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Potential seed dispersal agents of *Monoon liukiuense* on Iriomote Island, Japan

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Abstract

Monoon liukiuense (Annonaceae) is an endangered tree species distributed in Iriomote Island and Hateruma Island in the Ryukyu (Nansei) Islands, Japan, and in Orchid Island (Lanyu) in Taiwan. While its habitat is confined to small areas surrounded by human-altered landscapes, the matured trees bear abundant fruits, and many offspring grow under the mother trees. *M. liukiuense* is hypothesised to have lost effective seed dispersers. To test this hypothesis, fate of its seeds and the behaviour of frugivores were observed using time-lapse photography during three fruiting seasons from June 2015 to August 2016 in Iriomote Island, Japan. Although several animal taxa were observed to consume the fruit pulp, only two volant animals, namely the Yaeyama flying fox and large-billed crow, were proposed as seed dispersal agents for *M. liukiuense*. The present study shows that an average of 82% of the fruits in the canopies fell directly beneath the fruiting trees and an average of 90% of the seeds on the forest floor remained in their original positions. These results suggest that *M. liukiuense* has lost most of its seed dispersal agents and the chance to expand its distribution.

Introduction

Monoon liukiuense (Hatus.) B. Xue et R.M.K. Saunders (previously called *Polyalthia liukiuensis* Hatus.) is a tree species belonging to the family Annonaceae (Hatusima 1979, Xue et al. 2012). It grows on Iriomote Island (24.3°N, 123.7°E) and Hateruma Island (24.1°N, 123.7°E) in the Ryukyu (Nansei) Islands, Japan, and on Orchid Island (Lanyu, 22.0°N, 121.5°E) in Taiwan (Figure S1a). This species is distributed in the northernmost end of the distribution range of the other *Monoon* and *Polyalthia* species. Its habitats on all three islands are fragmented regenerating native forests surrounded by human-altered areas, such as rice paddies and sugarcane fields (Shinzato et al. 2018). Because of these threats to its existence, *M. liukiuense* is classified as a critically endangered species on the Red List of Japan (Ministry of the Environment, Japan 2020). Furthermore, two habitat fragments, one on Iriomote Island and the other on Hateruma Island, have been designated as natural heritage sites of Taketomi Town, Japan (Taketomi Town 2018). Both the Ministry of Environment and the Taketomi town government require the conservation of this rare tree species (Ministry of the Environment, Japan 2020, Taketomi Town 2018).

To conserve a plant species, it is not only essential to preserve its present habitat but also to maintain its regeneration processes, which are often highly species-specific (Saeki et al. 2013). Seed dispersal, for instance, is a crucial process in the reproductive cycle of plants (Wang & Smith 2002). Therefore, a conservation project should focus on preserving suitable areas and maintaining relationships between seed dispersers and plants.

M. liukiuense grows only in small areas, but the matured trees produce abundant fruit crops and many seedlings and saplings thrive under the fruiting trees (Figure S1b, c). A decrease in seed dispersal agents results in impacts on seed dispersal and an increased accumulation of seedlings under their parents (Howe & Miriti 2004). However, the seed disperser assemblage of *M. liukiuense* has yet been elucidated.

In this study, we hypothesised that *M. liukiuense* has lost effective seed dispersers in its present habitats. To test this hypothesis, fruit fate and frugivores were observed both in the canopy and on the ground of the habitats of *M. liukiuense* on Iriomote Island, Japan.

Materials and methods

Study site

The study was conducted on Iriomote Island (289.6 km^2, Figure S1a), Japan. Based on the meteorological data from 1991 to 2020 (Japan Meteorological Agency 2020), the average annual temperature of this region was 23.9 °C (ranging between 15.8 to 32.2 °C), the monthly rainfall ranged from approximately 120 to 265 mm, and the annual average precipitation was 2025 mm.

On Iriomote Island, *M. liukiuense* inhabits the limestone cliffs between rice paddies and sugarcane fields at approximately 20 m above sea level.

Study species

M. liukiuense is an evergreen arboreal species that grows to approximately 15 m tall (Ohashi 2015). The intact ripe fruits are oblong drupes: 2.3–4.0 cm long, 1.6–2.6 cm wide, and the weight of the fresh fruit ranges between 3.2 and 12.2 g ($n = 61$). Seeds without pulp are 1.4–2.8 cm long, 0.9–1.7 cm wide, and 0.6–5.2 g in fresh weight ($n = 191$).

Fruit removal from the canopies

Fruits in the canopies were observed from June 2015 to August 2016. During this period, *M. liukiuense* had approximately three fruiting seasons: June–July 2015, February–April 2016, and May–August 2016. Seven fruiting branches from five trees were observed. Two types of time-lapse photograph recorders were used. One was for diurnal observations (Recolo IR7, Kingjim Co., Ltd., Tokyo, Japan), and the other was a camera with infrared LEDs for nocturnal observations (DVR-HC7310A, Hanwha Q CELLS Japan Co., Ltd. Tokyo, Japan). Observations started when the fruits were greenish-yellow and finished when all fruits moved away from the focal branches. Photographs were taken every 5–12 s according to the reaction speed of each memory card and battery cell.

The time-lapse photographs were considered continuous footage of when and what animals visited and what they did. The fate of each fruit was determined using the photographs. Behaviours of animals in the photographs were categorised as 'visiting', 'eating', 'dropping', and 'carrying'. 'Visiting' indicated that animals appeared in photographs and handled no fruit, while 'eating' indicated biting fruits or ingesting pulp. Fruits were considered 'dropped' when successive photographs indicated the disappearance of fruits while the animals stayed. 'Carrying' indicated that animals with fruits in their mouths or bills disappeared from the photographs. When the fruits disappeared in successive photographs without any animals, it was considered 'falling', meaning that the fruits were dropped spontaneously.

Fruit removal from the ground

Fruits set on the ground under the fruiting crowns were observed for almost the entire period mentioned above. Observations were conducted in seven locations using the same type of cameras, as described above. A pair of cameras covered an area of approximately 2 m^2 on the ground. The observations started when the ripe fruits began to fall spontaneously and ended when almost all the fruits disappeared from the adjacent fruiting trees. During the observations, about 10 ripe fruits collected from the focal trees were placed on the ground, and new ripe fruits were added when all fruit pulp was eaten up. The behaviours of visitors were categorised as 'visiting, 'eating', 'moving', and 'carrying'. 'Visiting' indicated that the animals handled no fruit, and 'eating' indicated biting fruits or ingesting pulp. 'Moving' indicated that animals moved the fruits, but the moved fruits could still be seen in the photographs. 'Carrying' indicated that animals with the fruits in their mouths or bills disappeared from the photographs.

Results

Fruit removal from the canopies

The total observation duration was 7340 h. Photography failed for 423 h (5.8% of the observation duration) due to rain, wind, or other mechanical problems.

The fates of 358 fruits in the canopies were determined (Table 1). Although 13% ($n = 47$) of fruits were missing or unidentified, 7.5% ($n = 27$) were carried away by animals, 48% ($n = 171$) were dropped by animals, and 32% ($n = 113$) fell spontaneously. An average of 82% ± 3.1% (SEM, $n = 7$ branches) were dropped under their mother trees.

The most frequent visitor was the brown-eared bulbul (*Hypsipetes amaurotis stejnegeri* (Hartert, 1907)) (Table 2 and S1). The Yaeyama flying fox (*Pteropus dasymallus yayeyamae* Kuroda, 1933) was the most frequent animal dropping the fruits, followed by the brown-eared bulbul and large-billed crow (*Corvus macrorhynchos osai* (Ogawa, 1905)). These three volant animals were observed carrying away the fruits. The number of dispersed fruits per visit of the large-billed crow was 0.18, which was much higher than those of the Yaeyama flying fox (0.06) and brown-eared bulbul (0.01). The relative importance of dispersal for the large-billed crow and Yaeyama flying fox were comparable (48% and 44%, respectively), whereas that of the brown-eared bulbul was considerably less than the other two species.

Fruit removal from the ground

The total observation duration was 5844 h. Photography failed for 333 h (5.7% of observation duration), mainly due to mechanical problems.

The fate of 222 fruits on the ground was determined (Table 1). Animals carried away 4.1% of the fruits ($n = 9$), whereas 1.4% ($n = 3$) were moved by animals but could still be seen in the photographs. An average of 90% ± 8.7% (SEM, $n = 7$ locations) were consumed in their original locations, and their seeds were left behind.

The most frequent epigeal visitor was the yellow-margined box turtle (*Cuora flavomarginata evelynae* Ernst and Lovich, 1990) (Table 2 and S2). The turtles consumed almost all the pulp of a fruit. One fruit was bitten and carried out of the camera's view by a turtle when two individuals competed for it (Figure S2f). The large-billed crows were observed eight times and carried the fruits away on each occasion (Table 2 and S2). In this study, only these nine fruits were carried away from the ground.

Discussion

In the observations made in the canopies, an average of 82% of the fruits were dropped under the mother trees (Table 1). Howe & Vande Kerckhove (1981) observed fruit removal for wild nutmeg—whose seed size of similar to that of *M. liukiuense*—in Panama and revealed that an average of 38% of the fruits were either regurgitated by birds in the tree or were spontaneously dropped. The frequency of the fallen fruits in the present study (82%) was higher than for wild nutmeg. This result suggests that not all branches had sufficient primary seed dispersers.

On the ground, an average of 90% of the seeds were left in their original positions, while almost all pulp was consumed (Table 1). Several previous studies reported that terrestrial animals move

Table 1. Fates of the fruits of *Monoon liukiuense* (Hatus.) B. Xue et R.M.K. Saunders during three fruiting seasons from June 2015 to August 2016 on Iriomote Island, Japan

		Number of fruits		Percentage of fruits	
	N	Range	Mean ± SEM	Range	Mean ± SEM
In seven branches of five trees					
Carried away by animals*[1]	27 (7.5%)	0–8	3 ± 1	0–17	8 ± 2.0
Dropped by animals	171 (48%)	1–53	21 ± 5	0.1–95	48 ± 9.2
Fell spontaneously	113 (32%)	0–39	14 ± 5	0–77	34 ± 9.5
Subtotal in dropped fruits under the trees	284 (79%)	11–59	36 ± 6	0.6–95	82 ± 3.1
Unidentified	47 (13%)	0–24	6 ± 3	0–27	11 ± 2.8
Total in the branches	358 (100%)	13–90	45 ± 9		
On the ground at seven locations					
Carried away by animals*[1]	9 (4.1%)	0–8	1.3 ± 1.0	0–67	10 ± 8.7
Moved by animals*[2]	3 (1.4%)	0–1	0.4 ± 0.2	0–4	1 ± 0.6
Pulp consumed by the animals*[3]	210 (95%)	4–48	30 ± 5	33–100	90 ± 8.7
Total on the ground	222 (100%)	12–48	32 ± 4		

*[1] Animals disappeared with the fruits.
*[2] Fruits remained in the photographs.
*[3] Seeds were left on the spot.

most fruits from their original locations (e.g., Chauvet et al. 2004; Dennis 2003; Forget 1990, 1992; Kitamura et al. 2004; Kitamura et al. 2006). The frequency of the seeds remaining in their original positions in the present study was much higher than in the previous studies above mentioned. This result suggests that Iriomote Island has almost no secondary seed dispersers for *M. liukiuense*.

Various organisms, including most of the large omnivores and carnivores reported on the island (Ohdachi et al. 2015; Takano 1981), were observed both in the canopies and on the ground (Table S1 and S2). This suggested the exhaustive nature of my observations. Among the observed animals, the brown-eared bulbul, Yaeyama flying fox, yellow-margined box turtle, and large-billed crow carried the fruits of *M. liukiuense*.

Bulbuls (Pycnonotidae), such as the brown-eared bulbul, are the important avian dispersal agents for small (<14–15 mm) fruits in the Oriental region (Corlett 2017). However, the fruit of *M. liukiuense* may be too large (>16 mm) for the bulbul to fully swallow (Figure S2a, b). Although bulbuls picked some fruits with their bills from the branches, their visiting rates and the relative importance of dispersal were relatively low (Table 2). Thus, the brown-eared bulbul was not considered an effective seed disperser of *M. liukiuense* on Iriomote Island.

The Yaeyama flying fox could manipulate the fruit in both its mouth and foot (Figure S2c, d). The flying fox was considered a seed disperser of *M. liukiuense*, because some flying foxes held the fruits in their mouths and disappeared from the canopies. However, McConkey and Drake (2006) reported that an insular flying fox in Tonga (*Pteropus tonganus*) lost its function as an effective seed dispersal agent at sites where its abundance fell below a certain threshold. The Yaeyama flying fox is an endangered species with an unknown population size (Kinjo & Nakamoto 2017). Therefore, it is uncertain whether the flying fox on Iriomote Island is abundant enough to play a significant role as a seed dispersal agent. However, the Yaeyama flying fox remains a potential seed disperser of *M. liukiuense* because of its ability to fly with the fruit.

On the ground, the yellow-margined box turtle carried the fruit in its mouth on one occasion when two turtles fought over a fruit (Figure S2f). However, the turtles seemed unable to swallow the seed because their heads were only slightly larger or almost similar in width to the fruits (Figure S2e). Therefore, this carrying event may have happened accidentally, and the turtles may not be a seed dispersal agent for *M. liukiuense*. However, Corlett (2017) speculated that extinct Pleistocene giant tortoises (Testudinidae) of Wallacea had seed dispersal abilities. An extinct testudinid tortoise (estimated maximum carapace length of ca. 45 cm) was found in late Pleistocene deposits in the Ryukyu Islands (Takahashi et al. 2018). Its carapace length was 2.4 times larger than that of the yellow-margined box turtle, which grows to 19 cm in adults (Ota et al. 2009). This extinct tortoise might have swallowed the whole fruits of *M. liukiuense*.

The large-billed crows were observed to carry away the fruits in their bills, both in the canopies and on the ground (Figure S2g, h). One of the crows was photographed carrying a fruit of *Pandanus odoratissimus* L. fil., which is >2 cm in diameter (Figure S2i). Because the fruit of *M. liukiuense* is smaller than that of *P. odoratissimus*, the crow could carry *M. liukiuense* fruits. The number of dispersed fruits per visit was the highest for the crow among all visitors, both in the canopies and on the ground (Table 2). Thus, the large-billed crow was considered the most effective seed disperser of *M. liukiuense*. However, some crows removed the seeds from the fruits and held only the seeds in their bills (Figure S2g). These behaviours suggested that on Iriomote Island, the crow was not only a potential seed disperser but also a predator of *M. liukiuense* seeds.

The results suggest that *M. liukiuense* on Iriomote Island has two potential seed dispersers, the Yaeyama flying fox and large-billed crow. Other close relatives of *M. liukiuense*, including *Polyalthia* spp., have been suggested to rely on seed dispersal by

Table 2. Animals that handled the fruits of *Monoon liukiuense* (Hatus.) B. Xue et R.M.K. Saunders during three fruiting seasons from June 2015 to August 2016 on Iriomote Island, Japan

Taxon	Visiting	Number of handled fruits			Number of dispersed fruits per visit [*2]	Relative dispersal importance [*2]
		Eating	Dropping Moving[*1]	Carrying		
In the canopies						
Mammal						
Yaeyama flying fox (*Pteropus dasymallus yayeyamae* Kuroda, 1933)	211	113	92	12	0.06	44%
Rodentia spp.	6	4				
Bird						
Large-billed crow (*Corvus macrorhynchos osai* (Ogawa, 1905))	74	34	27	13	0.18	48%
Zosterops japonicus loochooensis Tristram, 1889	69	31	1			
Brown-eared bulbul (*Hypsipetes amaurotis stejnegeri* (Hartert, 1907))	322	153	42	2	0.01	7.4%
Treron formosae medioximus (Bangs, 1901)	1	1				
Invertebrates						
Blattodea spp.	264	187	8			
Orthoptera spp.	124	96	1			
Total of dropped or carried fruits in the canopies			171	27		
On the ground						
Bird						
Large-billed crow (*Corvus macrorhynchos osai* (Ogawa, 1905))	8			8	1.0	89%
Reptile						
Yellow-margined box turtle (*Cuora flavomarginata evelynae* Ernst and Lovich, 1990)	771	261		1	0.001	11%
Invertebrates						
Gecarcinidae spp.	435	7	3			
Total of moved or carried fruits on the ground			3	9		

[*1] 'Dropping' in the canopies and 'moving' on the ground.
[*2] Calculated assuming that 'carrying' causes 'dispersal'.

civets, hornbills, cassowaries, macaques, and flying foxes (Richards 1990; Sengupta et al. 2014; Sethi & Howe 2012; Stocker & Irvine 1983). These animals have not been reported on Iriomote Island, except for the Yaeyama flying fox (Ohdachi et al. 2015; Takano 1981). While terrestrial rodents might play important roles as seed dispersers in Malaysian tropical rain forests (Yasuda et al. 2000), no rodents were observed to carry any fruits in these observations (Table S1 and S2). Previous studies in intact forests reported that it was common for various frugivorous animals to disperse the fruit of any particular plant species (Gutier-Hion et al. 1985; Kitamura et al. 2002). The seed disperser assemblage of *M. liukiuense* on Iriomote Island is not diverse and provides a simple dispersal process with no ground-dwelling agents. Combinations of multi-step dispersal processes provided by various agents are more beneficial for seed dispersal than most single-step processes (Vander Wall & Longland 2004). The seeds of *M. liukiuense* may not benefit sufficiently from the simple dispersal process observed in this study. Furthermore, the effectiveness of each potential disperser remains unclear, and both quantitative and qualitative data are required to clarify their roles (Schupp 1993; Schupp et al. 2010). In this study, only a few quantitative components, such as the visitation rates of frugivores and the number of fruits moved by them, were estimated. Therefore, further studies are required to reveal where the Yaeyama flying fox and large-billed crow carry the seeds, whether the seeds can survive and germinate there, and how the simple seed dispersal process affects the survival prospects of *M. liukiuense*. Additionally, it might be worthwhile collecting the seeds and establishing new populations in other localities to enhance the persistence of *M. liukiuense*.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467423000056

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