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RESEARCH ARTICLE

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Plant–frugivore interactions across the Caribbean islands: Modularity, invader complexes and the importance of generalist species

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Abstract

Aim: Mutualistic interactions between plants and animals are fundamental for the maintenance of natural communities and the ecosystem services they provide. However, particularly in human-dominated island ecosystems, introduced species may alter mutualistic interactions. Based on an extensive dataset of plant–frugivore interactions, we mapped and analysed a meta-network across the Caribbean archipelago. Specifically, we searched for subcommunity structure (modularity) and identified the types of species facilitating the integration of introduced species in the Caribbean meta-network.

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Location: Caribbean archipelago (Lucayan archipelago, Greater Antilles, Lesser Antilles).

Methods: We reviewed published scientific literature, unpublished theses and other nonpeer-reviewed sources to compile an extensive dataset of plant–frugivore interactions. We visualized spatial patterns and conducted a modularity analysis of the cross-island meta-network. We also examined which species were most likely to interact with introduced species: (1) endemic, nonendemic native or introduced species, and (2) generalized or specialized species.

Results: We reported 3060 records of interactions between 486 plant and 178 frugivore species. The Caribbean meta-network was organized in 13 modules, driven by a combination of functional or taxonomic (modules dominated by certain groups of frugivores) and biogeographical (island-specific modules) mechanisms. Few introduced species or interaction pairs were shared across islands, suggesting little homogenization of the plant–frugivore meta-network at the regional scale. However, we found evidence of "invader complexes," as introduced frugivores were more likely to interact with introduced plants than expected at random. Moreover, we found generalist species more likely to interact with introduced species than were specialized species.

Main conclusions: These results demonstrate that generalist species and "invader complexes" may facilitate the incorporation of introduced species into plant–frugivore communities. Despite the influx of introduced species, the meta-network was structured into modules related to biogeographical and functional or taxonomic affinities. These findings reveal how introduced species become an integral part of mutualistic systems on tropical islands.

KEYWORDS

Antilles, biotic interactions, frugivory, introduced species, invader complex, island ecosystems, species networks, West Indies

1 | INTRODUCTION

Mutualistic interactions between plants and animals, such as pollinators and frugivores, are critically important for maintaining the functionality of natural communities (Jordano, 1987;Ollerton et al., 2011; Rech et al., 2016). While most flowering plants are dependent on animals for pollination and seed-set (Ollerton et al., 2011; Rech et al., 2016), animal frugivores may ingest or otherwise manipulate and consequently disperse millions of seeds annually (Bueno et al., 2013). Frugivory is thereby crucial for the maintenance of plant diversity (Harms et al., 2000), as it allows plants to populate new sites, maintains gene flow between distinct populations and decreases density-dependent mortality in proximity of the parent individuals (Rogers et al., 2021). In some tropical systems, approximately 90% of all woody plants depend on frugivores for seed dispersal (Almeida-Neto et al., 2008; Howe & Smallwood, 1982). In addition to providing direct dispersal to specific, favourable sites for the plant (Wenny & Levey, 1998), frugivores can enhance the probability of successful germination, for example through the passage of seeds in the intestinal system (e.g. Traveset et al., 2001). The most important frugivore groups are birds, mammals and reptiles with birds and reptiles being particularly important in tropical island ecosystems (Kaiser-Bunbury et al., 2010; Valido & Olesen, 2007).

Globally, co-evolved plant–frugivore communities are suffering from an array of drivers associated with global change, such as the introduction of species into new environments, where they become integrated into local communities through species interactions (Gallardo et al., 2016; Vilà et al., 2011). Species communities are thus being altered, which in turn may have consequences for biotic interactions and ecosystem functions, such as seed dispersal (Aslan et al., 2013; Lugo et al., 2012; Traveset & Richardson, 2006; Vizentin-Bugoni et al., 2021). Island ecosystems are particularly vulnerable to the disruption of native plant–frugivore interactions as island mutualists have evolved in isolation, and frequently developed specific traits, such as altered dispersal, or loss of defence traits in plants (Burns, 2019). Furthermore, as islands harbour many endemic species found nowhere else on Earth (Kier et al., 2009; Paulay, 1994), and have experienced disproportionally high

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extinction rates and numerous extant island species are threatened with extinctions (Blackburn et al., 2004; Fernández-Palacios et al., 2021; Groombridge, 1992), it is especially important to understand how introduced species integrate into island communities (Wood et al., 2017).

Introduced species may integrate into existing communities and establish themselves in different ways. For instance, the concept of "invader complexes" suggests that introduced species facilitate the establishment of other introduced species, resulting in groups of introduced species interacting strongly with each other and less with the remaining community (D'Antonio & Dudley, 1993). Alternatively, endemic species that have become superabundant and highly generalized species due to ecological release and density compensation may readily include new arrivals into their interactions and thereby facilitate the establishment of introduced species on islands (Olesen et al., 2002). Furthermore, a growing number of studies show that species with many mutualistic partners (i.e. generalized species irrespectively of being nonendemic native or endemic) are more likely to incorporate new partners into their networks (Bascompte & Stouffer, 2009; Maruyama et al., 2016). In network theory, this is called "preferential attachment" (Newman, 2001), and thus, most generalized species would be expected to interact with introduced species.

In addition to understanding which species are responsible for incorporating introduced species into native communities, we have little quantitative understanding of how introduced species affect the structure of native interaction networks and how this varies biogeographically (Fricke & Svenning, 2020). As for other mutualistic networks, plants and frugivores form complex interaction networks with reccurring structural properties (Bascompte & Jordano, 2007). One such property of interaction networks is modularity, which describes how interacting species aggregate into modules consisting of species that interact strongly within the respective module but much less with species of other modules (Thébault, 2013). The modular structure of mutualistic networks may reflect "co-evolutionary units" (Olesen et al., 2007) determined by an array of factors, such as phenological overlap, morphological traits, taxonomic relatedness and biogeography (Araujo et al., 2018; Dalsgaard et al., 2013; Donatti et al., 2011; Martín González et al., 2018; Maruyama et al., 2014; Schleuning et al., 2014). However, it is poorly understood whether introduced species influence the modular structure of mutualistic systems.

Here, we present an extensive dataset on plant–frugivore interactions compiled from published and unpublished resources across the islands of the Caribbean archipelago: Lucayan archipelago, Greater Antilles and Lesser Antilles. We use the data to (i) explore the distribution of frugivory records across the Caribbean islands; (ii) assess island connectivity through shared species and interactions; (iii) evaluate the modular structure of the regional plant–frugivore meta-network and (iv) determine whether generalized vs. specialized species and introduced vs. endemic species are more likely to integrate introduced plants and frugivores into native plant–frugivore communities in island systems.

2 | METHODS

2.1 | Data collection and study region

All our data were collected on the Caribbean islands, that is the Lucayan archipelago (The Bahamas and Turks and Caicos), the Greater Antilles (Cuba, Cayman Islands, Jamaica, Hispaniola and Puerto Rico) and the Lesser Antilles (a series of islands from the US and British Virgin Islands in the north to Grenada in the south). We did not include plant–frugivore interactions from islands such as Trinidad and Tobago, Curaçao, and Bonaire just north of South America, as these are continental islands with biotas with strong affinities to the South American mainland (Carstensen et al., 2012; Ricklefs & Bermingham, 2008). The low-lying sedimentary islands of the Lucayan Archipelago are part of the North American platform (Iturralde-Vinent & MacPhee, 1999; Trejo-Torres & Ackerman, 2001), and some of the islands have been interconnected in the Pleistocene (Murphy et al., 2004; Trejo-Torres & Ackerman, 2001). The mostly large and mountainous islands of the Greater Antilles are old with different geological origins (Graham, 2003; Iturralde-Vinent & MacPhee, 1999). The Greater Antilles emerged as fragments in the Eocene about 49 Ma; the geological history of the region has been highly dynamic with some parts connected in the past (Buskirk, 1985; Graham, 2003; Iturralde-Vinent & MacPhee, 1999; Ricklefs & Bermingham, 2008). The current biota of the Greater Antilles was only in small parts formed by vicariance, with dispersal facilitated by the Aves Ridge about 32–35 Ma (Iturralde-Vinent & MacPhee, 1999) or a more likely overwater dispersal at least for the avifauna (Buskirk, 1985; Graham, 2003; Ricklefs & Bermingham, 2008). The Lesser Antilles form a volcanic arc where the North and South American plates subduct under the Caribbean plate and likely originated at least 20 Ma (Ricklefs & Bermingham, 2008). To the east of the volcanic arc are some younger and low-lying islands such as Antigua and Barbuda, which consist of uplifted marine sediments (Ricklefs & Bermingham, 2008; Ricklefs & Lovette, 1999). Some islands were interconnected during the last glacial maximum, but most Lesser Antilles islands have never been interconnected (Ricklefs & Bermingham, 2004, 2008). The isolation of the Caribbean islands from the mainland differs greatly (Carstensen et al., 2012). Bimini in the Bahamas, for instance, is only approx. 87 km from the North American continent and Grenada in the Lesser Antilles is only 137 km from the continental landmass of South America. By contrast, islands such as Grand Turk (993 km) and South Caicos (999 km) are much more isolated from the mainland. On average, the isolation from any continental landmass in the Caribbean is over 500 km (Mean: 593 km ± 248 km SD; see details in Supporting Information Table S1). The distances between single islands are much smaller, for example the distance between Martinique and Dominica and Martinique and Saint Lucia is approx. 40 km. An island size threshold of 10,000 km^2 has previously been suggested to be important for islands to be considered sources for colonization (Weigelt & Kreft, 2013), and on average, the islands of the Caribbean are approx. 304 km (±174 km *SD*) from the nearest island that exceeds 10,000 km^2 (Table S1). Given

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the geological history and isolation of the Caribbean, the biota is characterized by being depauperate with high levels of endemism.

To collect data on interactions between plants and frugivores in the Caribbean, we screened the *Web of Science* (WoS) and *Google Scholar* search engines. We used the combination of the following search terms: ("frugivory" OR "seed dispersal" OR "seed removal" OR "mutualism") AND ("Caribbean" OR "Lesser Antilles" OR "Greater Antilles" OR "West Indies" OR "Bahamas" OR "Turks and Caicos" OR "Cayman Islands" OR "Jamaica" OR "Cuba" OR "Hispaniola" OR "Haiti" OR "Dominican Republic" OR "República Dominicana" OR "Puerto Rico" OR "Mona" OR "Virgin Islands" OR "Saint Martin" OR "Anguilla" OR "St. Kitts and Nevis" OR "Antigua" OR "Barbuda" OR "Montserrat" OR "Guadeloupe" OR "Dominica" OR "Martinique" OR "St. Lucia" OR "St. Vincent" OR "Grenadines" OR "Barbados" OR "Grenada"). To also include the grey literature, we contacted local ornithologists and ecologists working in the Caribbean region. This approach allowed us to obtain non-English publications, such as theses and dissertations not available online. We screened each of the studies manually, discarding studies where no appropriate data were presented (e.g. mutualistic interactions in marine environments). Interactions were only included when the respective authors presented original evidence for interaction events, that is evidence of fruits and/or seeds being ingested by frugivores. Thus, we discarded records where interactions between species were speculative (e.g. observation of frugivores on fruiting plant species without any evidence of fruit ingestion).

We standardized the species names of plants and frugivores using the R-package *taxize* (Chamberlain & Szocs, 2013; Global Names Resolver, 2021) and data from the Integrated Taxonomic Information System (ITIS, 2021). We also retrieved information about species taxonomies (i.e. class, order and family) from ITIS. Finally, we compiled information about the native status of species and classified them into nonendemic native (species native to the Caribbean, but also naturally occurring elsewhere), endemic (only occurring within the Caribbean) and introduced (not naturally occurring within Caribbean) species (see details in Supporting Information Text S1). Of the original records, 95 plant (approx. 16% of all reported plants) and one frugivore record were not identified to species level (e.g. only genus name reported) and were thus excluded from data analyses. The final data used in statistical analyses consisted of interactions between 486 plant and 178 frugivore species.

2.2 | Data analysis

2.2.1 | Cross-island patterns of shared species and interactions

We summarized patterns of shared species and interaction pairs across the Caribbean by calculating the proportion of shared species and interaction pairs across all islands. We calculated this proportion as the number of species/interaction pairs found on any two islands, divided by the total number of species/interaction pairs found on the given islands (Fricke & Svenning, 2020). We summarized these patterns separately for all reported records, for endemic, nonendemic native and for introduced plant and frugivore species and interaction pairs, respectively.

2.2.2 | Modularity of the Caribbean plant–frugivore meta-network

To detect a modular structure of the meta-network, that is the network of plant–frugivore interactions across all islands, we employed Beckett's DIRT-LPA algorithm in the *computeModules* function of the R-package "bipartite" (Dormann et al., 2008, 2009). We ran 10 independent runs of the algorithm on the binary meta-network containing interactions between all identified species and identified the run with the single best division into modules, that is the highest degree of modularity *Q*. For the run with the highest *Q* value, we recorded the *Q* value, the number of modules as well as the respective plant and frugivore species in each module (Schleuning et al., 2014) and the islands on which they were recorded. To test whether the identified modular structure of the meta-network differed from random, we compared our results to 100 null models. To this end, we used an algorithm proposed by Patefield (1981) to randomize the interactions between species, using fixed marginal totals to produce networks with randomly associated species without constraining the degree of specialization (Blüthgen et al., 2008; Schleuning et al., 2014). For each of the null models, we applied the same approach as with the original matrix, that is we identified the single best configuration from 10 independent runs (Schleuning et al., 2014). We then tested whether modularity of the original matrix was significantly different from the best 100 null models by looking at the proportion of null modularity values that were greater than the empirical one, that is if <5% of the null modularity values were greater than the empirical modularity, we concluded that the meta-network was significantly modular.

2.2.3 | Interaction with introduced species

We performed a series of tests to investigate how introduced species are integrated into insular plant–frugivore communities, that is which species the introduced species are most likely to interact with and whether that differs from random expectations provided by the pool of potential interaction partners. First, we identified the origins of interaction partners and classified them as endemic, nonendemic native and introduced, and tested whether these groups of species interacted more or less than expected at random. As the chances of a frugivore to interact with a certain plant vary from species that are exclusive from one (or few islands) to those that are present in many islands, we took species occurrence into account when examining this. For instance, we identified the islands where endemic plants were reported, and within this set of islands, we identified those islands with endemic frugivores. Across the resulting subset of islands,

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we calculated the expected proportion of interactions of endemic plants with endemic frugivores as the mean proportion of endemic frugivores in relation to the total pool of unique frugivore species available. The proportion of observed interactions between endemic plants and endemic frugivores should be similar to the proportion of endemic frugivore species in the pool of species. For example, if 40% of all potential interaction partners for endemic plants are endemic frugivores, then—if species interact at random—the proportion of reported interactions with this category of frugivores should similarly amount to 40%. To test this, we calculated the mean proportion of observed interactions between endemic plants and endemic frugivores across the islands where endemic species co-occurred in our data. We used a Chi-square test to test whether observed and expected number of interactions differed significantly. We performed the same approach for all possible combinations of interaction pairs between species of different origins (i.e. endemic, nonendemic native and introduced).

We also tested whether generalization level of species mattered for their interaction with introduced species, testing (1) whether generalized species were more likely to interact with introduced species and (2) whether generalized species were more likely to have a higher proportion of interactions with introduced species in their total set of interactions. To examine this, we first excluded all introduced species and constructed a meta-network based only on interactions reported between nonendemic native and endemic species. From this meta-network without the introduced species, we calculated the species degree for all nonendemic native and endemic plant and frugivore species using the R-package "bipartite" (Dormann et al., 2008, 2009). For each nonendemic native and endemic species, we then determined whether (1) or not (0) they interacted with introduced species by consulting the original meta-network containing also the introduced species. Likewise, for each nonendemic native and endemic species, we calculated the proportion of their interactions with introduced species in the original meta-network. We then fitted two generalized linear models with binomial error distribution with species degree as the predictor variable and (1) the probability of interacting with introduced species or (2) the proportion of the total set of interactions with introduced species as response variables, using the function *glm* (R Core Team, 2021).

All analyses were carried out in R version 4.1.0 (R Core Team, 2021).

3 | RESULTS

We retrieved a total of 3060 records of frugivory from a total of 581 plants and 179 frugivore observations, of which 486 plant and 178 frugivore records were identified to species level, respectively (see Supporting Information Tables S2 and S3 for detailed overview). Most plant and frugivore records were from the large islands of the Greater Antilles (Figure 1a). Puerto Rico was particularly well represented as approximately 50% of the entire species pool of plants and frugivores in the dataset was recorded there (247 plant species, 69 frugivore species; Tables S2 and S3). By contrast, the islands of the Lesser Antilles were particularly poorly represented in the dataset, with 63 plant and 24 frugivore species recorded for the entire region (approx. 13% of all plant and frugivore species, respectively; Tables S2 and S3).

Most frugivore species in the data were birds (79% of all frugivore species; Table S3 and Figure 1b). Reptiles were the second largest group of frugivores, with 13% of the species in the data; 8% of frugivores were mammals. Among mammal species, 71% were bats, and the remaining 29% were nonvolant mammals (rodents, primates and carnivores). Most species were either nonendemic native (53% plant and 27% frugivore) or endemic species (29% plant and 65% frugivore; Tables 1 and 2). Few species in the data were classified as introduced by humans (16% plant and 8% frugivore species). Most introduced frugivore species were birds (86%; Table 2), followed by mammals (14%; primates and carnivores). We could not determine the native status of nine plant species (2%).

3.1 | Cross-island patterns of shared species and interactions

All islands included in the study shared either plant or frugivore species and interaction pairs with other islands in the region (Figure S1 and Table S4). Nonendemic native and endemic plants were shared between 85% and 70% of the islands, and frugivores between 85% and 60% of the islands, respectively. Introduced plants were shared between 65% and frugivores between 25% of the islands. Interaction pairs were shared between 40%, 25% and 15% of the islands for nonendemic native, endemic and introduced species, respectively (Figure 2).

The maximum number of islands sharing the same plant species was 16 for nonendemic native (7.94 ± 5.09 Mean $\pm$ *SD*) and 11 for endemic species (4.71 ± 2.52 Mean $\pm$ *SD*). Introduced plant species were shared between a maximum of 10 islands (4.23 ± 2.83 Mean $\pm$ *SD*). The same frugivore species were shared between a maximum of 16 islands for nonendemic native frugivores (7.00 ± 5.28 Mean $\pm$ *SD*) and eight islands for endemic frugivores (4.33 ± 2.69 Mean $\pm$ *SD*). A maximum of four islands (2.00 ± 1.09 Mean $\pm$ *SD*) shared the same introduced frugivore species (see Table S4 for details). Interaction pairs were shared between a maximum of five (2.25 ± 1.39 Mean $\pm$ *SD*), four (2.00 ± 1.09 Mean $\pm$ *SD*) and two islands (1.33 ± 0.47 Mean $\pm$ *SD*), for nonendemic native, endemic and introduced species, respectively (Figure 2 and Table S4).

3.2 | Modularity of the Caribbean plant–frugivore meta-network

The plant–frugivore meta-network was significantly modular; the run with the single highest degree of the modularity index *Q* ($Q = 0.479$; $p < .001$) was divided into 13 modules of different sizes (Figure 3a,b and Table S5). Module size ranged from 9 (eight plants,

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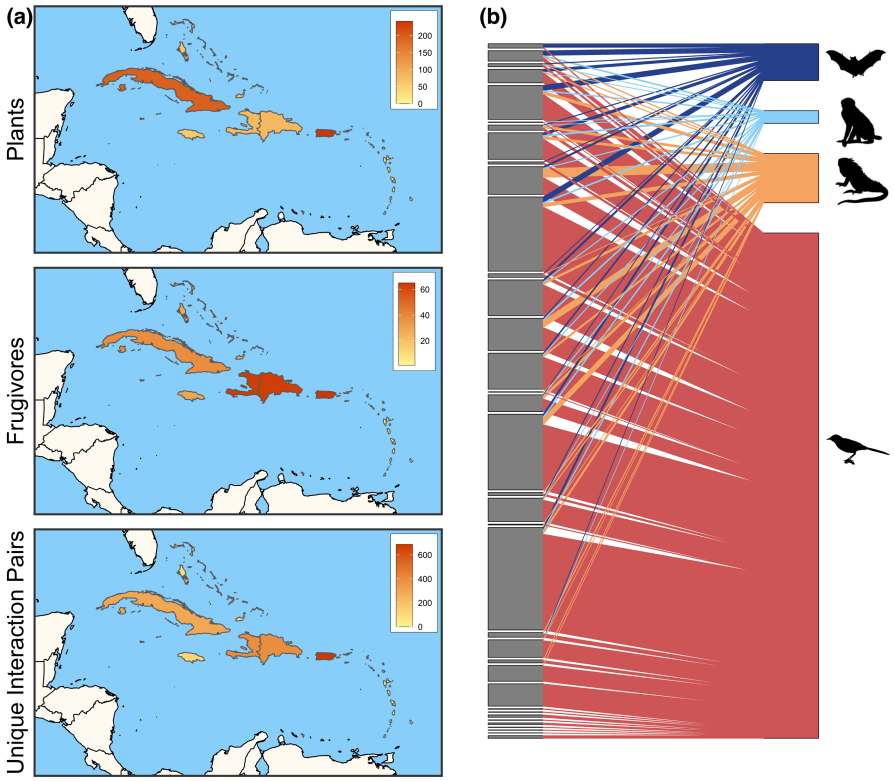

FIGURE 1 The Caribbean archipelago, showing the number of all plant–frugivore observations per island (a) and the plant–frugivore meta-network of the Caribbean (b). Note that observations are shown individually for single islands of the Greater and Lesser Antilles, but not for the Lucayan archipelago. Only fully identified species were included in these figures (compare Supporting Information Tables S2 and S3 for species numbers, see Github for original data). Unique interaction pairs show interactions between specific pairs of frugivore and plant species (a). For illustration purposes in the meta-network (b), plants on the left are grouped by order and frugivores on the right are grouped by class. Each line represents an observation of a frugivore species feeding on a particular plant species. Note that we separated volant bats (Chiroptera) from other, nonvolant mammals (Mammalia). Bats comprised approx. 71% of the mammal species reported in the data. Plants from top to bottom: Piperales, Malvales, Magnoliales, Solanales, Myrtales, Proteales, Brassicales, Zingiberales, Gentianales, Rosales, Poales, Fabales, Caryophyllales, Arecales, Asparagales, Boraginales, Malpighiales, Celastrales, Lamiales, Zygophyllales, Sapindales, Vitales, Laurales, Cucurbitales, Santalales, Apiales, Alismatales, Aquifoliales, Asterales, Liliales, Oxalidales, Picramniales, Pinales, Ranunculales.

one frugivore) to 98 (60 plants, 38 frugivores) species (47.61 ± 20.31 Mean ± *SD*). The separation of the meta-network into modules seemed driven partly by functional or taxonomic mechanisms, that is some modules were dominated by certain species groups such as Iguanas (Figure 3b and Table S5), and biogeographical mechanisms, that is some modules consisted of species recorded on specific islands or island groups (see also Section 4.3 in the Discussion).

3.3 | Interactions with introduced species

Nonendemic native (χ^2 = 47.95, $p < .001$) and endemic plants (χ^2 = 16.65, $p < .001$), respectively, interacted significantly less often with introduced frugivores than expected (Figure 4a,b). Introduced plants interacted with introduced frugivores as expected by the given pool of potential interaction partners, that is the proportion of interactions with introduced species corresponded to the proportion of introduced species in the pool of interaction partners (χ^2 = 0.05, p = .816; Figure 4c). Nonendemic native (χ^2 = 9.17, $p < .01$) and endemic frugivores (χ^2 = 33.14, $p < .001$), respectively, interacted significantly less often with introduced plants than expected (Figure 4a,b). Introduced frugivores interacted significantly more often with introduced plants than expected by the given pool of potential interaction partners (χ^2 = 15.85, $p < .001$; Figure 4c).

Irrespective of the species' native status, we found that generalized species, that is species with a higher degree value (number of partners) were more likely to incorporate introduced species into their interactions. This pattern was consistent from the plant (slope = 0.12, $p < .001$; Figure S2a) and the frugivore perspective (slope = 0.20, $p < .001$; Figure S2b). On the contrary, species with a higher degree did not have a higher proportion of their total set of interaction partners with introduced species than species with a lower degree, that is specialized species. This pattern was consistent both from the plant (slope = −0.006, $p > .05$; Figure S2c) and the frugivore perspective (slope = 0.003, $p > .05$; Figure S2d).

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TABLE 1 The native status of all records of plants observed to have their fruits eaten by a frugivore across the Caribbean archipelago. Shown are the numbers for each island/archipelago for all plants and for each plant class, respectively. Magnoliopsida are the dicotyledonous plants, and Pinopsida include most conifers. Nonendemic native (native to America but not restricted to the Caribbean); endemic to the Caribbean; introduced to the Caribbean; no data. LCA, Lucayan archipelago; C, Cuba; CI, Cayman Islands; H, Hispaniola; J, Jamaica; PR, Puerto Rico; VI, Virgin Islands; LA, Lesser Antilles; all: Total unique species. Note that we have no data about the native status of 104 reported plants, which includes records of species that were not fully identified (17.9% of all reported species)

	Status	LCA	C	CI	H	J	PR	VI	LA	All
All Plants	Nonendemic native	45	120	4	54	38	130	8	33	257
	Endemic	11	40	1	18	11	77	4	12	141
	Introduced	8	38	2	11	15	35	2	17	79
	No data	10	40	2	23	17	26	3	31	104
Magnoliopsida	Nonendemic native	45	120	4	54	38	129	8	33	256
	Endemic	11	40	1	18	11	76	4	12	140
	Introduced	8	38	2	11	15	35	2	17	79
	No data	10	40	2	23	17	26	3	31	104
Pinopsida	Nonendemic native	0	0	0	0	0	0	0	0	0
	Endemic	0	0	0	0	0	1	0	0	1
	Introduced	0	0	0	0	0	0	0	0	0

TABLE 2 The native status of all records of frugivore species across the Caribbean archipelago. Shown are the numbers for each island/archipelago for all frugivores and for each frugivore class, respectively. Nonendemic native (native to America but not restricted to the Caribbean); endemic to the Caribbean; introduced to the Caribbean; no data. LCA, Lucayan archipelago; C, Cuba; CI, Cayman Islands; H, Hispaniola; J, Jamaica; PR, Puerto Rico; VI, Virgin Islands; LA, Lesser Antilles; all: Total unique species. No native status could be determined for one frugivore record, as this record was not identified to species level

	Status	LCA	C	CI	H	J	PR	VI	LA	All
All Frugivores	Nonendemic native	14	15	2	26	10	28	3	5	49
	Endemic	14	24	3	32	30	30	2	16	115
	Introduced	0	0	0	5	1	11	0	3	14
	No data	0	0	0	0	0	1	0	0	1
Aves	Nonendemic native	14	14	2	25	9	26	2	4	47
	Endemic	8	17	3	28	26	18	0	14	81
	Introduced	0	0	0	5	1	10	0	2	12
Reptilia	Nonendemic native	0	0	0	0	0	1	0	0	1
	Endemic	5	1	0	4	4	7	1	1	23
	Introduced	0	0	0	0	0	0	0	0	0
	No data	0	0	0	0	0	1	0	0	1
Mammalia	Nonendemic native	0	1	0	1	1	1	1	1	1
	Endemic	1	6	0	0	0	5	1	1	11
	Introduced	0	0	0	0	0	1	0	1	2

4 | DISCUSSION

Here, we present a comprehensive review of published plant–frugivore interactions across the Caribbean archipelago, including the Lucayan archipelago, the Greater and Lesser Antilles. All islands shared species and unique interaction pairs with neighbouring islands and archipelagos, thereby forming a cohesive meta-network. We show that the meta-network of plant–frugivore interactions across the Caribbean was structured into modules, with at least some modules determined by a combination of functional or taxonomic (i.e. certain groups of frugivores) and biogeographical (i.e. island-specific modules) mechanisms. While relatively few species in the dataset were introduced to the Caribbean (16% plant and 8% frugivore species), we found support for the "invader complexes" theory, whereby introduced species facilitate the establishment of other introduced species (D'Antonio & Dudley, 1993; Olesen et al., 2002). Moreover, we found that generalized species were more likely to incorporate introduced species into their interactions, giving support for the "preferential attachment" theory (Newman, 2001). Below, we

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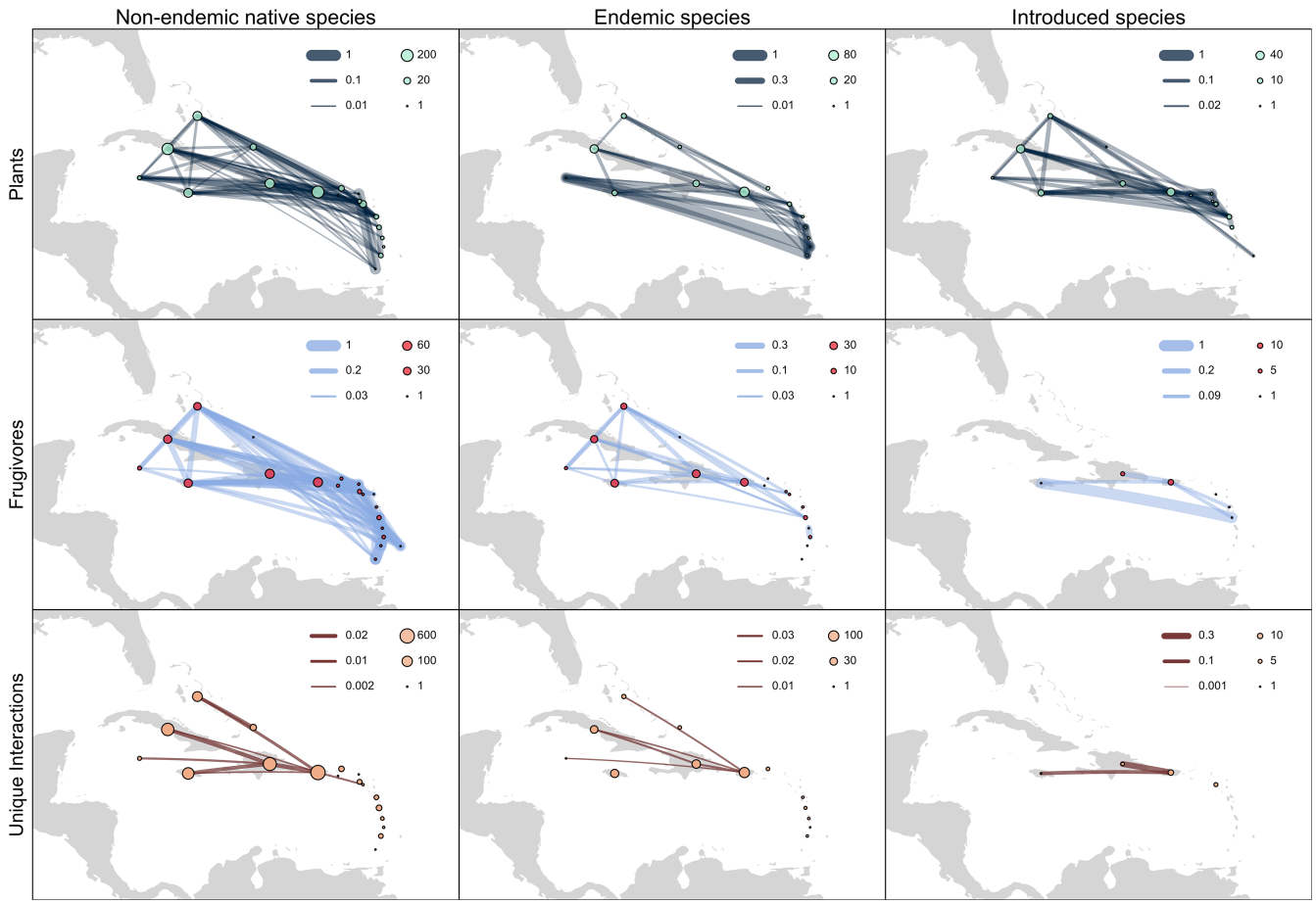

FIGURE 2 Shared species and interactions between the single islands in the Caribbean. The points lie in the centre of the respective islands. The size of the points indicates the number of recorded species or interaction pairs, respectively. The thickness of the lines connecting single islands indicates the proportion of species or interaction pairs, which the respective islands share in their total set of species. Note that the Lucayan archipelago was treated as a single unit, because of the lack of data on most islands. All other islands were shown as single islands. Included are only fully identified species. See Figure S1 for all observations combined.

first discuss the available data on frugivory in the Caribbean, whereafter we discuss how species and interactions are shared across islands. We end by discussing the drivers of modularity and the integration of introduced species into plant–frugivore communities across the Caribbean.

4.1 | Data on frugivores and their plants in the Caribbean archipelago

Across all islands, the vast majority of reported frugivores were birds (79%), followed by reptiles (13%) and mammals (8%), of which in turn the majority were bats (71%). These data thus reflect patterns that are typical for oceanic islands, as there is generally a lack of nonvolant, large-bodied, frugivorous mammals which may be ecologically replaced by birds and reptiles (Kaiser-Bunbury et al., 2010). The low number of mammal species in the dataset could also reflect past mammal extinctions particularly on the islands of the Greater Antilles (Turvey et al., 2021), potentially leaving some plants without their main seed dispersers.

A large proportion of the plant species (28%) and the majority of frugivore species in the dataset (65%) were classified as endemic to the Caribbean. High degrees of endemism in local species communities are characteristic of island ecosystems (Kier et al., 2009; Paulay, 1994). In a review of plant–frugivore interactions on the Galapagos archipelago, Heleno et al. (2011) found similarly high proportions of endemic frugivores in the species pool (71%), underlining the importance of endemic frugivores for island communities. By contrast, only a few species in the dataset were classified as introduced to the Caribbean (16% plants and 8% frugivores), which was lower than other studies on island ecosystems. Notably on Hawai'i, the proportion of introduced seed disperser species ranged from 50% to 100% for plants and from 60% to 100% for birds (Vizentin-Bugoni et al., 2019). On the Galapagos, the proportion of introduced plants and frugivores was 28% and 23%, respectively (Heleno et al., 2011). However, on the Galapagos, all introduced frugivore species were mammals, whereas in our data, the vast majority of introduced species were birds (86%) and only two species (14%) were mammals (a primate: *Chlorocebus pygerythrus* and a carnivore: *Herpestes javonicus*).

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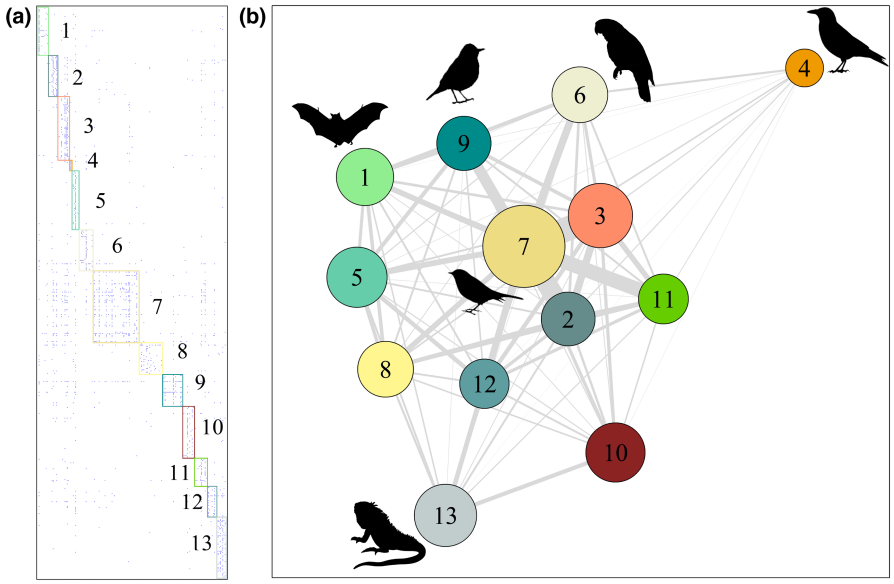

FIGURE 3 Modular structure of the plant–frugivore meta-network of the Caribbean. Plants are shown in rows and frugivores are shown in columns. (a) Species are sorted according to their modular affinity; the order of the 13 modules is arbitrary. (b) Graph of modules. The links between modules are weighted by the number of plant and frugivore species interacting between the respective modules. The Caribbean plant–frugivore meta-network was significantly more modular than expected by random ($p < .001$). Included are only fully identified species. Modularity was driven by functional or taxonomic and biogeographical mechanisms. For instance, module 13 consisted almost exclusively of rock iguanas found in the Bahamas and module one consisted mostly of bat species recorded in Cuba. For detailed list of species in each module compare Table S5 in Supporting Information.

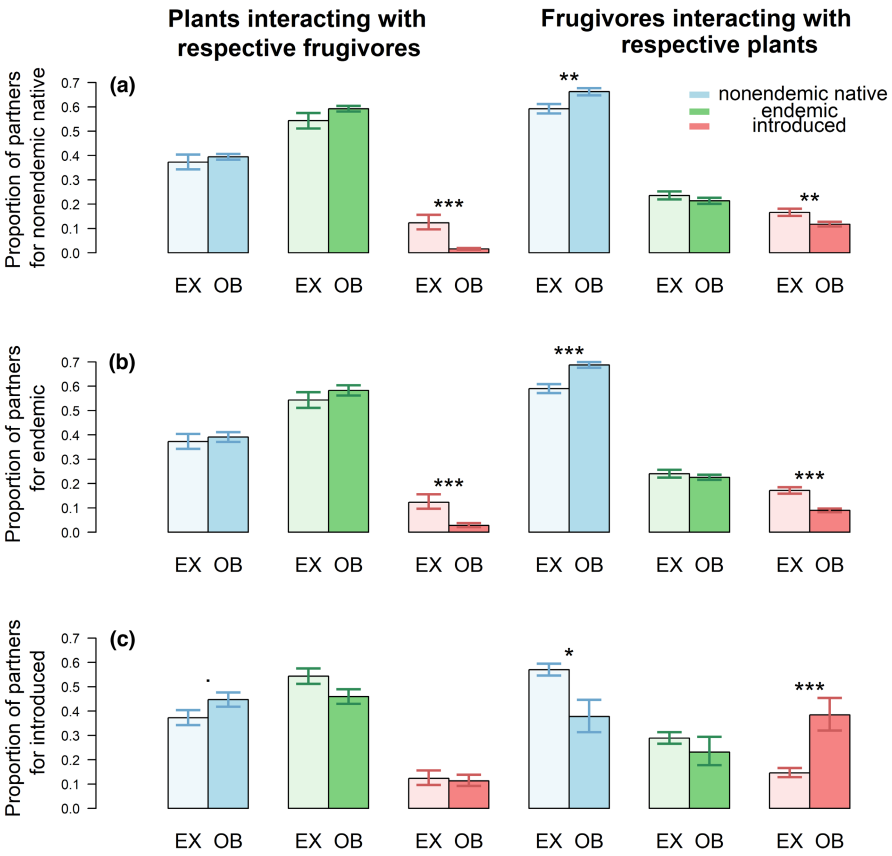

FIGURE 4 The expected (EX) compared with the observed (OB) proportion of interaction partners for plants and frugivores across the Caribbean. The relationships are shown for (a) nonendemic native, (b) endemic and (c) introduced species and their respective partners. Proportions were calculated from the species pools on islands, where species with the respective native status (e.g. introduced) co-occur, see methods for details. Bars indicate mean values across each respective subset of islands, where species categories co-occurred (±*SD*). Included are only fully identified species.

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4.2 | Cross-island patterns of shared species and interactions

When examining the role of different groups of plants and frugivores in connecting islands and archipelagos, we found that nonendemic native species and interaction pairs were shared most widely across islands (Figure 2), which is expected, as these species are widespread species occurring throughout the Caribbean and the Neotropical mainland. They are thus supposedly good dispersers, and their ranges often occur across multiple islands and cross-borders of archipelagos (Dalsgaard et al., 2014). Although endemic frugivores made up more than 60% of the frugivore species, generally they overlapped much less between islands compared to nonendemic natives, which only accounted for less than 30% of the frugivores in the data (Table 2). This pattern is not surprising, since the distributional ranges of endemic species are per definition confined within limited geographical areas (Kricher, 2011), many species being single-island endemics or occurring on few islands within each of the archipelagoes, that is the Lucayan archipelago, the Greater and Lesser Antilles (Dalsgaard et al., 2014). In the Caribbean, for instance, there is a high number of single-island endemic frugivorous birds, such as various species of parrots like the Saint Vincent Parrot *Amazona guildingii* (Birds Caribbean, 2021). Introduced plant species were shared widely across the Caribbean (Figure 2), which was expected, as most were agricultural and widely cultivated plants, reflecting that the Caribbean is historically heavily impacted by humans (Kemp et al., 2020; Walters & Hansen, 2013). By contrast, introduced frugivores were reported on few islands only (Table 2), and these islands shared mostly low proportions of introduced frugivores (Table S4); introduced interaction pairs were almost not shared between islands. Globally, a recent study showed how introduced species caused an increase in the proportion of regions sharing species and interactions (Fricke & Svenning, 2020), demonstrating that species introductions led to increasing similarity and homogenization in plant–frugivore communities across the world (Fricke & Svenning, 2020). In the Caribbean, however, given our data, especially nonendemic natives played a bigger role in interconnecting islands.

4.3 | Modularity of the Caribbean plant–frugivore meta-network

The Caribbean plant–frugivore meta-network was organized in modules, as are most mutualistic plant–animal interaction networks, both local networks (e.g. Dalsgaard et al., 2013; Dupont & Olesen, 2009; Mello et al., 2011a, 2011b; Olesen et al., 2007) and meta-networks (Araujo et al., 2018; Emer et al., 2018; Martín González et al., 2018). The separation of the meta-network into modules was at least partly driven by functional or taxonomic (i.e. modules dominated by certain species groups) and biogeographical (i.e. island-specific modules) mechanisms. For instance, one module consisted of small- to medium-sized bird species recorded in Jamaica (100% birds; 88% of frugivores recorded in Jamaica; module nine in Figure 4). Another module consisted mostly of various bat species (63% bats) recorded in Cuba (88% of frugivores recorded in Cuba; module one in Figure 4), whereas another module consisted almost exclusively of rock iguanas (*Cychlura* spp.) found in the Bahamas only (88% Iguanas; 88% of frugivores were recorded on the Bahamas only; module 13 in Figure 4). These modules associated with specific functional/taxonomic groups or specific islands were thus positioned in the periphery of the Caribbean meta-network (Figure 3). The separation into modules according to biogeographical affinities, such as single islands, was expected given that interactions between plants and frugivores are inherently spatial as species must be in the same place to interact (Morales & Vázquez, 2008) and many species are restricted to specific islands. Spatial patterns that correspond to insularity in the broad sense have previously been shown to partially explain the modular structure of mutualistic plant–animal networks in landscape matrices, where species are restricted to different types of patchily distributed habitats (Maruyama et al., 2014). Patterns of modularity have also previously been suggested to be explained by behavioural or functional traits of species (Dicks et al., 2002; Donatti et al., 2011; Maruyama et al., 2014). In plant–frugivore interactions, although plants typically aim to attract functionally diverse seed dispersers (Plein et al., 2013), there is evidence of functional matching between interaction partners, especially with birds (Vollstädt et al., 2017). Morphologically different frugivore species tend to forage on morphologically distinct sets of plant species (Dehling et al., 2016; Gautier-Hion et al., 1985; Lomáscolo et al., 2010; Mello et al., 2011b), which might be reflected in the modules composed primarily of specific frugivore groups with characteristic morphological and functional traits. Bats, for instance, consume different types of fruits than birds and may show a clear separation in their dietary composition (Gorchov et al., 1995). The patterns of modularity we detected were therefore in line with expectations of functional/taxonomic and biogeographical mechanisms as drivers of modularity. However, there were also modules consisting of a mix of species from various islands. One module consisted of about 50% of large parrot species (*Amazona* spp.), but the frugivores were recorded in the entire Caribbean (module six in Figure 4) and, notably, the module in the centre of the Caribbean meta-network consisted of various types of frugivores occurring throughout the Caribbean, thereby interconnecting islands and archipelagos in the Caribbean meta-network (module seven; Figure 3 and Table S5).

4.4 | Interactions with introduced species

Regarding how introduced species were integrated into the meta-network, we found that nonendemic native and endemic plants and frugivores interacted significantly less with introduced frugivore species than expected at random (Figure 4a,b). Among Caribbean frugivores and their fruiting plants, there is therefore no support for the idea that endemic super-generalists are the main facilitators of introduced species, as suggested for pollination networks on

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tropical islands (Olesen et al., 2002). On the contrary, introduced frugivores were recorded interacting with introduced plants significantly more often than expected at random (Figure 4c). This pattern suggests that introduced frugivores "prefer" to feed on introduced plants, which in turn suggests the presence of "invader complexes," that is introduced species interacting more among themselves than expected at random, thus facilitating their establishment (D'Antonio & Dudley, 1993). Such facilitation processes between introduced species can lead to "invasional meltdowns," as large groups of introduced species may have increasingly negative impacts on native communities (Jeschke et al., 2012; Simberloff & von Holle, 1999). Other island ecosystems have been found to be even more dominated by introduced frugivores, notably Hawai'i is almost exclusively dominated by introduced frugivores, as most of the endemic species have gone extinct (Vizentin-Bugoni et al., 2019; Vizentin-Bugoni et al., 2021). These findings from various archipelagos are concerning, regarding the potential impact of introduced species on native ecosystems. Such findings are particularly worrying when considering that on other island ecosystems, introduced species were also more often involved in seed-dispersal interactions (rather than seed/pulp predation) than native species (Heleno et al., 2011; Vizentin-Bugoni et al., 2019, 2021). For many of the interaction records, our data do not distinguish between seed-dispersal interactions or seed/pulp predation events; thus, it is not possible to estimate the effect of introduced species on local native and endemic plant communities in the Caribbean. Nevertheless, in Hawai'i, it was shown that introduced frugivores do not sufficiently replace the species roles of lost seed dispersers, since they preferentially disperse seeds of introduced rather than native plants (Vizentin-Bugoni et al., 2019). This raises the question why introduced plant species seem so attractive. One reason could be that introduced plants may have specific traits, such as longer fruiting duration, which increase the probability of encounters and are therefore more likely to be consumed by frugivores (Heleno et al., 2011; Sperry et al., 2021). In the Caribbean meta-network, many of the observations were from agricultural areas, where agricultural plants such as *Mangifera indica* (Mango) are often abundant with large crops, and although they are not dispersed by any native frugivore, they do overall attract many frugivores. Fruiting plant and thus resource abundance is in turn linked to increased fruit consumption, because frugivores often track available fruits in the landscape (Quitián et al., 2019), and consequently, the patterns we find may be partially driven by the high abundance of introduced agricultural plants and their crop sizes in human-dominated environments. Such patterns may be more pronounced on densely populated islands than on islands with few people and relatively more protected areas.

In addition to "invader complexes," we found that generalist species, that is species with many interaction partners, were more likely to interact with introduced species, which was consistent for both plants and frugivores (Figure S2a,b). These results are in line with previous findings, underlining the importance of highly generalized species for the establishment of introduced species, especially on islands (Maruyama et al., 2016). This gives support for the "preferential attachment" hypothesis (Newman, 2001), that is that species with wide ecological niches include and facilitate the establishment of new species, such as introduced species on islands. Our finding that generalized species do not have a higher proportion of interactions with introduced partners in their total set of interactions than specialized species (Figure S2c,d) reflects the overall low numbers of introduced species in the Caribbean data. Since only few of the potentially available interaction partners are introduced species, generalized species with many interaction partners would also be expected to have a decreasing proportion of their interactions with introduced species. Thus, although generalized species are likely to incorporate introduced species into their niche (Figure S2a,b), they do not have a specific preference for introduced species (Figure S2c,d).

5 | CONCLUSIONS

Based on a comprehensive review of accessible data on plant–frugivore interactions, we showed that the Caribbean meta-network is structured into modules and demonstrate how introduced species are integrated into native communities in the Caribbean archipelago. These results provide valuable insight into plant–frugivore interactions in insular biodiversity hotspots, showing how insular plant–frugivore systems are susceptible to invasion. Future studies are needed to demonstrate the importance of introduced species as seed dispersers compared with seed/pulp predators (Nogales et al., 2017). Specifically, research quantifying the relative importance of different frugivore groups as seed dispersers and their respective effectiveness is lacking for most plant–frugivore interactions in the Caribbean. This would provide valuable information and could help with the conservation of endemic plants in the Caribbean archipelago. Moreover, we also in general lack information on frugivory in the Caribbean. Kim et al. (2022) reported 4336 species of plants with animal-dispersal syndromes in the Caribbean archipelago, and our dataset represents only 11% of those species with some regional variation (Table S6). For instance, whereas Puerto Rican plants were covered relatively well (31% of the species), plants in Hispaniola (approx. 7%), Jamaica (approx. 8%) and the Lesser Antilles (approx. 9%) were less well represented. There may also be taxonomical differences in sampling completeness. Palms (Arecaceae) are highly diverse in the Caribbean representing 135 species (Roncal et al., 2008), and our dataset had only 23 palm species (17%). Several endemic and highly threatened fleshy-fruited plants do not have any information on the main seed dispersers (e.g. *Catesbea spinosa*, *Brunfelsia portoricensis*, *Diospyros* spp. and many cactus species). We also have limited and incomplete information on the fruit diet of several endemic frugivores (e.g. pigeons, thrashers and thrushes) that could play an important role for seed dispersal of Caribbean plants. There is therefore an urgent need to increment more scientific information on plant–frugivore interactions in the Caribbean, one of the world's insular biodiversity hotspots.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest to report.

DATA AVAILABILITY STATEMENT

All data used in this paper and relevant Supporting information are available available through GitHub (https://github.com/corvuscorax1/Caribbean-frugivory-overview-and-patterns).

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BIOSKETCH

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