



A Review on the State of the Art in Frugivory and Seed Dispersal on Islands and the Implications of Global Change

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Abstract

We provide an overview of the current state of knowledge of island frugivory and seed dispersal and identify knowledge gaps that are important for fundamental research on—and applied conservation of— island ecosystems. We conducted a systematic literature search of frugivory and seed dispersal on islands, omitting large, continental islands. This revealed a total of 448 studies, most (75%) published during the last two decades, especially after 2010. Nearly 65% of them were focused on eight archipelagos. There is a paucity of studies in Pacific archipelagos near Asia and Australia, and in the Indian Ocean. Data on island frugivory and seed dispersal are diverse but highly uneven in geographic and conceptual coverage. Despite their limited biodiversity, islands are essential reservoirs of endemic plants and animals and their interactions. Due to the simplicity of insular ecosystems, we can assess the importance of seed dispersal theory and mechanisms at species and community levels. These include the

ecological and biogeographical meaning and prevalence of non-standard mechanisms of seed dispersal on islands; the seed dispersal effectiveness and the relative roles of different frugivore guilds (birds and reptiles being the most important); and patterns of community organization and their drivers as revealed by interaction networks. Island systems are characterized by the extinction of many natives and endemics, and high rates of species introductions. Therefore, understanding how these losses and additions alter seed dispersal processes has been a prevailing goal of island studies and an essential foundation for the effective restoration and conservation of islands.

Keywords Conservation and restoration · Fleshy-fruited plants · Insular environments · Mutualistic interactions and ecological networks · Non-standard dispersal mechanisms · Seed dispersal effectiveness

Introduction

By definition, islands are geographically isolated, which results in lower species richness of plants and animals, but greater levels of endemism and occurrence of relict species when compared to continents (Darwin, 1859; Wallace, 1892). These characteristics have made islands ideal laboratories for studying ecological and evolutionary processes (Carlquist, 1974; MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007).

Islands also offer ideal frameworks for studying colonization processes and the characteristics of species that successfully arrive and establish. When a new species becomes established on an island, it engages in new interactions (and may alter existing local ones), including animal-plant mutualisms such as pollination and seed dispersal (see Traveset et al., 2013; Heleno et al., 2013a and references therein), or antagonisms, such as seed predation (Carpenter et al., 2020). Therefore, the varied assemblages of animals and plants that colonize different islands may give rise to unique interactions that shape the ecological and evolutionary trajectories of the species involved. In particular, interactions between animals and plants, and their ecological roles, often differ from those of their ancestors on continents or less isolated islands, and niche shifts are common (Banack, 1998; Valido & Olesen, 2019).

Birds and mammals are the most common seed dispersers on continents (Kitamura et al., 2002; Donatti et al., 2011; Fleming & Kress 2013; Timóteo et al. 2018), but they differ in their capacity for island colonization. As a consequence, whereas birds remain important on islands, the relative importance of certain groups of mammals (bats) and reptiles (mainly tortoises, iguanas, and other lizards) relative to birds increases, sometimes even surpassing that of birds in some isolated archipelagos (Olesen & Valido, 2003; Heleno et al., 2013a; Nogales et al., 2005, 2017; Valido & Olesen, 2019; Falcon et al., 2020; Albert et al., 2021).

Endozoochory (i.e., the dispersal of seeds by animals after ingestion) is an important dispersal mechanism during island colonization and establishment (Ridley, 1930). One of the peculiarities of island communities is their ‘disharmony’ as compared to continental ones (Darwin 1859). Disharmony occurs when taxa on islands are over- or

under-represented relative to comparable continental environments, at least in part because of differences in rates of long-distance dispersal over water (Whittaker & Fernández-Palacios, 2007). As a consequence, some animals (Nogales et al., 1999), but also plants (Price & Wagner, 2004) undergo niche shifts and perform different ecological roles after colonizing islands, filling niches that would be occupied by unrelated taxa on continents. Thus, when animal species arrive on islands, they often expand their niche breadth to occupy multiple trophic niches (i.e., the so-called *ecological release*) (Wright, 1980), which may involve the range of interactions that animals have with seeds, along the continuum from mutualism (dispersal) to antagonism (predation).

Therefore, island environments are advantageous for the in-depth assessment of a number of ecological processes that can be elusive to measure in more diverse continental sites. These include: the overlooked importance and role of non-standard dispersal mechanisms; determining the comparative effectiveness of seed dispersal interactions by disparate agents; the structure of interactions at community and ecosystem scales (e.g., ecological networks and fluxes); and the lasting effects of trait anachronisms and species extinctions, both of which are common on island systems.

Islands have suffered high rates of species decline and extinction, as well as species introductions, and are therefore in need of studies on the conservation biology and ecology of many species and communities (Fernández-Palacios et al., 2021). The breakdown of interactions as native species become rare or extinct, and the establishment of novel interactions as non-native species invade, offer opportunities to understand how ecological networks are assembled and how seed dispersal functions are altered (Vizentin-Bugoni et al., 2019, 2021).

The application of seed dispersal theory and knowledge can be used to inform the ecological restoration of altered island environments (Culliney et al. 2012; Albert et al., 2020, 2021). Studies of frugivory and seed dispersal on islands often claim that this important ecological interaction is understudied and therefore remains incompletely understood. However, it is hard to judge the extent to which these claims are true, as most literature is highly scattered and there has never been a global review on this topic.

This review has four goals. First, we present the current state of knowledge on mutualistic seed dispersal interactions between plants and frugivorous animals on islands worldwide. Second, we highlight the specific ecological and evolutionary characteristics of frugivory and seed dispersal phenomena on islands. Third, we assess the known conservation implications of altered seed dispersal on islands. Finally, we aim to identify major gaps in knowledge of frugivory and seed dispersal on islands, and suggest avenues for future research.

Methods

We focused our review on relatively isolated (mainly oceanic) islands, and excluded the larger continental islands (e.g., Great Britain, Madagascar, Japan, New Guinea, and New Zealand), though their respective offshore islands and islets have been included. These larger islands have more continental floras and faunas and have different ecological dynamics than the smaller islands (Whittaker & Fernández-Palacios 2007).

A systematic literature search was performed using Internet scientific search engines (<http://www.scholar.google.com> and <http://www.isiknowledge.com/WOS>), to identify all papers published until August 2022. Simultaneously, a search in each geographic region was carried out by people with expertise in each insular region to incorporate personal datasets, MSc and PhD theses, and potentially important grey literature. The key words used in the searches were: frugivory (consumption of fruits by animals), seed dispersal and seed predation (by ingestion), and island or insular. Because the study was basically focused on seed dispersal by frugivorous animals (or fruit- and seed-consuming animals) we concentrated our search on those contributions that include frugivory and fleshy-fruited plants. However, we included only studies in which data on frugivory and/or seed dispersal or predation by animals were provided, excluding those in which these interactions were treated collaterally. Although in the general search, the number of publications focused on islands was slightly more than 8000, we selected only those contributions whose basic topics were frugivory, seed dispersal and seed predation; this number was about 450. Those studies that included more than one of the three categories (i.e. both frugivory and dispersal, or both dispersal and predation, or all three) were counted more than once in the frequency analyses. While seed dispersal by frugivores is generally beneficial to plants, and seed predation by seed predators is harmful, we recognize that there is in fact a continuum of outcomes for seeds handled by animals (cf. Perea et al. 2013), and have therefore included seed predation along with frugivory and seed dispersal. We organised this information according to geographical region, following the hierarchical sequence: (1) the three main oceans—Atlantic, Pacific and Indian, (2) the main groups of archipelagos, and (3) the individual archipelagos or islands themselves (Appendix 1).

We compiled summary statistics for all references in the bibliography. Each contribution was scored for: (1) study site and date, (2) the type of interactions (frugivory, seed dispersal and/or seed predation), (3) experiments performed on seed germination or viability, (4) the origin of the studied plants (native or non-native), and (5) main disperser guilds involved.

Types of interactions (frugivory, seed dispersal and seed predation) and frugivores in the three oceans (Atlantic, Pacific and Indian) were analysed by Chi-square tests and they were performed by R (R Core Team, 2022), using ‘Bonferroni corrections’ to avoid type I Error in those cases in which multiple comparisons were carried out.

Results and Discussion

Geographical Areas and Studies

Information on frugivory and seed dispersal on islands is scattered and unevenly distributed across the world’s archipelagos (see Fig. 1 and Appendix 1 and 2 for general statistics of the contributions). Aside from 29 general contributions of wide geographical scope, 419 contributions covered specific islands, archipelagos, or

island groups, with nearly 65% of them focusing on eight archipelagos (Canaries: 19%, Puerto Rico: 10%, Japanese offshore islands: 11%, Galápagos: 8%, Hawai'i: 6%, New Zealand offshore islands: 5%, Balearics: 5% and the Marianas: 5%). Other islands have moderate coverage, but gaps clearly exist in the smaller Melanesian (e.g., Vanuatu or Solomon Islands) and Micronesian islands (e.g. Palau, Marshalls or Kiribati), where numerous archipelagos are located. Furthermore, coverage of the Indian Ocean was also patchy. In this regard, it is interesting to note that, of the 85,138 islands identified globally, based on the application of the Flanders Marine Institute (2021), 43% were located in the Pacific Ocean, 34% in the Atlantic and 12% in the Indian Ocean (A. Naranjo Cigala, pers. comm.). However, when considering those islands larger than 1 km², the percentage of islands in the Pacific is even higher (Weigelt et al., 2013), highlighting the large information gap existing in many of its islands and archipelagos.

Chronology of the Studies

The first reports on seed dispersal processes came from travellers and naturalists who described how seed morphology facilitated dispersal across oceans, and included descriptive information on frugivory and seed dispersal (Darwin, 1859; Wallace, 1892; Guppy, 1906, 1917; Ridley, 1930). Later, the seminal work of Snow & Snow (1971, 1988), sparked the field of frugivory and seed dispersal on islands with studies from birds and fruiting plants of Trinidad in the Caribbean. Subsequently, Carlquist (1974), Porter (1983) and Bramwell (1985) attempted to understand how plants, including species potentially dispersed by endozoochory, arrived on some oceanic archipelagos such as Hawai'i, Galápagos, and the Canary Islands, respectively. However, most publications on frugivory and seed dispersal (89%) on islands have been published since 1980 (Fig. 2; Appendix 3).

Types of Interactions

Considering the more specific papers, a total of 448 frugivory, seed dispersal, and seed predation studies were conducted on islands (see Fig. 3A; Appendix 1 and 2). Most (73%) of the publications focused on seed dispersal, followed by frugivory (30%), and seed predation (11%). Seed dispersal and frugivory have been studied more than seed predation ($\chi^2_4 = 29.10$; $P < 0.001$) in islands from all three oceans (Atlantic, Pacific and Indian). While most frugivory studies were conducted on the offshore islands of Japan, Canaries and Puerto Rico, seed predation studies were significantly more prevalent in the Pacific, especially in the Galápagos and Hawaiian archipelagos. Less than 20% of the studies included seed germination experiments. These were more frequently carried out in the Atlantic and Indian oceans, especially in the Canaries and Mauritius. Most of the total studies (81%) included native plants, and non-native plants featured in 30% of them.

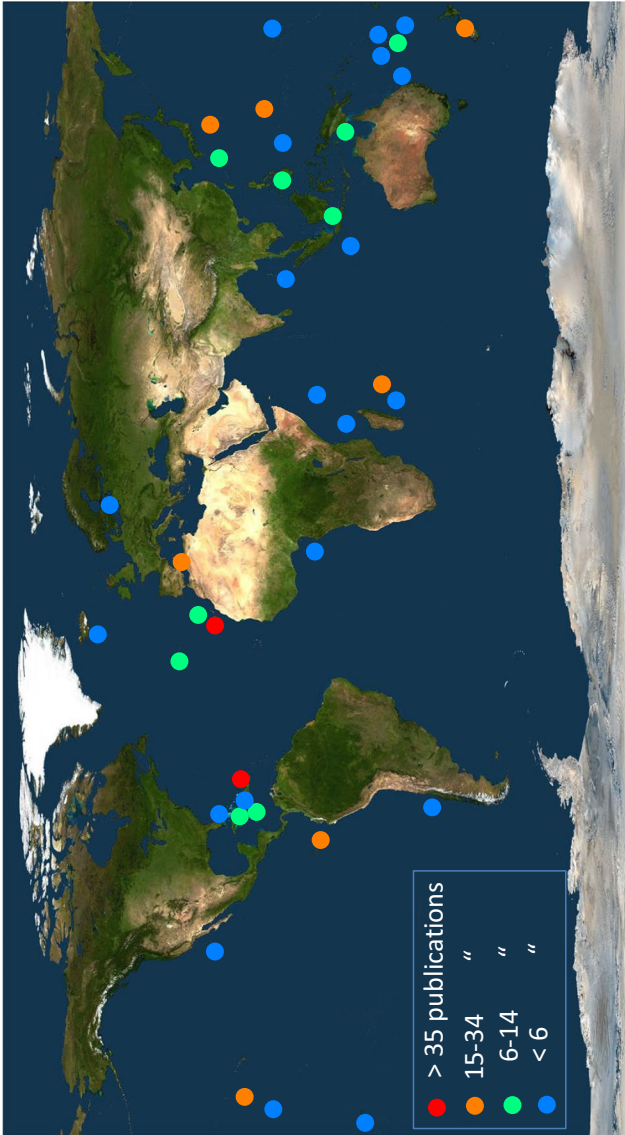


Fig. 1 A global view of the publications carried out on frugivory and seed dispersal on islands until 2022 inclusive

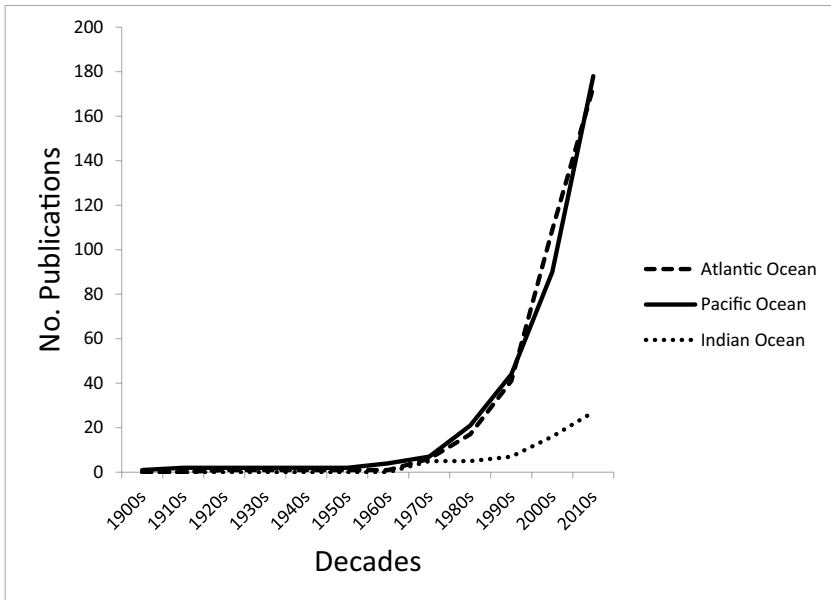


Fig. 2 Cumulative number of contributions on the topic of frugivory and seed dispersal on islands from different oceans since 1900

Types of Frugivores

There are three main guilds of vertebrate frugivores represented in these studies: reptiles, birds, and mammals (Fig. 3B). Among these, tortoises, lizards, passerine and non-passerine birds, and bats were the main groups. Invertebrates were uncommon, and included only land crabs ($n=8$) and orthopterans (New Zealand weta) ($n=1$).

Regarding reptiles, contributions on tortoises were frequent in the Pacific and Indian Oceans (this group having become extinct in the Atlantic islands; see López-Jurado & Mateo, 1993), whereas those on lizards were more frequent in the Atlantic ($\chi^2_4=51.08$; $P<0.001$). Studies on lizard seed dispersal were especially numerous in the Canary and Balearic archipelagos, and surprisingly scarce in the Caribbean islands, given the abundance of lizard taxa there and their potential importance as seed dispersers (Malone et al., 2000; Pinto et al., 2008; Seokmin et al., 2022). Most of these studies involved native species.

Native bird species have been studied more frequently than non-native species in the three oceans ($\chi^2_2=20.03$; $P<0.001$). However, in the Hawaiian Islands and the offshore islands of Japan and New Zealand, non-native birds have received considerable attention. The most frequently studied taxa across three oceans were passerines. Non-passerines (larger body size, mainly pigeons) were more frequently studied in Pacific archipelagos (e.g., offshore islands of Japan and New Zealand, Philippines, western and central Polynesia: Tonga, Samoa, Cook Islands, and Micronesia: the Marianas) than in the Atlantic and Indian Oceans ($\chi^2_2=6.52$; $P=0.038$).

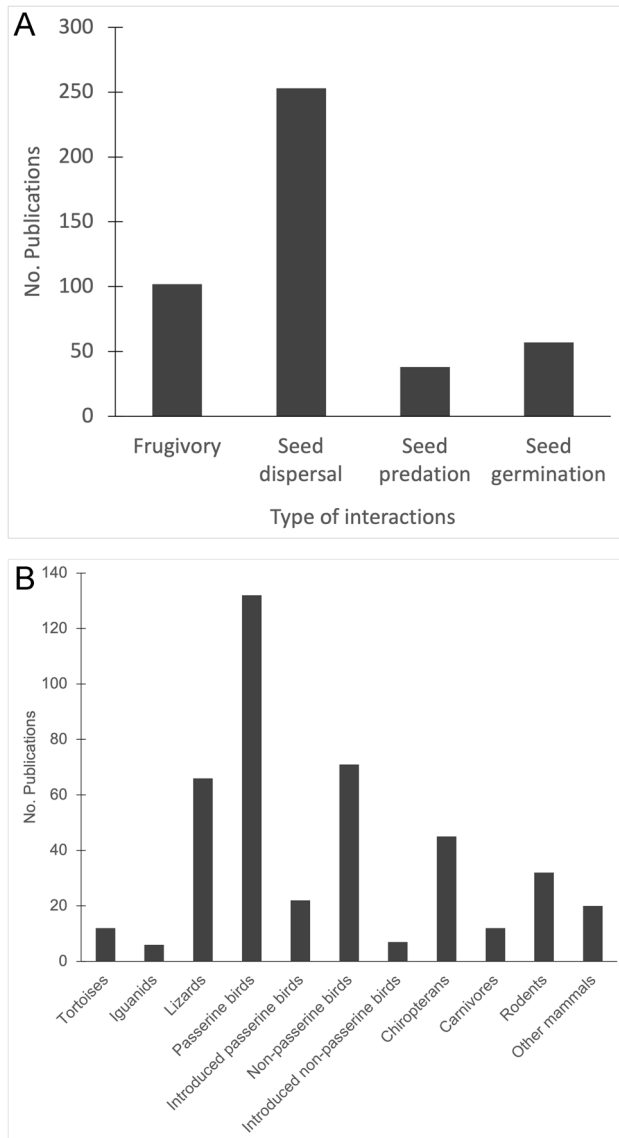


Fig. 3 **A.** Number of publications of the different types of interactions. **B.** Main guilds of frugivores included in the literature reviewed

Regarding mammals, native species were more often studied in the Pacific and Indian oceans whereas in the Atlantic, non-native mammals have received more attention ($\chi^2_4 = 20.40$; $P < 0.001$). Native bats were commonly studied in all three oceans, especially in archipelagos located at tropical latitudes (Atlantic Ocean: Caribbean islands; Pacific Ocean: Polynesia, Indonesia, and Melanesia; Indian Ocean: Andaman, Seychelles, and Mauritius). Primates (macaques) have been recently

studied in Mauritius where they were introduced (Reinegger et al., 2021), and in continental offshore islands of Japan, where they are native; they are naturally absent from all oceanic islands. Most contributions on non-native mammals have been carried out in the Atlantic and the Pacific, with rodents (especially rats, *Rattus* spp.) frequently being studied in many oceanic archipelagos worldwide. Other introduced mammals that have received attention include other rodents (ground squirrels in the Canaries and tree squirrels in Japan), as well as rabbits, carnivores (cats, pine martens, genets), insectivores (hedgehogs), and feral ungulates such as deer, goats, and pigs.

In summary, reptiles, birds, and mammals are the three main groups of animals in studies of island frugivory and seed dispersal. While birds feature in studies across all archipelagos, mammals are better represented in studies on tropical continental islands and some oceanic islands, and reptiles are more frequently involved on oceanic islands. In a global review on lizard seed dispersal, Valido & Olesen (2019) reported that seed dispersal by lizards is disproportionately common on islands. These authors also comment that insular ecosystems are commonly poor in arthropods, so lizards may have undergone a niche shift to forage for fleshy fruits as a supplementary food source. By contrast, seed dispersal by tortoises is not exclusively an island phenomenon (Falcon et al., 2020). With regard to birds, frugivorous species of pigeons are mostly represented on islands too (Marrero 2009).

Islands as Ideal Environments to Examine Seed Dispersal Theory and Mechanisms at Species and Community Levels

The Potential Importance of Non-Standard Dispersal Mechanisms

Seed dispersal by mechanisms other than those to which a species appears to be adapted has been defined as “non-standard dispersal mechanisms” (Higgins et al., 2003). These appear to be especially important—or at least easier to detect—on islands, whereas on continents they remain relatively unexplored. Several studies have recorded a high percentage of plants that lack obvious long-distance dispersal syndromes (hereafter LDD) (e.g., thalassochory, endozoochory, epizoochory or anemochory; sensu van der Pijl 1982) yet are capable of colonizing islands (Vargas et al., 2012; Heleno & Vargas, 2015; Arjona et al., 2018).

As determined by their morphological traits, the dispersal syndromes of plants (see van der Pijl, 1982) can usually be associated with mechanisms that generate predictable seed dispersal pathways. However, in some cases, the actual dispersal vector might be quite different from the expected one (Nogales et al., 2012; Heleno & Vargas, 2015). Seed dispersal by large, omnivorous birds (ravens and gulls; see Nogales et al., 1999, 2001; Thorsen, 2003), legitimate dispersal of seeds by ‘seed predators’ (sometimes migratory birds) (see Fridriksson, 1975; Heleno et al., 2011; Ando et al. 2022), and secondary dispersal by endozoochory of birds that prey upon smaller frugivorous vertebrates (lizards and birds) (Nogales et al., 1998; Padilla et al., 2012), could be typical of underappreciated mechanisms of LDD to and between islands. Furthermore, in some cases, shorebirds (Hancock & Prince, 2021)

and ducks (Soons et al., 2016) can carry out dispersal of seeds in the context of insular environments.

These non-standard LDD mechanisms have been partially evaluated on two recently-formed volcanic islands, Surtsey (Iceland, North Atlantic Ocean) and Anak Krakatau (Indonesia, Indian Ocean). Fifty years after the formation of Surtsey, 54% of the established angiosperms appear to have been transported to the island by birds (Fridriksson, 1992; Magnússon et al., 2014), whereas 23% of the seed plants established on Anak Krakatau during its first century were likely transported by birds and bats (Thornton, 1992). The differential role of birds in seed dispersal to the two islands is probably linked to the presence in Surtsey of birds with generalist feeding habits (a colony of gulls and a nest of ravens), and the importance of migratory birds (see Viana et al., 2017), some of them granivores and theoretically seed predators (Fridriksson, 1975). According to Fridriksson (1975) and Magnússon et al. (2014), many angiosperms appeared after these birds colonized the island, and they were established at their colonies and nests. Future research should focus on exploring the extent and importance of the non-standard LDD mechanisms presented here and seeking others not yet discovered.

The Measurement of Seed Dispersal Effectiveness as a Metric to Assess Threats to Island Communities

Seed dispersal effectiveness (SDE sensu Schupp, 1993; Schupp et al., 2010) estimates the combined contributions of dispersal quantity (number of seeds dispersed) and dispersal quality (the probability that a dispersed seed becomes a new adult plant) to plant recruitment. It is a key metric to assess the complementarity or redundancy of the contributions of different disperser groups to plant reproductive success (Rother et al., 2016; Lugon et al., 2017). However, estimation of parameters related to dispersal quality (e.g., the effect of gut treatment on seeds, spatial pattern of seed deposition, and habitat suitability for seed germination and seedling survival) is time-consuming and requires considerable effort, making thorough estimation of SDE at the community level inherently difficult. The lower species richness of island communities compared to continental ones makes such an endeavour more tractable on islands. There are an increasing number of studies based on the SDE framework in insular areas (e.g., González-Castro et al., 2015a; McConkey & Drake, 2015; Nogales et al., 2017; Muñoz-Gallego et al., 2019; Nakabayashi et al., 2019).

SDE studies worldwide are progressively increasing the number of animal species characterized (e.g., Howe, 1977; Reid, 1989; Graham et al., 1995; Jordano & Herrera, 1995; Stevenson 2000; Jordano & Schupp, 2000; Calviño-Cancela & Martín-Herrero, 2009; Li et al., 2016; Camargo et al. 2016). And, to our knowledge, the most comprehensive studies that have undertaken the challenge of studying many members at a plant community level (i.e., focusing on the dispersal service provided by animals to the many fleshy-fruited species in a local plant community) have been made on islands (Carlo et al., 2003; González-Castro et al., 2015a; McConkey & Drake, 2015; Nogales et al., 2017).

By and large, the use of the SDE conceptual framework to estimate dispersal by frugivores on islands has revealed high complementarity (i.e., low redundancy)

among vertebrate dispersers. This pattern suggests that plants could be vulnerable to the decline or extinction of their most crucial disperser group (González-Castro et al., 2015a; McConkey & Drake, 2015; Morán-López et al., 2020), perhaps as a result of earlier frugivore losses. It can explain the severe consequences of disperser loss for plant reproductive success which have been reported from different archipelagos (Meehan et al., 2002; Rodríguez-Pérez & Traveset, 2010; McConkey & Drake, 2006; Chimera & Drake 2010, 2011; Pérez-Méndez et al., 2016). However, the most comprehensive SDE studies at the community level have focused on only a few islands in just the Canary Islands and Galápagos. Dispersal quality is highly context-dependent and may change drastically in time and space (Schupp, 2007). Therefore, it is difficult to draw robust general conclusions about the complementarity of disperser effectiveness on islands worldwide. It is also desirable to validate models estimating SDE with empirical data on plant recruitment (Calviño-Cancela & Martín-Herrero, 2009). Islands with simple communities provide opportunities to look for consistent temporal and geographical patterns of disperser complementarity or redundancy, considering both quantitative and qualitative (with its direct and indirect effects on seedling recruitment) components of SDE.

Frugivory and Seed Dispersal Networks on Islands

Species interaction networks are an increasingly popular tool to explore the links between community structure and long-term persistence (Heleno et al. 2014; Jordano, 2016a). In frugivory networks, the interactions between fruiting plants and their frugivores may be characterised in terms of interaction frequency and outcome (e.g., pulp consumption, seed predation, legitimate seed dispersal) and developed into an interaction matrix, which can be used to explore species' functional roles and emergent community properties (Bascompte & Jordano, 2007).

The relative ecological simplicity that results from low biodiversity on oceanic islands makes them valuable research stepping stones towards understanding the mechanisms operating in the more complex communities on continents (Schleuning et al., 2014; Traveset et al., 2016). Nevertheless, despite the large number of island frugivory studies, remarkably few implement a community-wide network approach. The first such studies on islands include the work of Traveset (1992) in the Balearics and Carlo et al. (2003) on Puerto Rico, both exploring diet preferences of frugivorous birds. More recently, a network approach was implemented to show the re-establishment of seed dispersal function after habitat restoration in the Azores (Heleno et al., 2010). Other studies soon followed, either trying to identify community-level patterns in the structure of insular frugivory networks (e.g. González-Castro et al., 2012; Nogales et al., 2016) or exploring the consequences of plant invasions on islands. Biological invaders, especially plants, are a major conservation threat, and are particularly harmful on islands. Several studies have shown that insular frugivores readily integrate introduced plants in their diets, facilitating the spread of fleshy-fruited species in French Polynesia (Spotswood et al., 2012), Galápagos (Heleno et al., 2013a), Azores (Heleno et al., 2013b), Marianas (Fricke et al., 2017), the Mascarenes (Albert et al., 2021) and the Seychelles (Costa et al., 2022). A particularly extreme case of non-native plant integration was documented on O'ahu, Hawai'i, where all 1792 recorded

plant-frugivore interactions in seven forests included either an introduced plant or an introduced frugivore, or both (Vizentin-Bugoni et al., 2019, 2021); the few remaining native birds there consumed only non-native fruits, so there were no interactions between native birds and native plants.

The extent to which extant species may compensate for the decline or loss of a key disperser through rewiring is an open question in seed dispersal ecology, and islands have contributed significantly to answering it. For example, the island of Rota in the Marianas archipelago has a lower diversity and density of avian frugivores than the nearby island of Saipan (130 km away). Observations of fruit removal on both islands showed that the depauperate frugivore community on Rota favoured the plant species which had the highest interaction frequencies on Saipan, and ignored those species with low interaction frequencies, leading to a disproportionate dispersal advantage for the preferred species (Fricke et al., 2018). This study provides no support for the compensating mechanisms that are assumed in some theoretical network models, in which the functions performed by the missing frugivores are taken over by the remaining frugivores. This suggests that the cascading consequences of seed dispersal disruptions resulting from defaunation might be more negative than previously thought (Rogers et al., 2021). Seed dispersal by a simplified fauna composed of abundant and generalist species could instead accelerate species shuffling according to their abundance and thus accelerate the homogenization of biota, even if resulting in highly connected and highly nested (i.e., robust) communities (McKinney & Lockwood, 1999; Heleno et al., 2013a; Sperry et al. 2021). Recent co-extinction models that incorporate the dependence of species on mutualisms (Traveset et al., 2017; Fricke et al., 2017) suggest that networks might be more stable (i.e., more robust against co-extinctions) than predicted by models that did not do so. Using global databases and field experiments focused on seed dispersal interactions, Fricke et al. (2017) found that plants and animals that depend heavily on mutualistic interactions have higher partner diversity. This reduces the likelihood of species co-extinction because the species most likely to lose mutualists depend least on them. By incorporating such dependence on mutualism in co-extinction models, the importance of network structure (e.g., nestedness) was found to decrease (Fricke et al., 2017).

Recently, Schleuning et al. (2014) collated many datasets on island frugivory and found that island isolation increases network asymmetry, because isolated islands tend to have a lower ratio of animal/plant species, likely due to filtering effects restricting the number of dispersers that had colonized the island. This study shows that we are now reaching a position where it is possible to derive generalizations about seed dispersal at broad biogeographical scales. However, intrinsic variability among islands (e.g., island age, isolation, area, origin, conservation status), and methodological differences in sampling protocols (e.g., interaction frequency, interaction outcome, sampling completeness) still limit our capacity to identify reliable biogeographical patterns in network structure. Island networks might become increasingly similar to each other (and to continental networks) as many of the same non-native species from continents replace island endemics on multiple islands (Fricke & Svenning, 2020). Importantly, whereas most studies on continents report a downsizing of the seed dispersal services (i.e., favouring small-seeded plants) following the selective extinction of larger dispersers, the introduction of

often large frugivores on islands might cause an upsizing of seed dispersal services (i.e., towards larger seeds) as observed in the island of São Tomé (Heleno et al., 2022). On Mauritius, small extinct seed dispersers were replaced by large introduced seed predators (Heinen et al., 2023). However, it is critical to assemble more—and more accurate—community-wide frugivory networks, including multiple disperser guilds (Donatti et al., 2011; Costa et al., 2016; Jordano, 2016b; Heleno et al., 2022) to confirm this and other general patterns previously found.

The structural simplicity of insular networks might be particularly valuable for clarifying the relationships between different types of ecological functions, such as those between seed dispersal and pollination, for example using multi-layer networks (Hervías-Parejo et al., 2020), or among species on the continuum from seed dispersers and seed predators (Shiels & Drake, 2011; Perea et al., 2013; Carpenter et al., 2020). As mentioned above, the relative simplicity of island communities has allowed to scientists not only to obtain comprehensive data on effectiveness of mutualistic interactions, but also to incorporate them into the mutualistic network approach from both the perspective of plants and dispersers (González-Castro et al., 2022). The intense interest in characterizing island frugivory networks to understand the underlying mechanisms of their structure is likely to provide significant advances in the field in the near future.

Conservation Approach: Extinction, Effects of Invasive Species, and Ecological Restoration

Impact of the Extinction of Dispersers on Islands

In contrast to abiotically-dispersed species, plants that depend on animals for seed movement are susceptible to dispersal failure when their seed vectors become rare or extinct (Traveset & Richardson, 2006, 2014). Disruption of seed dispersal mutualisms can have serious consequences for the recruitment success, population maintenance, metapopulation dynamics, and colonization ability of the organisms involved, especially plants, which are likely more dependent upon animals (due to their lack of motility) than the animals are on the plants. Furthermore, because networks typically contain more plants than animals, the impact of losing an animal can be greater than that of losing a plant. Most studies reporting such mutualism disruptions come from island ecosystems (see Traveset & Richardson, 2014 and Rogers et al., 2017 and references therein), from both tropical and temperate zones. In a global analysis, Heinen et al. (2018) investigated recent extinctions of frugivorous birds, mammals, and reptiles on 74 (sub)tropical oceanic islands in 20 archipelagos worldwide. Nearly half (45%) of these islands have on average lost a third (34%) of their frugivore species, while some islands from the Pacific (e.g., Cook Islands, Hawaiian Islands, and Tonga) and the Indian Oceans (Mascarenes, Seychelles) have lost more than half. Furthermore, large and flightless species showed a higher extinction probability than small or volant species, leaving the island communities with only smaller frugivores available to disperse seeds. Therefore, large-seeded plants that depend on large-bodied frugivores are those most likely to be negatively affected by frugivore extinction, as has been

found in numerous habitats worldwide (e.g., Meehan et al., 2002; Donoso et al., 2017; Schlenning et al., 2014; Case & Tarwater, 2020; Albert et al., 2021). However, the role of large-bodied introduced species as potential dispersers on islands should be carefully considered alongside the role of native dispersers before firm conclusions can be drawn regarding lack of seed dispersal (Heleno et al., 2022; Costa et al. 2022). The loss of native frugivores could have negative cascading effects on plant populations, especially when they cannot be replaced by remaining native or newly-introduced frugivore species. On many islands, the collapse of seed dispersal has affected plant demography by decreasing or totally preventing seedling recruitment of some species (Traveset & Riera, 2005; Hansen & Galetti, 2009; Chimera & Drake, 2010, 2011; Rodríguez-Pérez & Traveset, 2012; Caves et al., 2013; Pérez-Méndez et al., 2015, 2016) and by suppressing dispersal-mediated gene flow (Calviño-Cancela et al., 2012; Pérez-Méndez et al., 2016).

Recently, reductions in seed dispersal distances resulting from loss of large- and medium-bodied frugivores have been documented along a gradient of human-driven defaunation in the Canary Islands (Pérez-Méndez et al., 2016), where smaller effective population sizes and a higher genetic similarity within local plant neighbourhoods occurred when large, frugivorous lizards declined or became extinct (because the remaining, medium-sized, frugivores provide less efficient seed dispersal). This demonstrates how the deterioration of mutualisms affects plant population dynamics over large spatial scales. This can result in reduced plant population connectivity, together with increased isolation by distance, within the most defaunated island (La Gomera) when compared to the islands where lizards still maintain their seed dispersal function (Gran Canaria and Tenerife) (Pérez-Méndez et al., 2018). Large-bodied frugivores are thus crucial in maintaining seed dispersal and genetic cohesiveness, as well as the adaptive potential of plant species across the landscape and their entire geographical range.

The Effect of Invasive, Non-Native Species on Islands

Non-native species can have wide-ranging impacts on frugivory and seed dispersal interactions on islands, from causing declines or extinctions of native plants and frugivores (Sax & Gaines, 2008), to facilitating the spread of non-native mutualistic partners (Huenneke & Vitousek, 1990; Woodward et al., 1990; Chimera & Drake, 2010), to compensating for the loss of native mutualists (Foster & Robinson, 2007; Chimera & Drake, 2010). Most plant and animal extinctions in the past 500 years have happened on islands (Sax & Gaines, 2008). Vertebrate extinctions were primarily driven by invasive mammalian predators (Sax & Gaines, 2008). Changes to the frugivore community can dramatically alter, directly or indirectly, the interactions between frugivores and native plants (reviewed in Traveset & Richardson, 2011, 2014). Detailed studies have documented dispersal disruptions resulting from non-native animals in oceanic archipelagos, such as the Canary Islands (Nogales et al., 2005, 2015; López-Darias & Nogales, 2008), Hawai'i (Chimera & Drake, 2010), and the Marianas (Rogers et al., 2017).

Competition between native and non-native species for mutualistic partners is often claimed, although it is not yet clear to what extent such potential competition

negatively influences native population dynamics in ways other than by facilitating the spread of non-natives. However, it seems likely that plant seed-disperser interaction networks will be irreversibly altered in these novel communities in response to the spread and increasing local dominance of non-natives (Ghazoul, 2005; Spotswood et al., 2012; Vizentin-Bugoni et al., 2019, 2021). Further work is needed across different species and ecosystems to better understand the overall 'cost' of disrupting native mutualisms, but the evidence so far indicates that the cost can be high (Traveset et al., 2012; Rogers et al., 2021).

While many impacts of non-native species are negative, some native plants that have lost their native dispersers currently benefit from non-native seed dispersers. In one of the most extreme cases, many common native plants in Hawaiian forests are dispersed mainly or exclusively by non-native birds that have replaced at least some of the functions of rare or extinct native birds (Foster & Robinson, 2007; Chimera & Drake 2010; Vizentin-Bugoni et al., 2019, 2021). Elsewhere, in the Balearic Islands, some plants formerly dispersed by now-extinct native lizards are dispersed mainly by a completely novel type of frugivore: a non-native mammal (pine marten; *Martes martes*; Traveset et al., 2012; Celedón-Neghme et al., 2013). This seems to have had evolutionary consequences for the plant, as pine martens exert a selective pressure on seed size (by choosing larger fruits, which contain larger seeds) different from that exerted by native lizards (Traveset et al., 2019). Non-native frugivores may not always compensate for the loss of native dispersers, especially on oceanic islands where their seed dispersal effectiveness is low (e.g., Wu et al., 2014), or where they are too small to disperse large-seeded species (Chimera and Drake 2010; Case & Tarwater 2020).

Long-distance seed dispersal has caused surprisingly fast invasion rates for many non-native plant species (Nathan, 2006). Both native and invasive frugivores can facilitate the spread of non-native plants. Native lava lizards were the most important dispersers of non-native plants in the Galápagos (Heleno et al., 2013a). A year-long study of frugivory networks in seven forests on O'ahu, Hawai'i, documented 1792 frugivory interactions, most involving non-native birds consuming non-native (93.2%) and native (6.6%) plants. Native birds rarely consumed non-native plants (0.2%), and never consumed native plants (Vizentin-Bugoni et al., 2019). Even animals normally considered seed predators, such as black rats (*R. rattus*), may be facilitating the spread of some non-native plants in Hawai'i (Shiels, 2011; Shiels & Drake, 2011), Tonga (Drake & McConkey, 2021) and in the Marianas (Gawel et al. 2018, 2023). Fruit production by non-native plants that is asynchronous with native plants, thus providing frugivores with a food source when few other options are available, has been identified as a key factor facilitating dispersal of non-native plants (López-Darias & Nogales, 2008; Chimera & Drake, 2010; Heleno et al., 2013a; Wotton & McAlpine, 2015). Indeed, the timing of fruit production by both native and non-native plants seems to be a critical factor for understanding the functional changes imposed by introduced plants and animals on frugivory and seed dispersal. However, these effects are still insufficiently explored (Costa et al., 2022). This is likely not unique to islands but illustrates how studies in relatively simple insular ecosystems can reveal phenomena that may be more widespread.

Conservation and the Role of Frugivory and Seed Dispersal in Ecological Restoration

Deforestation and landscape transformations have significantly altered nearly all islands that have been colonised by people (Kirch, 1997; Walker & Bellingham 2011; Fernández-Palacios et al., 2021). Human impacts pose a paradox for the maintenance of plant populations. On one hand, disturbances create new opportunities for plant colonisation and spread from remnant sources, but on the other hand they can pose strong barriers for dispersal if dispersal agents are negatively affected by changes or the new environments hamper recruitment (Holl, 1999; Zimmerman et al., 2000). Disturbances may also provide opportunities for the spread of non-native species, many of which have become integrated into dispersal networks (as described above). Frugivory and seed dispersal are responsible for the regeneration of forests in situ (i.e., cyclic regeneration), and for new successional forests recolonizing deforested landscapes (Carlo & Morales, 2016; Wandrag et al., 2015, 2017; González-Castro et al., 2019; Albert et al., 2020).

In Puerto Rico, for example, birds disperse about 70% of the woody tree and shrub species (Carlo & Morales, 2016). Thus, the conservation of frugivore populations is critical for the health of entire ecosystems there, given that a myriad of other life forms and processes also depend, directly or indirectly, on habitats formed by frugivore-dispersed plants. However, deforestation results in lower population sizes for native frugivores and fruiting plants; this, when accompanied by the introduction of non-native species into island communities, can deeply alter interaction networks (Heleno et al., 2013a, 2013b, 2022; Vizenin-Bugoni et al., 2019, 2021; Costa et al., 2022). Aside from increasing population sizes, ensuring restoration of the interaction functionality between species (with sufficient habitat range overlap, encounter, and success rates) is necessary to achieve self-sustaining island ecosystems (Heinen et al., 2020).

In the context of forest regeneration and restoration efforts, the combined reduction in numbers of frugivores and plants creates a dual problem of *source limitation* (dispersal limited by the availability of seeds) and of *dispersal limitation* (dispersal limited by the lack of seed dispersers) (Nathan & Muller-Landau, 2000), which may be particularly acute on islands. Source limitation may potentially be dealt with if plant species can be cultivated, strategically planted, and then set fruit in areas where they become integrated into active networks of frugivory and seed dispersal (Peters et al., 2016). This means increasing the seed sources where there are strong numbers of frugivores naturally active. This can work in most cases because most island frugivores are generalists with broad diets that feed on a variety of fruiting species (Banack, 1998; Whelan et al., 1998), resulting in positive (facilitative) interactions between different species that co-occur in the same locality (Carlo, 2005). For example, Costa et al. (2022) have recently shown that well-preserved native forest fragments in Seychelles' inselbergs do act as sources of native seed propagules to the surrounding invaded forests due to the action of frugivores, thus providing a critical insurance service for future forests.

In contrast, for those species whose dispersal agents are extinct or extirpated, as described for many large-seeded plants and large-bodied frugivores, then assisted dispersal by humans, by reintroduced frugivores, or even by rewilding with non-native taxon

substitutes may be necessary. In a dramatic example of the latter, dispersal and subsequent recruitment of a critically-endangered, large-seeded tree (*Diospyros egrettarum*) were restored when Aldabran tortoises (*Aldabrachelys gigantea*) were introduced to replace the function of extinct tortoises on Ile aux Aigrettes off Mauritius (rewilding) (Griffiths et al., 2011). However, in many cases, seed dispersing animals may recover, recolonise, or be reintroduced following habitat restoration, for example by eradicating invasive mammalian predators or herbivores (Anderson et al., 2006; Bellingham et al., 2010). In some cases, seeds may be dispersed in sufficient numbers, but to areas where they have little chance of recruitment (Holl, 1999). Understanding the structure of frugivore-plant networks on islands, and how they change across habitat boundaries, can reveal which frugivore species are keystones in the dispersal process owing to their greater ability to cross habitat boundaries and disperse seeds into degraded habitats (Carlo & Morales, 2016; Rehm et al., 2017; Thierry et al., 2022; Costa et al., 2022). On the other hand, effective disperser communities can lead to undesirable outcomes for attempts to restore deforested islands and for securing remaining remnants of forests, if dispersers favour (through high abundance of fruit) non-native plant species over native plant species with slower growth rates (e.g., *Pittosporum undulatum* in Jamaica, Bellingham et al., 2018) and the Azores (Heleno et al., 2013a, b), *Miconia calvescens* in Tahiti (Spotswood et al., 2012), *Morella faya* (Huenneke & Vitousek, 1990; Woodward et al., 1990) or *Clidemia hirta* (Sperry et al., 2021) in Hawai'i, *C. hirta* and *Cinnamomum verum* in the Seychelles (Costa et al., 2022), *Bischofia javanica* in the Ogasawara Islands (Abe et al., 2018) or *Aristotelia chilensis* in Juan Fernández (Smith-Ramírez et al., 2013). This is especially pertinent on islands where natural disturbance regimes (e.g., cyclones, volcanoes) may enhance opportunities for expansion of populations of non-native, fast-growing species (Fernández-Palacios et al., 2021). At the same time, strategic planting of a species with properties that make it a strong interactor in frugivory networks (e.g., long fruiting periods, González-Castro et al., 2015b; Peters et al., 2016) can make it serve as an attractor and facilitation nexus for the formation of forest nuclei (Holl et al., 2017). It is clear that restoration efforts should be guided by theoretical advances in our understanding of mutualistic networks (Peters et al., 2016). Therefore, more studies in island settings are needed to test and develop appropriate strategies to restore and conserve communities of native plants that rely on frugivorous agents of dispersal.

Conclusions, Information Gaps and Future Avenues of Research

This is the first review on frugivory and seed dispersal studies carried out on islands worldwide. Despite the descriptive observations of voyagers and naturalists in earlier centuries, most information on frugivory and endozoochory has been published during the last two decades. One of the first patterns emerging from the review is that knowledge measured as the number of papers published on frugivory and seed dispersal on islands is unevenly distributed among biogeographic regions, with most information deriving from the subtropics, especially the Canary Islands and Puerto Rico. The disproportionate contributions to the literature from a subset of authors/researchers account for some of this biogeographic disparity. Much of the research is concentrated in the archipelagos where there are research universities or research

stations. Furthermore, a serious gap clearly exist in parts of the Indian Ocean and in the Pacific Ocean (e.g. the smaller Melanesian and Micronesian islands), where numerous archipelagos are located. This uneven distribution among biogeographic regions gives us an incomplete view of frugivory and seed dispersal on islands.

To advance our knowledge of frugivory and seed dispersal on islands, it would be valuable to compile complete lists of fleshy-fruited plants and frugivorous animals for each archipelago, or at least a significant representation of them, given the great number of existing islands. These lists would be further improved if they were supplemented with functional trait data for the existing species of plants and animals (native and non-native), and inferred traits of extinct species. Compiling these lists requires considerable effort and time, but if they were available for many islands and archipelagos across all biogeographic regions, they would facilitate macroecological studies and allow us to determine whether patterns that have been described from individual islands and archipelagos are general. The compilation of this information would also advance our understanding of how islands differ from continental systems.

Islands are ideal places to study ecological drivers of key interactions, especially if studies are coordinated among islands by using comparable methods to examine questions across gradients of diversity, isolation, or disturbance. A parallel situation may exist with respect to vertebrate seed predators and the plants they consume. On many oceanic islands, the original seed predators were largely endemic birds, including parrots, pigeons, and a variety of large, flightless species. Today, roughly 90% of the endemic, seed-eating vertebrates on some islands have been replaced by globally invasive species of birds, rodents, and pigs (Carpenter et al., 2020). The non-native rodents, with their teeth and generalist diets, may interact with plants very differently from native granivorous birds, for example by adding a novel secondary-dispersal stage to bat-dispersed seeds (McConkey et al. 2003; Drake & McConkey 2021).

One aspect of islands that both complicates our understanding of frugivory and seed dispersal, while also offering unprecedented opportunities, results from the fact that ecosystems on nearly all islands have been strongly modified by humans. In addition to habitat destruction, islands have experienced high rates of species extinctions and invasions of both plants and animals relative to comparable continental ecosystems (Fernández-Palacios et al., 2021). These changes have resulted in profound impacts on interactions among native species, while simultaneously creating novel interactions among species brought together for the first time (Fricke & Svenning 2020). However, we still have incomplete knowledge about the disruption of seed dispersal (and seed predation) interactions caused by extinctions and/or by novel interactions with invasive animals, especially those that show wide distributions, such as rodents (rats and mice), ungulates (especially goats), lagomorphs (mainly rabbits) and carnivores (feral cats, ferrets, or mongooses).

As we gain knowledge about how patterns of frugivory and seed dispersal on islands have changed through time, we can apply that knowledge to conservation. Conservation efforts can be focused on species identified as playing key roles in networks. Introduced alien species can be assessed for their ability to replace the roles of extinct native species or to reconnect species that had dropped out of networks when their native partners were lost. Conversely, problematic invasive species can

be identified and removed from networks if they are determined to be facilitating invasion (invasional meltdown).

Though much island biodiversity has been lost, it may be possible to halt or reverse the ongoing decline by gaining a deeper understanding of key biological interactions that maintain biodiversity, such as frugivory and seed dispersal, and employing that knowledge to conserve and restore functioning island ecosystems.

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Declarations

Conflict of Interest The authors declare that the present work has non-financial interest and that there is no conflict of interest regarding the publication of this article. All data that support the findings of this study will be available contacting with the first author of the manuscript (MN).

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