

Dispersal of fig seeds in the Cook Islands: introduced frugivores are no substitutes for natives

S. C. Staddon · S. G. Compton · A. Portch

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Abstract Across the Pacific, island vegetation is altering in response to changes in seed disperser assemblages brought about by extinctions and introductions of birds and other animals. On the Cook Islands in the South Pacific, the Pacific Banyan (*Ficus prolixa*, Moraceae) is undergoing little if any recruitment, possibly linked to a lack of dispersal agents. On Rarotonga, where *F. prolixa* is found in semi-urban and agricultural environments, there is no recent recruitment in contrast to the situation on Atiu where the tree is common in native forest. We examined the quality and quantity of seed dispersal offered to *F. prolixa* by the available frugivores on these islands, comparing the effectiveness of extant native and introduced species. The native Cook Islands fauna, particularly birds and bats, appear to be the most effective seed dispersers of *F. prolixa*, both in terms of quantity and quality. Whilst these are relatively numerous on Atiu, they rarely visit *F. prolixa* on Rarotonga. The native Chocolate hermit crab *Coenobita cavipes* is a previously unreported additional native seed disperser, conferring low quantity, but high quality dispersal. Introduced birds and mammals are the most numerous *F. prolixa* frugivores on Rarotonga and in non-forest environments on Atiu, but they act mainly as seed predators. Consequently, the losses and rarity of remaining native frugivores have not been compensated for by introduced species on Rarotonga which may be contributing to the absence of recruitment there.

Keywords Atiu · *Ficus* · Extinction · Frugivory · Introduction · Rarotonga · Seed dispersal

S. C. Staddon (✉)
Institute of Geography, University of Edinburgh, Edinburgh EH8 9XP, UK
e-mail: s.c.staddon@sms.ed.ac.uk

S. C. Staddon · S. G. Compton · A. Portch
Centre for Biodiversity and Conservation, Faculty of Biological Sciences, University of Leeds,
Leeds LS2 9JT, USA

Introduction

Up to ninety percent of tropical tree species rely on fruit-eating animals for their seed dispersal (Howe and Smallwood 1982) and the potential effects of changing frugivore assemblages on ecosystems and individual plant species is of great concern. Frugivore assemblages may be altered through forest degradation and fragmentation (Cordiero and Howe 2001; Serio-Silva and Rico-Gray 2002; Babweteera and Brown 2009), through the introduction of exotic species (Christian 2001; Delgado Garcia 2002; Foster and Robinson 2007) and through human-induced extinctions or near-extinctions (Cox et al. 1991; Meehan et al. 2002). These studies of altered assemblages emphasise the importance of frugivore diversity for the maintenance of individual plant species and of suites of species within communities.

Consequences of the alteration of seed disperser assemblages are potentially far reaching in environments with naturally depauperate faunas, such as on isolated islands. Island plants have been shown to be vulnerable to extinction through the loss of pollinators (Cox et al. 1991) and, potentially, dispersers (Meehan et al. 2002; Riera et al. 2002). Introduced species may however functionally substitute native frugivores in their seed dispersal activities. Foster and Robinson (2007) report that introduced birds in Hawaii are the principal dispersers of native plant seeds into exotic-dominated vegetation, whilst Cox (1983) found that extinct pollinators of native Hawaiian plants have been replaced by an introduced bird.

Across the Pacific, habitat alteration, hunting, predation by exotic animals and the introduction of diseases by exotic birds has led to widespread faunal, and in particular avifaunal, decline over the last 2500 years (Steadman 1995, 2006). The Cook Islands archipelago in the South Pacific is no exception and whilst in the past the islands were home to a ‘medium sized’ frugivore community comprising ground doves, fruit doves, fruit pigeons, lorikeets and a fruit bat (Steadman 1997), only various remnants of that community now survive. Concurrent with extinctions, exotic plant and animal species have been introduced to the islands by both the Polynesians around 500–700AD and since the 1820s by Europeans (Allen and Wallace 2007; Pimm et al. 1995).

Compton and McCormack (1999) considered the situation of the fleshy-fruited Pacific Banyan fig tree *Ficus prolixa* in the Cook Islands, where on certain islands it is undergoing little if any recruitment. They compared the size of *F. prolixa* populations on various islands with the number of potential dispersers present and concluded that the abundance of *F. prolixa* is unrelated to the extent of potential disperser extinctions and introductions, and of disperser richness *per se*. This led them to pose the question—does the disruption of seed disperser mutualisms matter?

Frugivores differ in their ‘effectiveness’ of seed dispersal however and without knowledge of both the quality and quantity of seed dispersal by native and introduced frugivores the importance of alterations in frugivore assemblages cannot readily be assessed. The effectiveness of a seed disperser is defined as the contribution it makes to the future reproduction of a plant and comprises both quantitative and qualitative components (Schupp 1993). Quantity of seed dispersal depends on the number of visits made to the plant by a disperser and the number of seeds dispersed per visit. Quality of dispersal depends primarily on the treatment given in the mouth and gut and the quality of deposition and is determined by the probability that a deposited seed will survive and become an adult.

Here we describe both the quality and quantity of seed dispersal offered to *F. prolixa* by the frugivores that are potentially available on Rarotonga and Atiu in the Cook Islands. No recent recruitment of *F. prolixa* has been detected on Rarotonga, whereas on Atiu the tree

is common in native forest (Compton and McCormack 1999). In particular, we aimed to compare the dispersal abilities of the remnant extant native fauna with those of the frugivores introduced to the islands. Taxa not normally considered in such comparisons, including invertebrates, were assessed. By determining the effectiveness and contribution of native and introduced frugivores, we assess the likely consequences of further extinctions of native species or introductions of aliens.

Methods

Study area

The Cook Islands comprise numerous geologically diverse islands in the southern Pacific Ocean. Rarotonga (21°14'S, 159°46'W) is the largest and is a 'high volcanic island', reaching 653 m above sea level. Its approximately 10,000 inhabitants live on the narrow (<1 km wide) fertile coastal plain, whilst native forest covers the inland mountainous area (Robertson et al. 1994). Atiu (19°58'S, 158°08'W) is a 'raised island' composed of an elevated coral limestone platform, known by the Polynesian name of *makatea* (Franklin and Steadman 1991). The makatea surrounds a central plateau upon which the approximately 1,000 inhabitants live. Sinkholes, caves and clay-filled cracks are features of the makatea, which supports relatively undisturbed forest.

Study species

Ficus prolixa, the Pacific banyan or *ava* as it is known in Cook Island Maori, is a monoecious fig tree distributed across the South Pacific (Corner 1963). It is found on all the major Cook Islands and is largely a coastal species, capable of living on seashores and coral rock, although it also grows as an epiphytic strangler of other trees (Compton and McCormack 1999). *Ficus prolixa* have a fruiting phenology typical of monoecious fig trees, with between-tree fruiting asynchrony and within-tree fruiting synchrony, but larger plants can also spread vegetatively, forming clumps of semi-independent trunks that can fruit at different times. The figs reach up to about 10 mm in diameter, ripening from pale green to dark red or purple in colour. *Ficus prolixa* is rare on Rarotonga, where less than 20 individuals are known, all from the coastal plain, but it is common in the native forest on Atiu (Compton and McCormack 1999). *Platyscapha innumerabilis* is the host-specific fig wasp which pollinates *F. prolixa* and is present on both Rarotonga and Atiu (Vougioukalou 2000).

Nine species of pigeons (Columbidae) and three species of *Pteropus* fruit bats are recorded as dispersers of *F. prolixa* throughout its range (Shanahan et al. 2001). It is thought that the Cook Islands would once have been home to five or six species of Columbids (Franklin and Steadman 1991, Steadman 1995), of which two remain today on the islands studied; the Cook Islands fruit-dove *Ptilinopus rarotongensis* and the Pacific pigeon *Ducula pacifica*. The Insular flying fox *Pteropus tonganus* is the only indigenous mammal to the Cook Islands and is found on Rarotonga and another of the southern islands, Mangaia. The species is considered a recently arrived native on Rarotonga, having arrived there from Mangaia in around 1873; it is possible however that it was deliberately introduced (Smith 1898). Whilst only a small number of potential native seed dispersers remain, these have been supplemented by numerous introductions of species that will also eat fruit (Table 1). Non-volant potential dispersers, such as reptiles and land crabs, are considered in this study, as their role in both promoting and depressing seed dispersal is

Table 1 The potential dispersers of *Ficus prolixa* seeds on Rarotonga and Atiu, the Cook Islands

Potential dispersers		Frugivory	Rarotonga	Atiu
Native species				
<i>Ptilinopus rarotongensis</i>	Cook Islands fruit dove	O	✓	✓
<i>Ducula pacifica</i>	Pacific pigeon	O	✓	✓
<i>Aplonis cinerascens</i>	Rarotonga starling	F	✓	x
<i>Pteropus tonganus</i>	Insular flying fox	O	✓	x
<i>Coenobita cavipes</i>	Chocolate hermit crab	F	✓	✓
Introduced species				
<i>Acridotheres tristis</i>	Indian mynah	F	✓	✓
<i>Gallus gallus</i>	Domestic fowl	F	✓	✓
<i>Rattus exulans</i>	Pacific rat	F	✓	✓
<i>Rattus rattus</i>	Ship rat	F	✓	✓
<i>Rattus norvegicus</i>	Norwegian rat	F	✓	✓
<i>Gehyra oceanica</i>	Forest gecko	F	✓	✓
Total native species			5	3
Total introduced species			6	6
All species			11	9

O obligate frugivore; F facultative frugivore; ✓ present; x not present

increasingly being recognised, especially in island environments (Valido and Nogales 1994; Green et al. 1997; Whiting and Greef 1997; Nogales et al. 1998; Campbell and Atkinson 1999; Olesen and Valido 2003). On Rarotonga five native and six introduced frugivores are potential dispersers of *F. prolixa*, whilst on Atiu there are three native and six introduced.

Quantity of frugivory and seed dispersal

Between May and July 2000, crop sizes of three *F. prolixa* trees on Rarotonga and three on Atiu were estimated on a 3 point scale; <50, 50–500, >500 (Table 2). All trees studied on Rarotonga were located in semi-urban or agricultural (i.e., non-forest) environments whilst those on Atiu ranged from semi-urban environments to native forest. On Rarotonga, the rates of fig removal by diurnal frugivores (all birds) and nocturnal frugivores (bats, rats and crabs) were estimated using fruit traps made of plastic sheeting placed beneath fruiting branches. The number of figs on the branches were counted at the start of the survey period and then at dusk and dawn for 7 days. The number of figs collected in the traps beneath the branches was subtracted from these counts, leaving the number of figs removed by frugivores each day and night.

Frugivore activity at the trees was observed with binoculars from a suitable distance in order to minimise disturbance. Observations on Rarotonga were made at dawn (13.5 h in total), at dusk (5.5 h) and throughout one whole day (10 h), totalling 29 h. Observations on Atiu were carried out from dawn until midday, totally 21.5 h. For each visiting animal, the following were recorded: species, arrival and departure times, group size and main activities. During foraging, the numbers of figs eaten or knocked from the trees were also recorded. A Fruit Removal Index (FRI) was calculated for each frugivore species as the number of visits *times* mean length of visit *times* feeding rate (after Bronstein and Hoffman 1987).

Table 2 Characteristics of fruiting *Ficus prolixa* studied on Rarotonga and Aitut

Tree	Rarotonga			Aitut		
	1	2	3	4	5	6
Grid reference	4221E 76547N	4226E 76544N	4232E 76539N	5934E 77864N	5915E 77906N	5928E 77887N
Habitat	Non-forest (disturbed woodland)	Non-forest (mixed agriculture)	Non-forest (mixed agriculture)	Forest (forest on <i>makatea</i>)	Forest (forest on edge of <i>makatea</i>)	Non-forest (semi-urban)
Description	Large self-strangling	Large self-strangling	Large self-strangling	Medium self-strangling	Large self-strangling	Large, some descending roots
Crop size*	>500	>500	>500	50–500	>500	<50
Human disturbance	High	High	High	Low	Medium	High

* After Compton and McCormack 1999

Quality of frugivory and seed dispersal

Dispersal quality was measured as the germination success of dispersed seeds. The germination of fig seeds that had been eaten and subsequently defecated were compared with that of seeds obtained directly from the same parent trees. After counting, seeds were germinated in moistened filter paper-lined petri-dishes under ambient temperature and light conditions and recorded daily. The number of seeds per dish varied according to the number passed by each individual frugivore and the number of replicates per species also varied (see Table 3). The number of seeds germinating was recorded each day and the trials were ended after 21 days. Seeds from the Cook Islands fruit dove *Ptilinopus rarotongensis* and Pacific pigeon *Ducula pacifica* were obtained from droppings collected beneath fruiting trees on Atiu. On Rarotonga, most animals were trapped and underwent feeding trials to obtain seeds, thereby also yielding information on gut passage times. Indian mynah *Acridotheres tristis* were mist netted while feral domestic fowl *Gallus gallus* were caught in a ground-level trap and additional droppings were obtained from birds roosting in one of the *F. prolixa*. Rats *Rattus* spp and Chocolate hermit crab *Coenobita cavipes* were caught using Sherman traps and purpose-built treadle-release traps. Forest gecko *Gehyra oceanica* were caught using a noose and by hand. The animals were given time to empty their gut contents before each was provided with ten ripe figs for 3 h (birds) or overnight (rats, crabs and lizards). The number of figs eaten and faeces produced were recorded every 15 min during the day and every hour during the night. Faeces were collected immediately in order to calculate minimum gut passage times. All animals were subsequently released at their capture sites at an appropriate time of day.

Results

Quantity of frugivory and seed dispersal

Combining results for Rarotonga and Atiu, native frugivores contributed 22% of visits and introduced frugivores 78%; but these differed significantly depending on the habitat. On Rarotonga, where all *F. prolixa* are found in non-forest habitats, and on Atiu in non-forest habitats, the vast majority of frugivore visits (81%) were made by introduced species, primarily *A. tristis* (Fig. 1). Other frugivore species observed in this non-forest environment included *Rattus* spp., which were trapped beneath all trees on Rarotonga and observed on trees in non-forest environments on Atiu. *Gallus gallus* were only observed in one tree on Rarotonga (in which they roosted) and whilst *C. cavipes* were not observed visiting *F. prolixa*, they were trapped beneath a tree on Rarotonga. *Pteropus tonganus* accounted for only 2% of visits on Rarotonga, but due to the lack of nocturnal observations this may be a considerable underestimate. There was no significant difference between diurnal and nocturnal fig disappearance rates from marked branches (2 ± 1.4 (mean + SE) figs during a day compared with 2.0 ± 2.9 during a night (Mann–Whitney U = 7.5, $P = 0.56$, $n = 5$ nights)), suggesting high visitation rates by *P. tonganus* at night on Rarotonga. No equivalent data was unfortunately collected on Atiu to allow a comparison with an island on which there are no bats.

In the native forest on Atiu, *P. rarotongensis* and *D. pacifica* accounted for 78 and 14% of visits respectively (Fig. 1), although neither of these species were recorded visiting *F. prolixa* in non-forest environments on either Rarotonga or Atiu. *Aplonis cinerascens*; a native avian frugivore found on Rarotonga (but not Atiu) was not observed at any

Table 3 Feeding behaviour of frugivores and results of feeding trials and germination trials of ingested *F. prolixa* seeds

Native species	Feeding observed in wild	N. animals in trials	N. animals eating figs in trials	N. figs eaten per animal (mean ± SD) (max = 10)	N. seeds recovered (mean ± SD)	Gut passage time (h min) (mean and range)	% Germination success		
							Frugivore	Control	
<i>Ptilinopus rarotongensis</i> *	Y	4	-	-	173 ± 193	-	0.4	0	
<i>Ducula pacifica</i> *	Y	5	-	-	366 ± 391	-	0.2	0	
<i>Coenobita cavipes</i>	N	3	1	1 ± 1.7	1 ± 0	15h30 (2h–35h 30)**	50	3.5	
Introduced species									
<i>Acridotheres tristis</i>	Y	4	3	3.3 ± 4.6	38 ± 66	9h (9h)	3.5	6.5	
<i>Gallus gallus</i>	N	10	10	8.2 ± 2.9	13 ± 8	2h15 (15–4h15)	5.8	5.1	
<i>Rattus</i> spp.***	N	10	8	7.3 ± 2.3	2.9 ± 3.7	6h (1h–19h45)	3.3	5.4	
<i>Gehyra oceanica</i>	N	5	0	-	-	-	-	-	

* Based on data from droppings collected below *F. prolixa*, not from feeding trials

** The high time is based on a minimum passage time in the individual that ate a fig in the wild, prior to capture

*** *Rattus* spp. combine results for eight *R. exulans*, one *R. rattus* and one *R. norvegicus*

Y yes; N no

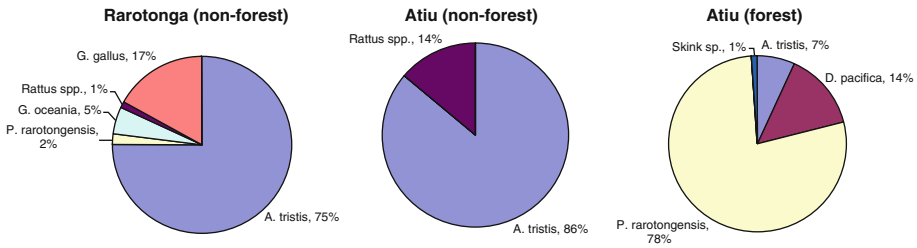


Fig. 1 Frequencies of visits by frugivores to *Ficus prolixa* on Rarotonga and Atiu, according to habitat type

F. prolixa there. Introduced frugivores made very few visits to *F. prolixa* in Atiuan forest; only *A. tristis* visited, accounting for 7% of the total. This introduced bird was the only species observed visiting all the trees on both islands.

The length of individual visits made to fruiting *F. prolixa* by frugivorous birds was related positively to bird size, with the large *D. pacifica* spending longer (mean = 10 min 25 s, $n = 14$ observations) than medium-sized *P. rarotongensis* (6 min 40 s, $n = 70$) and small *A. tristis* (2 min 54 s, $n = 46$). One *P. tonganus* remained in a tree for 20 min, but most visits by this species could not be timed. *Gehyra oceanica* and *Rattus* spp. were observed briefly scurrying about on *F. prolixa* branches, whereas *G. gallus* spent hours roosting in the one tree where they were present.

Ptilinopus rarotongensis, *D. pacifica* and *A. tristis* were the only frugivores directly observed removing *F. prolixa* figs in the wild (although *G. gallus* fed on the ground beneath one tree). Rates of feeding in the trees were also positively related to body size, with *D. pacifica* (on Atiu) eating on average one fig every 3 min ($n = 43$ figs), *P. rarotongensis* (on Atiu) one every 6 min ($n = 70$ figs) and *A. tristis* (on Rarotonga) only one every 50 min ($n = 3$ figs). Fruit handling success varied between species, with *D. pacifica* dropping 5% of the figs ($n = 2$ figs dropped), *P. rarotongensis* 7% ($n = 5$ figs dropped) and *A. tristis* none. The Fruit Removal Index, combining the number of visits, mean visit length and feeding rates, was calculated as 126 for *P. rarotongensis*, 69 for *D. pacifica* and 10 for *A. tristis*; indicating that the two former native birds are more effective seed dispersers than the latter introduced bird.

Quality of frugivory and seed dispersal

Ptilinopus rarotongensis and *D. pacifica* were observed swallowing *F. prolixa* figs whole whilst in the tree, indicating that all seeds in the fruit will be ingested intact (Table 3). Feeding methods of *A. tristis* and *G. oceanica* were not directly observed, however they have gape widths of 13.72 mm ($n = 1$) and 12.03 ± 0.51 mm ($n = 5$) respectively, which are well in excess of the diameter of ripe *F. prolixa* figs (mean = 7.13 ± 1.08 mm; $n = 93$), meaning they should not be 'gape limited' (Whiting and Greef 1997). Captive *G. gallus* either swallowed figs whole or pecked off pieces, whilst *Rattus* spp. were observed in captivity nibbling the figs offered to them; indicating that fewer seeds from each fig may be ingested by these species. The feeding method of *P. tonganus* was not observed.

Individuals of *P. rarotongensis* and *D. pacifica* could not be captured for feeding trials, so droppings of each species were collected beneath *F. prolixa* on Atiu as the basis of analysis (Table 3). The number of seeds in the droppings did not differ significantly between the two species (Mann–Whitney U test, $U = 5.0$, $P = 0.286$, $n = 5$). All other frugivore species were trapped and underwent feeding trials, in which all species ate at

least some of the figs offered them except *G. oecania* (Table 3). *Gallus gallus* and *Rattus* spp. individuals ate the greatest number of figs during trials. The number of seeds recovered during the trials varied both between and within species, with *A. tristis* passing the most per animal and *C. cavipes* the least (excluding *P. rarotongensis* and *D. pacifica*). The *C. cavipes* individual which passed one fig seed had not eaten any of the figs offered during the feeding trial, indicating that it had fed on figs in the wild prior to capture. Gut passage time in the feeding trials varied widely both between and within species (Table 3). *G. gallus* had the fastest mean passage times and *C. cavipes* the slowest.

All seed germination rates in the trials were low (Table 3). Germination success was however higher amongst seeds passed by the native frugivores *P. rarotongensis*, *D. pacifica* and *C. cavipes* than amongst control seeds collected from the same tree. Seeds passed by the introduced frugivores *A. tristis* and *Rattus* spp. on the other hand, had lower success rates than control seeds. Those seeds passed by *G. gallus* had similar rates to controls. Unfortunately, given the small sample sizes, these results can not be statistically tested.

Discussion

Our results demonstrate that native pigeons and doves were the most effective of the native seed dispersers we examined, both in terms of quantity of fig eating and quality of seed treatment. Previous studies demonstrate the dove also to be effective in dispersing seeds away from parent trees (McConkey et al. 2004). Whilst the native fruit bat may be an effective disperser (Shilton et al. 1999; McConkey and Drake 2006), it was not studied in full in the present research. The hermit crab *C. cavipes*, is fairly ubiquitous on the Cook Islands (E. Saul, personal communication), and was demonstrated to eat figs both in the wild and in captive situations. Very few intact seeds were defaecated by this species, but half those that were proved to be viable. Its gut passage time was long in comparison to those of other frugivores studied and is in general agreement with those calculated for other species of land crab (Greenaway and Linton 1995). *Coenobita cavipes* can be found up to several metres high in trees (Barnes 1997) so individuals could potentially deposit small numbers of seeds in microsites suitable for this hemiphytic fig tree, as well as on rocks which are the other germination site for *F. prolixa* in the Cook Islands. Any such contribution by this crab will nonetheless be tiny compared with that possible by vertebrates.

The introduced Indian mynah *A. tristis* accounted for a large proportion of frugivore visits to *F. prolixa*, particularly those in non-forest environments, but its visits were short and it fed infrequently. In feeding trials, although many seeds were recovered from its faeces, germination rates were low. This may be explained by its relatively long gut passage times. Other starlings display a wide range of gut passage times, from 5 min to 15 h (Proctor 1968; Midya and Brahmachry 1991). Despite being so common in non-forest areas, *A. tristis* provides low quantity, low quality dispersal relative to native pigeons and doves. Feral domestic fowls *G. gallus* did eat figs in feeding trials, but few seeds survived, presumably because of their grit-filled gizzard (Corlett 1998). Germination rates amongst the seeds that survived were equal to control seeds. *Gallus gallus* is therefore a fairly ineffective disperser of *F. prolixa* seeds. Small numbers of the introduced rats *R. exulans*, *R. rattus* and *R. norvegicus* were observed on fruiting *F. prolixa*, but feeding on the figs in the wild was not confirmed. These are omnivorous animals and all three species ate the figs offered during captivity. These rodents nibbled the figs, rather than swallowing them whole, so only small numbers of seeds may have been ingested; certainly few seeds were

passed and their germination success was low, as has been reported for other plant species dispersed by rats (Price and Jenkins 1986; Delgado Garcia 2002). Despite the highlighted importance of reptiles as seed dispersers in island environments (Valido and Nogales 1994; Green et al. 1997; Whiting and Greef 1997; Nogales et al. 1998; Olesen and Valido 2003), we found no evidence that the widespread facultatively frugivorous lizard *G. oceanica* is willing to feed on the figs of *F. prolixa*.

All of the alien frugivores introduced to the Cook Islands therefore only offer poor seed dispersal services to *F. prolixa* (and probably other fleshy-fruited native plants), both in terms of quantity and quality. Consequently, the losses and declines in abundance of native frugivores; which have been shown to be the most effective dispersers, are unlikely to have been compensated for by the introduction of species from elsewhere. This is in contrast to the situation on Hawaii, where introduced birds have been found to aid the recruitment of native plant species in areas of exotic-dominated vegetation (Foster and Robinson 2007). Clearly the behaviour and habitat preferences of those particular introduced species has a large influence on whether or not they can be ecological equivalents for lost native species. The Cook Islands have not been lucky in this regard. The diverse alien frugivores present nonetheless can provide some seed dispersal, and this may be significant in situations where native species are entirely absent. On the island of Mangaia, for example, there are no remaining native frugivorous birds, and its fruit bat is close to extinction (Cousins and Compton 2005). Even rare, poor quality, biotic seed dispersal events may be better than none.

Ficus prolixa occupies forests on Atiu where native birds are still common and they contributed over 93% of the frugivore visits we recorded. The situation is different on Rarotonga and in non-forest environments on Atiu, where native birds are scarce and only rarely visit fruiting *F. prolixa*. A large, mixed age population of *F. prolixa* is present in the forests of Atiu, in contrast to the situation on Rarotonga, where recruitment has apparently been absent for some years, despite the persistence of a quite large population of fruit bats (Cousins and Compton 2005) and several native frugivorous birds. Consequently, the lack of recruitment on Rarotonga may be partially explained by a spatial mis-match between the distribution of *F. prolixa*; which occurs in the non-forested lowlands, and that of the native frugivores, which are concentrated in the central upland forest and descend to the lowlands rather infrequently. It is mainly introduced frugivores which are abundant in the areas occupied by *F. prolixa* on Rarotonga and these have been shown to be ineffective seed dispersers. Seed dispersal is thus very limited in lowland Rarotonga and it is possible that this is contributing to the lack of *F. prolixa* recruitment there, where it has already been hard-hit by extensive habitat modification which has led to the loss of its closed lowland forest and suitable germination sites (Compton and McCormack 1999).

Given the small sample sizes and limited scope of the present study it is not possible to make comparisons or generalisations to other island environments, however it is possibly indicative of situations throughout the Pacific and further afield.

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