NUSANTARA BIOSCIENCE
Volume 18, Number 1, June 2026
Pages: 10

ISSN: 2087-3948
E-ISSN: 2087-3956
https://doi.org/10.13057/nusbiosci/n180103

Functional guild complementarity and morphological filtering in Annonaceae seed dispersal within a managed tropical garden

TRI HANDAYANI[1,♥], HARY WAWANGNINGRUM[1], YUZAMMI[2], MUHAMMAD EFENDI[1,♥♥], TITUT YULISTYARINI[3]

[1]Research Center for Applied Botany, National Research and Innovation Agency. Jl. Jakarta-Bogor Km. 46, Cibinong 16913, West Java, Indonesia. Tel.: +62-811-1933-3639, ♥email: irtri@yahoo.co.id, ♥♥email: muhammadefendi05@gmail.com

[2]Research Center for Biosystematic and Evolution, National Research and Innovation Agency. Jl. Jakarta-Bogor Km. 46, Cibinong 16913, West Java, Indonesia

[3]Research Center for Ecology, National Research and Innovation Agency. Jl. Jakarta-Bogor Km. 46, Cibinong 16913, West Java, Indonesia

Manuscript received: 14 October 2025. Revision accepted: 11 May 2026.

Abstract. *Handayani T, Wawangningrum H, Yuzammi, Efendi M, Yulistyarini T. 2026. Functional guild complementarity and morphological filtering in Annonaceae seed dispersal within a managed tropical garden. Nusantara Bioscience 18 (1): n180103. https://doi.org/10.13057/nusbiosci/n180103.* Understanding the mechanisms that structure plant-frugivore interactions in managed ex situ environments is essential for maintaining Seed Dispersal Effectiveness (SDE), genetic diversity, and long-term plant persistence. This study assessed the possible morphological filtering effect of Annonaceae fruit and seed traits on four co-existing frugivore guilds (birds, bats, squirrels, and civets) in the protected environment of the Bogor Botanical Gardens (BBG), Indonesia. To ensure a comprehensive dataset, we performed detailed morphological measurements and conducted twice-weekly observations across 22 Annonaceae species to identify fruit consumption patterns. We recorded fruit color, size, and shape, and statistically tested the classical morphological filtering hypothesis using Chi-Square, ANOVA, and Spearman correlation analyses. Our results showed a generally generalist interaction system, with the apocarpous fruit type being the most prevalent (12 species). The morphological specialization hypothesis was rejected, as fruit and seed size dimensions did not significantly correlate with specific visitor guilds ($\chi^2 = 9.793$, df = 18, P = 0.938). Spearman's rank correlation confirmed strong internal morphological constraints within the fruit ($\rho > 0.70$, P < 0.05), while no external ecological filtering regarding animal attraction was detected ($\rho > 0.70$, P > 0.05). This pattern indicates that frugivores in these managed collections exhibit high behavioral flexibility, utilizing a broad range of resources regardless of specific morphological traits. Despite this lack of strict matching, SDE is maintained through functional guild complementarity: bats act as long-distance dispersal specialists, while civets provide niche coverage for the largest fruits. However, the aggregated seed clumps deposited by civets remain a concern for recruitment. These findings show that generalist interactions, supported by complementary guild functions, underpin effective seed dispersal. Conserving the full frugivore assemblage is therefore critical to sustaining ecological processes in botanical gardens and should directly inform faunal management strategies.

Keywords: Annonaceae, Bogor Botanical Gardens, frugivory, morphology, Seed Dispersal Effectiveness (SDE)

INTRODUCTION

Whether found in wild forests or managed botanical gardens, fruit-producing plants are essential to tropical ecosystems. This is mostly down to their deep connection with frugivores, or fruit-eating animals (Fleming and Kress 2011; Forget et al. 2011). In this mutualistic setup, birds, bats, and mammals get a reliable food source, while the plants receive a hand with pollination and getting their seeds moved to new locations (Howe and Smallwood 1982; Hodgkison et al. 2006; Fleming and Kress 2011; Adyn et al. 2022). Traits like fruit size, color, and scent aren't just random; they act as visual or smell-based cues to attract specific animal groups, a result of long-term natural selection shaped by how these animals prefer to eat (Partasasmita 2015; Partasasmita et al. 2017; Campagnoli et al. 2025).

Annonaceae is a diverse family of about 2,440 species worldwide, noted for its significant variety in fruit and seed forms (van Setten and Koek-Noorman 1992; Couvreur et al. 2012). While many species produce fleshy fruits attractive to birds and mammals, quantitative data from tropical Asia is still lacking compared to the Neotropics and Africa. Furthermore, how fruit morphology attracts frugivores in ex situ conservation sites like botanical gardens is poorly understood. This leaves a gap in our knowledge regarding the connection between Asian Annonaceae traits and their specific frugivore groups (Jordano 2000; Corlett 2017).

Out in the wild, fruits from the Annonaceae family are a staple food for many tropical vertebrates, including giants like elephants and rhinos. There's plenty of evidence for this; for example, in Sulawesi's protected forests, *Cananga odorata* is a key resource for anoa (Ranuntu and Mallombasang 2015), while *Maasia glauca* is a known favorite for rhinos at the Sumatran Rhino Sanctuary (Awaliah et al. 2018). Over in Thailand, *Platymitra macrocarpa* has been documented supporting a wide array of mammals, ranging from primates to bears (McConkey et al. 2018). We see similar patterns in Mexico (Coates-

Estrada and Estrada 1988) and Africa (Gautier-Hion et al. 1985). Ecologists describe these interactions through 'morphological filtering'-a process where a fruit's physical traits basically decide which animal gets to eat it.

Birds, for one, tend to go for small fruits with those eye-catching colors like red, black, or blue (Gautier-Hion et al. 1985; Kissling et al. 2007; Duan et al. 2014; Wang et al. 2023). It's a different story for bats and mammals; they're more into fruits that are larger, smell stronger, and have meatier pulp (Muscarella and Fleming 2007; Duan et al. 2014; Steele and Yi 2020; Aziz et al. 2021). While a squirrel might just nibble on the fruit and leave seeds right where they found them, civets help by moving seeds to open spots like riverbanks or canopy gaps (Gautier-Hion et al. 1985; Nakashima et al. 2010; Tsuji et al. 2024). In Southeast Asia, fruit bats (*Cynopterus* spp.) are especially vital for dispersal (Hodgkison et al. 2006). Right here in the Bogor Botanical Gardens, they've been recorded eating fruits from over 50 species, including Annonaceae (Soegiharto et al. 2010). All these diverse animal tastes eventually put selective pressure on how fruit traits evolve (Howe and Smallwood 1982; Fleming and Kress 2011).

Botanical gardens are actually great places for ecological research because they offer a controlled yet natural setting. They're perfect for studying things like fruit-frugivore ties or plant phenology (Primack and Miller-Rushing 2009; Heywood 2011; Chen and Sun 2018; Girmay 2023). The Bogor Botanical Gardens (BBG) in Indonesia, itself is a major ex situ conservation hub in Southeast Asia, housing a huge Annonaceae collection (Safarinanugraha et al. 2018; Ariati and Widyatmoko 2019). This current study builds on earlier work that looked at ten species here (Handayani 2022). By expanding our scope to 22 species, we can really dig into how different fruit sizes and shapes drive animal preferences in these managed landscapes, giving us a much better grasp of this family's diversity

We aim to evaluate whether traditional morphological filtering holds true for the 22 Annonaceae species at BBG. Our objectives are (i) to quantify fruit and seed morphological variation, and (ii) to test how these traits associate with observed frugivore guilds. By documenting consumption signs (Russo et al. 2006; McConkey et al. 2012), we offer a fresh look at fruit-frugivore relationships in managed environments where traditional filters might be diluted. Our findings support a framework of functional guild complementarity, essential for effective conservation strategies in ex situ collections.

We tested the classical filtering hypothesis, predicting that fruit color and size would selectively attract specific guilds, such as birds preferring small fruits and mammals handling larger, aromatic ones. We also hypothesized that mechanical constraints would limit large fruits to mammals with greater gape width. Alternatively, we proposed that if these filters fail in BBG, seed dispersal effectiveness would be maintained through functional complementarity, where different guilds, like bats and civets, perform distinct but complementary roles.

MATERIALS AND METHODS

Study area

The research took place at the Bogor Botanical Gardens (BBG), an 87-hectare ex situ conservation area located in the heart of Bogor City, West Java, Indonesia (6°35'50"S, 106°47'40"E), at about 250 meters above sea level (Figure 1). The site is mostly flat with gentle slopes (3-15%) and has a humid tropical climate, with temperatures ranging from 22-32°C, annual rainfall of 1.500-3.000 mm, and relative humidity between 34-80%. The BBG harbors a rich diversity of tropical plants, including a well-established collection of Annonaceae, mainly found in the lowland forest. The trees grow under a partially closed canopy that creates microclimates with moderate light and temperature, offering suitable conditions for fruit-eating animals such as bats and civets. Although the area is managed, it still maintains a semi-natural structure that makes it relevant for observing fruit-frugivore interactions.

Plant selection and observation

The Annonaceae collection at the Bogor Botanical Gardens was the main subject of this study. Following initial observations in 2018 that included ten species, we increased the sampling effort during the primary research periods (May, June, July, October, November, December 2022 and 2023). This resulted in the inclusion of twenty-two species in total. Species were selected not only based on fruit availability during the observation period but also to represent a wide variety of fruit morphologies, critically including both apocarpous (where the carpels remain separate and distinct) and syncarpous (where the carpels are fused together into a single unit) types. Furthermore, we have included species with moniliform fruits, which are characterized by a beaded appearance due to the distinct constrictions between each seed, as noted in Table 1

All of the mature, fruiting individuals of each selected species in the collection were observed in order to capture the possible temporal and spatial variation in frugivore interactions. As a result, the sample size for each species ranged from one to five trees. The fact that a single individual represented some species is recognized, which naturally restricts the ability to draw general spatial conclusions for those particular taxa. For each species, the exact locations and number of individuals observed are listed in Table 1.

Our observation protocol adhered to Handayani's (2022) framework, with minor modifications to prioritize important feeding times. Observations were made twice a week: once in the early morning (06:00-09:00) to document diurnal frugivores, and again in the late afternoon (16:00-18:00) to document crepuscular activity, the transitional feeding peak commonly associated with bats and nocturnal mammals. This regular bi-weekly schedule was strictly followed during both six-month fruiting seasons to minimize the possibility of missing intermittent feeding events that were crucial to the study.

We acknowledge that the methodological constraint of the twice-weekly observation schedule, alongside the reliance on indirect signs (e.g., bite marks and scat) for guild identification, introduces a possibility of misclassification, particularly among similar terrestrial mammals. Therefore, the data analysis focuses on robust guild-level associations, ensuring the broad ecological conclusions remain sound, as discussed further in the limitations section.

Fruit morphological data collection

The current study collected data on frugivore interactions and Annonaceae morphological traits in the Bogor Botanical Gardens using a descriptive-observational method. We gathered both qualitative (such as type, shape, and color) and quantitative parameters from fully ripe fruits for morphological evaluation. To ensure the integrity of the morphological analysis, only fully ripened and intact fruits were selected for measurement. Data were strictly excluded for malformed fruits or individuals showing signs of prior damage or decay. We regularly measured ten fully ripe fruits and ten seeds per species to guarantee accurate averages for our analysis and to take into consideration potential natural variation among individuals of the same species. In order to reduce the possibility of bias resulting from variations in developmental stages or environmental influences on fruit size, this rigorous sampling technique was required. The specific measurements for seed morphology were based on the methods described by Subrata and Syahbudin (2016) and Fuzessy et al. (2018), with minor necessary modifications to adapt to the unique characteristics of Annonaceae carpels and fruit structure. The summary of sample sizes used for both morphological and consumption data analysis is presented in Table 2.

Characteristics of qualitative data

We focused on qualitative traits mainly to figure out how the fruits, if at all, function as visual cues for frugivore attraction. This process meant carefully noting three key features: the dominant ripe color (things like black, brown, dark green, glaucous, red, or yellow), the fruit's overall shape (was it globose, ovoid, ellipsoid, or perhaps cylindrical), and finally, the fruit type, which we categorized them simply as apocarpous, syncarpous, or moniliform. For our classification work, the schemes for fruit shape and type drew heavily on established ecological sources (Gautier-Hion et al. 1985; Wheelwright and Janson 1985; Jordano 2000; Onstein et al. 2019), using minor necessary adjustments for the Annonaceae family specifically.

To properly test the visual cue hypothesis, recording the dominant color visually in the field was a crucial step. We made it a strict rule to ensure lighting conditions remained consistent during observation. Importantly, we prioritized the most apparent color for a generalized visual signal, rather than getting distracted by secondary hues or blemishes. This attention to detail on the primary signal is ultimately what drove our initial classification work and formed the basis for our subsequent Chi-Square analysis.

Characteristics of quantitative data

Quantitative parameters were measured to test the physical constraint hypothesis. We recorded fruit length (measured from base to tip) and fruit diameter (measured at the widest point) for ten fully ripe fruits per species. Similarly, seed length, width, and diameter were measured for ten seeds per species. All linear measurements were taken using a digital caliper for precision, supplemented by a tape measure for larger dimensions where necessary.

For descriptive purposes and to facilitate comparative discussion, fruits and seeds were subsequently categorized into size classes based on their dimensions: Fruit size categories (based on diameter): small (2 cm), medium (2-7 cm), and large (> 7 cm). Seed size categories (based on length and diameter): small (length 0.5-1 cm; diameter < 0.5 cm), medium (length 1-2 cm; diameter 0.5-1 cm), and large (length > 2 cm; diameter > 1 cm). The measurements of seed morphology are referred to the works of Subrata and Syahbudin (2016) and Fuzessy et al. (2018), with modifications.

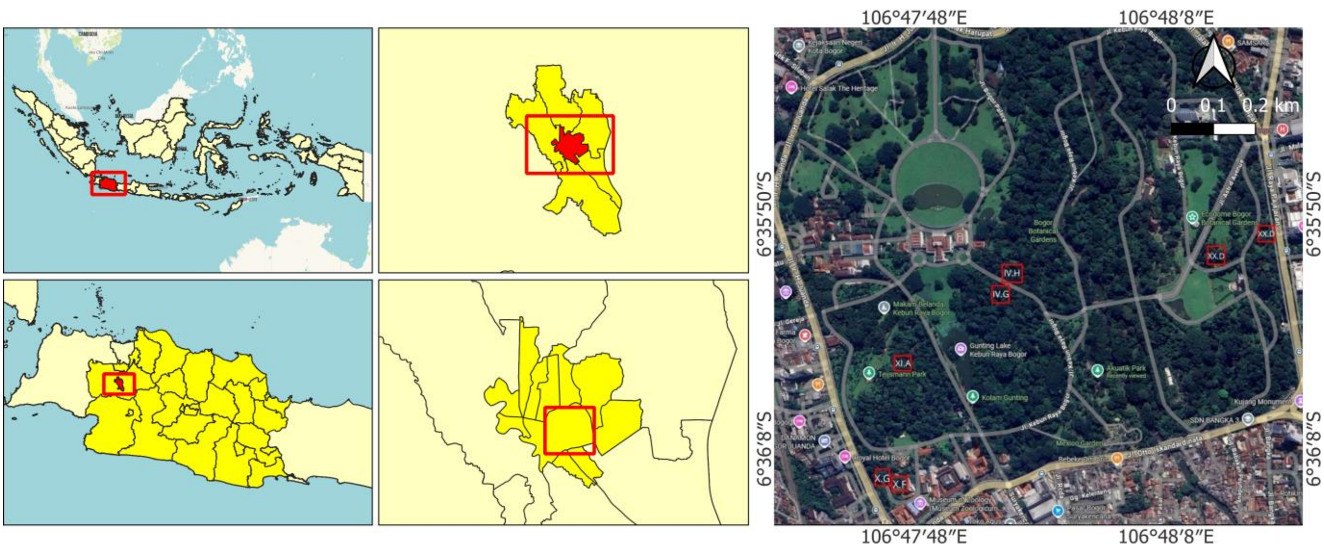

Figure 1. Study site in the Bogor Botanical Gardens, Paledang, Bogor Tengah, Bogor City, West Java, Indonesia. Red boxes indicate the number of the gardens' collections of the Annonaceae

Table 1. Species list, sampling effort, and habit of Annonaceae in Bogor Botanical Gardens, Bogor City, West Java, Indonesia

Species name	Number of individuals observed	Location of origin	Plant habit	Fruit type
Alphonsea elliptica Hook.f. & Thomson	2	Bangka Island	Tree	Apocarpous
Alphonsea javanica Scheff.	1	Java	Tree	Apocarpous
Annona glabra L.	3	Tropical America	Tree	Syncarpous
Annona montana Macfad.	1	Central America	Tree	Syncarpous
Annona muricata L.	1	Northern South America	Tree	Syncarpous
Annona reticulata L.	1	Tropical America	Tree	Syncarpous
Annona squamosa L.	1	Tropical America	Tree	Syncarpous
Artabotrys hexapetalus (L.f.) Bhandari	4	South China	Woody climber	Apocarpous
Cananga odorata (Lam.) Hook.f. & Thomson	6	Malesia	Tree	Apocarpous
Cyathocalyx sumatranus Scheff.	2	Sumatra	Tree	Syncarpous
Dasymaschalon dasymaschalum (Blume) I.M.Turner	4	Southeast Asia	Shrub	Moniliform
Meiogyne virgata (Blume) Miq.	2	Central Sulawesi	Tree	Apocarpous
Mezzettia parviflora Becc.	2	Kalimantan	Tree	Syncarpous
Miliusa horsfieldii (Benn.) Pierre	3	Java	Tree	Apocarpous
Monodora tenuifolia Benth.	3	Tropical Africa	Shrub	Syncarpous
Mitrephora polypirena (Blume) Miq.	2	Java	Tree	Apocarpous
Platymitra macrocarpa Boerl.	2	Java	Tree	Apocarpous
Maasia glauca (Hassk.) Mols, Kessler & Rogstad	4	Western Indonesia	Tree	Apocarpous
Polyalthia lateriflora (Blume) Kurz	5	Southeast Asia	Tree	Apocarpous
Marsypopetalum littorale (Blume) B.Xue & R.M.K.Saunders	3	Java	Shrub	Apocarpous
Hubera rumphii (Blume ex Hensch.) Chaowasku	6	Java, Sumatra	Tree	Apocarpous
Stelechocarpus burahol (Blume) Hook.f. & Thomson	4	Java	Tree	Syncarpous

Table 2. Summary of sample sizes (*N*) for morphological and consumption data used in the statistical analysis

Data category	Trait description	Sample size (N)
Species	Total Annonaceae species in the study	N = 22 spesies
Plant specimens	Number of individuals observed	N = 62 individuals
Fruit morphology	Total mature fruits measured (length, diameter, color)	N = 220 fruits
Seed morphology	Total seeds measured (length, diameter)	N = 220 seeds
Consumption frequency	Total observation records (feeding events) used for χ^2	N = 62 frugivore associations
Fruit colors	Total fruit color categories used for χ^2	N = 7 categories
Frugivore guilds	Total guilds used in statistical comparison	N = 4 guilds

Frugivore interaction data

Interactions between frugivores and fruiting Annonaceae trees were recorded throughout the collection. We consistently covered the morning (diurnal) and late afternoon (crepuscular) feeding times during our two observation sessions per week protocol. To minimize the impact of human presence and garden maintenance, we specifically scheduled our observation sessions during the early morning and late afternoon. These windows coincide with peak frugivore activity but are typically the quietest times for visitors. Furthermore, because our study focused on the 'presence' of frugivore guilds rather than the absolute frequency of feeding events, the data remained reliable despite the garden’s managed environment. We also cross-referenced our observations with insights from garden technicians who are present during daily maintenance to ensure no key interactions were overlooked. Importantly, observations were not aimed at measuring the frequency or intensity of feeding events, but rather at recording the presence and nature of interaction. Although it does not measure actual consumption preferences, this methodology produced qualitative and observational data on possible connections within the Annonaceae-frugivore network. All frugivorous species were identified using either indirect indicators or direct confirmation of presence (Table 3). Interviews with botanical garden technicians, who frequently supplied insightful field notes about fruit-eating behavior and consumption residues, were used to augment these observations further.

Data analysis

Fruit color association (visual cue hypothesis)

The association between ripe fruit color (grouped into binary categories such as bright vs. dark/dull) and the four identified frugivore guilds was assessed using the Chi-Square Test of Independence (χ^2). The unit of analysis was the number of interacting Annonaceae species. This test determined if the consumption pattern was non-randomly associated with the categorical fruit traits.

Fruit and seed size filtering (physical constraint)

To test the physical constraint hypothesis, One-way Analysis of Variance (ANOVA) was performed to compare the mean fruit size and seed size across the identified frugivore guilds.

Functional and morphological

Furthermore, Spearman Rank Correlation (**ρ**) was used to assess the functional relationship within morphological traits (e.g., fruit length vs. fruit diameter, seed length vs. seed diameter) and the potential constraint between external and internal dimensions (e.g., fruit size vs. seed size). Non-parametric Spearman Correlation was selected due to the nature of morphological data and the relatively small sample size (N = 22)

Statistical

All coefficients and P-values for ANOVA, Chi-Square, and Spearman Rank Correlation were calculated using standard, ecologically verified online statistical analysis functions.

RESULTS AND DISCUSSION

General morphological diversity and frugivore linkages

The collection of 22 Annonaceae species at the Bogor Botanical Gardens showed remarkably high variation across their morphological traits. This confirms that the collection offers a broad and highly heterogeneous spectrum of resources available to frugivore guilds. The initial descriptive analysis, summarized in Figure 2, provides the necessary foundation before delving into the deeper statistical testing. Figure 2 clearly visualizes the frequency distribution for fruit type (Figure 2.A) and fruit shape (Figure 2.B) across the sampled species.

Our study of the 22 Annonaceae in Bogor Botanical Gardens revealed a striking level of variation in fruit morphology and development (Figure 2). This diversity is not just a physical trait; it’s a key factor in how these plants serve as food resources within the garden's managed landscape. From our data, the apocarpous fruit type clearly stands out as the most common structure, while syncarpous and moniliform types appeared less frequently (Figure 2.A). We also saw a lot of variety in fruit geometry. While ovoid shapes were the most prominent, the collection also showed plenty of globose and rounded forms (Figure 2.B). This mix of structures creates a very diverse resource pool for different frugivore guilds, which likely reflects how these species have adapted their seed dispersal strategies to thrive in such a varied environment.

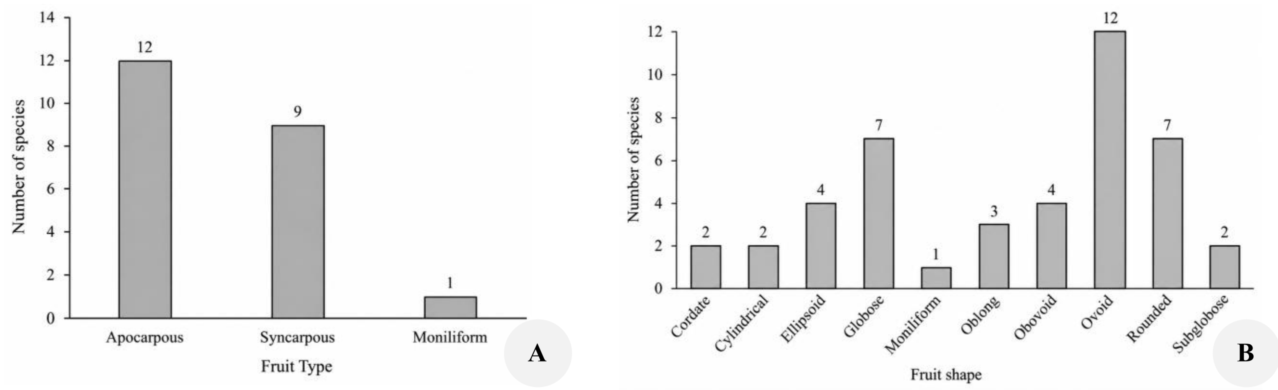

Figure 2. Morphological characteristics of the 22 Annonaceae species sampled in the Bogor Botanical Gardens, Bogor City, West Java, Indonesia. A. Distribution of fruit types (apocarpous, syncarpous, and moniliform). B. Distribution of fruit shapes. Note: The shape frequency count totals 44 because several individual species contributed more than one observed fruit shape category to the data set

Table 3. Evidence used for guild identification

Frugivore guild	Primary observation method	Evidence recorded
Birds	Direct observation of feeding, examination of fallen fruit	Fruit with characteristic beak marks on the tree or on the ground
Squirrels	Direct observation, identification of fruit remains beneath trees	The presence of discarded skins and scattered seeds indicates consumption and dropping
Civets (Nocturnal)	Scat analysis in known foraging areas (riverbanks, paths, under trees)	Presence of identifiable Annonaceae seeds within civet scat
Bats (*Cynopterus* spp.)	Examination of common roosting sites (e.g., building terraces) and trees	Piles of spat-out fruit remains and peels, often indicating juice extraction and subsequent seed discarding

Table 4. Summary of qualitative and quantitative characteristics of observed Annonaceae species

Characteristics	Category	Range	Most common frequencies
Fruit type	Qualitative	Apocarpous, syncarpous, moniliform	Apocarpous (54.5%)
Fruit shape	Qualitative	Cordate, globose, ovoid, cylindrical, ellipsoid, moniliform, oblong, obovoid, ovoid, rounded, subglobose	Ovoid (27.27%)
Dominant color	Qualitative	Black, brown, dark green, glaucous, greenish yellow, red, yellow	Black (22.72%) Brown (22.72%)
Fruit length	Quantitative	1.3-20 cm	Medium (54.55%)
Fruit diameter	Quantitative	0.8-16 cm	Medium (54.55%)
Seed length	Quantitative	0.8-3.9 cm	Medium (50.0%)
Seed diameter	Quantitative	0.6-2.6 cm	Medium (50.0%)

We also want to point out that the total counts for frugivore associations (N = 62) and fruit shape categories (N = 44) don't match the number of species sampled (N = 22). This isn't a mistake in the data; rather, it reflects the actual biological complexity we saw in the gardens. Many Annonaceae species don't just fit into one neat box-some individuals display multiple fruit shapes due to phenotypic plasticity or changes during ripening. Similarly, when it comes to dispersal, a single plant species often interacts with several different frugivore guilds at once. We decided to use these cumulative frequency counts because they give a much more honest picture of the ecological network. A simple species-to-species count would have been too thin and would have missed the multifaceted nature of how these plants actually function as a resource for the local wildlife.

The Annonaceae family in the Bogor Botanical Gardens collection exhibits a notable morphological diversity in both fruit and seed characteristics, reflecting the potential for adaptation to a range of dispersal syndromes. The summary of the distribution of these particular traits among the 22 species under study is shown in Table 4.

Descriptively, our study found that the apocarpous fruit type stands out as the most dominant structure within the collection, as visualized in the frequency distribution. The distribution of fruit shapes is primarily characterized by ovoid and globose/rounded forms. Other shapes, such as ellipsoid, obovoid, oblong, cylindrical, cordate, and moniliform, appear much less frequently in our samples. Most significantly, a large portion of the species (over 50%) falls into the medium categories for both fruit length and seed size, suggesting a stabilized morphological trend within this managed environment.

This observed dominance of medium-sized traits is consistent with studies indicating that tropical plant communities, especially those found in botanical gardens or secondary forests, favor generalist dispersal syndromes (Jordano 2000). Medium-sized fruits and seeds frequently avoid the handling restrictions placed by the smallest frugivores (birds) but remain manageable for medium- and large-sized consumers, such as bats and civets (Wheelwright and Janson 1985).

In addition to size, frugivores are subject to crucial handling restrictions based on fruit type and shape. Of particular note is the preponderance of apocarpous fruits (54.5%) in the sample. Instead of requiring frugivores like birds and squirrels to handle the entire large fruit at once, apocarpous fruits, which mature as separate segments (monomers), allow them to consume smaller, individual portions. This mechanism maximizes the feeding efficiency of smaller dispersers by effectively reducing the handling time and the overall gape size constraint. This result is consistent with studies that indicate small, monocarpic fruits are better at drawing in small to medium-sized frugivores (Saunders 2020; Cabral et al. 2025). Similarly, the prevalence of ovoid and globose shapes indicates a tendency to produce compact, easily accessible fruit. Globose shapes are generally practical for birds and bats to bite or swallow, while ovoid shapes are also utilized by land mammals (Herrera 2002; Fleming and Kress 2011). This suggests that the Annonaceae species in Bogor Botanical Gardens have primarily evolved or been selected for traits that facilitate handling by generalized guilds rather than traits that impose rigid specialization.

Fruit color and guild association

Our data in Table 5 shows that black and brown are the most common fruit colors in the collection. The association between these color categories and the observed frugivore guilds was tested using the Chi-Square Test of Independence.

Dominance of non-visual cues (aroma and nutritional content)

The non-significant Chi-square test results regarding fruit color preference (Table 5) strongly imply that non-visual cues are probably predominating, and that local ecological factors are superseding color’s function as a primary selection cue. The descriptive data confirm that bats (nocturnal) consume fruits across all seven color categories and that nocturnal/crepuscular civets also eat dull colors (brown, dark green). This aligns with the hypothesis that these guilds rely primarily on olfactory cues (aroma) and nutritional content rather than color, a finding strongly supported by studies on multimodal cues and foraging decisions in bats (Mahandran et al. 2021). Since bats exhibit minimal color preference, their high interaction rate acts to statistically mask any potential specialized visual preferences exhibited by diurnal guilds when tested collectively.

The true complexity of fruit color data

The true color complexity of the Annonaceae fruits studied beyond the dominant category used for the Chi-Square test indicates that the dominant color may not be the only functional signal. While the highest frequency in the dominant category was shared by the dull hues (black and brown), the overall spectrum observed across all fruits includes ten distinct categories, ranging from basic yellow and red to more complex colors like dark purple and purplish black (based on comprehensive field notes). This significant visual diversity suggests that the presence of minor colors (such as yellowish spots or reddish hues on a dominant green fruit) likely serves as a close-range cue. These cues would be crucial for frugivores already present in the canopy (especially birds and squirrels), helping them detect the optimal stage of ripeness even when the dominant color offers poor contrast against the foliage. This behavior is also seen in capuchin monkeys, whose reliance on olfactory cues increases when fruit color changes are poor or when color vision is limited (Melin et al. 2019). This multi-sensory signaling approach suggests that reliance on a single visual cue may be an oversimplification in this complex ex-situ habitat.

Physical constraints as the true ecological filter

Since color association is statistically weak, this emphasizes that morphological constraints (size) are likely the true ecological filters in this system. The lack of specialization by color suggests that frugivores are generalists choosing fruits based on energy needs and handling feasibility (which is dictated by size), rather than visual preference.

Overall, while color diversity in Annonaceae fruits is associated with a diversity of frugivores (as shown in Table 4), this relationship is not statistically strong enough to indicate color as the sole or primary factor determining guild specificity. Therefore, this warrants a deeper analysis of the role of fruit and seed size as the dominant mechanical factor shaping interaction outcomes.

Absence of frugivore filtering but presence of morphological constraint

The lack of external filtering is consistently supported by statistical analysis, where no significant differences were found in mean fruit and seed size dimensions across the four identified frugivore guilds (Table 6). However, while external filtering is absent, the analysis of internal biophysical relationships revealed strong morphological constraints. The Spearman Rank Correlation revealed highly significant positive correlations between dimensions within the fruit and seed structure (Table 7).

Table 5. Contingency table of Annonaceae species count associated with frugivore guilds based on dominant fruit color

Dominant colors	Bats	Birds	Civets	Squirrels	Total species
Black	5	5	0	3	13
Brown	5	1	2	4	12
Dark green	2	2	2	2	8
Glaucous	3	2	1	1	7
Greenish yellow	2	2	2	2	8
Red	2	2	0	0	4
Yellow	3	3	2	2	10
Total interacting species	22	17	9	14	62

Table 6. Actual ANOVA results and mean fruit/seed size across frugivore guilds

Morphological traits	Frugivore guild	Mean (cm)	ANOVA (F)	P-value (Actual)	Conclusion
Fruit length	Bats	6.02	1.2379	0.3042	Not Significant
	Birds	6.31			
	Civets	9.83			
	Squirrels	7.62			
Fruit diameter	Bats	4.17	0.76	0.5211	Not Significant
	Birds	4.08			
	Civets	6.22			
	Squirrels	4.74			
Seed length	Bats	1.87	0.7942	0.5021	Not Significant
	Birds	1.55			
	Civets	1.71			
	Squirrels	1.94			
Seed diameter	Bats	1.22	0.7499	0.5268	Not Significant
	Birds	0.99			
	Civets	1.09			
	Squirrels	1.24			

Note: The ANOVA tested the difference between all four guilds for each trait. All morphological traits showed no significant difference among guilds at $\alpha = 0.05$

Table 7. Functional correlation between fruit and seed morphological traits (Spearman's Rank Correlation)

Correlated traits	Spearman (ρ)	P-value
Fruit length vs. fruit diameter	0.748**	< 0.001
Seed length vs. seed diameter	0.771**	< 0.001
Fruit length vs. seed length	0.057	0.800
Fruit diameter vs. seed diameter	-0.058	0.798

Note: Functional and morphological constraints assessed using Spearman Rank Correlation (*ρ*) among morphological traits in Annonaceae species (N = 22). P-value: level was set at P < 0.05 for all correlations. Significance: Correlations marked with an asterisk (*) are statistically significant P < 0.05). Correlations marked with two asterisks (**) are highly significant (P < 0.001)

Morphology vs guilds

It is important to note that the total number of observed associations presented in Figure 2 (N = 62) exceeds the total number of Annonaceae species sampled (N = 22, as listed in Table 1). This is because the figure represents the cumulative frequency count of frugivore associations, where a single Annonaceae species may have been recorded as being consumed by multiple distinct frugivore guilds

While the One-way ANOVA results showed no morphological trait served as a statistically significant filter for frugivore guilds, Spearman's Rank Correlation revealed strong internal constraints within the fruit's morphology. This finding of non-filtering stands in direct contrast to widely established models of seed dispersal, where large-gaped frugivores impose strong selective pressures (e.g., Galetti et al. 2013). According to our analysis, the fruit and seed have highly integrated shapes that are separate from one another. Specifically, there was a strong positive correlation between fruit length and fruit diameter (ρ = 0.748, P < 0.001), and likewise a very strong positive correlation between seed length and seed diameter (ρ = 0.771, P < 0.001). This implies that the size of seeds is structurally limited by their own dimensions.

Crucially, while our analysis confirmed strong internal morphological constraints within the fruit structure (*ρ* > 0.70, P < 0.05), the dimensions were completely uncoupled across the fruit-seed barrier. The non-significant correlations between the external fruit measures and internal seed measures (e.g., fruit length vs. seed length, (*ρ* = 0.057, P = 0.800), strongly reinforce our overall conclusion regarding the generalist frugivore strategy. Of particular note is the correlation between fruit diameter and seed diameter (*ρ* = -0.058, P = 0.798), which shows a slight negative trend. This provides the strong empirical support suggesting that the size of the fruit's container does not restrict the size of the seed within it, which further confirms that animal attraction is not limited by these specific morphological traits (*ρ* > 0.70, P > 0.05). This lack of linkage suggests that frugivores here are not constrained by an evolutionary trade-off where the size of the fruit they swallow is rigidly linked to the size of the seed they must handle. Instead, this finding aligns with the concept of ecological fitting (Janzen 1985), where resource availability in a non-native or managed habitat drives consumer behavior more than strict evolutionary co-adaptations.

Rejecting classical filtering

The Chi-Square (χ^2) test revealed no statistically significant association between dominant fruit color and frugivore guild, contrasting the predictions of classical visual filtering ($\chi^2 = 9.793$, df = 18, P = 0.938). Contrary to the traditional assumption that fruit morphology should align with specific visual cues for diurnal dispersers, the highest observed consumption frequencies were shared by dull colors, specifically black (22.72%) and brown (22.72%) (Gautier-Hion et al. 1985). This pattern suggests that color may not function as the primary attractant in this ex-situ environment. This non-significant result may partly stem from a methodological limitation, as our analysis relied on classifying fruit color into a single 'dominant' category. This limitation may obscure subtle color variations that could still be visually salient. Therefore, the non-significant correlation should be interpreted while considering the low resolution of our color categorization method.

Collectively, the statistical results largely deviate from the traditional morphological filtering hypotheses in this managed environment: neither fruit color nor fruit and seed size operates as a significant ecological filter determining consumption patterns. The fact that dominant fruit color is not a significant predictor of frugivore guild association contradicts the classical seed dispersal syndrome theory, which posits that visual cues drive specialization. Instead, descriptive analysis shows that frugivore behavior, even among diurnal guilds like birds, exhibits flexibility in fruit choice. This finding aligns with the concept of ecological filtering, where resource availability in a managed habitat may drive consumer generalist behavior more than strict evolutionary specialization.

Functional complementarity

The statistical analysis of both visual signals (color) and mechanical constraints (size) has critical implications for the Seed Dispersal Effectiveness (SDE) of Annonaceae in this managed ecosystem. Based on the established SDE framework, this lack of morphological filtering is balanced by functional niche partitioning. While a generalist strategy dominates the system, the SDE role played by each guild remains highly specialized. Our data suggest that functional SDE relies on a functional division of labor (or complementarity), primarily between two main guilds. The Civet guild holds a crucial role as the only group capable of processing fruits at the maximum end of the size spectrum (mean fruit length at 9.83 cm). They essentially provide the essential niche reach, which is a capacity vital for large-seeded plants, particularly in managed or degraded habitats (Nakashima and Sukor 2010; Nakashima et al. 2010).

However, field observations present an interesting finding: despite moving the seeds, consumption by civets often results in low dispersal quality (Schupp et al. 2010). This is mainly because seeds are frequently observed scattered in highly aggregated clumps deposited directly beneath the parent tree, a pattern we identified as biological dispersal based on fecal signatures, distinguishing it from human garden maintenance. Such clumped dispersal by civets may trigger density-dependent mortality, where high seedling density attracts more seed predators or pathogens, effectively reducing the chances of successful recruitment compared to the long-distance dispersal provided by bats.

In contrast to the civets, bats provide a unique complementary function focused on dispersal quality. While bats are physically limited to handling medium-sized fruits (mean 6.02 cm), they consistently deliver optimal dispersal quality. Bats invariably carry fruits away from the parent tree to their resting sites (roosts). This behavior results in Long-Distance Dispersal (LDD) and places the seeds in new, spatially separated areas with significantly less competition. In the context of a managed or limited area like the Bogor Botanical Gardens, the bat's role in providing this distance quality is absolutely crucial for the long-term persistence of Annonaceae species (Fleming and Kress 2011). Therefore, this paper proposes that despite the lack of fruit specialization, Annonaceae achieves functional SDE through guild complementarity. The loss of either guild, whether the civet (which provides maximum size reach) or the bat (which provides maximum distance reach), could lead to serious loss of ecological function within the seed dispersal system.

Ecological and conservation implications

The results on functional complementarity show the importance of conserving all frugivore guilds to keep the full range of ecological functions required for Annonaceae survival in ex situ landscapes. Since neither fruit size nor color strictly filters consumption, the system relies on the balanced contributions of specialists, bats for long-distance dispersal and civets for maximal size-niche coverage. Because of this, losing a single guild could eliminate a specific and vital ecological function, a mechanism essential for the long-term existence of Annonaceae in this managed tropical landscape.

We must acknowledge that the frequency and type of frugivore observations are the main limitations of our methodology. We planned our field visits for twice-weekly sampling, as daily monitoring in such a large area was not feasible. This constrained schedule prevented us from recording quantitative aspects like actual dispersal rates or feeding frequencies. Future research should include seed-tagging to measure dispersal kernels, increased sampling across seasons, and higher-frequency or automated monitoring. The goal is to better understand the behavioral mechanisms of guild complementarity in ex situ environments by incorporating fruit chemistry, scent cues, and nocturnal surveys.

The presented study offers notable empirical support challenging the use of classical morphological filtering in support of a complementary generalist strategy for the seed dispersal mechanism in Annonaceae. The functional division of labor, with bats acting as long-distance specialists and civets providing size-niche coverage, maintains ecological function even when strict morphological cues are absent. These findings call for the urgent need to rework management strategies in ex situ conservation to give higher priority to maintaining diversity in frugivorous communities in order to make plant collections viable in the long term.

In conclusion, our work at the Bogor Botanical Gardens suggests a clear variety in Annonaceae fruit traits and how they relate to different frugivore interactions. We found that apocarpous fruits and ovoid shapes are particularly common across the sampled species. While these interactions with birds, bats, and civets are notable, the managed environment of a botanical garden may influence these patterns differently than in natural forests. We acknowledge that the sampling period was relatively short, meaning some seasonal visitors might have been missed. Future research should include longer, multi-season monitoring to get a more complete picture. It would also be worth looking into how well seeds survive when dropped in clumps compared to those spread further away-this would reveal more about how Annonaceae actually succeed in managed landscapes .

ACKNOWLEDGEMENTS

The authors would like to express their sincere gratitude to Mr. Harto and Mrs. Mimin, the technical staff of Bogor Botanical Gardens, Indonesia, for their invaluable assistance and unwavering support during the fieldwork and data collection for this study. Their support greatly facilitated the smooth implementation of this research. We also extend our deep appreciation to the field technicians who diligently look after the Annonaceae collection. Their consistent, everyday observations and excellent local ecological knowledge about the frugivores in that specific area proved instrumental to the final data validation and overall success of this study.

REFERENCES

Adyn MF, Sibarani MC, Utoyo L, Surya RA, Sedayu A. 2022. Role of siamang (*Symphalangus syndactylus*) as seed dispersal agent in a Sumatran lowland tropical forest. Biodiversitas 23 (4): 2101-2110. https://doi.org/10.13057/biodiv/d230445.

Ariati SR, Widyatmoko D. 2019. Bogor Botanic Gardens. Sibbaldia Intl J Bot Garden Hortic 17: 11-28. https://doi.org/10.24823/Sibbaldia.2019.265.

Awaliah ATS, Dewi BS, Winarno GD. 2018. Palatabilitas badak sumatera (*Dicerorhinus sumatrensis*) di Suaka Rhino Sumatera. J Sylva Lestari 6 (3): 64-72. https://doi.org/10.23960/jsl3664-72. [Indonesian]

Aziz SA, McConkey KR, Tanalgo K, Sritongchuay T, Low MR, Yong JY, Mildenstein TL, Nuevo-Diego CE, Lim VC, Racey PA. 2021. The critical importance of old world fruit bats for healthy ecosystems and economies. Front Ecol Evol 9: 641411. https://doi.org/10.3389/fevo.2021.641411.

Cabral A, Bender IMA, Couvreur TLP, Faurby S, Hagen O, Hensen I, Kühn I, Rodrigues-Vaz C, Sauquet H, Tobias JA, Onstein RE. 2025. Seed-dispersing vertebrates and the abiotic environment shape functional diversity of the pantropical Annonaceae. New Phytol 246 (5): 2263-2279. https://doi.org/10.1111/nph.70113.

Campagnoli M, Christianini A, Peralta G. 2025. Plant and frugivore species characteristics drive frugivore contributions to seed dispersal effectiveness in a hyperdiverse community. Funct Ecol 39 (1): 238-253. https://doi.org/10.1111/1365-2435.14697.

Chen G, Sun W. 2018. The role of botanical gardens in scientific research, conservation, and citizen science. Plant Diver 40 (4): 181-188. https://doi.org/10.1016/j.pld.2018.07.006.

Coates-Estrada R, Estrada A. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. J Trop Ecol 4 (2): 157-172. https://doi.org/10.1017/S0266467400002650.
Corlett RT. 2017. Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. Glob Ecol Conserv 11: 1-22. https://doi.org/10.1016/j.gecco.2017.04.007.
Couvreur TLP, Maas PJM, Meinke S, Johnson DM, Keßler PJ. 2012. Keys to the genera of Annonaceae. Bot J Linn Soc 169 (1): 74-83. https://doi.org/10.1111/j.1095-8339.2012.01230.x.
Duan Q, Goodale E, Quan RC. 2014. Bird fruit preferences match the frequency of fruit colors in tropical Asia. Sci Rep 4: 5627. https://doi.org/10.1038/srep05627.
Fleming TH, Kress WJ. 2011. A brief history of fruits and frugivores. Acta Oecol 37 (6): 521-530. https://doi.org/10.1016/j.actao.2011.01.016.
Forget PM, Jordano P, Lambert JE, Böhning-Gaese K, Traveset A. 2011. Frugivores and seed dispersal (1985-2010); the 'seeds' dispersed, established, and matured. Acta Oecol 37: 517-520. https://doi.org/10.1016/j.actao.2011.09.008.
Fuzessy LF, Janson C, Silveira FA. 2018. Effects of seed size and frugivory degree on dispersal by Neotropical frugivores. Acta Oecol 93: 41-47. https://doi.org/10.1016/j.actao.2018.10.004.
Galetti M, Guevara R, Côrtes MC, Fadini R, Matter SV, Leite AB, Labecca F, Ribeiro T, Carvalho CS, Collevatti RG, Pires MM, Guimarães Jr PR, Brancalion PH, Ribeiro MC, Jordano P. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340 (6136): 1086-90. https://doi.org/10.1126/science.1233774.
Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Moungazi A, Roussilhon C, Thiollay JM. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65 (3): 324-337. https://doi.org/10.1007/BF00378906.
Girmay M. 2023. Roles of botanical gardens for conservation and requirements for their establishment: Review. Daagu Intl J Basic Appl Res 5: 182-192. https://doi.org/10.20372/dijbar.81657.
Handayani T. 2022. Pemencaran Biji Jenis-Jenis Tanaman Suku Annonaceae di Kebun Raya Bogor, Indonesia. Prosiding Seminar Nasional Masyarakat Biodiversitas Indonesia 8 (2): 136-141. https://doi.org/10.13057/psnmbi/m080205. [Indonesian]
Herrera CM. 2002. Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds.). Plant-Animal Interactions. An Evolutionary Approach. Blackwell Science, Oxford, UK.
Heywood VH. 2011. The role of botanic gardens as resource and introduction centres in the face of global change. Biodiver Conserv 20: 221-239. https://doi.org/10.1007/s10531-010-9781-5.
Hodgkison R, Balding ST, Zubaid A, Kunz TH. 2006. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35 (4): 491-502. https://doi.org/10.1111/j.1744-7429.2003.tb00606.x.
Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Ann Rev Ecol Syst 13: 201-228. https://doi.org/10.1146/annurev.es.13.110182.001221.
Janzen D. H. 1985. On ecological fitting. Oikos 45 (3): 308-310. https://doi.org/10.2307/3565565.
Jordano P. 2000. Fruits and frugivory. In: Fenner M (eds.). Seeds: The Ecology of Regeneration in Plant Communities. 2nd ed. CABI Publisher, Wallingford, UK. https://doi.org/10.1079/9780851994321.0125.
Kissling WD, Rahbek C, Böhning-Gaese K. 2007. Food plant diversity as a broad-scale determinant of avian frugivore richness. Proc Biol Sci 274 (1611): 799-808. https://doi.org/10.1098/rspb.2006.0311.
Mahandran V, Murugan CM, Gang W, Jin C, Nathan PT. 2021. Multimodal cues facilitate ripe-fruit localization and extraction in free-ranging pteropodid bats. Behav Proces 189: 104426. https://doi.org/10.1016/j.beproc.2021.104426.
McConkey KR, Nathalang A, Brockelman WY, Saralamba C, Santon J, Matmoon U, Somnuk R, Srinoppawan K. 2018. Different megafauna varieties in their seed dispersal effectiveness of the megafaunal fruit *Platymitra macrocarpa* (Annonaceae). PLoS One 13 (7): e0198960. https://doi.org/10.1371/journal.pone.0198960.
McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L. 2012. Review seed dispersal in changing landscapes. Biol Conserv 146 (1): 1-13. https://doi.org/10.1016/j/biocon.2011.09.018.
Melin AD, Nevo O, Shirasu M, Williamson RE, Garrett EC, Endo M, Sakurai K, Matsushita Y, Touhara K, Kawamura S. 2019. Fruit scent and observer color vision shape food-selection strategies in wild capuchin monkeys. Nat Commun 10 (1): 2407. https://doi.org/10.1038/s41467-019-10250-9.
Muscarella R, Fleming TH. 2007. The role of frugivorous bats in tropical forest succession. Biol Rev Camb Philos Soc 82 (4): 573-590. https://doi.org/10.1111/j.1469-185X.2007.00026.x.
Nakashima Y, Inoue E, Inoue-Murayama M, Sukor JRA. 2010. Functional uniqueness of a small carnivore as a seed dispersal agent: A case study of the common palm civets in the Tabin Wildlife Reserve, Sabah, Malaysia. Oecologia 164 (3): 721-730. https://doi.org/10.1007/s00442-010-1714-1.
Nakashima Y, Sukor JA. 2010. Importance of common palm civets (*Paradoxurus hermaphroditus*) as long-distance dispersers for large-seeded plants in degraded forests. Tropics 18 (4): 221-229. https://doi.org/10.3759/tropics.18.221.
Onstein RE, Kissling WD, Chatrou LW, Couvreur TLP, Morlon H, Sauquet H. 2019. Which frugivory-related traits facilitated historical long-distance dispersal in the custard apple family (Annonaceae)? J Biogeogr 46 (8): 1874-1888. https://doi.org/10.1111/jbi.13552.
Partasasmita R, Mardiastuti AN, Solihin DD, Widjajakusumah R, Prijono SN. 2017. Frugivorous birds are characteristic of seed dispersers in the shrubland tropical forest of West Java, Indonesia. Biodiversitas 18 (1): 263-268. https://doi.org/10.13057/biodiv/d180134.
Partasasmita R. 2015. The role of frugivorous birds in the dispersal of shrubs in the submontane zone of tropical forest, West Java, Indonesia. Nusantara Biosci 7 (2): 144-148. https://doi.org/10.13057/nusbiosci/n070214.
Primack RB, Miller-Rushing AJ. 2009. The role of botanical gardens in monitoring plant responses to climate change. New Phytol 182 (2): 30-313. https://doi.org/10.1111/j.1469-8137.2009.02712.x.
Ranuntu RA, Mallombasang SN. 2015. Studi populasi dan habitat anoa (*Bubalus* sp.) di Kawasan Hutan Lindung Desa Sangginora Kabupaten Poso. e-Jurnal Mitra Sains 3 (2): 81-94. [Indonesian]
Russo SE, Portnoy S, Augspurger CK. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87 (12): 3160-3174. https://doi.org/10.1890/0012-9658(2006)87[3160:IABISD]2.0.CO;2.
Safarinanugraha D, Gunawan A, Mugnisjah WQ. 2018. The development of Bogor Botanic Garden Design from 1817 to 2017 is based on spatial and functional considerations. IOP Conf Ser Earth Environ Sci 179: 012026. https://doi.org/10.1088/1755-1315/179/1/012026.
Saunders RMK. 2020. The evolution of key functional floral traits in the early-divergent angiosperm family Annonaceae. J Syst Evol 58 (4): 369-392. https://doi.org/10.1111/jse.12645.
Schupp W, Jordano P, Gómez JM. 2010. Seed dispersal effectiveness revisited: A conceptual review. New Phytol 188 (2): 333-353. https://doi.org/10.1111/j.1469-8137.2010.03402.x.
Soegiharto S, Kartono AP, Maryanto I. 2010. Pengelompokan kelelawar pemakan buah dan nektar berdasarkan karakteristik jenis pakan polen di Kebun Raya Bogor, Indonesia. Jurnal Biologi Indonesia 6 (2): 225-235. https://doi.org/10.47349/06022010/225. [Indonesian]
Steele MA, Yi X. 2020. Squirrel-seed interactions: The evolutionary strategies and impact of squirrels as both seed predators and seed dispersers. Front Ecol Evol 8: 259. https://doi.org/10.3389/fevo.2020.00259.
Subrata SA, Syahbudin A. 2016. The common palm civet is a potential seed disperser of important plant species in Java. AIP Conf Proc 1744: 020053. https://doi.org/10.1063/1.4953527.
Tsuji Y, Tatewaki T, Farajallah A, Tanaka H, Widayati KA, Suryobroto B. 2024. Food habits of the common palm civet (*Paradoxurus hermaphroditus*) in Pangandaran Nature Reserve, West Java, Indonesia: A preliminary report. Hayati J Biosci 31 (4): 687-692. https://doi.org/10.4308/hjb.31.4.687-692.
van Setten AK, Koek-Noorman J. 1992. Fruits and seeds of Annonaceae. Morphology and its significance for classification (Studies in Annonaceae XVII). Bibliothec Bot Heft: 142. https://www.schweizerbart.de/publications/detail/isbn/9783510480135/Bibliotheca_Botanica_Heft_142.
Wang G, Huang Y, Yao W, Huang Q, Huang Y, Wei L, Zhou Q. 2023. Structure and characteristics of the plant-frugivore bird network from the Guilin Botanical Garden. PeerJ 11: e15028. https://doi.org/10.7717/peerj.15028.
Wheelwright NT, Janson CH. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. Am Nat 126 (6): 777-799. https://doi.org/10.1086/284453.