yai National Park, Thailand. XSBN and MS FDPs are ideal sites to study the potential fate of large-seeded plants in changing landscapes. Both FDPs are in protected forest, but there has been relatively little anthropogenic disturbance around the MS FDP since Khao Yai National Park was established in 1962, whereas the surroundings of the XSBN FPD have experienced higher deforestation rates and agricultural development (Zhang, 1986; Liu et al., 2013; Sreekar et al., 2015; Chanthorn et al., 2019; Chang et al., 2019). Although *B. ramiflora* is widely distributed in southern China and Southeast Asia, there are no quantitative data on the interactions between this common large-seeded tree and its dispersers. We sought to determine whether the differences in frugivores, especially mammal faunas, between the plots could affect the consumption of fruits and dispersal of seeds on the respective plots, and hence the possible survival of the tree species.

2. Materials and methods

2.1. Study sites

The study was conducted in two FDPs in China and Thailand (Fig. 1). The two FDPs were set up according to the standards of the long-term permanent plot network of the Center for Tropical Forest Science (CTFS), Smithsonian Tropical Research Institute, Smithsonian Institution, Washington D.C (Condit, 1998). and now are part of the forestGEO network (forest-geo.si.edu). The 20-ha XSBN FDP is located in Yunnan Province, southwestern China (21°36′ N, 101°34′ E). The altitude within this plot ranges from 709 to 869 m (Cao et al., 2008; Lan et al., 2012). The 30-ha MS FDP is located inside Khao Yai National Park, central Thailand (14° 26′ N, 101° 22′ E), with altitude ranging from 725 to 815 m (Brockelman et al., 2017). The forest on the

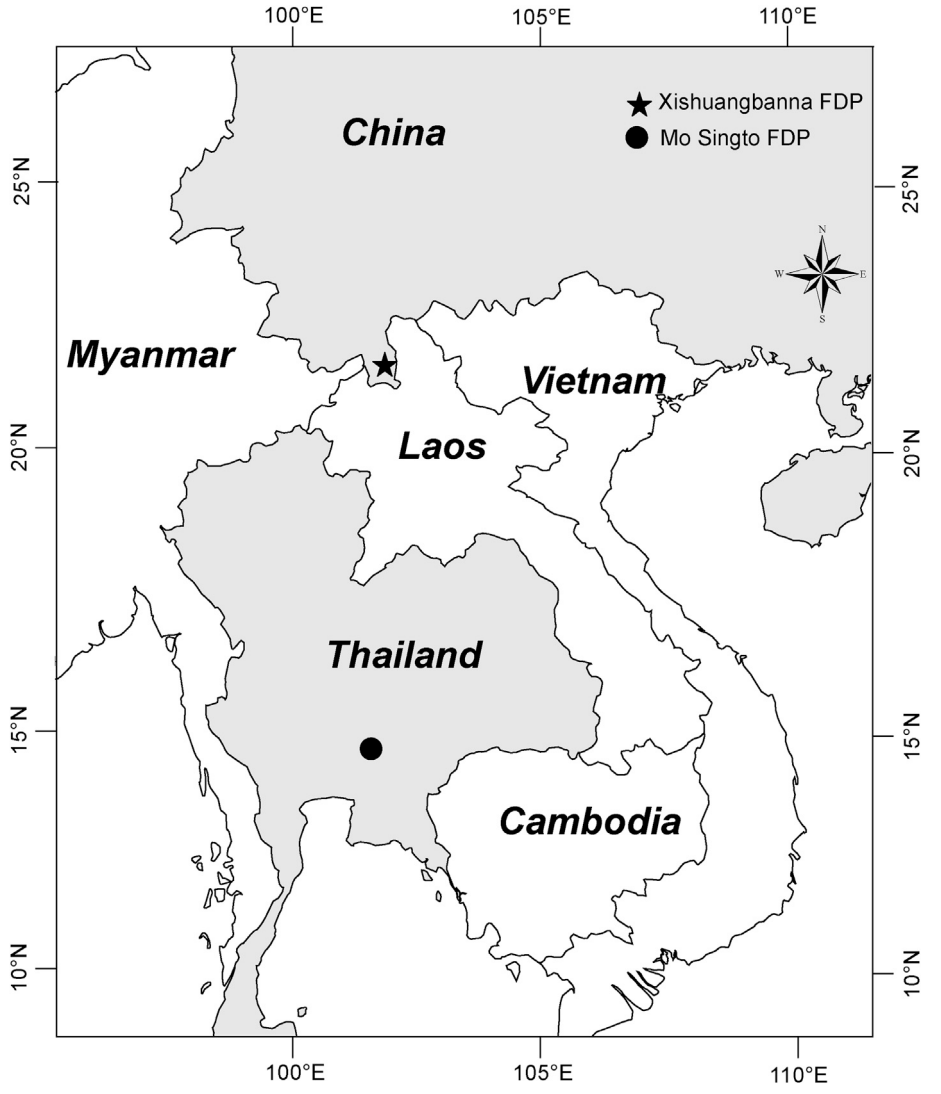

Fig. 1. Map showing the location of the 20-ha Xishuangbanna FDP (star) in Yunnan, China and the 30-ha Mo Singto FDP (point) within Khao Yai National Park, Thailand.

two plots has been classified as northern seasonal evergreen forest (Ashton, 2014; Brockelman et al., 2017) and there are many genera, though not so many species, in common between them. Average annual precipitation at XSBN FDP was 1532 mm and at MS FDP was 2073 mm. Average annual temperatures are 21 °C and 22.4 °C, respectively (Lan et al., 2012; Brockelman et al., 2017). These two FDPs are both partly dominated by tall dipterocarps: *Parashorea chinensis* at XSBN FDP, and *Dipterocarpus gracilis* in the MS FDP.

2.2. Study species

The plant species *Baccaurea ramiflora* Lour. (Phyllanthaceae [Euphorbiaceae]), is a semi-evergreen species reaching 5–25 m in height (Pammenter and Berjak, 1999). It is distributed from Nepal, India, Bhutan, Myanmar, Bangladesh, South China, Thailand, the Andaman Islands and Peninsular Malaysia through Indo-China, chiefly in moist tropical forests (Sundriyal and Sundriyal, 2003; Abdullah et al., 2005). It is a common understory species in both FDPs, with 3221 individuals ≥1 cm (3.35% of total stems) and 533 individuals ≥ 10 cm DBH (diameter at breast height) in XSBN FDP (census in 2007), and 630 individuals ≥1 cm (0.47% of total stems) and 27 individuals ≥ 10 cm DBH in MS FDP in MS FDP (census in 2011) (Cao et al., 2008; Brockelman et al., 2017).

B. ramiflora is dioecious. It sets fruit from May to July in XSBN and from April to June in MS. The fruit is oval to round, velvety and 2–3 cm in diameter. There are 3–4 seeds (0.8 by 1.2 cm in size) embedded in pinkish white pulp within the berry with yellowish to red leather pericarp (Singh et al. 2017). The fruit of this plant species is used as a novel food additive because of its high content of vitamin C, protein and iron (Amin and Nabi, 2015). Other plant parts (i.e., leaves, roots, seeds, fruits) are believed to have medicinal value and health benefits (Pammenter and Berjak, 1999).

The fruits of *B. ramiflora* are consumed by various vertebrates such as monkeys (Albert et al., 2013), deer (Datta and Rawat, 2008), squirrels, gibbons and civets (Kitamura et al., 2002), although the fruit characteristics are typical of “primate fruits” (Gautier-Hion et al., 1985). There were also reports that hornbills (captive individuals) (Kitamura et al., 2005) and wild pigs (Datta and Rawat, 2008) could consume *B. ramiflora* fruits; however, the most effective dispersers remain unknown. The camera trapping survey carried out by National Forest Ecosystem Research Station at Xishuangbanna around the XSBN FDP from 2012 to 2017 recorded potential frugivores including northern pig-tailed macaque (*Macaca leonina*), sambar deer (*Rusa unicolor*), red muntjac (*Muntiacus muntjak*), lesser mouse deer (*Tragulus kanchil*), wild boar (*Sus scrofa*), binturong (*Arctictis binturong*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*), small-toothed ferret-badger (*Melogale moschata*) and several species of Sciuridae and Muroidea (Zhang et al., 2014; National Forest Ecosystem Research Station at Xishuangbanna, Unpublished data). All the potential frugivores from XSBN FDP, aside from masked palm civet, were also recorded around MS FDP (Lynam et al., 2006). Other potential frugivores in and around MS include white-handed gibbon (*Hylobates lar*) and pileated gibbon (*Hylobates pileatus*), Asian elephant (*Elephas maximus*), Asiatic black bear (*Ursus thibitanus*), Malayan sun bear (*Helarctos malayana*) and four species of hornbills (Lynam et al., 2006).

2.3. Fruit tree survey and setting up camera traps

B. ramiflora trees within and around the two FDPs were surveyed in early 2018. At the start of the fruiting period, fruit production of *B. ramiflora* trees was estimated by counting the number of fruits on the trees and the fallen capsules around the fruiting trees. The species is cauliflorous, which facilitates counting the fruit crop. Nine trees (≥10 cm DBH, > 4 m high) from each FDP were selected in the study based on size and the fruiting status (Table S1), including three trees with high fruit production (>2000 fruits), three with medium fruit production (1000–2000 fruits) and three with low fruit production (<1000 fruits). The trees varied from 14.3 cm to 30.2 cm (median 25 cm) in the MS plot, and 14.7–31.0 cm in DBH (median 26.2 cm) in the XSBN plot. For each focal tree, the tree tag identification number and coordinates were recorded (Table S1).

After focal trees selection, we fixed three to five cameras at each focal tree. To record both arboreal and ground dwelling species, camera traps were secured to the trunks of trees surrounding each focal tree aimed at the focal tree itself and the ground beneath it. Camera traps were sometimes set on the focal tree itself if there were no ideal locations on neighboring trees. Camera traps were secured to maximize detection of visiting animals; hence, the position varied per focal individual. Auto-focus camera traps were set with the following settings: real-time clock, high-quality full-color resolution, day/night auto-sensor, programmable trigger interval of 1–2 s, photo plus video mode with three photos per trigger, and a 10 s lengths video, with 30 s gaps between videos. All photos and videos were saved in 16 GB memory cards. Camera traps ran on 8 to 12 1.5-V alkaline batteries. Camera traps settings were double checked and tested by taking photos and videos of operators before set in the field.

During the fruiting season (May–July in XSBN, April–May in MS, 2018), camera traps were checked daily until the fruiting season finished. Camera ID, date, time and temperature will be stamped on each photo and video. Photos and videos were transferred from memory card to a computer and were examined carefully to (1) identify the animal species captured in the photos and videos (following Lekagul and Round, 1991; Smith and Xie, 2009), (2) record the date, time, location and number of photos and videos taken, (3) determine whether fruits were consumed during the visit (through time-delay sequence), and (4) count the number of fruits remaining in front of the cameras. We expected to distinguish “no fruit-consumer” (species not observed to consume fruits) from actual “frugivores and seed dispersers” (species observed to consume fruits either from the tree or those fallen on the ground). We also expected to determine the most important dispersers and predators of *B. ramiflora* seeds based on the number of fruits consumed by each frugivore.

2.4. Environmental factors

We hypothesized that high fruit abundance on the focal trees, high number of neighboring fruit trees and nearby streams would attract frugivores (Beck and Terborgh, 2002; Côrtes and Uriarte, 2013; Trisurat et al., 2014). In addition, ground cover and slope of the habitat could also affect frugivore visitation and consumption (Levey, 1990; Côrtes and Uriarte, 2013). We therefore collected information on these factors for all individual *B. ramiflora* trees in this study. Neighboring fruit trees and ground cover were estimated within a 20 m × 20 m quadrat with the focal tree at the center. The 20 m × 20 m quadrat was divided into four 10 m × 10 m subquadrats, where neighboring fruit trees and ground cover were visually estimated. The average measurement of the four subquadrats was taken as the value for that focal tree. Slope was measured using a mobile application (iOS Compass application).

2.5. Data analysis

After camera trap photos and videos were transferred from the memory cards, each photo and video were carefully checked to (1) compare the number of fruits in earlier and later photos in the sequence, (2) estimate the number of available fruits consumed by each frugivore, and (3) assess how long (in minutes) the frugivores stayed at the fruiting trees (visit length). On an Excel spreadsheet, photos and videos were grouped by tree individual and animal species, with date and time. Photos and videos of one species captured within 30 min were recorded as one independent record following O'Brien et al. (2003). After grouping the photos and videos to independent records, the following aspects were examined (formulas shown in Table S2):

Relative abundance of frugivores and no fruit-consumer*:* Based on the photos and videos from camera traps, we identified animal species that were observed to consume and remove *B. ramiflora* fruits as frugivores, while other animals not observed removing or eating fruits were classified as no fruit-consumers. From these data, the number of species visiting *B. ramiflora,* as well as the number and types of frugivores were recorded. The number of independent photograph records for each species was counted and used to calculate the relative abundance index (RAI) for each species (Kawanishi et al., 1999; Azlan and Sharma, 2006).

B. ramiflora *visitation and fruit consumption**:* We first recorded the number of times each species visited the focal trees and calculated the relative frequency of visits following Prasad et al. (2010). We then compared the number of fruits seen in earlier and later photos and videos to count the number of available fruits consumed by each frugivore species per visit and relative fruit consumption (%), as well as the time the frugivores spent at the fruiting tree (average visit length). Following Kitamura et al. (2004), we used relative fruit consumption (%) to determine the top frugivores of *B. ramiflora* in the two FDPs.

We also categorized the frugivores into size classes (large >45 kg, medium 1–45 kg, small <1 kg), following Corlett (2007) and Smith and Xie (2009). We used student's t-test to compare the frugivore activity in the two plots based on body size.

Factors affecting visitation fruit removal: For each focal tree, the following response variables were calculated (for the formulas, see Table S2): frugivore species richness, frequency of frugivore visits, average visit length, amounts for fruits consumed, fruits consumed per day and fruits consumed per visit (data were showed in Table S3). The predictor variables considered include fruit abundance, neighboring fruit trees, ground cover, distance to water, slope and site. Generalized linear models (GLMs) were used to detect the influence of these predictors on *B. ramiflora* visitation and frugivory. Frugivore species richness and frequency of frugivore visits were modelled using Poisson (or quasi-Poisson) distribution while others were modelled using Gaussian distribution (response variables were logged prior to analysis). Models using Poisson distribution were evaluated for over-dispersion. When over-dispersed, we used quasi-Poisson distribution instead to account for over-dispersion. Stepwise regression analysis was employed where all predictor variables were included in the first model (full additive model) and then removing one parameter at a time for the succeeding models (Korine et al., 2000). To evaluate nested models, analysis of variance (ANOVA) using 'Chisq' test statistic was conducted, followed by measurement of the Akaike Information Criterion (AIC) values. The model with the lowest AIC value was then selected as the best model for each of the response variables. All analyses were conducted using R Statistical Software (R Core Team, 2018).

3. Results

3.1. Frugivores and no fruit-consumer of B. ramiflora

A total of 2336 independent records of 27 frugivore and 12 no fruit-consumers from both plots were captured (Table 1). In XSBN, 15 frugivore and six no fruit-consumers were captured in 1660 independent records. In MS, 22 frugivore and six no fruit-consumers were captured in 676 independent records. Of all frugivore species in the two plots, five were recorded only in XSBN, 12 were observed only in MS, and 10 species were found in both plots (Table 1).

The most abundant frugivore species (RAIs) in XSBN were *Callosciurus erythraeus* (40.5%), Muroidea sp. (29.2%) and *Dremomys rufigenis* (12.8%), while in MS they were *Ratufa bicolor* (44.5%), *Macaca leonina* (14.7%) and *Rusa unicolor* (11.6%; Table S4).

Table 1
Occurrence of species captured by camera traps with their body mass in Xishuangbanna (XSBN) and Mo Singto (MS) FDPs. Asterisk indicates that the species was captured consuming *B. ramiflora* fruits (frugivore); 1 and - indicate presence and absence, respectively.

Family	Common name	Scientific name	IUCN status	XSBN	MS	Body mass (Kg)
Birds						
Phasianidae	Siamese fireback	*Lophura diardi**	*LC*	–	1	0.6–1.4
	Silver pheasant	*Lophura nycthemera**	*LC*	1	1	0.9–2
	Red junglefowl	*Gallus gallus**	*LC*	1	1	0.5–1.3
	Green-legged partridge	*Arborophila chloropus**	*LC*	–	1	0.25–0.3
Cuculidae	Coal-billed ground cuckoo	*Carpococcyx renauldi**	*VU*	–	1	0.4
Columbidae	Grey capped emerald dove	*Chalcophaps indica**	*LC*	–	1	0.08–0.14
Bucerotidae	Oriental-pied hornbill	*Anthracoceros albirostris*	*LC*	–	1	0.6–1.2
Leiothrichidae	White-crested laughingthrush	*Garrulax leucolophus**	*LC*	1	1	0.1–0.13
Corvidae	Common green magpie	*Cissa chinensis*	*LC*	1	–	0.13–0.2
Eurylaimidae	Long-tailed broadbill	*Psarisomus dalhousiae*	*LC*	1	–	0.05–0.07
	Silver-breasted broadbill	*Serilophus lunatus*	*LC*	1	–	0.03–0.05
	Bird (Unknown)	*Cyornis* sp.		–	1	<1
Mammals						
Elephantidae	Asian elephant	*Elephas maximus**	*EN*	–	1	>2000
Cervidae	Sambar deer	*Rusa unicolor**	*VU*	–	1	185–260
	Southern red muntjac	*Muntiacus muntjak**	*LC*	1	1	17–40
Tragulidae	Lesser mousedeer	*Tragulus kanchil**	*LC*	1	1	2.5–4.5
Suidae	Wild boar	*Sus scrofa**	*LC*	1	1	50–200
Felidae	Leopard cat	*Prionailurus bengalensis*	*LC*	1	–	1.5–5
Viverridae	Large Indian civet	*Viverra zibetha**	*LC*	–	1	1.6–4
	Small-toothed palm civet	*Arctogalidia trivirgata**	*LC*	–	1	2–2.5
	Binturong	*Arctictis binturong**	*VU*	–	1	9–14
	Masked palm civet	*Paguma larvata**	*LC*	1	–	3–7
	Owston's civet	*Chrotogale owstoni**	*EN*	1	–	2.4–3.4
	Small Indian civet	*Viverricula indica*	*LC*	1	–	1.6–4
Canidae	Dhole	*Cuon alpinus*	*EN*	–	1	10–20
Mustelidae	Small-toothed ferret-badger	*Melogale moschata*	*LC*	1	–	0.5–1.6
Cercopithecidae	Northern pig-tailed macaque	*Macaca leonina**	*VU*	1	1	11–14
Hylobatidae	White-handed gibbon	*Hylobates lar**	*EN*	–	1	3.9–7
Sciuridae	Variable squirrel	*Callosciurus finlaysonii**	*LC*	–	1	0.16–0.2
	Grey-bellied squirrel	*Callosciurus caniceps**	*LC*	–	1	0.2–0.3
	Pallas's squirrel	*Callosciurus erythraeus**	*LC*	1	–	0.28–0.3
	Red-cheeked squirrel	*Dremomys rufigenis**	*LC*	1	–	0.21–0.34
	Black giant squirrel	*Ratufa bicolor**	*NT*	1	1	1.3–2.3
	Himalayan striped squirrel	*Tamiops macclellandii**	*LC*	1	1	0.07–0.09
	Indochinese ground squirrel	*Menetes berdmorei*	*LC*	–	1	0.21
	Flying squirrels (Unknown)	*Hylopetes* sp.*		1	–	<1
Muroidea	Rat (Unknown)	Muroidea sp.*		1	1	<1
Hystricidae	Malayan porcupine	*Hystrix brachyura*	*LC*	–	1	10–18
Reptiles						
Varanidae	Common water monitor	*Varanus salvator*	*LC*	–	1	15–70
		Total number of species: 39		21	28	
		Number of frugivore species: 27		15	22	

IUCN status: LC–least concern, NT–near threatened, VU–vulnerable, EN–endangered.

3.2. *B. ramiflora* visitation and fruit consumption

Frugivores visited *B. ramiflora* a total of 1664 times in XSBN and 633 times in MS. In XSBN, most of the visits (~83%) were made by Muroidea sp. (743), *C. erythraeus* (420) and *D. rufigenis* (274). In MS, *R. bicolor* (141), *M. leonina* (131) and *Callosciurus caniceps* (75) accounted for most of the visits (~55%). In XSBN, Muroidea sp., *C. erythraeus, Sus scrofa* and Hylopetes *sp. made the most visits per day. R. bicolor* spent the longest time per visit (mean = 26.7 min), followed by *C. erythraeus* and *M. leonina*. In MS, *the frugivores making the most visits per day were Hylobates lar, M. leonina and R. bicolor* while the frugivores which had the longest average visit length were *R. bicolor* (mean = 27.2 min), followed by *H. lar* and *M. leonina* (Fig. 2 and Table S4).

Amount of fruits consumed was relatively higher in MS than in XSBN. In both plots, consumption up in the canopy was higher than consumption on the ground (Table S4). In XSBN, *M. leonina* consumed the highest number of fruits per visit (34.6 fruits). while in MS, *H. lar* consumed the most fruits per visit (41.4 fruits; Fig. 2 and Table S4).

The top rank of frugivores in XSBN (based on relative fruit consumption) were *C. erythraeus* (65.6%), *D. rufigenis* (16.2%) and *R. bicolor* (6.1%) whereas the top frugivores in MS were *M. leonina* (36.5%), *R. bicolor* (31.1%) and *H. lar* (23.5%) (Fig. 2 and Table S4).

Activities (average visit length, frequency of visits, visitation rates per day and fruit consumed per day) of large and medium-sized frugivores were relatively greater in MS than in XSBN. On the other hand, small frugivores showed higher activity in XSBN than in MS (Table S5).

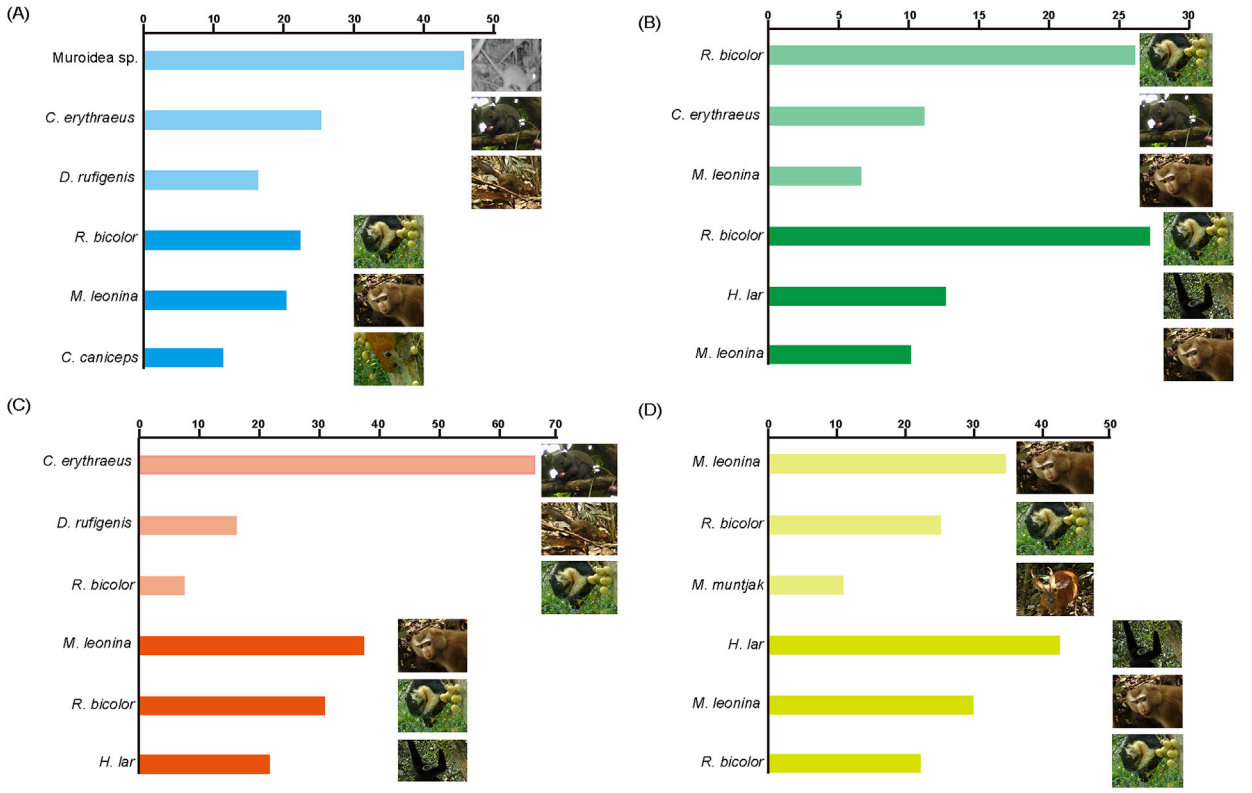

Fig. 2. Top three ranked frugivores in Xishuangbanna forest dynamic plot (upper three light color) and Mo Singto forest dynamic plot (below three dark color). (A) Relative frequency of visit; (B) Average visit length (min); (C) Relative fruit consumption (%) and (D) No. of fruits consumed per visit. All the photos were taken by camera traps in this study. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.3. Effects of environmental factors on frugivory

Fruit abundance showed a positive correlation with frequency of frugivore visits, frugivore visitation rate per day, amount of fruits consumed and fruit consumption rate (fruits consumed per day and per visit) (Table 2 and Table S6). Ground cover was also an important predictor of average visit length, amount of fruits consumed and consumption rate. Moreover, visitation and consumption parameters (except frugivore visitation rate per day) showed significant differences between the two sites. Specifically, frequency of frugivore visits was higher in XSBN while average visit length and fruit consumed per day were higher in MS. Average visit length was positively (but not significantly) affected by the number of neighboring fruit trees and slope. Lastly, variation in frugivore species richness could not be explained any of the predictor variables (Table 2).

4. Discussion

4.1. Frugivore diversity, relative abundance and frequency

Our results showed that Mo Singto had more *B. ramiflora* frugivore species than Xishuangbanna. The most abundant and most frequent frugivores in Mo Singto were relatively larger compared with those in Xishuangnanna. Xishuangbanna is famous for having the richest flora and fauna in China; it represents only 0.2% of the area of China, but contains more than 20% of China's mammal and bird species (Zhang and Cao, 1995), Forests covered approximately 70% of this region in 1976 (Li et al., 2007). From the late 1970s, rubber plantations developed rapidly in the region and forest cover decreased to 52% by 2018 (Zhang et al., 2019). Unlike the well-protected Mo Singto area of Khao Yai Park, the primary forest around the Xishuangbanna plot has become fragmented by road and rubber plantations. Deforestation and agricultural development threaten local species diversity, which has become reduced and simplified on the Xishuangbanna plot (Li et al., 2013).

Another main cause of biodiversity loss, specifically of larger species, in Xishuangbanna is hunting pressure (Chang et al., 2019). Previous animal surveys in southern China have reported reduction in population sizes of many large and medium-sized mammals (Fellowes et al., 2004; Corlett, 2007). They also found out that many mammals had already become locally extinct or depleted in many areas (Fellowes et al., 2004). For example, white-cheeked gibbon (*Nomascus leucogenys*) was common in the region surrounding the Xishuangbanna plot before 1970 (Ma and Wang, 1986). An interview survey in 2008

Table 2
Summary of generalized linear models after AIC model selection to test the influence of the environment on frugivore activity (visitation and consumption) on *B. ramiflora*. Candidate models for best model selection were presented in Table S6. * denotes that the corresponding predictor variable explained significant variation in the response. SE = standard error; NS; non-significant; NA = not available (Modelled with "quasi-Poisson" family distribution).

Response variable	Explanatory fixed variable	Estimate	SE	t-value	P-value	Model AIC
Frugivore species richness ~	Intercept*	1.735	0.099	17.520	<0.001	78.009
Frequency of frugivore visits ~	Intercept	1.369	1.118	1.224	NS	NA
	Site: Mo Singto*	−0.685	0.246	−2.786	0.014	
	Fruit abundance (logged)*	0.446	0.153	2.917	0.011	
Frugivore visitation rates/day ~	Intercept	0.943	0.700	1.347	NS	21.584
	Fruit abundance (logged)	0.188	0.098	1.924	0.072	
Average visit length ~	Intercept	0.735	0.754	0.975	NS	26.680
	Site: Mo Singto *	1.129	0.389	2.903	0.012	
	Number of neighboring fruit trees	0.114	0.062	1.856	0.086	
	Ground cover*	−1.686	0.556	−3.034	0.010	
	Slope	0.015	0.012	1.285	NS	
Amount of fruits consumed ~	Intercept	−0.544	1.707	−0.465	NS	40.880
	Site: Mo Singto	0.536	0.328	1.633	NS	
	Fruit abundance (logged)*	0.529	0.164	3.221	0.006	
	Ground cover	1.293	0.793	1.630	NS	
Fruits consumed per day ~	Intercept	0.052	1.275	0.041	NS	43.960
	Site: Mo Singto*	0.851	0.358	2.380	0.032	
	Fruit abundance (logged)*	0.414	0.179	2.315	0.036	
	Ground cover*	1.889	0.864	1.187	0.046	
Fruits consumed per visit ~	Intercept	0.872	1.314	0.664	NS	45.002
	Site: Mo Singto	0.603	0.368	1.637	NS	
	Fruit abundance (logged)	0.290	0.184	0.158	NS	
	Ground cover	1.282	0.890	1.440	NS	

showed this species on the edge of extinction in China, with only three separate localities holding small populations (Fan and Huo, 2009). Meanwhile, the better protected Mo Singto area of Khao Yai National Park still retains its large species (Chanthorn et al., 2019).

4.2. *B. ramiflora* frugivory

Based on the relative number of fruits consumed, we identified *M. leonina* as potentially the most important disperser of *B. ramiflora* in the two FDPs. In general, *Macaca* species are important components of the seed dispersal assemblage of Indo-Malayan forests (Albert et al., 2013). They may play important roles in different successional stages given that they are able to cross a range of habitat types within the same day. In our study, *M. leonina* visited the trees irregularly, foraged on both canopy and ground, and always came in groups of up to nine individuals. Despite spending relatively short visits, *M. leonina* consumed more fruits than other frugivores of *B. ramiflora*. They appeared to be good seed dispersers as they have a diverse diet and process seeds in several ways (swallowing, spitting out, or dropping them) (Albert et al., 2013). Moreover, *M. leonina* was demonstrated to carry numerous seeds away from the parent tree and could serve as long-distance dispersal agents within their relatively large home ranges (Albert et al., 2014).

The other main disperser in Mo Singto was the gibbon *H. lar* (not present in Xishuangbanna). *H. lar* visited fruit trees regularly when fruiting. Like *M. leonina*, they consumed only the seed and flesh of the fruits and dropped the skin. Their guts seem to process seeds with care (Kanwatanakid, 2000; McConkey, 2000). However, *H. lar* checked the fruit first and would not eat fruits that were unripe or those with insects or insect damage. Thus, they consumed less fruit than *M. leonina*. *H. lar* were also believed to be an important quality dispersers of *B. ramiflora*, but *M. leonina* has been found to process as many, or even more, seeds than *H. lar* (McConkey, 2000; McConkey and Brockelman, 2011). The macaques often disperse seeds by spitting them from their cheek pouches while travelling across their home range (Albert et al., 2013). Furthermore, macaques use more habitat types than do gibbons, including degraded areas and human-dominated landscapes, and most macaque species are tolerant of human disturbance. Thus, we infer the *M. leonina* is potentially a more important seed disperser than the gibbons for *B. ramiflora* over landscapes with variable habitat types.

Most remaining fruits were taken by rodents. Rodents were among the main arboreal consumers of *B. ramiflora* fruits in both Xishuangbanna and Mo Singto. In fact, the camera trap surveys from 2012 to 2017 showed that the Xishuangbanna plot had a high diversity of rodent species. Previous studies have found that rodent diversity and abundance increases with disturbance intensity (Basuta and Kasenene, 1987; Stanford, 2000; Babweteera and Brown, 2010). High abundance of rodents in Xishuangbanna may also be a result of loss of most carnivores that prey upon them (such as Felidae and Canidae: Corlett, 2007). Lower species abundance of macaques and the absence of other dominant arboreal frugivores in Xishuangbanna left a lot of fruits for other frugivores. Due to low predation risk, rodents (Muridae and Sciuridae) were able to focus on taking as many fruits/seeds as they could and become the most dominant frugivores of *B. ramiflora* in Xishuangbanna.

However, unlike the two primate species, squirrels are known to be pre-dispersal seed predators (Corlett, 2014) that normally chew off the husk and eat only the seeds (McConkey, 2000). Meanwhile, rats were believed to be responsible for consuming most fruits that dropped from the canopy (Kitamura et al., 2004). We have observed Muroidea species consuming numerous *B. ramiflora* fruits in both plots. However, the number of fruits consumed by Muroidea species could not be determined from the photos and videos. It is possible that squirrels and rats may disperse some *B. ramiflora* seeds when they scatter-hoard seed, as scatter-hoarding rodents are reportedly important in dispersal of many large-seeded plants (Kitamura et al., 2008; Briggs et al., 2009; Hirsch et al., 2012; Wang et al., 2019). In fact, rodents could perform as seed dispersers in the absence of predators (Sunyer et al., 2013). Without predators, rodents could focus less on perceiving predation risk and more on taking fruits/seeds, therefore, damaging fewer seeds in the process which results in higher number of dispersed seeds (Sunyer et al., 2013). Thus, rodents may be of particular importance in Xishuangbanna, where many large terrestrial frugivores and carnivores were already lost. Unfortunately, we could not count the seeds taken by the rats and did not track the seeds taken by the rodents, therefore, we have no idea about the fate of these seeds. Nonetheless, the predominance of small frugivores in Xishuangbanna would limit the distance over which the seeds of *B. ramiflora* are dispersed, and hence recruitment of *B. ramiflora* in Xishuangbanna could suffer from dispersal limitation.

The relative importance of large terrestrial frugivores to *B. ramiflora* seed dispersal appears to be small in our study, as they only have access to fruits that fall to the ground. Terrestrial frugivores such as deer are attracted to the commotions created by the feeding of arboreal species and usually return to consume the fallen fruits in the night (Brodie et al., 2013; WYB unpublished observations). Large ground frugivores could potentially be efficient dispersers as they are able to forage across several habitats and may carry seeds from the forest; however, no study has yet reported these large animals as dispersers of *B. ramiflora*. The non-ruminant pigs (wild boar) and the ruminant deer (sambar, mouse deer and muntjac) have teeth and jaws adapted to breaking up tough plant materials (Corlett, 2017) and could either chew up or swallow seeds as large as those of *B. ramiflora* (Sridhara et al., 2016).

4.3. The effects of environment on frugivory

We found that fruit abundance consistently influenced frugivore activity (visitation and consumption). This was not surprising as food availability heavily influences frugivore behavior (Kissling et al., 2007). Frugivores prefer to visit areas with larger resource concentrations over areas with smaller concentrations (Beck and Terborgh, 2002). This is further supported by our finding that frugivores stayed longer at focal trees where neighboring fruit tree number was higher. Higher number of fruit trees translates to shorter distances between neighboring trees, shorter travel time, and less foraging effort (McConkey et al., 2015). Therefore, frugivores can spend more time in one tree and can save energy for travelling to other food trees (Normand et al., 2009).

Ground cover was also a predictor for average visit length and fruit consumption. Dense ground cover could allow predators to hide from terrestrial frugivores. We found a positive correlation between ground cover and fruit consumption per day; however, we also found a negative relation between ground cover and average visit length (Table 2). In Mo Singto, it may be that there are few predators of large terrestrial frugivores (tigers have recently been extirpated) so that frugivores do not need to worry about the risk of predation, and ground cover only makes it difficult to find fruits on the ground. However, the same may not be true in Xishuangbanna. It is possible that the smaller terrestrial frugivores in Xishuangbanna are very cautious of predation risk and naturally stay for short durations at fruiting trees, as they just need to secure a few fruits then move away from the focal tree.

Lastly, we found that visitation and consumption parameters varied between the two plots, which may be explained by differences in their animal communities. Mo Singto plot has relatively larger frugivores, which ought feed for longer at fruiting trees and, consequently, make fewer visits. On the other hand, the relatively smaller frugivores (mostly rats and squirrels) in Xishuangbanna plot made relatively shorter but more frequent visits to the focal trees, resulting in fewer fruits removed from the tree.

5. Conclusions

Species such as *B. ramiflora* mainly depend on medium- and large-bodied mammalian frugivores for dispersal. It is important to understand the quantitative role of frugivores in the dispersal of fruit species in order to identify plant species that might need our assistance in moving across fragmented landscapes in response to changing climate. This study suggests potential consequences of anthropogenic change (chiefly habitat degradation and hunting) on the fate of large-seeded plants. In Mo Singto, where more large frugivores remain, *B. ramiflora* seeds could be potentially dispersed over longer distances. Conversely in Xishuangbanna where most large frugivores have already been lost, large-seeded species will be dispersed over shorter distances. Seed dispersal services for such plant species are threatened by the loss of large frugivores (Brodie et al., 2013). Large-scale surveys across Xishuangbanna could be conducted to identify the remaining fauna within the region. Stricter implementation of policies against hunting is one way to help prevent loss of large vertebrates, which in turn could help plant species maintain links in fragmented landscapes, facilitate plant movements in response to climate change, and aid the recovery of forests on abandoned agricultural land.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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