

REVIEW

Frugivory and seed dispersal in the Galápagos: what is the state of the art?

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Abstract

The Galápagos are considered a model oceanic archipelago, with unique flora and fauna currently threatened by alien invasive species. Seed dispersal is an important ecosystem function with consequences for plant population dynamics and vegetation structure. Hence, understanding the seed dispersal abilities of the assemblages of frugivores will inform scientists and managers of the dynamics of plant invasions and improve management planning. Here we provide the first comprehensive review of published information on frugivory and animal seed dispersal in the Galápagos. We collected data from a variety of sources, including notes of the first naturalist expeditions, gray literature available only in Galápagos collections, and peer-reviewed journal articles. Plant–animal frugivorous interactions were retrieved from 43 studies and compiled into an interaction matrix describing 366 unique interactions. Most studies focused on fruit consumption as a driving force for natural selection, but seed fate was seldom considered. Although most (71%) of the interactions involved native plants, more than one-quarter (28%) involved introduced species. Interactions involving birds are considerably more common than those of reptiles and mammals, probably reflecting a research bias towards birds. Despite the historical importance of the archipelago as the laboratory for evolutionary and ecological research, understanding of its seed dispersal systems is limited. We end the review by suggesting 3 priority areas of research on frugivory and seed dispersal in the Galápagos: (i) target research to close knowledge gaps; (ii) the use of a network approach to frame seed dispersal at the community level; and (iii) evaluation of the effect of seed dispersal as a selective pressure acting upon plants and frugivores. Finally, the output of this research has to be properly delivered to the Galápagos National Park Services to help increase management effectiveness.

Key words: conservation planning, oceanic islands, plant invasions, plant–animal interaction, seed predation.

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INTRODUCTION

For sessile organisms, such as plants, for which seeds usually represent the only mobile stage, seed dispersal is a key service that increases the likelihood of seeds surviving and becoming established adults (Ridley 1930; Van

der Pijl 1982; Nathan & Muller-Landau 2000). Seed dispersal allows plants to occupy newly available niches, avoid competition, find suitable physical conditions for the germination of seeds, expand their area of distribution, and escape high mortality rates close to the parent plant due to shading or a high abundance of natural enemies (Janzen 1971; Howe & Smallwood 1982). By directly dispersing seeds to favorable recruitment sites (Wenny & Levey 1998) or by virtue of the treatment offered to ingested seeds (Verdú & Traveset 2004; Traveset *et al.* 2007), animals play an important role as seed dispersers for many plants (Levey *et al.* 2002; Dennis *et al.* 2007). Three classes of vertebrates assume particular relevance as seed dispersers, namely reptiles, birds, and mammals (Stiles 2000). Although birds and mammals are important in continental systems, birds and reptiles have a more significant role on islands, at least on those located at tropical and subtropical latitudes (Olesen & Valido 2003; Kaiser-Bunbury *et al.* 2010).

Seed dispersal communities around the globe are being altered by many factors, including pesticide poisoning, hunting, habitat fragmentation, and biological invasions. The likely consequences of such disruptions include a reduction in the diversity of mutualistic species and changes in the densities of survivors (Bond 1994). Given the global scale of lost and degraded habitats, understanding the processes that dictate the movement of seeds (and

therefore plants) between disturbed and pristine areas could prove crucial for effective conservation programs.

Despite their poverty in terms of the absolute number of species (MacArthur & Wilson 1967), oceanic islands are critically important for the particular biodiversity they harbor (Carlquist 1974; Porter 1976). Island ecosystems typically support unique biotic communities, with a higher proportion of endemic taxa than continents (Paulay 1994). Consequently, these species-poor island communities evolve under low pressure from competitors and natural enemies, rendering island ecosystems especially vulnerable to the introduction of exotic species (for a review, see Van Leeuwen *et al.* 2005). Therefore, it is not surprising that 80% of the recorded extinctions since ca. 1600 have occurred on islands (Groombridge 1992).

There is now an increasing recognition that species lists alone provide limited information to guide conservation efforts because they ignore complex networks of antagonistic and mutualistic interactions that maintain functional natural communities (Bond 1994; Bascompte *et al.* 2003). These interactions, although recognized by early ecologists (Darwin [1859] referred to them as nature's “entangled bank”), are still not given the attention they deserve in conservation planning (Memmott *et al.* 2007), particularly on oceanic islands (Kaiser-Bunbury *et al.* 2010). This is due, in large part, to a scarcity of information on frugivory and seed dispersal on oceanic islands,

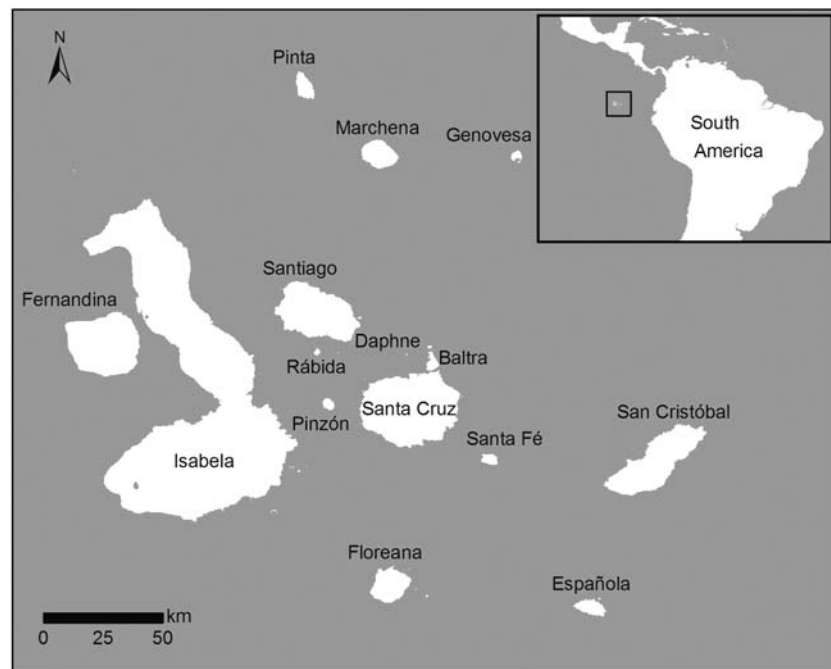


Figure 1 Map of the Galápagos archipelago, showing its global location (inset) and the main islands.

as well as to the high investments in sampling effort and financial resources required.

Owing to their relative ecological simplicity, their spatial isolation, and the high degree of endemism, islands are frequently referred to as “natural laboratories” for the study of evolutionary and ecological processes. Despite the central role of the Galápagos for the origin and development of new concepts in ecology and evolution, our understanding of several important ecological processes, particularly that of seed dispersal, in the archipelago remains basic. Here, we begin filling this gap by assembling and synthesizing information from disparate sources into a review of the knowledge of endozoochorous seed dispersal systems in the Galápagos. Our objectives are 2-fold: (i) to compile existing information on the interactions between plants and frugivorous animals in the Galápagos; and (ii) to highlight particular areas where research on frugivory and seed dispersal can prove particularly relevant in both theoretical and applied terms.

The Galápagos archipelago

The Galápagos archipelago straddles the equator (1°40'N–1°36'S, 89°16'–92°01'W) in the Eastern Pacific, approximately 960 km west of mainland Ecuador (Fig. 1). With an area of 7882 km², the archipelago consists of 123 islands of volcanic origin, rising from a few meters to approximately 1700 m above sea level (Tye *et al.* 2002). Seven of the islands are larger than 100 km² and 18 are greater than 1 km² (Snell *et al.* 1996). The oldest lava flows on the eastern islands have been aged to no more than 4 million years, whereas the youngest islands, Fernandina and Isabela, to the west, are less than 0.5 million years old (White *et al.* 1993). The isolation and location of the archipelago with respect to oceanic currents and trade winds have favored a high degree of endemism: 59% of all vertebrates are endemic (Tye *et al.* 2002), with endemism especially high among terrestrial birds (84%).

The flora of the Galápagos is closely related to that of South America, from where most plant propagules originated (Hooker 1847), probably transported to the archipelago by oceanic currents, wind, or birds (either as ingested seeds or attached to the body; Porter 1983). Differences in the dispersal efficiency of plant families resulted in a disharmonic flora, typical of oceanic islands (Baur 1891). The Galápagos flora consists of approximately 557 native (including 62 doubtfully native) vascular plant species, of which approximately 185 are endemic and 825 are exotic species (Galápagos flora database, Charles Darwin Research Station 2010; but see also Van Leeuwen *et al.* 2008).

The native vegetation is distributed in distinct zones that are largely related to local climatic conditions (Wiggins & Porter 1971). These zones are classified as follows: (i) the littoral zone, including the mangroves; (ii) the arid zone, which dominates the archipelago, found on all but the smallest islets, and contains the highest plant endemism (including *Opuntia* and other Cactaceae) and has the greatest diversity of plant communities (Tye *et al.* 2002); (iii) the transition zone, located between the arid and humid zones, containing a mixture of plants from these 2 zones; and (iv) the humid zone, which forms the wettest and most biologically productive regions of the archipelago because of high precipitation (Wiggins & Porter 1971; Tye *et al.* 2002). Only 7 islands are high enough to develop a humid zone (San Cristóbal, Santa Cruz, Floreana, Fernandina, Santiago, Isabela, and Pinta).

Plant invasions are concentrated, but not limited to, the 4 inhabited islands (Santa Cruz, San Cristobal, Isabela, and Floreana), particularly impacting humid habitats surrounding the agricultural and urban zones (Guerrero *et al.* 2007; Guézou *et al.* 2010).

Several invasive plant species, including the fleshy-fruited *Psidium guajava* (guava) and *Rubus niveus* (blackberry), have severely altered the composition and structure of the natural ecosystems (Jaramillo 1999; Tye *et al.* 2007). The Galápagos National Park maintains a permanent control program for invasive species in areas of high ecological value on the 4 populated islands, investing approximately US\$0.5 million each year (Parque Nacional Galápagos 2009).

The seasonal climate of the Galápagos is atypical of other equatorial oceanic islands because of its location in the eastern Pacific, which means that it is influenced by several weather systems and oceanic currents (Colinvaux 1984). There are 2 distinct climatic seasons in the Galápagos. The hot season prevails from January to May and is characterized by warm sea and air temperatures (24–29 °C) with a highly variable rainfall (ranging between 64 and 2769 mm annually on the coast). The cool season occurs from June to December and is characterized by prolonged cloud cover and perpetual drizzle in the highlands, little or almost no rain throughout the dry lowlands, and temperatures ranging between 19 and 23 °C (Trueman & d'Ozouville 2010). The cyclic El Niño events cause prolonged intense rains, usually followed by a period of drought (Snell & Rea 1999). Rainfall is lowest on the coast and increases with altitude, especially on the southern slopes of the highest islands (Tye *et al.* 2002).

Because of their relatively late discovery (1535), the

harsh conditions faced by settlers, and the early establishment of the Galápagos Natural Park, the archipelago has remained relatively unspoiled (Gardener *et al.* 2010). Throughout the last century, the establishment of permanent human settlements and, in particular, the deliberate introduction of exotic plants and animals severely impacted large areas of the archipelago (Mauchamp 1997; Sulloway 2009; Guézou *et al.* 2010). Nevertheless, the Galápagos is today one of the best-preserved oceanic archipelagos, where human impacts on many ecological processes are still relatively low (Thornton 1971; Loope *et al.* 1988), particularly in the uninhabited islands. Therefore, and notwithstanding the permanent threat posed by invasive species, the Galápagos archipelago offers one of the last opportunities to study little-altered natural processes, including seed dispersal.

MATERIALS AND METHODOLOGY

A thorough literature search was performed using Internet scientific search engines (<http://www.scholar.google.com> and <http://www.isiknowledge.com/WOS>), as well as by searching the publications available in the library of the Charles Darwin Foundation (Puerto Ayora, Santa Cruz, Galápagos).

All interactions that described the consumption of fruits or seeds by animals were extracted and coded according to 4 categories as follows: (i) “frugivory” if fruit consumption is confirmed without clear information on seed fate; (ii) “seed predation” if there is evidence of the physical or chemical destruction of seeds; (iii) “potential seed dispersal” if entire seeds are identified in stomach contents or feces, but there is no confirmation of seed viability; and (iv) “seed dispersal” if viability of the dispersed seeds is observed. Broad or ambiguous taxonomic groups, such as finches, birds, or grasses, were not included in the analysis but, when relevant, are discussed in the literature review. Differences in the interaction frequency between animals and plants were explored applying likelihood ratio tests. For analysis, multiple interaction types (e.g. seed predation, seed dispersal) assigned to the same plant–animal pair were treated as independent observations.

RESULTS

Chronological literature overview

The first naturalists to explore the Galápagos Islands, including Charles Darwin, focused chiefly on the taxonomy and morphology of the fauna and flora, with little account of any interactions observed between the two. At the begin-

ning of the 20th century, particularly with the expedition of the California Academy of Sciences (1905–1906), explorers provided the first systematic records of frugivory in the archipelago (Stewart 1911; Gifford 1919), although most attention was still devoted to establishing the taxonomic borders of species and only a few feeding records were provided of the most conspicuous interactions, usually from giant tortoises (*Chelonoidis nigra*) and land iguanas (*Conolophus* spp.) (Beebe 1924).

Despite his short stay in the Galápagos, ornithologist David Lack’s observations supported the idea that access to food, particularly fruit and seeds, could be the selective pressure driving the morphological differences among Galápagos finches (Lack 1947). Lack’s work, and subsequent studies (e.g. Bowman 1961), brought considerable attention to frugivory and granivory among this group of birds, although none of the studies considered the potential role of seed dispersal. Although the potential role of Galápagos finches as seed dispersers did not strike Richard Bowman, giant tortoises did and, in 1961, Charles Rick and Bowman published the first study on animal seed dispersal in the Galápagos (Rick & Bowman 1961). They explored the positive effect of seed ingestion by giant tortoises on the germination of Galápagos tomato (*Solanum cheesmanii*) seeds, which experienced extremely low germination rates in the absence of tortoise dispersal. Later, the same experimental approach was extended to birds and showed that Galápagos mockingbirds (*Mimus parvulus*) enhanced the germination of *S. cheesmanii*, whereas Galápagos finches (*Geospiza magnirostris* and *Platyspiza crassirostris*) acted mainly as seed predators (Rick 1964). Although thorough investigations, the work of Rick and Bowman was based on fruit fed to captive animals and seed dispersal in the wild remained unstudied, with only a passing reference to seeds of *S. cheesmanii* recovered from the feces of *Rattus* sp. that did not germinate (Rick 1964). More recent studies have shown that consumption by giant tortoises and land iguanas increases the germination rate of *Opuntia echios* (Estupiñán & Mauchamp 1995) and that Galápagos mockingbirds generally pass the seeds of ingested fruits intact, whereas medium (*Geospiza fortis*) and small (*G. fuliginosa*) ground finches usually crush the seeds before ingesting them (Buddenhagen & Jewell 2006).

The long-term studies by Peter and Rosemary Grant and their students, chiefly on Daphne Major but also in Genovesa and several other islands, are a milestone in our understanding of how selective pressures shape species evolution and of plant–animal interactions in the Galápagos. Their long-term datasets follow the evolution-

ary ecology of ground finches from what was probably the worst drought of the century (1977) to the extraordinary El Niño of 1982–1983 (the year of the “great flood” [Grant & Grant 1987; Weiner 1995]). On what is an extremely dry archipelago, rain is a limiting factor for vegetation productivity and, consequently, for frugivorous and granivorous animals (Boag & Grant 1984). The Grants and their colleagues established that the 4 species of ground finches on Daphne Major are highly dependent on seeds. During years of average or above average rainfall, all species can find enough seeds to survive and reproduce and there is considerable overlap in their diets. However, in years of low rainfall, and consequently low fruit and seed availability, birds that cannot compete successfully will not survive. Under such conditions, each species specializes in a particular niche for which its beak shape confers some advantage: small ground finches specialize in eating small, soft seeds (e.g. *Paspalum galapageia*, *Aristida repens*), the medium ground finches diversify their diets to encompass most seeds available, large ground finches (*G. magnirostris*) specialize cracking large, hard seeds (e.g. *Tribulus cistoides*, *Bursera graveolens*) and cactus finches (*G. scandens*) specialize in *Opuntia* spp. seeds (Grant 1981; Schluter 1982a; Boag & Grant 1984). These studies also resulted in the first detailed descriptions of the diet of Galápagos birds. However, the authors focused on fruits and seeds as sources of energy for birds coping with difficult environments and did not quantify variables related to seed dispersal *per se*, such as the proportion of seeds that avoid finch predation and thus achieve dispersal (Grant & Grant 1982; Schluter 1982b). An important exception is the only study on secondary seed dispersal in the Galápagos by Grant *et al.* (1975), who discussed the role of predatory birds (short-eared owls [*Asio flammeus*] and Galápagos hawks [*Buteo galapagoensis*]) as seed dispersers because these species prey upon finches and rats, which regularly feed on fruits. The authors concluded that, although rare, secondary seed dispersal by these species might be disproportionately important for the long-distance, interisland dispersal of plants.

Two studies (Racine & Downhower 1974; Downhower & Racine 1976) took a different approach and framed plant–animal evolution from the plant’s perspective. These studies revealed that the morphology of *Opuntia* spp. and *Croton scouleri* is likely shaped by selective forces exerted by frugivores. Although highly speculative, these 2 studies represent the only attempt to make a link between the selective forces exerted by birds (predators and dispersers) on plant morphology and phenology.

Among reptiles, and although well represented on the Galápagos, the 7 species of endemic lava lizards (*Microlophus* spp.) have received relatively little attention from ecologists. In one of the few ecological studies on these species, Schluter (1984) discovered that herbivory increases with body size and that the seeds of *Lantana peduncularis* passed intact through the lizards’ digestive tract. Given the distribution and abundance of the genus, they are likely an underappreciated group in terms of their seed dispersal capacity. Carpenter (1969) provided another example of saurochory by describing seed dispersal of *Opuntia* spp. by land iguanas (*Conolophus* spp.). He also found several other species of seeds in droppings, but did not identify them. Although they are likely to be important dispersers, the only published accounts of frugivory in land iguanas are *Opuntia* spp., *Psidium galapageium*, and *Scutia spicata* (McMullen 1999).

The diet of the giant tortoises was studied by Cayot (1987), who compiled historical diet records and conducted her own studies with wild tortoises in Santa Cruz and Pinzón. She described over 60 taxa of plant foods, but only in 3 cases (*Citrus* sp., *Hippomane mancinella*, and *P. galapageium*) was the consumption of fruits confirmed. However, in an ongoing study on Santa Cruz, Steve Blake and colleagues have so far found at least 46 species of intact seeds from dung piles (Blake *et al.*, unpubl. obsv., 2010).

Studies of fruit consumption by mammals in the Galápagos are restricted to those of Deborah and David Clark on black rats (*Rattus rattus*) on Santa Cruz, Pinzón, and Santiago. Black rats include several fruits in their diet and, although they act primarily as seed predators, the dispersal of intact seeds was shown only for seeds of *Miconia robinsoniana* (Clark 1980; Clark 1981). In the same study, Clark and Clark (1981) observed that 10 years after the extermination of feral goats (*Capra hircus*) on the island of Santa Fé, the population of *Bursera graveolens* consisted of 2 distinct groups: (i) old, large adult trees; and (ii) juveniles recruiting away from the canopy of adult plants. The authors therefore speculated that animal seed dispersal must play an important role in the recruitment of this species. More recently, the use of the spool-and-line method suggested that the coexistence between the endemic Santiago rice rat (*Nesoryzomys swarthi*) and the invasive black rat could be maintained by differential fruit consumption (Gregory & Macdonald 2009). However, although this method is useful to detect plant visitation trends, it cannot accurately inform whether fruits are consumed, or on the treatment conferred to the seeds.

In his classic book on Galápagos natural history, Ian

Thornton (1971) first brought attention to the increasing threat that exotic vegetation poses to the native flora by suggesting that feral goats were dispersing the exotic guava (*P. guajava*). However, until recently, the role of animals as vectors of plant invasions was only supported by anecdotal references (e.g. cattle and birds; Schofield 1989; Lawesson & Ortiz 1994). Later, quantitative research evaluated the role of the introduced garrapatero (*Crotophaga ani*) as a potential seed disperser for both native and exotic plant species (Ballesteros 1984; Jara 1995; Soria 2006).

Most recently, 2 studies have attempted to quantify seed dispersal and measure dispersal effectiveness by conducting viability tests and germination trials of dispersed seeds. Soria (2006) assessed the role of 7 bird species on the dispersal of blackberry (*R. niveus*), one of the most problematic invasive plants in the archipelago. Of the 7 bird species investigated, 5 dispersed viable seeds, with the introduced garrapatero (*C. ani*) being the most effective. Contrary to general opinion, Guerrero and Tye (2009) found that Galápagos finches are not simply seed predators, but that they can also be important seed dispersers. All 9 species studied ate fruits and 7 species defecated viable seeds. Interestingly, feces from 2 species generally assumed as insectivorous, namely the woodpecker finch (*Camarhynchus pallidus*) and warbler finch (*Certhidia olivacea*), contained high proportions of intact seeds.

Frugivory and seed dispersal: a quantitative analysis

Plant–animal frugivorous interactions were retrieved from 43 studies (Appendix 1) and compiled into an interaction matrix (Table 1). Table 1 describes 366 unique interactions between 26 animal species and fruits or seeds of 136 plant species. Most of these interactions (174; 48%) refer to the consumption of fruits or seeds with no indication on seed fate (i.e. frugivory). Seed predation was confirmed in 150 (41%) of the interactions and seed dispersal was assumed in 83 (23%) cases, but seed viability was only confirmed on 6 occasions (1.6%).

Although the majority (72%) of interactions involve seeds of native species, more than one-quarter (28%) involve introduced species. Seed dispersal has more often been confirmed for Solanaceae and Cactaceae, due, in part, to the disproportionate influence of *Solanum lycopersicum* and *Opuntia echios*, respectively. Poaceae species dominate the records of frugivory and seed predation. Regarding animals, interactions involving birds are considerably more numerous than those involving reptiles and mammals, in terms of both seed dispersal (63%, 10%, and 27%, respectively) and

seed predation (68%, 0%, and 32%, respectively). There were no significant differences between the proportion of introduced fruits consumed by birds (28%), mammals (30%), and reptiles (22%; $G = 0.47$; $df = 2$; $P = 0.791$). Seed dispersal was more often confirmed or suggested (i.e. potential seed dispersal) for introduced plants (28% of the interactions) than for native plants (17%; $G = 6.63$; $df = 2$; $P = 0.036$). Similarly, seed dispersal (confirmed and potential) was proportionally more common among reptiles (50% of the interactions) than among birds (16%) or mammals (32%; $G = 62.6$; $df = 2$; $P < 0.001$).

DISCUSSION

Advances in our understanding of frugivory and seed dispersal in the Galápagos can be summarized in 3 general phases defined by 3 distinct time frames. For most of the 20th century, the debate has been dominated by the influence of seed consumption as a driving force for the morphological adaptations of animal species. This debate provided vast information on the consumption of fruits mostly by Galápagos finches; however, it has neglected the role of animals as seed dispersers. In the second phase, several studies focused on seed dispersal from at least 3 perspectives: (i) the treatment conferred to seeds by captive animals; (ii) the role of animal seed dispersal in assisting plant invasions; and (iii) the potential importance of secondary seed dispersal. Finally, 2 recent studies (Soria 2006; Guerrero & Tye 2009) applied stronger scientific protocols to assess seed dispersal effectiveness for focal groups of plants (*R. niveus*) and birds (Galápagos finches).

The data suggest that, despite the historical importance of understanding the diet of Galápagos finches, the critical ecosystem function of seed dispersal remains largely unknown for the archipelago. Given the relatively low animal diversity, plants on oceanic islands are generally served by a reduced number of seed dispersers (Kaiser-Bunbury *et al.* 2010). Therefore, shifts in the assemblage of frugivores can more easily influence future vegetation, and hence ecosystem structure, by altering seed deposition patterns. Clear examples of such disruptions have been documented in other oceanic archipelagos, such as Hawaii (Chimera & Drake 2010) and the Canary Islands (Nogales *et al.* 2005; López-Darias & Nogales 2008).

That introduced plants participate in 28% of the interactions compiled in the present study is a worrying statistic considering the uniqueness of the Galápagos endemic flora and particularly considering that introduced plants were more often involved in seed dispersal interactions (compared with frugivory and seed predation) than native plants.

Table 1 Interaction matrix between frugivores and seeding plants in the Galápagos based on published literature

Plant	Animal																										
	Origin	Mammalia					Aves							Reptilia													
		<i>Bos taurus</i>	<i>Capra hircus</i>	<i>Sus scrofa</i>	<i>Equus asinus</i>	<i>Rattus rattus</i>	<i>Oryzomys galapagoensis</i>	<i>Asio flammeus</i>	<i>Crotophaga ani</i>	<i>Mimus parvulus</i>	<i>Zenaida galapagoensis</i>	<i>Camarhynchus pallidus</i>	<i>Camarhynchus parvulus</i>	<i>Camarhynchus pauper</i>	<i>Camarhynchus psittacula</i>	<i>Certhidia olivacea</i>	<i>Geospiza conirostris</i>	<i>Geospiza difficilis</i>	<i>Geospiza fortis</i>	<i>Geospiza fuliginosa</i>	<i>Geospiza magnirostris</i>	<i>Geospiza scandens</i>	<i>Platyspiza crassirostris</i>	<i>Conolophus pallidus</i>	<i>Conolophus subcristatus</i>	<i>Chelonoidis nigra</i>	<i>Microtophus pacificus</i>
Acanthaceae																											
<i>Blechnum pyramidatum</i>	N					F							P							P							
<i>Tetramerium nervosum</i>	N					P																					
Aizoaceae																											
<i>Trianthes portulacastrum</i>	N															F	P	F			P						
Amaranthaceae																											
<i>Alternanthera echinocephala</i>	N																	F	P			F					
<i>Amaranthus sclerantoides</i>	E									F																	
Anacardiaceae																											
<i>Spondias purpurea</i>	i											F						F	F		F	F					
Apocynaceae																											
<i>Vallesia glabra</i>	N							F										F									
Asteraceae																											
<i>Adenostemma platyphyllum</i>	i										d									d							
<i>Ageratum conyzoides</i>	N																			P							
<i>Bidens pilosa</i>	i											P							F	F							
<i>Blainvillaea dichotoma</i>	N					P																					
<i>Lactuca sativa</i>	i																		F	F							
<i>Porophyllum ruderale</i>	i					P																					
<i>Pseudelephantopus spiralis</i>	i																			P							
<i>Scalesia incisa</i>	E																			P							
<i>Scalesia pedunculata</i>	E					d									d			P	P								
<i>Sonchus oleraceus</i>	i																			P							
Boraginaceae																											
<i>Cordia leucophlyctis</i>	E																		P	F		F					
<i>Cordia lutea</i>	N					P	d	F	d				F	P				P		d							
<i>Heliotropium angiospermum</i>	N					P				F								F	P			F					
<i>Tournefortia psilostachya</i>	N					F		d				P							P	d	P	F					
<i>Tournefortia pubescens</i>	E							d													P						
<i>Tournefortia rufo-sericea</i>	E								d			P							P	P	P						
Brassicaceae																											
<i>Brassica oleracea</i>	i																		F	F							
Burseraceae																											
<i>Bursera graveolens</i>	N					d		F		d	F	F				F		d	F	d	F						
<i>Bursera malacophylla</i>	E																		F	F	F	F					
Cactaceae																											
<i>Opuntia echios</i>	E					P			d	d									d	d		d	F	d	d		
<i>Opuntia galapageia</i>	E																				P					F	
<i>Opuntia helleri</i>	E								F								d				F						
<i>Opuntia megasperma</i>	E																P									d	
Caesalpinaceae																											
<i>Parkinsonia aculeata</i>	N					P																					
Cannaceae																											
<i>Canna lambertii</i>	N					d																					
Caricaceae																											
<i>Carica papaya</i>	i																							F			
Celastraceae																											
<i>Maytenus octogona</i>	N										F								F	d	F		F				

continued

continued

Plant	Origin	Animal																									
		Mammalia				Aves						Reptilia															
		<i>Bos taurus</i>	<i>Capra hircus</i>	<i>Sus scrofa</i>	<i>Equus asinus</i>	<i>Rattus rattus</i>	<i>Oryzomys galapagoensis</i>	<i>Asio flammeus</i>	<i>Crotophaga ani</i>	<i>Mimus parvulus</i>	<i>Zenaida galapagoensis</i>	<i>Camarhynchus pallidus</i>	<i>Camarhynchus parvulus</i>	<i>Camarhynchus pauper</i>	<i>Camarhynchus psittacula</i>	<i>Certhidia olivacea</i>	<i>Geospiza conirostris</i>	<i>Geospiza difficilis</i>	<i>Geospiza fortis</i>	<i>Geospiza fuliginosa</i>	<i>Geospiza magnirostris</i>	<i>Geospiza scandens</i>	<i>Platyspiza crassirostris</i>	<i>Conolophus pallidus</i>	<i>Conolophus subcristatus</i>	<i>Chelonoidis nigra</i>	<i>Microlophus pacificus</i>
Commelinaceae																											
<i>Commelina diffusa</i>	N																			P							
Convolvulaceae																											
<i>Evolvulus convolvuloides</i>	N					P																					
<i>Ipomoea linearifolia</i>	E									F							F	F	F								
<i>Ipomoea triloba</i>	N					P											F	F	F								
<i>Merremia aegyptica</i>	N					P				d																	
Cucurbitaceae																											
<i>Momordica charantia</i>	i										F		F					d	F					F			
Cyperaceae																											
<i>Cyperus andersonii</i>	E																			P							
<i>Cyperus confertus</i>	N																			P							
<i>Kyllinga brevifolia</i>	N											d							d	d							
<i>Rhynchospora rugosa</i>	N																			P							
<i>Scleria melaleuca</i>	N																		P								
Euphorbiaceae																											
<i>Acalypha parvula</i>	E																		F		F			F			
<i>Chamaesyce amplexicaulis</i>	E						d			F							F	F	d	F		F					
<i>Chamaesyce ophthalmica</i>	i					P													F								
<i>Chamaesyce recurva</i>	E									F							F		F			F					
<i>Chamaesyce punctulata</i>	E																		P								
<i>Croton scouleri</i>	E					P			F								F	F	F	F	F	F	F				
<i>Hippomane mancinella</i>	N																		F	F		F				d	
Fabaceae																											
<i>Crotalaria pumila</i>	N					P																					
<i>Neptuna plena</i>	N																F				F						
<i>Pisum sativum</i>	i																							F			
<i>Rhynchosia minima</i>	N																		F	P	P						
Lauraceae																											
<i>Persea americana</i>	i		d																								
Loasaceae																											
<i>Mentzelia aspera</i>	N					d																					
Malvaceae																											
<i>Abutilon depauperatum</i>	E					P																F					
<i>Bastardia viscosa</i>	N					P																					
<i>Hibiscus diversifolius</i>	N					P																					
<i>Sida rhombifolia</i>	i											P								P							
<i>Sida salviifolia</i>	i																	F	F			F					
<i>Sida spinosa</i>	N																		F								
Melastomataceae																											
<i>Miconia robinsoniana</i>	E					d					d	d	d	d						d				d			
Mimosaceae																											
<i>Prosopis juliflora</i>	N					d											F				F					F	
<i>Acacia macracantha</i>	N					P																					
<i>Acacia rorudiana</i>	N											F									P						
<i>Desmanthus virgatus</i>	N					P											F										
Moraceae																											
<i>Ficus benjamina</i>	i																						F	F			

continued

continued

Plant	Origin	Animal																									
		Mammalia					Aves					Reptilia															
		<i>Bos taurus</i>	<i>Capra hircus</i>	<i>Sus scrofa</i>	<i>Equus asinus</i>	<i>Rattus rattus</i>	<i>Oryzomys galapagoensis</i>	<i>Asio flammeus</i>	<i>Crotophaga ani</i>	<i>Mimus parvulus</i>	<i>Zenaida galapagoensis</i>	<i>Camarhynchus pallidus</i>	<i>Camarhynchus parvulus</i>	<i>Camarhynchus pauper</i>	<i>Camarhynchus psittacula</i>	<i>Certhia olivacea</i>	<i>Geospiza conirostris</i>	<i>Geospiza difficilis</i>	<i>Geospiza fortis</i>	<i>Geospiza fuliginosa</i>	<i>Geospiza magnirostris</i>	<i>Geospiza scandens</i>	<i>Platyspiza crassirostris</i>	<i>Conolophus pallidus</i>	<i>Conolophus subcristatus</i>	<i>Chelonoidis nigra</i>	<i>Microlophus pacificus</i>
Musaceae																											
<i>Musa acuminata</i>	i					P																					
Myrtaceae																											
<i>Psidium galapageium</i>	E				F																			F	d		
<i>Psidium guajava</i>	i		d	d														F	F							d	
Nyctaginaceae																											
<i>Boerhaavia caribaea</i>	N																F	F	F	F							
<i>Boerhaavia erecta</i>	N															F	F	F									
<i>Commicarpus tuberosus</i>	N																		P								
<i>Cryptocarpus pyriformis</i>	N																		P	F	d						
<i>Pisonia floribunda</i>	E																						F				
Orchidaceae																											
<i>Epidendrum spicatum</i>	E					d																					
Oxalidaceae																											
<i>Oxalis dombeyi</i>	N						P																				
Passifloraceae																											
<i>Passiflora edulis</i>	i	d	d																P							d	
<i>Passiflora foetida</i>	E					d												P		P							
<i>Passiflora incarnata</i>	i																									F	
<i>Passiflora suberosa</i>	N					F		d																			
Plumbaginaceae																											
<i>Plumbago scandens</i>	N									F																	
Poaceae																											
<i>Antheophora hermaphrodita</i>	i					P																					
<i>Aristida repens</i>	E																		P								
<i>Aristida subspicata</i>	E															F	F	F			F						
<i>Bouteloua disticha</i>	i					P																					
<i>Cenchrus platyacanthus</i>	E															F	F		F	F							
<i>Digitaria horizontalis</i>	i										P								P	P							
<i>Eleusine indica</i>	i																			P							
<i>Eragrostis cilianensis</i>	i															F	F	F									
<i>Eragrostis ciliaris</i>	N									F										P							
<i>Ichmanthus nemorosus</i>	i					d																					
<i>Panicum dichotomiflorum</i>	N																				P						
<i>Panicum hirticaule</i>	N								P												P						
<i>Panicum maximum</i>	N											P									P						
<i>Urochloa multiculma</i>	E					P										F	F	F			F						
<i>Paspalum conjugatum</i>	i					P						d							P	d							
<i>Paspalum galapageium</i>	E																		P	P	P						
<i>Pennisetum purpureum</i>	i																			P							
<i>Setaria parviflora</i>	N																			P							
<i>Setaria setosa</i>	N																		P	P							
<i>Sporobolus indicus</i>	N											P								P							
<i>Zea mays</i>	i																		F								
Portulacaceae																											
<i>Portulaca howellii</i>	E									F									F			F					
<i>Portulaca oleracea</i>	i					P													d	d	P	P					
<i>Portulaca umbraticola</i>	i					P																					
<i>Sesuvium edmonstoneii</i>	N									F																	
<i>Sesuvium portulacastrum</i>	N																				d						

continued

continued

Plant	Origin	Animal																										
		Mammalia					Aves					Reptilia																
		<i>Bos taurus</i>	<i>Capra hircus</i>	<i>Sus scrofa</i>	<i>Equus asinus</i>	<i>Rattus rattus</i>	<i>Oryzomys galapagoensis</i>	<i>N. Asio flammeus</i>	<i>Crotophaga ani</i>	<i>Mimus parvulus</i>	<i>Zenaida galapagoensis</i>	<i>Camarhynchus pallidus</i>	<i>Camarhynchus parvulus</i>	<i>Camarhynchus pauper</i>	<i>Camarhynchus psittacula</i>	<i>Certhidia olivacea</i>	<i>Geospiza conirostris</i>	<i>Geospiza difficilis</i>	<i>Geospiza fortis</i>	<i>Geospiza fuliginosa</i>	<i>Geospiza magnirostris</i>	<i>Geospiza scandens</i>	<i>Platyspiza crassirostris</i>	<i>Conolophus pallidus</i>	<i>Conolophus subcristatus</i>	<i>Chelonoidis nigra</i>	<i>Microlophus pacificus</i>	
Rhamnaceae																												
<i>Scutia spicata</i>	N							F			F							P	F	P	d	F		F				
Rosaceae																												
<i>Rubus niveus</i>	i				P			D		D	D		F	F				P	D	D								
Rubiaceae																												
<i>Chiococca alba</i>	N							F			F													F				
<i>Coffea arabica</i>	i																							F				
<i>Psychotria rufipes</i>	E				d					F	F			F					F				F					
Rutaceae																												
<i>Zanthoxylum fagara</i>	N				P						F							P		P								
Sapindaceae																												
<i>Cardiospermum galapageium</i>	E							F																				
Scrophulariaceae																												
<i>Capraria biflora</i>	N																			d								
Simaroubaceae																												
<i>Castela galapageia</i>	E				F																F							
Solanaceae																												
<i>Capsicum frutescens</i>	i																							F				
<i>Grabowskia boerhaaviaefolia</i>	N				P														F		F							
<i>Iochroma ellipticum</i>	E				P																							
<i>Nicotiana tabacum</i>	i													F					F									
<i>Physalis galapagoensis</i>	E				d																							
<i>Physalis pubescens</i>	N				d																							
<i>Solanum americanum</i>	i				d			d		F	d								d	d								
<i>Solanum cheesmaniae</i>	E				d																							
<i>Solanum lycopersicum</i>	i				d				d		d		d						d	d			d			D		
Sterculiaceae																												
<i>Waltheria ovata</i>	N									F																		
Urticaceae																												
<i>Pilea baurii</i>	E				d																							
Verbenaceae																												
<i>Lantana peduncularis</i>	E				P				F								F	F	F	F	F	F					d	
<i>Stachytarpheta cayennensis</i>	i																			P								
Viscaceae																												
<i>Phoradendron henslovii</i>	E										F		F											F				
Zygophyllaceae																												
<i>Tribulus cistoides</i>	i									F						F		F		F	P							

Interaction types: F, frugivory; D, seed dispersal; d, potential seed dispersal, results inconclusive; P, seed predation.

Origin: E, endemic; N, native; i, introduced.

Taxonomy and origin follow the information of the Galápagos flora database maintained by the Charles Darwin Research Station and consulted in January 2011.

Interestingly, and despite the large information deficit, 9 of the 18 interactions between plants and reptiles are of seed dispersal and there are no records of seed predation among this group. The apparent high effectiveness of rep-

tiles as seed dispersers contrasts with the lower effectiveness (*sensu lato*) of birds (56 dispersal interactions of 349 interactions in total). However, given the different research interests that have dominated reptile and bird studies in

the archipelago (with most avian studies focusing on seed predation), further unbiased studies are needed to clarify this pattern in the Galápagos, as shown for other tropical and subtropical archipelagos (Nogales *et al.* 2005).

Given the absence of specialized frugivores in the Galápagos, the potential importance of seed dispersal and its impacts has been underappreciated (Soria *et al.* 2002). However, recent studies in the Galápagos and elsewhere call for a re-evaluation of the role of animals typically disregarded as seed dispersers (Soria 2006; Guerrero & Tye 2009; Heleno *et al.* 2011).

Future avenues of research

Based on the present literature review, we highlight 3 promising avenues for future research and important steps to translate research output into action, as outlined below.

Systematic, un-biased and targeted baseline research

Data on frugivory and seed dispersal have not been collected either randomly or systematically, neither in space, time, nor through taxonomic groups. For logistic reasons, most studies have focused on inhabited or easily accessible islands (with some important exceptions) and, within these, on most accessible habitats (particularly the dry zone). Future studies should address these weaknesses by conducting multiyear studies and collecting data from poorly studied islands (e.g. Fernandina) and habitats (e.g. humid zone). Similarly, most studies have been conducted during non-random time frames, generally during the wet/hot season and only rarely including El Niño years, which hampers the ability to detect temporal trends. Most worrisome is that in some studies that encompass several islands, it is often not clear where each interaction was detected, something that should be corrected in future studies. Finally, studies have been biased towards birds, with much less information from other taxonomic groups (e.g. mammals and reptiles) and, within birds, considerably more effort has been devoted to identifying trophic rather than mutualistic interactions. A community-level approach to the implications of frugivory and seed dispersal for ecosystem functioning should be developed, particularly focusing on the challenge of maintaining functional habitats threatened by invasive plants.

Despite the status of “natural laboratory” often conferred to the Galápagos Islands (Jäger *et al.* 2007; but see also Deem *et al.* 2010), there has been no rigorous study on interisland seed dispersal. Secondary seed dispersal by raptors has been suggested to be disproportionately important to interisland seed dispersal (Grant *et al.* 1975). Molecular analysis suggests negligible interisland gene flow in the Galápagos hawk (Bollmer *et al.* 2005), sug-

gesting that it may not be important for seed dispersal between distant islands. Conversely, the recent discovery of several rodent skulls in short-eared owl (*A. flammeus*) pellets in Champion, a rodent-free islet by the coast of Floreana (Heleno, unpubl. data, 2010), strengthens the case for frequent interisland movements of these birds and their potential role as secondary seed dispersers, at least between nearby islands. As in other oceanic islands (Nogales *et al.* 2007), the importance of this mechanism remains largely underevaluated in the Galápagos. Given the good knowledge of each island’s flora and fauna, the archipelago offers a privileged situation for testing hypotheses related to interisland seed dispersal, such as the relative effectiveness of dispersal syndromes.

Finally, long-term information on the productivity of fruit-bearing plants would be extremely valuable when identifying patterns regarding the diet preferences of frugivorous animals. Grant and Grant (1990) pointed out that “This gap in our knowledge has pinpointed a general deficiency; there are no seed- and fruit-production values for any plant species in the Galápagos archipelago”. Even if progress has been made, there is still the need for consistent long-term patterns of fruit production.

A network approach

Ecological networks have provided useful tools for understanding and managing environmental threats, such as biological invasions, global change, habitat fragmentation, and the pollination crisis (Kremen & Hall 2005; Tylianakis *et al.* 2008; Heleno *et al.* 2009). Due to the simplified communities of oceanic islands, such an approach can be particularly insightful, although seed dispersal networks on islands are extremely rare (Kaiser-Bunbury *et al.* 2010). Ongoing research is taking this network approach for the first time in the Galápagos and is providing information on new interactions, on how the community of seed dispersers is structured, and on how alien invasive species may affect the topology of such networks.

High-quality, quantitative ecological networks, such as food webs or seed dispersal networks, can prove important in 3 stages of ecological conservation: (i) as a tool to detect and quantify direct and indirect impacts of a particular threat; (ii) as a roadmap to aid in the preparation of effective management plans aiming to manage communities as a whole; and (iii) as a benchmark to measure the success of restoration programs.

To implement such a holistic approach implies a large and systematic sampling effort to make sure all interactions (e.g. birds, mammals, and reptiles) are given the same detection probability; however, data obtained in this way

could be used to detect and predict often elusive impacts in species interactions patterns (Simberloff 2004; Kremen & Hall 2005).

Frugivory as a selective pressure

Dispersal is critically important for the biogeography and evolution of biodiversity on oceanic islands (Cowie & Holland 2006). The Galápagos archipelago has provided key information on how plants affect frugivores by changing food supply, but little is known about how frugivores affect plant population dynamics and evolution. Like frugivorous animals, plants too have to face reciprocal selective pressures by attracting legitimate seed dispersers while avoiding physical and chemical destruction from seed predators. Thus, natural selection is likely to benefit the recruitment of seeds not preferred by predatory finches. As described by Racine and Downhower (1974), the different assemblages of seed predators and seed dispersers in each island (Table 1) make the Galápagos an excellent location in which to test hypotheses in this field. For example, it has been suggested that the now extinct race of *Geospiza magnirostris* var. *magnirostris* of Floreana had an abnormally large beak that allowed it to exploit the similarly abnormal seeds of the endemic variety of *Opuntia megasperma* var. *megasperma* (Steadman & Zousmer 1988). In fact, the range loss of this plant, largely consumed by domestic animals, may explain the local extinction of this bird. Although highly plausible, both hypotheses are impossible to test *a posteriori*, highlighting the need for timely data.

The relative ecological simplicity and presence of a megaherbivore (the giant tortoise) in the Galápagos provides an excellent opportunity to study the impact of a potential ecosystem engineer on plant dynamics and community structure, with highly relevant practical applications. Galápagos tortoises can attain high biomass and are generalist herbivores with rather simple digestive processes; thus, much of their food passes through the gut relatively intact. Tortoises, especially giant tortoises, are keystone species in some environments (Hansen *et al.* 2010) and, with a body size an order of magnitude larger than any other terrestrial vertebrate, are likely to be so on the Galápagos. Galápagos tortoises are extinct on several islands, although there are plans for repatriation to restore these ecosystem processes (Tapia 2009). A critical component of these restoration programs will be to dedicate research to understanding the role of the tortoise in the Galápagos ecosystem functioning.

The dispersal of highly different seeds by a multitude of vectors, across habitats, and for highly variable distances is inherently hard to follow. Traditional methods of direct observations of movement patterns based on ra-

diotelemetry or mark–recapture methods do not render appropriate data to assess the extent of seed dispersal and plant colonization. Nevertheless, solutions are now available, such as stable isotopes analysis (Wang & Smith 2002; Carlo *et al.* 2009), radioactive labeling (Vander Wall 1994), and molecular genetic markers (Cain *et al.* 2000; Jordano *et al.* 2007).

In particular, the introduction of molecular techniques has made it possible to estimate gene flow and population genetic structure, and thus the colonization and evolutionary history, of populations. For example, the distribution of molecular lineages (phylogeography) of *Bursera* spp. is congruent with high interisland genetic exchange via seed dispersal by birds (Weeks & Tye 2009), a pattern shared by *Opuntia* spp. (Helsen *et al.* 2009).

Translating research outputs into management action

To become practically relevant, the results of the research described above needs to be communicated properly to the Galápagos National Park and other stakeholders. Information regarding seed dispersal may prove important in the conservation of threatened species and ecological restoration (Ingle 2003). The incorporation of a fleshy-fruited exotic plant into the diet of native frugivores, particularly birds (Timmins & Williams 1987), is frequently an important step in that species becoming invasive (Bartuszevige & Gorcho 2006; Buckley *et al.* 2006). Therefore, information on seed dispersal is most important when dealing with fleshy-fruited plant invasions (Williams & Karl 1996), possibly the threat with most potential impact in the Galápagos biota. Given the severe impact of invasive plants in the Galápagos and the amount of research dedicated by the Charles Darwin Foundation and the Galápagos National Park to the problem of invasive species, it is surprising that there is not a robust unified assessment of seed dispersal vectors in the archipelago.

Given the increasing prevalence of alien species worldwide (D'Antonio & Chambers 2006), restoration ecologists are frequently faced with the challenge of managing invaded ecosystems (Vander Zanden *et al.* 2006; Forup *et al.* 2008). As an ecosystem function with direct consequences for the biologic community, seed dispersal has often been suggested as an integrated yardstick with which to measure the effectiveness of ecological restoration (Olesen & Valido 2003; Heleno *et al.* 2010; Kaiser-Bunbury *et al.* 2010).

Another use of seed dispersal information is to identify the consequences for plants of the local extinction of

frugivores (Kaiser-Bunbury *et al.* 2010). In the Galápagos, there have been few local extinctions since human arrival (e.g. giant Tortoises on Pinta [now reintroduced], Santa Fé, and Floreana; the Floreana Mockingbird [*Mimus trifasciatus*] and the large-ground-finch [*G. magnirostris*] from Floreana; 3 endemic species of rice rat [*Oryzomys* spp.] from San Cristóbal; and possibly the vermilion flycatcher [*Pyrocephalus rubinus*] also from San Cristóbal). Without baseline information on the interactions that these species established in the communities they were integrated in and on the ecosystem functions they performed, it is now impossible to rigorously assess the community-wide effect of their absence.

Three applied problems where seed dispersal information is only recently being implemented for the first time, but where advances are most expected, are in improving eradication protocols for invasive plants, planning conservation strategies based on the manipulation of seed dispersal, and preventing further introductions. Finally, there is now a solid body of evidence suggesting that climate change will affect fruit production, seed dispersal, and the spread of exotic vegetation throughout the world (Dukes & Mooney 1999; Mainka & Howard 2010). Again, islands are at greater risk than continents (Kaiser-Bunbury *et al.* 2010); thus, accurate predictions and strategies to mitigate different kinds of impacts are critically needed (Mainka & Howard 2010).

The need of direct cooperation between scientists and conservation managers has been more often preached than put into practice. However, when cooperation has been possible, it has generally resulted in positive results for scientists, managers, and the ecosystems in which they work. The Galápagos is no exception and plant–frugivore interactions represent a highly desirable bridge.

The importance of seed dispersal for the Galápagos is reflected by the current research interest devoted to filling some of the information gaps highlighted in the present article. These studies include an assessment of the ecological role of giant tortoises as megaherbivores, the effectiveness of non-finch birds as seed dispersers, and the study of seed dispersal networks at the community level. We therefore expect that the coming years will substantially consolidate our understanding of the seed dispersal systems in this unique archipelago.

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APPENDIX I

References used to compile the plant–animal interactions described in Table 1.

	Disperser	References
Mammalia	<i>Bos taurus</i>	1–4
	<i>Capra hircus</i>	5
	<i>Sus scrofa</i>	1–3
	<i>Equus asinus</i>	6
	<i>Rattus rattus</i>	7–12
	<i>Oryzomys galapagoensis</i>	13, 14
Aves	<i>Asio flammeus</i>	13
	<i>Crotophaga ani</i>	12, 15
	<i>Mimus parvulus</i>	2, 13, 14, 16–18
	<i>Zenaida galapagoensis</i>	2, 13, 19
	<i>Camarhynchus pallidus</i>	12, 20, 21
	<i>Camarhynchus parvulus</i>	10, 12, 20–22
	<i>Camarhynchus pauper</i>	22
	<i>Camarhynchus psittacula</i>	10, 12, 20, 21
	<i>Certhidia olivacea</i>	21
	<i>Geospiza conirostris</i>	23–25
	<i>Geospiza difficilis</i>	24
	<i>Geospiza fortis</i>	2, 10, 12, 13, 20–22, 24–34
	<i>Geospiza fuliginosa</i>	10, 12, 20–22, 24, 28, 29, 31, 34
	<i>Geospiza magnirostris</i>	12, 13, 20, 21, 24–26, 28, 30, 32–34
<i>Geospiza scandens</i>	14, 20–24, 28, 29	
<i>Platyspiza crassirostris</i>	10, 21, 22, 25, 29	
Reptilia	<i>Conolophus pallidus</i>	35
	<i>Conolophus subcristatus</i>	2, 14, 20, 36–38
	<i>Chelonoidis nigra</i>	3, 6, 10, 14, 37–42
	<i>Microlophus pacificus</i>	43

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