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RESEARCH ARTICLE

Resurrecting plant–animal interactions in the Caribbean can benefit large-fruited plants

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Many plants benefit from seed dispersal by frugivorous animals. This mutualistic interaction depends largely on interaction-relevant matching of functional traits (i.e. fruit size of plants and gape size of frugivores). With declines in large-bodied animal populations, it is likely that fruit–frugivore interactions have eroded, leading to the loss of seed dispersal of large-fruited plants. Such erosion could be especially evident in vulnerable island ecosystems such as those in the Caribbean, where most large-bodied frugivore populations have collapsed due to human activities. Here, we aim to understand the consequences of this decline by first quantifying gaps in frugivory function between common, smaller frugivores (birds, smaller reptiles, and bats) and rarer or regionally extinct, larger reptiles (*Cyclura* spp. and *Chelonoidis* spp.) in the Caribbean archipelagos. We then assess the benefits of reestablishing these interactions by determining the effects of large reptile ingestion on seed germination for 10 fruiting species, representing a range of fruit sizes, native to the Caribbean. We found that there are significant gaps in frugivory function, with smaller frugivores having many times smaller mean gape sizes than larger reptiles. Furthermore, we found that most fruiting species used in this study could germinate after being consumed by large reptiles, with two species having their germination speed significantly accelerated post-ingestion. These results indicate that fruiting plants could benefit from reestablishing frugivorous interactions between larger reptiles and fruiting plants. Given the existing gap in frugivory function, additional attention should be given to the possibility of rewilding defaunated islands to restore plant–frugivore networks.

Key words: *Chelonoidis*, *Cyclura*, frugivory, germination, seed dispersal

Implications for Practice

- We find significant gaps in frugivory function in the Caribbean, with current frugivores largely unable to compensate for the loss of large reptilian frugivore populations.
- Given that we demonstrate that larger frugivores such as iguanas and tortoises can benefit large-fruited plant dispersal, we show that plants could benefit from reestablishing populations of large reptiles.
- While native Caribbean tortoise populations have gone extinct, this study shows that Galapagos tortoises could be an appropriate substitute for reestablishing fruit–frugivore interactions.

Introduction

Defaunation, the decline of animal populations (Dirzo et al. 2014), is driven by anthropogenic disturbances (Gallego-Zamorano et al. 2020). This loss can have important ecological consequences, particularly on plant communities, with greater than 90% of tropical woody plants benefiting from animal-based seed dispersal (Almeida-Neto et al. 2008; Onstein et al. 2017). Frugivory, or the consumption of fruits by animals, plays a major role in seed dispersal (Jordano 2000). Germination enhancement, or the increased rate of germination post-ingestion, has been considered a principal advantage of frugivory-based seed dispersal (van der Pijl 1982; Traveset & Verdú 2002; Rogers et al. 2021*a*). Furthermore, the capacity of seeds to simply germinate, independent of any germination enhancement, post-ingestion has also been shown to be important (Traveset 1998), as any frugivore-dispersed viable seeds can potentially (1) escape the high mortality zone near the parent tree, (2) be deposited in a favorable microhabitat, and (3) promote gene flow between populations through this process (Schupp et al. 2010).

Author contributions: SK, LL, MG conceived and designed the experiments; SK, LL, FLT-T, JA, ML, TP, AM-P performed the experiments; SK analyzed the data and wrote the manuscript; MG, CS provided editorial advice.

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Plant–frugivore mutualism largely depends on "matching" functional traits between the interacting partners (Onstein et al. 2017). One of the most important characteristics shaping a frugivore's ability to interact with fruits is its gape size (i.e. the broadest oral dimension; Lord 2004). This trait correlates with the maximum sized fruit that a frugivore can consume and thus helps define a species' functional role in frugivory and seed dispersal networks through trait-matching between frugivore and fruit (Bender et al. 2018). For seed dispersal, plants with big fruits tend to require large-bodied animals with large gape sizes to swallow the fruit and the seeds within (Onstein et al. 2017). However, due to defaunation, many tropical plants have lost their interaction partners, which could negatively affect plant recruitment and diversity (Ruxton & Schaefer 2012).

Island ecosystems are particularly vulnerable to defaunation and the resulting losses in mutualistic interactions, with researchers finding most plants having significant losses in pollination and seed dispersal potential on defaunated islands (Fricke et al. 2018). For instance, in Guam, Wandrag et al. (2017) found that the loss of avian frugivores led to a halving of plant richness in comparison to neighboring islands where seed dispersers were present. Additionally, on the island of La Réunion, Albert et al. (2020) demonstrated that the extinction of frugivores has led to the loss of large-fruited plant diversity. Given this vulnerability, one region of interest is the Caribbean, where most large-bodied frugivore populations have collapsed in the last 7000 years due to human activities such as overharvesting or habitat loss (Kehlmaier et al. 2017).

Two groups of large-bodied frugivores of interest in the Caribbean archipelagos are giant tortoises (*Chelonoidis* spp.) and iguanas (*Cyclura* and *Iguana* spp.). Both reptile groups existed throughout the region and were widely frugivorous (Fig. 1; Shaney et al. 2020; Steadman et al. 2020), thus likely playing important roles in plant–frugivore mutualisms. This is especially important as they are relatively big, possess large gape sizes, and can interact with a wide variety of plants (Lord 2004). Although all *Chelonoidis* spp. became extinct in the Caribbean (Steadman et al. 2020), species of the same genus continue to exist in the Galapagos archipelago and South America (e.g. *Chelonoidis niger*, *C. carbonaria*, and *C. denticulata*). Meanwhile, 11 species of native iguana (*Cyclura carinata*, *C. collei*, *C. cornuta*, *C. cychlura*, *C. nubila*, *C. lewisi*, *C. pinguis*, *C. ricordii*, *C. rileyi*, *C. stejnegeri*, and *Iguana delicatissima*) as well as two non-native iguanas (*Ctenosaura similis* and *Iguana iguana*) still exist within the region and are the current largest extant frugivores within the Caribbean. However, all native iguanas are highly threatened and restricted to small, localized populations on a limited number of islands (Fig. 1), with some species being eliminated from most islands within their historical ranges (Malone et al. 2000; Bradley & Gerber 2005). Due to the declines in both groups, many fruiting plants, particularly those with larger fruits, may have lost their main frugivore partners, as existing frugivores (mostly birds, smaller reptiles, and bats) cannot reliably consume their large fruits due to having smaller gape sizes (e.g. Lim et al. 2020).

Large fruits possessed by some plants can thus be a form of anachronism, where their traits, which evolved due to the existence of large frugivorous partners, no longer benefit from plant–frugivore interactions due to defaunation (Guimarães et al. 2008). In this study, we aim to understand the consequences of this anachronism in the Caribbean by first quantifying potential gaps in frugivory function between smaller frugivores (bats, birds, and smaller lizards: *Anolis* spp., *Leiocephalus* spp., etc.), and rarer, larger frugivorous reptiles (*Cyclura* spp., *Chelonoidis* spp.). We then artificially reestablish anachronistic relationships by feeding large-fruited Caribbean plants to *Chelonoidis* spp. and *Cyclura* spp. and determining their effects on germination. We focus on addressing the following questions: (1) How much larger are *Cyclura* spp. and *Chelonoidis* spp. gape sizes than those of smaller, widespread lizards and frugivorous birds? (2) How does ingestion by *Chelonoidis* and *Cyclura* affect the germination of Caribbean fruits? We expect to find a significant gap in ingestion capabilities between smaller common frugivores and larger rare frugivores in the region. We also predict that plants ingested by *Cyclura* and *Chelonoidis* will benefit from having accelerated germination speeds and higher germination percentages, which would imply that the absence of large reptiles would negatively affect large-fruited plants.

Methods

Reptile and Fruit Measurements

We compiled the gape sizes of 12 species of frugivorous bats, 100 species of frugivorous reptiles, and 248 species of frugivorous birds native to the Caribbean archipelagos. We defined the Caribbean archipelagos as all islands within the Antillean biogeographic dominion, which is a region of biogeographic similarity that includes the Greater and Lesser Antilles and the Lucayan archipelago (the Bahamas and Turks and Caicos islands) (Morrone 2014). An exception to our focus on native species was the tortoise (*Chelonoidis* sp.), as all tortoises native to the Caribbean (*Chelonoidis alburyorum*, *C. cubensis*, *C. dominicensis*, *C. marcanoi*, *C. monensis*, and *C. sombrerensis*) have gone extinct (Rhodin et al. 2015). Therefore, we complemented our measurements of Caribbean tortoise fossils with live measurements of the Galapagos tortoise (*C. niger*), as it is a species of the same genus as the extinct Caribbean giant tortoises.

We defined "small lizards" as any reptilian species smaller than iguanas (*Iguanidae*). Then, using a catalog of frugivorous reptiles in the Caribbean as a guide (Kim et al. 2022), in which only lizard species (Squamata) were found to be frugivorous, we gathered and measured the gape size of up to 30 individuals from each species found within the Florida Museum of Natural History (Gainesville, FL, U.S.A.) by measuring the greatest width of the base of the mouth for each individual with digital calipers. Tarazona-Tubens (in prep) performed a similar process for measuring frugivorous bird and bat gape sizes, and their measurements were used to supplement our analyses.

For larger reptiles, we focused on iguanas (Iguanidae) and giant tortoises (*Chelonoidis*), as these were the main reptilian frugivorous megafauna in the Caribbean. This group was considered separate from the "small lizards" not only for their size but also for their relatively threatened status. In addition to specimens

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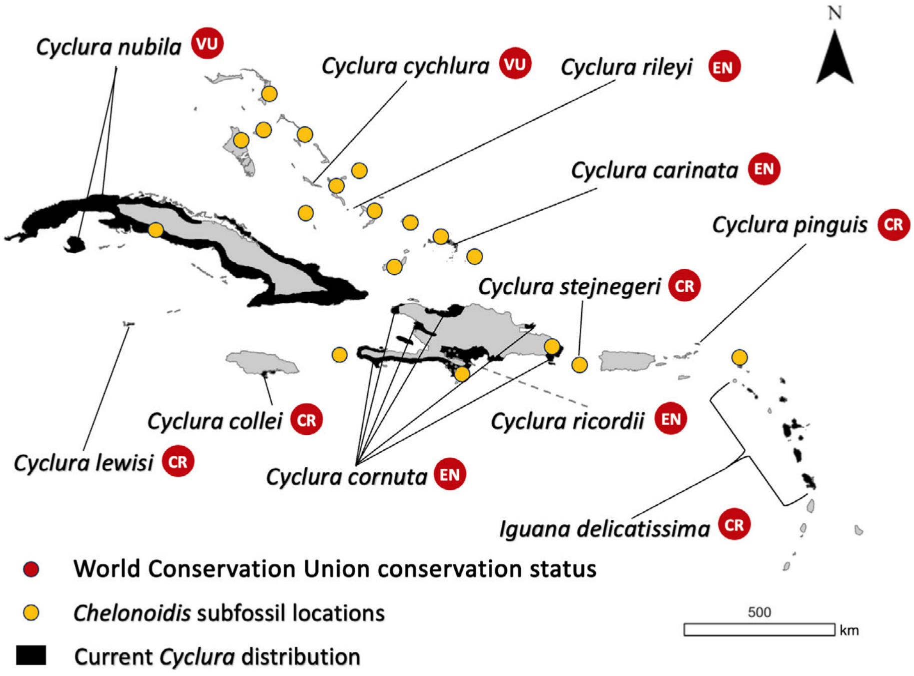

Figure 1. Distribution of *Chelonoidis* subfossil locations (adapted from Steadman et al. 2020) and distribution of extant *Cyclura* species as estimated by World Conservation Union and Buckley et al. (2016), as well as their conservation status.

available within the museum, we also obtained access to captive *Cyclura* specimens (*Cyclura lewisi-nubila* hybrids and *C. pinguis*) from Iguanaland, a reptile zoo, education, and conservation center in Punta Gorda, Florida, United States, and Mike Lloret's Breeding Facility, a privately owned and licensed reptile facility in Miami, Florida, United States. For giant tortoises, we measured gape sizes from captive individuals from Three Jay's Tortoise Sanctuary, a Species Survival Plan participant located in Miami, Florida, United States, which is dedicated to the captive management and conservation of the Galapagos giant tortoise. However, it is important to note that Caribbean tortoises were likely smaller than those currently in the Galapagos (Kehlmaier et al. 2017). As such, we also obtained gape size measurements from two Caribbean tortoise sub-fossils housed at the Florida Museum of Natural History as a reference for the difference in gape size between the extinct and extant *Chelonoidis* spp.

We obtained fruits from 10 fruiting plants native to the Caribbean: *Acrocomia crispa*, *Catesbaea spinosa*, *Chrysobalanus icaco*, *Coccoloba uvifera*, *Coccothrinax barbadensis*, *Cordia sebestena*, *Goetzea elegans*, *Pseudophoenix vinifera*, *Syagrus amara*, and *Theophrasta jussieui*. We selected these species due to their availability and as they ranged from being common throughout the Caribbean (*C. icaco*, *C. uvifera*, and *C. sebestena*) to being either rare or endemic to specific regions (*A. crispa*—Cuba, *C. spinosa*—Bahamas, *C. barbadensis*—Lesser Antilles, *G. elegans*—Puerto Rico, *P. vinifera*—Hispaniola, *S. amara*—Lesser Antilles, *T. jussieui*—Hispaniola). These species also encompassed a wide range of sizes, which is directly associated with their interaction potential with frugivores (Lord 2004; Bender et al. 2018).

We obtained all fruits used for ingestion trials from Montgomery Botanical Center, the Gifford Arboretum at the University of Miami, Fairchild Tropical Botanical Garden, and Biscayne National Park, all near Miami, Florida, United States. To minimize any effects of individual variation on germination, we obtained the fruits of a specific species for each treatment from either a single parent tree or, if that was not possible, from a group of individuals from within the same area. Then, for each species, we measured the diameter (the smallest axis) of at least 10 specimens with digital calipers, but measured more for species with higher availability. To put these measurements in the context of broader Caribbean fruiting plants, we used information from a dataset of 250 Caribbean fruiting plants' traits (Tarazona-Tubens in prep), which were measured in a similar manner to this study.

To statistically compare the gape sizes of the three frugivore groups (birds, small lizards, and large reptiles) and fruit sizes, we first calculated the mean size of each species in our dataset. Then, we conducted a Kruskal–Wallis rank-sum test ($\alpha = 0.05$) and followed up with post hoc pairwise comparisons using the Dwass-Steele-Critchlow-Fligner all-pairs test through the "*PMCMRplus*" R package (Pohlert 2022).

Ingestion Treatments

Between June and October 2021, we collaborated with Three Jay's Tortoise Sanctuary, Iguanaland, and Mike Lloret's Breeding Facility to conduct feeding trials with either *Cyclura* spp. or *C. niger*. *Cyclura* spp. (consisting of similarly sized *C. cornuta*, *C. nubila-lewisii* hybrids, or *C. pinguis*) were housed in small groups in either 2 m × 6 m × 2.1 m (Iguanaland) or

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3.7 m × 3.7 m × 2.1 m (Mike Lloret's Breeding Facility) enclosures. Meanwhile, all *C. niger* individuals from the Three Jay's Tortoise Sanctuary were housed within an area of approximately half an acre. *Cyclura* spp. were typically fed romaine lettuce, kale, collards, papaya, *Opuntia* cactus, squash, and Mazuri tortoise chow three times per week, while *C. niger* regular feed consisted of a variety of fresh-cut hay grasses (orchard grass, alfalfa, Timothy and Coastal, etc.), fresh-picked *Opuntia* sp. cactus pads, natural grazing on low-hanging leaves and grasses, and Mazuri brand zoological, extruded tortoise chow (both "regular" and their "low starch" varieties).

Before *Cyclura* feeding trials, selected individuals were not fed for 2–3 days to encourage fruit consumption. For each trial, we offered at least 20 fruits of a single, selected fruit species to a group of enclosed *Cyclura* by placing them either on the enclosure floor or on top of prepared feeding trays; feces were collected and examined afterwards for the presence of seeds. All feces within the enclosures were found by scanning the enclosure floor every day for up to 2 weeks after the feeding event. We collected all feces found within each enclosure in plastic zip-loc bags and then stored them in a refrigerator for later processing to minimize the risk of fungal infections. To minimize the effects of storage on germination, we removed every fecal collection from storage no longer than 1 week after the first fecal samples were collected and searched for seeds. Every seed found within was cleaned manually with water, identified, and sorted for planting.

As with *Cyclura*, *C. niger* feeding trials consisted of offering at least 20 fruits of each species to the tortoises. However, the tortoises were fed fruits directly into their mouths in addition to placing the fruits on the enclosure floor, as the tortoises were easier and safer to handle than *Cyclura*. Additionally, we determined that a fasting period was unnecessary due to the tortoises' large appetite. All tortoise feces found within the enclosure between 1 and 3 weeks from consumption were collected within a large plastic bag and stored within a shaded area as they could not be accommodated within a refrigerator due to their large size. At the end of the second and third weeks of this period, we processed every fecal sample collected, and for each seed found, we cleaned, identified, and sorted them by species for the germination experiment.

Greenhouse Germination Tests

All germination trials took place at the University of Miami greenhouse in the Gifford Arboretum for 200 days (July 2021 to January 2022). Seeds from the three treatment groups (i.e. "Control" [defleshed/depulped seeds], "iguana ingestion," and "tortoise ingestion") were individually planted into 5.5 × 7.5 × 5.5 cm rectangular prism plastic pots that were filled with approximately 4 cm of garden soil (Miracle-Gro Potting Mix). While using vermiculite provides a more sterile environment for the seeds (Kumar 2013), common garden soil was used to better imitate how the seeds would grow under less artificial conditions. Meanwhile, although defleshing fruits is one method through which frugivores benefit the recruitment success of plants (Rogers et al. 2021*b*; Albert et al. 2022), we used defleshed/depupled seeds as Control as our goal is to assess the potential benefit of larger frugivores in fully ingesting seeds, whereas smaller frugivores such as small lizards and birds are still able to deflesh fruits without the presence of larger animals. Pots were grouped by species, placed within the same area of the greenhouse to limit microclimate variations, and watered manually approximately every 2 days, at which time they were also monitored for signs of germination. Only seedlings that "sprouted" (had their radicle protrude out of the soil) were considered germinated (Hermann et al. 2007).

At the end of the monitoring period, all non-sprouted pots were emptied, and the seeds were checked for signs of germination. If roots were visible on a seed, the seed was considered germinated but not included in the germination speed calculations since it did not match our pre-determined definition of germination and we could not specify when sprouting occurred. If no roots were visible on a seed, the seed was dissected longitudinally to visually decide whether it was dead. Any seeds with signs of rot (brown or absent endocarp, structurally unsound seed capsule, etc.) were considered dead, as were those that we could not find within the pot.

Analysis of Germination

We evaluated how ingestion affected survivability or germination success by comparing the number of dead or successfully germinated seeds by different treatment groups (Control, iguana ingestion, and tortoise ingestion) through a series of Fisher's exact tests for each of the study species (Fisher 1934) with the Benjamini–Hochberg false discovery rate correction (Benjamini & Hochberg 1995). For each significant result, we followed up with a post hoc test between the treatments for each species through the *rstatix* R package (Kassambara 2022).

We assessed the speed of germination using two metrics: peak value (PV) and germination value (GV), calculated using the equations below. PV is the highest mean daily germination percentage (MDG), which is the cumulative total percentage of germinated seeds divided by the exact germination day (Iroko et al. 2021). GV is a widely used metric created by Czabator (1962) and is an expression of the speed and totality of germination and their interaction. These were calculated through the *germinationmetrics* R package (Aravind et al. 2022).

$$\text{Germination percentage} = \frac{\text{Total seeds germinated}}{\text{Total seeds sown}}$$

$$\text{MDG percentage} = \frac{\text{Cumulative germination percentage}}{\text{Exact germination day}}$$

$$\text{PV} = \text{MAX}(\text{MDG percentage})$$

$$\text{GV} = PV \times \text{MDG percentage}$$

To assess whether ingestion treatment significantly affected seed germination speed for each species, we used a modified survival analysis approach through the *survival* R package (Therneau & Grambsch 2000). This method is commonly used in public health to assess and compare the effectiveness of

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specific traits or treatments on patient survival rates (Lee & Go 1997). We modified this approach to evaluate effects on germination speed as suggested by Onofri et al. (2010) and considered the time it took for each plant to germinate as part of our analysis. As our germination trials likely terminated before every potentially viable seed was able to germinate, non-germinated, potentially viable seeds were considered censored observations, while dead seeds were removed from our survival analysis (Onofri et al. 2010). First, we conducted a series of log-rank tests for each species to determine if there were significant differences in germination speed throughout all treatments. We then supplemented this through Cox regression models (Cox 1972), which quantify effect sizes for each treatment through the "hazard ratio" (HR) metric to identify the probability that an individual has a germination event at a given time while also providing a pairwise comparison between treatments. Our regression models pursued a mixed, "frailty" model approach as advocated by Hougaard (1995), Chuang et al. (2005), and Onofri et al. (2010).

Results

Gape Size Comparisons

We measured 1752 individuals from 91 small lizard species (*Anolis* spp., *Aristelliger* spp., *Celestus* spp., and *Leiocephalus* spp.) with a mean gape size of 8.62 mm (±0.07 mm SE), 1984 individuals from 247 frugivorous bird species with a mean gape size of 9.26 mm (±0.19 mm SE), and 142 individuals from 12 frugivorous bat species with a mean gape size of 7.77 mm (±0.71 mm SE). For iguanas (Iguanidae), we measured 69 individuals from six species (*Iguana delicatissima*, *Cyclura cornuta*, *C. carinata*, *C. cychlura*, *C. lewisi-nubila* hybrids, and *C. pinguis*). This group had a mean gape size of 62.1 mm (±3.4 mm SE). For tortoises, we measured 12 individuals of *Chelonoidis niger* with a mean gape size of 91.0 mm (±7.3 mm SE) (Table S1). Additionally, we included the gape size of one individual each of *C. alburyorum* and *C. dominicensis*, which previously inhabited the Caribbean, as reported by Albury et al. (2018). These gape sizes were smaller than the mean gape size of *C. niger*, with gape sizes of 58.9 and 50.8 mm for *C. alburyorum* and *C. dominicensis*, respectively. Placed in the context of all known frugivorous species in the Caribbean islands (Kim et al. 2022), we sampled 65, 83, 80, 46, and 40% of all cataloged frugivorous species for small lizards, birds, bats, iguanas, and tortoises, respectively.

We found that the sizes of small lizard, bird, bat, and large reptile gapes were significantly different ($\chi^2 = 31.781$, degrees of freedom [df] = 3, $p < 0.001$), with large reptile gapes being significantly larger than those of all the other groups, which were in turn all statistically equivalent to each other (Fig. 2). The smallest member of the large reptile group (*C. carinata*), with a mean gape size of 25.1 mm, could consume 50% of the fruits used in our trials. Meanwhile, 67% of the large reptiles could consume all the fruit species used in our trials. In contrast, the largest species outside of the large-reptile category (*Anolis equestris*) could consume 50% of the fruits used in our trials with a mean gape size of 24.5 mm. Meanwhile, 79, 50, and 92% of small lizards, birds, and bats could consume none of the fruits fed to larger reptiles in this study.

Germination Trial Results

Fruits that were part of the ingestion trials ranged from 10.18 mm (*Coccothrinax barbadensis*) to 55.75 mm (*Theophrasta jussieui*) in diameter (Table S2; Fig. 2). When compared to the available fruit traits dataset in the Caribbean ($n = 250$; Tarazona-Tubens in prep), our study species range from the 65th (*C. barbadensis*) to the 99th percentile (*T. jussieui*) of all species sizes measured. We fed every fruit species to both iguanas and tortoises, except for *Syagrus amara*, which possesses the largest seeds in our study (33.12 ± 0.35 mm SE). Due to this large size, we only fed eight fruits of this species to tortoises to avoid harming any individuals. Overall, we recovered at least 10 seeds for all species-treatment combinations, except for iguana-ingested *Cordia sebestena*, *Pseudophoenix vinifera*, and *T. jussieui* (4, 8, and 3 seeds recovered, respectively).

Germination occurred after ingestion for 7 of the 10 plants in our study (*Acrocomia crispa*, *Catesbaea spinosa*, *Chrysobalanus icaco*, *Coccoloba uvifera*, *C. sebestena*, *S. amara*, and *T. jussieui*). Iguana-ingested *C. sebestena* had the highest proportion of seeds germinating, with 100% of sown seeds germinating. However, this was with only four seeds having been sown for this species. The next best categories were iguana-ingested *C. uvifera* and uningested *C. spinosa* (94.1 and 93.3%, respectively). Meanwhile, none of the ingested *C. barbadensis*, *Goetzea elegans*, and *P. vinifera* seeds germinated, with none of the seeds from the Control group of *G. elegans* germinating either (Tables 1 & S3).

Ingestion affected the likelihood of germination and survivability for several species. *Syagrus amara* and *C. uvifera* seeds had significantly higher germination (*S. amara*: $p = 0.026$, *C. uvifera*: $p = 0.001$) and survivability likelihoods (*S. amara*: $p = 0.026$, *C. uvifera*: $p = 0.002$) after ingestion. A post hoc test showed that only iguana ingestion significantly affected *C. uvifera* germination/survivability likelihoods. In contrast, *C. barbadensis*, *C. icaco*, and *T. jussieui* seeds had significantly lower germination (*C. barbadensis*: $p < 0.001$, *C. icaco*: $p = 0.033$, *T. jussieui*: $p < 0.001$) and survivability likelihoods (*C. barbadensis*: $p < 0.001$, *C. icaco*: $p = 0.048$, *T. jussieui*: $p < 0.001$) after ingestion. The subsequent post hoc test showed that while both iguana and tortoise ingestion significantly affected the likelihood of germination and survivability for *C. icaco* and *T. jussieui*, only iguana ingestion significantly affected the likelihood of germination and survivability for *C. barbadensis*.

Iguana-ingested *C. spinosa* germinated most quickly, with the highest PV and GV at 3.85 and 11.66, respectively. However, tortoise-ingested *C. uvifera* had the highest HR compared to Control with a value of 7.4 (Table 1). A comparison of germination speed among ingestion treatments showed significant variation for both *C. uvifera* ($\chi^2 = 12.6$, $df = 2$, $p = 0.002$) and *C. sebestena* ($\chi^2 = 5.9$, $df = 1$, $p = 0.02$), with

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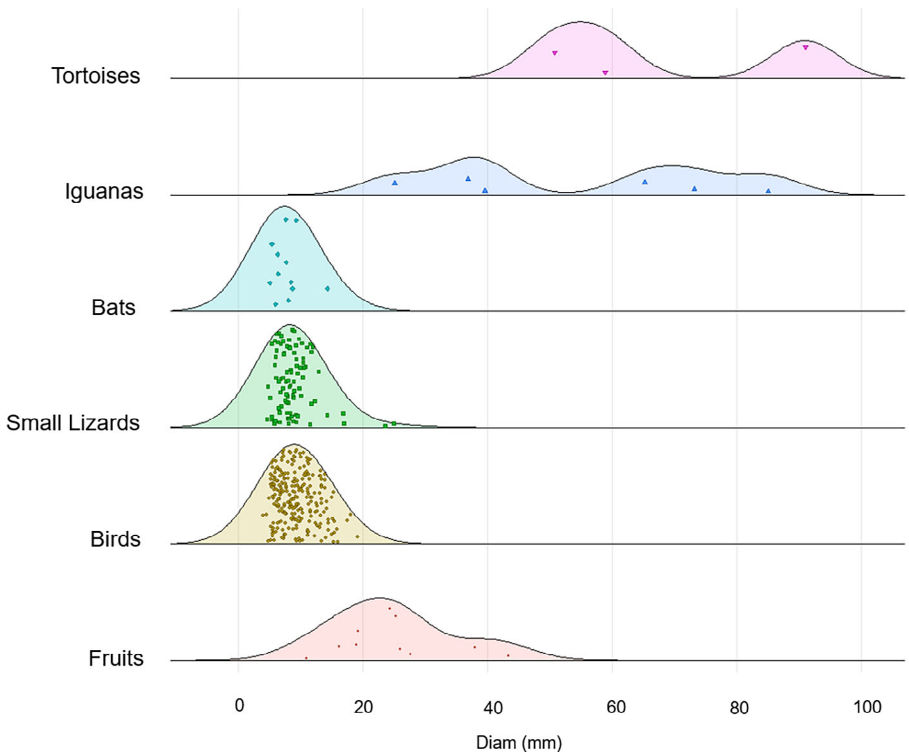

Figure 2. Distributions of fruit diameters for species used for ingestion trials (26.20 ± 0.44 mm SE), and gape sizes of tortoises (66.88 ± 12.26 mm SE), iguanas (54.15 ± 9.65 mm), bats (7.77 mm ± 0.71 mm SE), small lizards (8.62 ± 0.07 mm SE), and birds (9.34 ± 0.2 mm SE).

ingested seeds showing higher germination speed than uningested seeds for both species. An evaluation of the Cox regression results showed that tortoise ingestion was more responsible for the increase in germination speed than iguana ingestion for *C. uvifera*, with only the tortoise-ingestion treatment providing a significant difference in germination speed (Table 1; Fig. 3).

Discussion

Fruit traits play an important role in determining interactions with seed dispersers (Schupp 1993), with larger-fruited plants being disproportionately dependent on large vertebrate frugivory for dispersal and recruitment (Onstein et al. 2017). With Caribbean megafauna being depleted (Steadman et al. 2020), it is crucial to gage the strength of missing interactions and their effects on germination. Our analysis of gape sizes showed a significant gap in frugivore function, with the gape sizes of common, smaller frugivores (birds, smaller lizards, and bats) being many times smaller on average than rarer, larger reptiles. This size distribution dramatically limits the ability of the existing frugivore community to consume and interact with fruits in the Caribbean, leaving many large-fruited plants functionally orphaned from their frugivore dispersers, with potentially negative effects on their recruitment (e.g. Lim et al. 2020). We evaluated the presence of such negative effects by assessing the impacts of ingestion by two large reptiles (iguanas and tortoises) on large-fruited plant species. Our trials showed that most of these large-fruited plants could indeed germinate post-ingestion. As seed dispersal is in and of itself beneficial to a plant, independent of germination speed, by moving seeds away from the parent tree (Schupp et al. 2010), this finding indicates that the reestablishment of frugivorous interactions could be beneficial to plants by restoring seed dispersal.

Exceptions to the pattern of plants germinating post-ingestion were *Coccothrinax barbadensis*, *Goetzea elegans*, and *Pseudophoenix vinifera*. None of the *G. elegans* individuals, including those in the Control group, germinated in our study, potentially indicating an issue outside of zoochory, such as climatic or edaphic conditions (Koger et al. 2004). However, for *C. barbadensis*, the ingestion appears to have actively inhibited germination, likely by damaging the seed coat during digestion and harming the embryo (Traveset 1998; Lautenschlager et al. 2022). Given this, it seems possible that this species does not benefit from large reptilian frugivory. Instead, other forms of zoochory, such as from birds, could be responsible for dispersing this species, as the effects of bird digestion could be different than those of large reptiles, likely due to differences in gut retention time (Janzen et al. 1985) and digestion process (Stevens 2001). This is supported by personal observations (S.K. and M.G.) of *Patagioenas leucocephala* consuming and dispersing *Coccothrinax* spp. and warrants further investigation, especially as it is unknown if those seeds germinated after deposition. Indeed, the role of generalist birds as seed dispersers cannot be underestimated, as they are known to play keystone roles in forest regeneration and the maintenance of frugivory

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Table 1. Effect of iguana and tortoise ingestion compared to control on survival and germination likelihood, mean germination time (mean GT), and germination speed of all species that germinated. "HR" stands for "hazard ratio," where higher values indicate a higher chance of germination in comparison to Control. Reported *p* values are from the survival analyses. "GV" and "PV" indicate "germination value" and "peak value", respectively, with higher values indicating faster germination. Tortoise-ingestion treatments did not occur for *Cordia sebestena* and *Pseudophoenix vinifera*. An iguana-ingestion treatment did not occur for *Syagrus amara*. None of the *Goetzae elegans* individuals germinated, so this species is not included in the table. Effect, compared to controls, is listed as positive (+), neutral (0), or negative (−) depending on the change in percent germinated seeds. "na" stands for "not applicable".

Germination (viable)									
Species	*Treatment*	*% Alive*	*% Germinated*	*Effect*	*Mean GT*	*HR*	p *Value*	*GV*	*PV (%)*
Acrocomia crispa	Control	93.3	20	0	81.5	na	na	0.012	0.13
	Iguana	70	30	+	148.5	2.07	0.4	0.033	0.18
	Tortoise	61.9	0	−	na	na	na	0	0
Catesbaea spinosa	Control	93.3	93.3	0	25.5	na	na	3.66	2.12
	Iguana	60	60	−	25.6	2.06	0.1	11.66	3.85
	Tortoise	66.7	66.7	−	26.5	1.94	0.14	9.18	3.03
Chrysobalanus icaco	Control	86.7	86.7	0	101.9	na	na	0.28	0.59
	Iguana	48	48	−	99.1	1.08	0.8	0.32	0.63
	Tortoise	60	46.7	−	58.4	1.15	0.8	0.23	0.68
Coccoloba uvifera	Control	40	33.3	0	38.4	na	na	2.02	1.7
	Iguana	94.1	94.1	+	28.6	2.77	0.05	3.49	2.45
	Tortoise	66.7	66.7	+	20.7	7.4	<0.001	4.97	3.48
C. sebestena	Control	80	80	0	99.5	na	na	0.5	0.81
	Iguana	100	100	+	58	4.91	0.029	0.76	1.22
	Tortoise	na	na	na	na	na	na	na	na
Coccothrinax barbadensis	Control	50	50	0	100.2	na	na	0.60	0.77
	Iguana	0	0	−	na	na	na	0	0
	Tortoise	0	0	−	na	na	na	0	0
P. vinifera	Control	73.3	13.3	0	130	na	na	0.013	0.12
	Iguana	50	0	−	na	na	na	0	0
	Tortoise	na	na	na	na	na	na	na	na
S. amara	Control	16.7	16.7	0	na	na	na	0	0
	Iguana	na	na	na	na	na	na	na	na
	Tortoise	87.5	87.5	+	82	na	na	0.31	0.17
Theophrasta jussieui	Control	86.7	86.7	0	96.2	na	na	0.35	0.59
	Iguana	0	0	−	na	na	na	0	0
	Tortoise	6.7	6.7	−	na	na	na	0	0

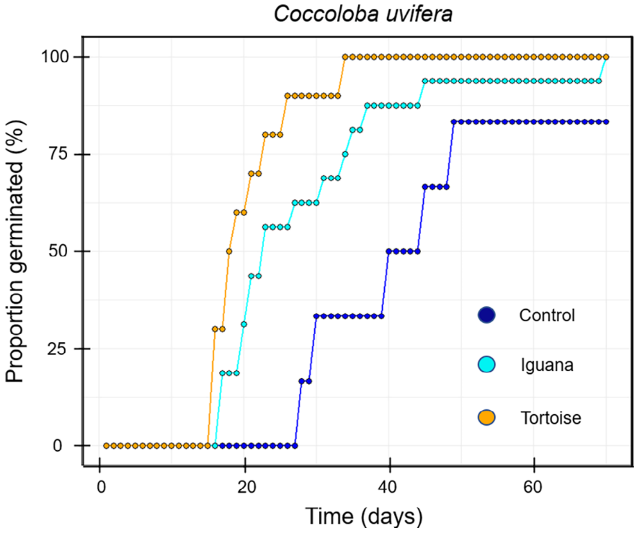

Figure 3. Effects of iguana (light blue) and tortoise (orange) consumption on the proportion of seeds that germinated for *Coccoloba uvifera* compared to the Control treatment (dark blue).

networks (Carlo & Morales 2016). However, as shown by our trait comparison results, iguanas and tortoises have even greater potential as frugivores by being able to interact with a wider variety of fruits, including those that are too large to be consumed by smaller frugivores such as birds.

Scarification of the seed coat through mechanical or acidic means during ingestion can also benefit plants by accelerating the germination process (Aliero 2003). Quicker germination would provide ingested seeds a competitive advantage by allowing those individuals to take priority over potentially limited resources (Vaughn & Young 2015). Moreover, certain plants have developed a dependence on ingestion by megafauna to trigger germination (Moolna 2007; Setlalekgomo & Sesinyi 2014).

Our results did not demonstrate that this occurred for most plants, with only *Coccoloba uvifera* and *Cordia sebestena* having significantly faster germination speeds post-ingestion. Interestingly, these large-fruited plants are widely distributed throughout the region (GBIF 2022), indicating that these plants, which most benefitted from megafauna ingestion in our study, have some alternative dispersal mechanism to ingestion by

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large-bodied reptiles, as their fruit sizes are too large to be readily consumed by common, native frugivores (i.e. birds and smaller lizards). This runs counter to many theories regarding the high dependence of tropical fruiting plants on interaction-dependent zoochoric dispersal (Beaune et al. 2013) and is particularly interesting given that other large-fruited plants in our study (*Acrocomia crispa*, *Catesbaea spinosa*, and *Syagrus amara*) possess limited distributions in the region (GBIF 2022). Understanding the mechanisms behind the success of certain large-fruited plants in contrast to others could highlight the importance of specific non-zoochoric dispersal strategies such as hydrochory (Gillespie et al. 2012) or the emergence of new zoochoric interactions through the proliferation of non-native animals (Pedrosa et al. 2019), providing a glimpse of future plant distributions in the face of defaunation. Furthermore, it is important to note that our greenhouse experiments do not fully replicate natural conditions, which could have biased our understanding of the effects of frugivore ingestion on plants. For instance, the effect of the Aldabra tortoise (*Aldabrachelys gigantea*) scat on plant germination has been shown to have varied effects on seed germination and seedling growth (Hansen et al. 2008). Regardless, our trials still illustrate the generally positive effects of ingestion on Caribbean plants by allowing most species in our study to germinate post-ingestion.

*Re*establishing interactions between plants and animals is one method of recreating lost seed dispersal dynamics (Falcón & Hansen 2018; Falcón et al. 2020; Moorhouse-Gann et al. 2021; Lautenschlager et al. 2022). This can be done by introducing species with similar ecological function or that are taxonomically related to extinct and/or endangered species (Hansen et al. 2008). Such rewilding efforts could reverse the consequences of lost interactions (Falcón et al. 2020) and, in the case of frugivory, benefit plant germination, genetic population connectivity, and allow plants to reach potentially more suitable areas for recruitment (Falcón & Hansen 2018). For instance, in the Mascarene Islands, rewilded Aldabra giant tortoises (*A. gigantea*) have been shown to restore functions previously performed by extinct tortoises by effectively consuming and dispersing large-seeded plants (Griffiths et al. 2010). A similar finding was made in the Atlantic Forests of Brazil with the Red-footed and Yellow-footed tortoises (*Chelonoidis carbonarius* and *C. denticulatus*; Sobral-Souza et al. 2017). By demonstrating the viability of ingested seeds, we show that *C. niger* could be a potential candidate for such rewilding efforts in the Caribbean. This is of special interest as native giant tortoises have been completely extirpated from the region and their ecological function has it. Although it is important to consider the potential risks of introducing exotic animals to any ecosystem (e.g. facilitating the spread of invasive plants, damaging native plant communities, or competing with existing native animals; see Ruesink et al. 1995; Falcón et al. 2013), island rewilding with a functional analogue has generally been considered less controversial due to the relative recency of island species extinctions and the smaller size of their extinct megafauna (Falcón & Hansen 2018). Meanwhile, additional effort should be invested to reinforce and understand iguana–plant interactions through further *Cyclura* conservation efforts and studies on the effects of invasive green iguanas (*Iguana iguana*) on shaping seed dispersal interactions in the Caribbean islands.

In conclusion, studying plant–frugivore interactions and how they affect plant germination is of great relevance to our understanding of ecosystem structure and resilience. We show that there are considerable gaps in animal functional traits relevant to plant–frugivore networks in the Caribbean, and our study is the first to present this pattern for such a variety of fruits in the Caribbean. We also demonstrate the usefulness of reestablishing lost interactions between larger reptiles and large-fruited plants by proving the viability of ingested seeds for multiple species. We suggest future studies expand on this research by examining other zoochoric interactions, such as those with non-native species, as well as non-zoochoric dispersal, such as hydrochory in island systems.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. All fruit diameter and gape width data used for this study.
Table S2. Expanded fruit information for those used for the study.
Table S3. Summary information of germination and survival for all plants used in this study.

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