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Elevated threat status of large-fruited plants is associated with the extinction of large frugivores in the Caribbean islands

Fabio L. Tarazona-Tubens[a,1], Seokmin Kim[a], Alcides L. Morales-Pérez[b], Eleanor M. Hay[a], Maximilian G. R. Vollstädt[c,d], Thomas F. Johnson[e], Fernando Gonçalves[c,f], Benno I. Simmons[g], Christopher N. Kaiser-Bunbury[g], Bo Dalsgaard[c], Mauro Galetti[a,h], and Christopher A. Searcy[a]

Affiliations are included on p. 7.

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Anthropogenic activities severely impair biodiversity and ecosystem functionality. A prime example is the loss of frugivores and their corresponding seed dispersal services due to defaunation (the decline of animal populations), ultimately affecting the continued persistence of plant species that lack their ecological partners. Loss of frugivores and their biotic interactions can be particularly severe on islands due to their isolation and relatively small area, which is often associated with low functional redundancy. From field observations on the Caribbean Virgin Islands, we found that only 1% of documented seed dispersal events occurred in large-fruited plants, with dispersal probability closely tied to overlap between fruit width and gape size of the largest nonthreatened frugivore. Using fruit–frugivore trait matching to extrapolate this pattern to the rest of the Caribbean, we found that large-fruited plant species are effectively "orphaned" due to the absence of animal dispersers, resulting in elevated rates of endangerment across islands. Threat status of plant species was better explained by trait matching than other pressures such as human use, suggesting that extinction or reduced abundance of large-bodied frugivores is compromising their plant mutualists' ability to persist. These results argue strongly for the need to restore populations of large-bodied frugivores across the Caribbean, either through population enhancement of currently endangered species or rewilding with close relatives of extinct species.

mutualism | seed dispersal | defaunation | functional traits | rewilding

Our planet is experiencing dramatic losses in animal populations, mostly as a result of anthropogenic threats, such as destruction of habitat, introduction of exotic species, and overharvesting (1, 2). Such threats have historically led to changes in the abundance and distribution of species and, in extreme cases, to extirpation and extinctions (2, 3). The most dramatic reductions in the abundance and distribution of species due to anthropogenic activity are seen among large-bodied animals (2), especially on oceanic islands where the majority of human-induced extinctions have occurred (4). Species loss also leads to the concomitant loss of functional traits—the measurable characteristics that influence organismal performance (5). Ultimately, species functional traits mediate species interactions and ecosystem functions, such as those between plants and frugivorous animals (6–8). Consequently, contractions in functional trait distributions can have detrimental effects on mutualistic partners as well as overall ecosystem function (9).

Physical traits of seed dispersers and fleshy fruiting plants determine which fruits are consumed, the rate of consumption, and the dispersal distance of those seeds (10–12). Generally, large-bodied species tend to have a larger gape size, longer gut retention times, and increased mobility (13). These traits facilitate consumption of a wide variety of fruits with larger size and promote the deposition of seeds farther away from parent trees than for small-bodied dispersers (14, 15), ultimately increasing plant genetic connectivity by moving seeds between fragmented habitat patches or between islands (16, 17).

Even in cases where extinction is avoided, lower abundances of large-bodied frugivores may still lead to functional extinctions if the species is no longer able to fulfill its role in the ecosystem (18). As an example, 61% of iguana species, a clade that has an important role in seed dispersal in the Neotropics, are currently under threat of extinction (19), with all Caribbean species of *Cyclura* rock iguanas having experienced dramatic reductions in their abundance and distribution. Loss of species and their ecological roles disrupt natural interactions and the ecosystem services they provide, ultimately affecting stability of seed dispersal mutualisms with direct effects on plant reproduction and recruitment (20, 21).

Islands have high levels of species endemism, which is often threatened by human activity and natural hazards (22–24), making them particularly vulnerable to the disruption of mutualisms due to species extinctions and population declines (25, 26). The

Significance

The loss of frugivores and their seed dispersal abilities can have detrimental effects for plant communities that depend on them, especially on islands where functional diversity is low. Here, we use a combination of field observations and a dataset of fruit–frugivore functional traits in the Caribbean islands to evaluate the current and future status of seed dispersal interactions if currently threatened large frugivores become functionally extinct. We demonstrate that size traits are significantly related to extinction threat in frugivores and plants. Furthermore, based on empirical and trait-based projections using fruit–gape size matching, we show that large-fruited plants experience severe dispersal limitations, and demonstrate that loss of frugivores is associated with a fourfold increase in extinction risk of large-fruited plant species.

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[1] To whom correspondence may be addressed. Email: fabio.tarazona08@gmail.com.

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Caribbean islands constitute a key biodiversity hotspot (27), particularly for avian and reptile frugivores and the plants that depend on these species for seed dispersal services (28–30). However, defaunation as a result of human activities has led to extinctions and significant changes in Caribbean species' functional trait diversity. These species losses seem to have occurred in waves, with the extinction of megafauna (e.g., giant sloths, giant tortoises) occurring during early Amerindian colonization (~6,000 to 5,000 y ago), followed by more recent events in which approximately 70% of known extinctions occurred during the arrival of Taino cultures (~1,500 y ago) and European colonization (~500 y ago) (31, 32). In addition to the extinction of Caribbean megafauna, at least 47% of bat species were eliminated from one or more islands (33), and parrot diversity and distributions have declined significantly since human arrival in the Caribbean (31). Furthermore, many extant large frugivores are under conservation concern, and, although studies evaluating this are much needed, it is likely that they are already functionally extinct due to reduced abundances and contracted distributions. For instance, the Jamaican Crow (*Corvus jamaicensis*), which was once abundant across forested areas of Jamaica, is now restricted to isolated and threatened populations (34). In extreme cases, the effects of habitat destruction have resulted in island-wide extirpations, such as the White-necked Crow (*Corvus leucognaphalus*), formerly widespread throughout St. Croix, Puerto Rico, and Hispaniola, now being restricted to isolated Hispaniolan populations (35). The functional traits of these lost and threatened frugivores might play an important role in determining which fruits are consumed and ultimately dispersed.

Here, we utilize field-based observations across seven defaunated Caribbean Islands, combined with functional traits of fleshy fruits and the main frugivore groups (i.e., birds, reptiles, mammals) in the region to examine the effects of defaunation on seed dispersal interactions and plant conservation status across the Caribbean archipelagos. We first conducted field observations on the Virgin Islands, where large-bodied frugivores are now extinct or severely reduced in number, to determine which portions of the plant community experience seed dispersal given the observed defaunation. Based on our field observations, we identified the maximum fruit size that can be effectively dispersed via endozoochory (i.e., dispersal through ingestion and subsequent passage through the digestive tract), given the gape size and relative abundance of members of the frugivore guild on the Virgin Islands. Based on fruit and gape size measurements collected from multiple museums and living collections, we then applied the identified size cutoff as a rule for fruit–frugivore trait matching across the rest of the Caribbean. With this approach we aimed to identify "orphaned" plants, i.e., large-fruited plant species that have likely lost their seed disperser, and examined whether their conservation status has declined compared to plants with extant dispersers. Using this trait matching approach, we show the importance of key threatened frugivore groups and the strong negative effect their loss has on the conservation status of large-fruited plants in the Caribbean.

Results

Extant Frugivores Do Not Disperse Large-Fruited Plants. Across the seven surveyed islands, we conducted observations on 200 individual fruiting plants of 53 species, recording 297 frugivory interactions with 16 frugivore species. To test whether larger fruits experience reduced seed removal events as a result of defaunation, we conducted a Bayesian phylogenetic logistic regression between seed removal events and fruit size. This model allowed us to incorporate phylogenetic relatedness as a random effect to account for shared ancestry between plant species. Overall, we found a strong, negative relationship between fruit size and seed removal ($\beta = -1.61$, 95% CI: –2.67 to –0.73; Fig. 1), indicating that large-fruited plants experience reduced seed dispersal services by the extant frugivore community in the Virgin Islands. We found good model convergence as indicated by R-hat values and posterior diagnostic plots (*SI Appendix*, Fig. S1). We utilized the posterior distribution of the intercept and slope parameters to calculate the inflection point, allowing us to identify the fruit size at which the majority of seeds were no longer removed (Fig. 1). Based on this model, we found that seeds of fruits larger than 16.4 mm (95% CI: 11.0 to 24.0) were unlikely to be removed from the parent plants. The surveyed plant species included 38 small-fruited plants (<16.4

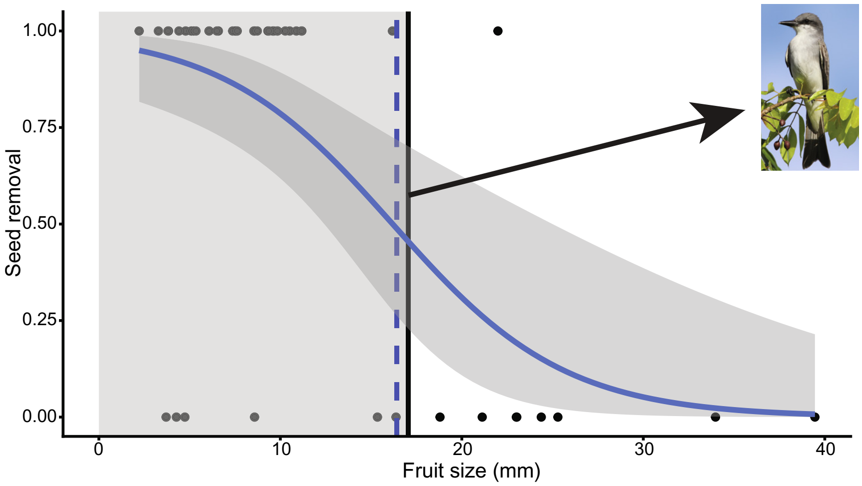

Fig. 1. Field observations revealed that the probability of seed dispersal decreased significantly with increased fruit size (n = 48 plant species; $\beta_{\text{fruit size}} = -1.61$; 95% CI: −2.67 to −0.73). Results are from a Bayesian phylogenetic logistic regression based on frugivory observations in the Virgin Islands. Each point represents an observed plant species along with its mean fruit size. The dashed blue line represents the inflection point at which the majority of seeds were no longer dispersed by frugivores (fruit size > 16.4 mm). We also include a representation of our trait matching approach, where the shaded region represents fruit sizes that can be consumed by the Gray Kingbird (*Tyrannus dominicensis*, upper 95% gape size = 17.0 mm, solid black line), the nonthreatened frugivore with the largest gape size in the local community. The dispersal event greater than the inflection point represents bird interactions with *Pilosocereus royenii* (Cactaceae), in which birds pecked and removed pulp of the large fruit along with its small seeds (<1 mm). Gray Kingbird image sourced from Wikimedia Commons (Author: Aitor; CC BY-SA 4.0).

mm), which experienced 99% of total seed removal events, while the 10 large-fruited plant species (>16.4 mm) only experienced 1% of seed removal interactions.

Comparing this fruit size to the community of common (nonthreatened) native frugivores present in the Virgin Islands, we found the species with the largest gape to be the Gray Kingbird (*Tyrannus dominicensis;* mean gape size = 14.5 mm). The upper size limit of fruits that are commonly dispersed (16.4 mm) matches closely with the largest Gray Kingbird gape sizes (upper 95% CI = 17.0 mm; Fig. 1), providing a trait matching guide for identifying orphaned plant species that lack effective animal dispersers.

Threatened Frugivores and Plants Have Larger Gape and Fruit Sizes. Based on measured museum specimens from across the Caribbean (n = 333 species; *SI Appendix*, Table S1), we found that frugivores in higher IUCN threat categories have progressively larger gape sizes ($F_{5,327}$ = 22.1, $P < 0.0001$; Figs. 2 and 3*A*). The extinct Giant Tortoises (*Chelonoidis* spp.) had the largest mean gape size (85.3 mm ± 25.5 mm SD) followed by the Critically Endangered Anegada Rock Iguana (*Cyclura pinguis;* 85.0 mm ± 12.9 mm SD), while the Common Ground Dove (*Columbina passerina*) had the smallest gape size (4.6 mm ± 0.5 mm SD). Across the Caribbean islands, we found that threatened extant frugivores, specifically those in the Iguanidae (eight species), Psittacidae (six species), and Corvidae (two species) families have the largest gape sizes (Fig. 2 and *SI Appendix*, Table S3). With the exception of Puerto Rico, which has no extant native iguanas on its main island, *Cyclura* iguanas were the largest extant frugivores across the Greater Antilles and Bahamas island groups (Fig. 2 and *SI Appendix*, Table S3), highlighting the critical role of this large-bodied, highly endangered, endemic frugivore clade. Across the Lesser Antilles, the Critically Endangered Lesser Antillean Iguana, *Iguana delicatissima,* (39.6 mm ± 2.9 mm SD) was the largest native frugivore. For plants, we measured a total of 259 species native to the Caribbean (*SI Appendix*, Fig. S5 and Table S1). Similar to frugivores, we found that threatened plants have larger fruit sizes (16.9 ± 1.47 mm SE) than nonthreatened plants (11.9 ± 0.84 mm SE; $t_{234} = -3.86$, $P = 0.0001$; Fig. 3*B*).

Limited Seed Dispersal as Driver of Threatened Plant Conservation Status. To determine whether seed dispersal status (orphaned vs. dispersed) is associated with the conservation status of large-fruited plants, we performed fruit–frugivore trait matching across the Caribbean by comparing fruit size with the gape size of co-occurring frugivores. We assumed an orphaned classification if fruit size was larger than the gape size of co-occurring frugivores and dispersed if fruits were equal or smaller than frugivore gape sizes. We found that Puerto Rico has the highest percentage of orphaned plants (19%; Fig. 2), likely

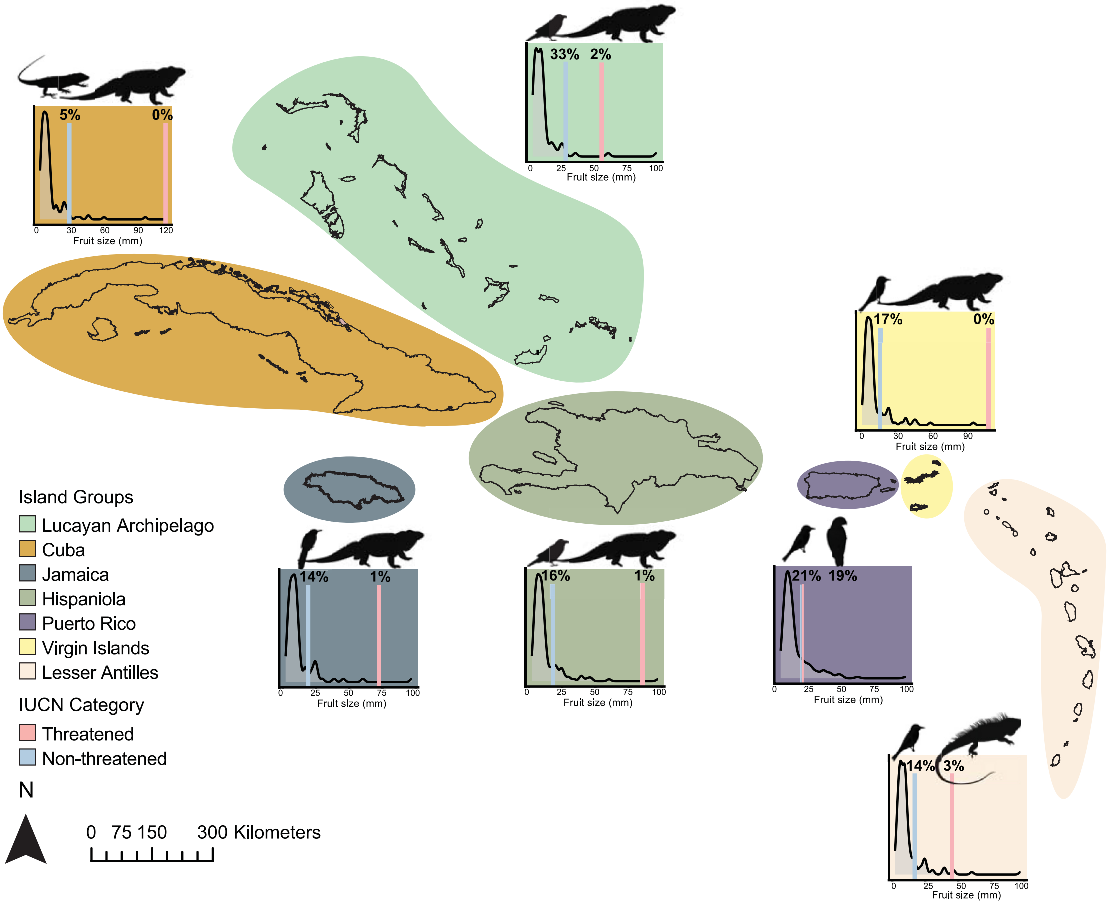

Fig. 2. Caribbean islands were separated into seven island groups within which we performed fruit–frugivore trait matching to identify orphaned plants (those that lack a biotic disperser). Shown here is the fruit size distribution (as obtained from our measured fruits) within each island group and the percentage of orphaned species when all extant frugivores are considered as potential dispersers (solid pink line) vs. when currently threatened frugivores are considered to be functionally extinct (solid blue line). Frugivore silhouettes above each line represent the largest potential disperser in each island group under each of the two scenarios. Puerto Rico has the largest percentage of orphaned plant species due to lack of extant native iguanas, which were found to have the largest gape size on all other island groups. If these rare iguanas are considered functionally extinct, then the percentage of orphaned plants on all island groups, except Cuba which has a large frugivorous anole, converges at ~20% with birds as their largest functioning frugivores.

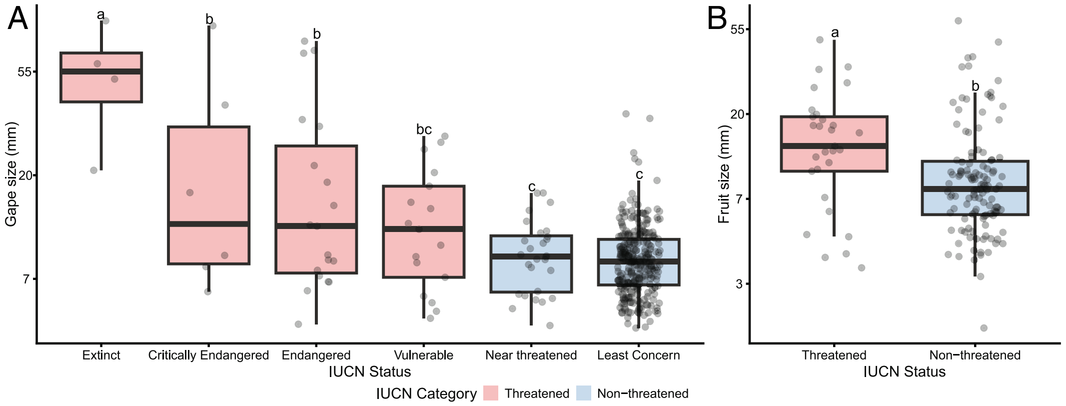

Fig. 3. (*A*) Boxplots comparing gape size of frugivores in each of the IUCN threat categories; letters denote significance grouping based on Tukey tests. Gape size varies significantly between threat categories ($F_{5,327} = 22.1$; $P < 0.0001$), with progressively larger species in higher threat categories. (*B*) Boxplots comparing fruit size of measured species in Threatened and Nonthreatened IUCN categories. Threatened species had significantly larger fruits than nonthreatened species ($t_{234} = -3.86$; $P = 0.0001$). Both gape and fruit sizes were log-transformed to meet assumptions of parametric statistics.

due to lack of extant rock iguanas. Contrastingly, Cuba and the Virgin Islands have no orphaned species, while remaining island groups have few orphaned species (Fig. 2). A Fisher's Exact Test revealed that orphaned plants were more likely to be threatened than nonorphaned plants (n = 229 species; $P < 0.0001$; Fig. 4*A*), with 82% of orphaned plants being threatened compared with only 18% of nonorphaned plants. A Bayesian phylogenetic logistic regression also found a strong effect of a plant's dispersal status on its probability of being threatened (n = 229 species; $\beta_{\text{Orphan}} = 2.57$; 95% CI: 1.26 to 3.93). We again found good model convergence as indicated by R-hat values and posterior diagnostic plots (*SI Appendix*, Fig. S2). In addition, we calculated a latent-scale phylogenetic intraclass correlation coefficient (ICC), which represents the proportion of variance that is explained by the phylogenetic signal. The ICC indicated no strong phylogenetic effect on a plants' conservation status (mean ICC = 0.005). This suggests that conservation risk is not phylogenetically clustered and the higher conservation concern for large-fruited plants is likely related to the absence of large frugivores able to consume and disperse their seeds. If currently Threatened frugivores are considered functionally extinct, as suggested during the field observations in the Virgin Islands, during which only a single frugivory interaction was documented by an endangered Anegada Rock Iguana, then the number of orphaned plant species increases fourfold (Figs. 2 and 4*B*). With this much larger sample size of orphaned plants, the higher probability of orphaned plants being in a Threatened IUCN category remains consistent (n = 234; $P = 0.04$; Fig. 4*B*). After a phylogenetic correction (Bayesian phylogenetic logistic regression), this effect fell just below the level of significance (n = 235; $\beta_{\text{Orphan}} = 0.88$; 95% CI: −0.01 to 1.76; ICC = 0.006). We assessed the sensitivity of our findings by repeating our analyses using different frugivore gape size cutoffs (upper 90% and 97.5% CI) and sources for plant conservation status; we found our results remained consistent across all scenarios (*SI Appendix*, Fig. S6).

Thus, elevated plant extinction risk can only be confidently identified for those with extinct dispersers, although there is some indication for elevated risk among plants with currently Threatened frugivores as well. This is highly concerning given that the set of orphaned plant species expands fourfold if currently Threatened frugivores are no longer able to perform their seed dispersal services. To rule out other sources of anthropogenic threat to plants' conservation status, we separately evaluated the relationship between fruit size and both wood density (as a proxy for desirability in timber products) and overall human use. We found no significant relationship between fruit size and either wood density or human use (*SI Appendix*, Figs. S3 and S4), leaving absence of large frugivores as the leading potential cause of Caribbean plants' elevated extinction risk.

Discussion

Frugivore losses have been hypothesized to explain plant declines on oceanic islands (36–38). Our work identifies seed dispersal limitations of large-fruited plants in the Virgin Islands through field observations, from which we expanded to predict the influence of large-bodied frugivore extinctions on the endangerment of large-fruited plants across the Caribbean archipelagos. We found that gape and fruit sizes of threatened Caribbean species are significantly larger than those of nonthreatened species. We also found that plant species currently lacking a biotic disperser are more likely to be classified as Threatened by the IUCN. This finding suggests that loss of large-bodied frugivores and their corresponding functional diversity has cascading negative effects on the plant species dependent upon them. Changes in frugivore functional traits due to species losses can have detrimental effects on mutualistic partners, as the maintenance of these beneficial relationships is dependent on existing functional diversity (39–42). Therefore, we argue that the protection and restoration of threatened large-bodied frugivores is critical for the conservation of large-fruited plants.

Large vertebrates and the ecosystem functions they provide are at increased risk from anthropogenic threats, a pattern particularly prominent in insular systems (6, 43–45). Our work in the Virgin Islands found strong evidence that large-fruited plants (>16.4 mm) are effectively orphaned, with no extant frugivores providing seed dispersal services for these species. Such findings have significant implications for long-term persistence of these plant species (46, 47). In fact, we already observed negative effects on the conservation status of similarly orphaned large-fruited plants across the Caribbean islands. Furthermore, all interactions observed in the Virgin Islands were carried out by native frugivores, suggesting that exotic species introduced in these islands (e.g., Green Iguana, *Iguana iguana*) are not currently playing a prominent disperser role, likely because they tend to be associated with anthropogenic habitats where they are less likely to encounter native plants (48). In addition, associated traits of exotic frugivores in the Caribbean are smaller in size than those of historic frugivore assemblages (28), a pattern consistent with other insular systems (6, 42). For example, despite being introduced across many of the Caribbean

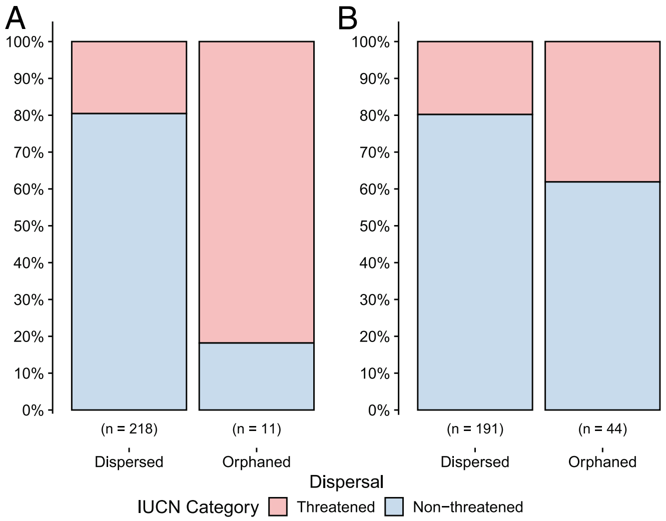

Fig. 4. (*A*) Mosaic plots demonstrating that the probability of being Threatened is fourfold higher among orphaned plant species than nonorphaned plant species ($P < 0.0001$). (*B*) Number of orphaned plant species increases fourfold when currently Threatened frugivores are considered functionally extinct. Elevated extinction risk among this larger set of potential orphans cannot be definitely concluded as the associated test falls just below significance after phylogenetic correction.

islands, the Green Iguana has a gape size 1.25 times smaller than our smallest measured rock iguana species (*Cyclura carinata*).

Although there is strong evidence showing how the removal of larger fauna can negatively affect seed dispersal interactions (49, 50), few studies have assessed the conservation impact on plants. Research suggests that declines of large Caribbean frugivores started with the arrival of native cultures and that a second larger extinction wave occurred after European colonization (33, 51). For example, rock iguanas in Puerto Rico seem to have been extirpated before European arrival (52, 53), while other frugivores such as the White-necked Crow persisted until the 1960s (35). Thus, the time interval in which large-fruited plants have experienced seed dispersal limitations varies from several centuries to the last 60 y. While extinction risk was not significantly elevated for plants with currently endangered, but still extant, frugivores, there is reason to expect that these large-fruited plants are next in line to suffer from frugivore defaunation, and thus it is alarming that the extinction of this group would increase the number of orphaned plants fourfold. While there is likely a time lag between loss of frugivores and plant declines due to the long lifespan of the latter, we could expect the conservation status of these imminent orphans to be negatively affected within the coming centuries.

Frugivore losses have been hypothesized to explain plant declines on other islands. For instance, population declines have been observed in the donne' sali chili (*Capsicum frutescens*) following frugivore extinctions in Guam (38), while lemur extinctions have led to local extirpations of the large-fruited plant *Eligmocarpus cynometroides* in Madagascar (37). Our study found that fruit size was not associated with other forms of anthropogenic threat, such as high wood density that would lead to harvesting for timber, or other forms of human usage. We therefore argue that lack of alternative explanations, derived from correlations across the Caribbean, combined with the clear dispersal limitation experienced by large-fruited plants, indicates that lack of large-bodied frugivores may be the mechanism leading to heightened threat status among large-fruited plants in the Caribbean.

While this study does not consider alternative sources of seed dispersal (e.g., stomatochory—dispersal in which seeds are carried externally by frugivores, hydrochory—dispersal facilitated by water), it is possible that some of the plant species considered here benefit from such means of dispersal. For example, while the large-fruited plant *Andira inermis* is classified as orphaned based on the gape sizes of co-occurring frugivores, it has been documented that the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*) can disperse this species via stomatochory (54). Similarly, *Annona glabra,* which is also classified as orphaned, is known to be dispersed by hydrochory (55). Both of these plant species are classified as Least Concern under IUCN and seem to be unaffected by lack of endozoochory by extant frugivores. However, our findings suggest that these alternative means of dispersal are insufficient to maintain most large-fruited plants, as the majority of the remaining orphaned species have already been assigned elevated threat statuses.

Our data also suggest that current methods may underestimate the true threat status of native Caribbean plants, as it is possible that species' global IUCN classification may be masking regional biodiversity losses (i.e., a species may be common on one island group and thus assessed as Least Concern even though it has been extirpated from other island groups where it once occurred). For example, 21% of plants in our dataset are threatened according to their IUCN global assessments, while regional assessments of the conservation status of plants in the Lesser Antilles, Cuba, and Puerto Rico report 70%, 50%, and 33% of their species, respectively, to be under some level of threat (56–58). Although these higher estimates are not specific to large-fruited plants, they highlight that the threat status of orphaned species might locally be more extreme than what we report here, especially considering the high number of Caribbean species with Unknown conservation status. The estimate of 21% of Caribbean plants being threatened does not include species whose extinction risk has not been assessed by IUCN, which comprise 42% of the plants in our dataset. Given that the Caribbean is considered a biodiversity hotspot with 72% plant endemism (59), it is essential to prioritize the conservation of plants within this region (60). Expansion of protected areas is one way forward and is ongoing, but more focus should be placed on ensuring the future coexistence of plants and their mutualists throughout the Caribbean biodiversity hotspot, for instance by habitat restoration and through species reintroductions or by introducing taxon substitutes of extirpated frugivores (25, 61, 62).

Species conservation, beyond the direct action of preserving species in their natural environment, also provides indirect benefits through the conservation of ecological interactions and improved ecosystem function. We argue that, beyond conservation efforts to preserve frugivores in the areas where they currently exist, conservation plans should also focus on restoring the ecological interactions they provide by reintroducing them to parts of their former range. Some successful examples of species reintroductions include the increase in extant populations of the Critically Endangered Puerto Rican Parrot (*Amazona vittata*) and the establishment of additional populations of the Anegada Rock Iguana in Guana and Necker islands (63). Continued conservation of these threatened frugivores should also positively impact the conservation of large-fruited Caribbean plants by restoring lost seed dispersal interactions. Direct monitoring of the reestablishment of lost plant interactions is an important way to quantify the effectiveness of frugivore reintroductions, as has been documented with increased germination and dispersal of ebony seeds (*Diospyros egrettarum*) following the introduction of Aldabra Giant Tortoises (*Aldabrachelys gigantea*) to Ile aux Aigrettes, a small island off Mauritius (64). Many current plant conservation plans focus on establishing additional populations through direct planting without subsequent monitoring for vital information like germination success, population structure, spatial distribution, and genetic connectivity. The need for such monitoring is demonstrated by current assessments of the orphaned cobana negra (*Libidibia monosperma*) and matabuey (*Goetzea elegans*). Both species are threatened endemics for which little to no recruitment has been identified in existing populations of the species, along with clustered spatial distribution of seedlings, and even local extinctions (65, 66)—most likely caused by eroded frugivore communities. We warn that without monitoring and restoration of frugivore populations, the continued persistence of many large-fruited orphaned plant species in the Caribbean, and most likely across oceanic islands in general, remains uncertain.

Methodology

Frugivory Observations in the Field. To determine if large-fruited plants experience less seed dispersal by extant frugivore species than small-fruited plants, we conducted observations of frugivores visiting focal trees on seven defaunated islands in the Caribbean where large-bodied frugivores have been extirpated or exist at very low densities. Specifically, we sampled the U.S. Virgin Islands (St. Thomas, St. John, and St. Croix) and Vieques and Culebra during June-July 2022, and a subset of the British Virgin Islands (Tortola and Anegada) during June 2023. These months encompass the typical wet season for this region and the peak of fruiting. Observations of frugivory interactions were conducted during the day in natural protected areas within each island and consisted of observing a focal fruiting individual for 30 min, repeated for up to 10 individuals of each species; 30-min focal observations were also conducted opportunistically outside of protected areas when fruiting plants were observed. Given that species cannot be considered statistically independent due to shared ancestry, we employed a Bayesian phylogenetic logistic regression, with fruit size as the predictor and seed removal (removed/not removed) as the response (*SI Appendix*). Seed removal was modeled using the Bernoulli family and uninformative priors, and fruit size was standardized. Based on the phylogenetic logistic regression, we identified the inflection point (fruit size) at which the probable outcome changed from primarily dispersed seeds to primarily nondispersed seeds. Specifically, we estimated the inflection point by dividing the intercept by the slope parameter, using the means of their posterior distributions. We then compared this fruit size with the gape size of the largest common (non-Threatened) frugivore documented in our frugivory interactions and identified that the size of the largest fruits likely to be dispersed matched the upper 95% CI of the gape size distribution of this largest frugivore. We then utilized this as a rule to infer which plant species experience seed dispersal across the Caribbean ("*Plant and Frugivore Interactions and Conservation Status*" section below).

Frugivore and Fruit Functional Traits. We compiled a list of frugivores (reptiles, mammals, birds) and fleshy-fruited plant species within the Caribbean from Kim et al. (29). Additionally, we collected data on each species' risk categorization under the International Union for Conservation of Nature (IUCN) Red List, and the species' occurrence across the Caribbean. Overall, the conservation status of 42% of our measured plants had not been assessed by IUCN (*SI Appendix*, Table S1). Given the high number of plants with Unknown conservation status, we used the model from Bachman et al. (67) to obtain estimated conservation status for additional species based on their endemicity, human related threats, preferred climate, and evolutionary history, reducing the species ultimately classified as Unknown to only 6% (*SI Appendix*, Table S1).

We then measured gape size and fruit width of species present in the compiled dataset. We collected data on gape size from museum specimens at the Florida Museum of Natural History in Gainesville, Florida, and the Ornithology collection in the Department of Biology of the University of Puerto Rico in Mayagüez, Puerto Rico. For fleshy-fruited plants, we measured fruits collected from botanical collections in Florida, Puerto Rico, and the Virgin Islands. Fruits were also collected from wild individuals across the Lesser Antilles, Puerto Rico, and the Virgin Islands. Overall, our dataset includes representation of 94% and 68% of native frugivore and fleshy-fruited plant families, respectively. To determine if gape size was related to frugivore species' risk status, we utilized ANOVA with post hoc Tukey tests to determine which IUCN categories differed significantly in log-transformed gape size. To determine if fruit size significantly differs between Threatened and Non-threatened plants, we performed a two-sample *t* test comparing log-transformed mean fruit size between the two groups.

Plant–Frugivore Interactions and Conservation Status. We subsetted our dataset to develop occurrence datasets of native frugivores and plants within each of the following island groups: Bahamas and Turks and Caicos (Lucayan archipelago), Cuba and Cayman Islands, Jamaica, Hispaniola, Puerto Rico, Virgin Islands (U.S. and British), and the Lesser Antilles (*SI Appendix*, Table S2). Using our field observations in the Virgin Islands as a guide, we identified the largest (based on gape size) frugivore with which each plant species co-occurred (*SI Appendix*, Table S3) within each of the island groups and compared its mean fruit width with the upper 95% CI of the gape size distribution for this largest frugivore, as calculated using a t-based approach. Plant species whose mean fruit size was below that of the upper 95% CI for gape size distribution of the largest co-occurring frugivore would be dispersed, while any plant species with mean fruit size above this cutoff were orphaned. For plant species that occur across multiple island groups, we used their modal dispersal classification (orphaned vs. dispersed) when assessing the overall relationship between threat status and dispersal classification. We performed this analysis twice, first including all extant frugivores, and second including only nonthreatened frugivores under the assumption that frugivores with a Threatened IUCN status may soon go extinct (68) and/or may already be functionally extinct. For each analysis, we constructed a contingency table comparing the number of orphaned and dispersed plant species in each of the IUCN categories. For ease of interpretation, we grouped all Critically Endangered, Endangered, and Vulnerable species as Threatened species, while Least Concern and Near Threatened species were classified as Nonthreatened. Plant species with "Unknown" conservation status were excluded from analysis. We determined whether there was a relationship between threat categorization and orphan vs. dispersed status using Fisher's exact tests in R (69).

To account for phylogenetic effects on the plants' predicted dispersal status, we used package "brms" (70) to fit a phylogenetic logistic regression under a Bayesian framework, using dispersal status (orphaned/dispersed) as the predictor, conservation status (threatened/nonthreatened) as the response variable, and plant phylogeny as a random effect. Conservation status was modeled using the Bernoulli family and uninformative priors. We used package "ape" (71) to generate a phylogenetic variance–covariance matrix from a plant phylogeny built with package "V.PhyloMaker2" (72). Last, we computed a latent-scale phylogenetic intraclass correlation coefficient (ICC) to assess how much of the model variance was explained by phylogeny. This metric is obtained by dividing the variance explained by the phylogenetic random effect by the total variance. In addition to the approach explained above, we conducted a sensitivity analysis to explore how the relationship between plant dispersal and conservation status might change with varying thresholds for identifying orphaned species and sources of classification of plant conservation status (*SI Appendix*). To account for uncertainty in the estimated threat categories by Bachman et al. (67), we conducted additional sensitivity analyses by repeating our models using only species with official IUCN threat assessments. As the results remained consistent, we present the outcomes obtained using the results obtained from using Bachman et al. (67), while the results obtained from only using IUCN assessments are included in the *SI Appendix*.

To account for additional sources of threat related to anthropogenic use, we also evaluated independent phylogenetically corrected models considering fruit size as a predictor and wood density and human use as response variables (*SI Appendix*).

Data, Materials, and Software Availability. Datasets and code data used in this study are available at ref. 73. Other data are included in the article and/or *SI Appendix*.

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Author affiliations: [a]Department of Biology, University of Miami, Coral Gables, FL 33146; [b]Fideicomiso de Conservación de Puerto Rico, Para La Naturaleza, San Juan 00927, Puerto Rico; [c]Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, Copenhagen 1350, Denmark; [d]Instituto Mediterráneo de Estudios Avanzados, Esporles, Mallorca, Balearic Islands 07190, Spain; [e]Ecology and Evolution, School of Biosciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; [f]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich 8057, Switzerland; [g]Centre for Ecology and Conservation, Faculty of the Environment, Science and Economy, University of Exeter, Cornwall Campus, Penryn TR10 9FE, United Kingdom; and [h]Departamento de Biodiversidade, Centro em Pesquisa em Biodiversidade e Mudanças no Clima, Universidade Estadual Paulista, Rio Claro, SP 13506-900, Brazil

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