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To cite this version:

Quiterie Duron, Oriana Garcia-Iriarte, Fabrice Brescia, Eric Vidal. Comparative effects of native frugivores and introduced rodents on seed germination in New-Caledonian rainforest plants. Biological Invasions, 2017, 19 (1), pp.351-363. 10.1007/s10530-016-1284-1 . hal-01681563

HAL Id: hal-01681563

https://hal.science/hal-01681563v1

Submitted on 11 May 2018

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Comparative effects of native frugivores and introduced rodents on seed germination in New-Caledonian rainforest plants

Quiterie Duron · Oriana Garcia-Iriarte · Fabrice Brescia · Eric Vidal

Abstract Native frugivores play an important role in native plant community dynamics by participating in seed dispersal. Today many island forests are invaded by introduced omnivores, such as rats, but their role in dispersing native plants is still little known. Here, we evaluated whether native seeds from New-Caledonian rainforests can germinate after passing through an invasive rat digestive tract and compared seed germinability and germination time between seeds ingested by invasive rats and native frugivores. We offered native fruits of *Ficus racemigera* and *Freycinetia sulcata* to the rats *Rattus rattus* and *R. exulans*, three flying foxes *Pteropus* spp. and the pigeon *Ducula goliath.* Our results showed that seeds can germinate after passing through an invasive rat digestive tract, and suggest that rats can disperse seeds of both plant species. However, invasive rats may be less efficient than native frugivores, as more seeds were destroyed when passing through rat digestive tracts than through native frugivores, and because germinability was lower and germination time was longer for seeds passing through invasive rats than through native frugivores. The reduced efficiency of rats may result from their generalized diet, the structure of their digestive tract, and/or their feeding behavior. In New-Caledonian rainforests, dispersal services on both plant species are likely well fulfilled by flying foxes and *Ducula* pigeons, but rats do not seem to be as efficient dispersers. Consequently, management measures to protect native frugivores should help to conserve seed dispersal services.

Keywords Seed dispersal · Seed destruction · *Rattus* · Flying foxes · Frugivorous pigeon

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Introduction

Seed dispersal is a key process in plant community dynamics as it allows species to colonize new areas and avoid competition with siblings, predation, and spread of pathogens (Traveset et al. 2014). Frugivorous vertebrates, especially mammals and birds, play an important role in seed dispersal (Jordano 2014). Vertebrates disperse seeds from 70 to 94 % of all woody species in tropical rainforests, and seeds from 65 to 74 % in subtropical humid forest (Jordano 2014). One of the main ways for frugivores to disperse seeds is by endozoochory, i.e. by the ingestion and excretion of seeds. While frugivores benefit by obtaining energy

and nutrients from the fruit pulp, endozoochory benefits the plant by facilitating the transport of seeds away from the parent plant location, and can also help germination (Traveset 1998; Reid and Armesto 2011; Jordano 2014). Passage through a frugivore's digestive tract can enhance germination success by abrasion of the seed coat and the removal of the pulp (Barnea et al. 1991; Traveset 1998; Jordaan et al. 2011). Endozoochory is crucial for the dispersal of many fleshy fruited plants (Traveset et al. 2014) and it is recognized that these mutualistic interactions are currently threatened by human disturbance and the drivers of global environmental change, such as invasive species (Tylianakis et al. 2008; Markl et al. 2012). On islands, endozoochory relations are even more particularly prone to be disturbed by invasive species because of the uniqueness and the low diversity of native frugivore assemblages (Traveset and Richardson 2006; Traveset et al. 2014).

Invasive species can affect dispersal processes negatively by disrupting plant-seed disperser interactions (Kelly et al. 2006; Traveset and Richardson 2006), or positively by compensating when native seed dispersers are few or have disappeared (Kaiser-Bunbury et al. 2010; Pattemore and Wilcove 2011). For example, the efficiency of introduced birds as native seed dispersers was already demonstrated in Hawaiian forests (Foster and Robinson 2007), and the capacity of invasive rats to disperse small seeds of both native and invasive plants was studied in New Zealand and Hawaiian forests (Williams et al. 2000; Grant-Hoffman and Barboza 2010; Shiels 2011; Shiels and Drake 2011). However, invasive species can belong to groups or taxa that did not exist among native species, in particular flightless terrestrial mammals that have historically been absent from most oceanic islands (Lever 1985; Whittaker and Fernandez-Palacios 2007; Scheiner and Willig 2011) and did not evolve together with native plant species (Nogales et al. 2005). These two particularities may result in lower seed dispersal performances of invasive vertebrates versus native vertebrates. The effects of invasive species on seed dispersal can be ambiguous and our objective was to study the relative capacities of invasive rats and native frugivores to facilitate the dispersal process in an island system.

On islands, native vertebrate frugivores include birds, flying foxes and many Squamata but few terrestrial mammals (Olesen and Valido 2004; Nogales et al. 2005). Nonetheless, most islands have been invaded by exotic terrestrial mammals (Courchamp et al. 2003; Blackburn et al. 2004), some of them being partly frugivorous like pigs, deer, rabbits and rats. These species can strongly affect plant communities and mutualisms directly, through predation and competition (Traveset and Richardson 2006; Traveset et al. 2009). Invasive rats (*Rattus* spp.), and particularly the Black rat *Rattus rattus*, even if their diet is omnivorous and depends on seasonal resource availability (Caut et al. 2008; Shiels et al. 2014), feed mainly on plant material (seeds, fruits, vegetative parts; Sugihara 1997; Meyer and Butaud 2008; Grant-Hoffman and Barboza 2010; Shiels et al. 2012). Invasive rats are generally considered to be seed predators and are known for their detrimental effects on plants (Meyer and Butaud 2008; Grant-Hoffman and Barboza 2010; Shiels and Drake 2011), but they may also have positive effects by acting as seed dispersers (Williams et al. 2000; Grant-Hoffman and Barboza 2010). When eating fleshy fruits, small seeds may pass intact through the rat digestive tract and may be dispersed by endozoochory (Traveset 1998; Williams et al. 2000; Bourgeois et al. 2005; Grant-Hoffman and Barboza 2010; Shiels 2011). The length limit of seeds reported to pass intact through the rat digestive tract was about 2.0–2.5 mm for *R. rattus* and 0.11 mm for the Pacific rat *R. exulans* (Williams et al. 2000; Shiels 2011). However, our knowledge on the capacity of invasive rats to participate in native seed dispersal is still limited (Shiels and Drake 2011).

Since most of the world's islands (82 %) are now occupied by invasive rats (Atkinson 1985; Capizzi et al. 2014), a better understanding of the role of invasive rats in their host ecosystems is essential before considering their management. In the New Caledonia archipelago, two common invasive rats *R. exulans* and *R. rattus* coexist in all natural areas from sea level to 1629 m a.s.l (Beauvais et al. 2006). *R. exulans* reached the archipelago 3000 years ago with the initial Melanesian settlements, while *R. rattus* arrived with European colonization about 150 years ago (Beauvais et al. 2006). New Caledonia is listed as one of 35 biodiversity hotspots with exceptional rates of floral endemism that reach 83.2 % in rainforests (Mittermeier et al. 2011; Morat et al. 2012). A study conducted on 123 new-Caledonian rainforest tree species revealed that 72 % have adaptations for dispersal by vertebrates (Carpenter et al. 2003), and

pinpointed the importance of conserving native frugivorous species to maintain dispersal processes of endemic plants. Native frugivores on New Caledonia's main island (Grande Terre) include 47 species of Squamata (42 gekkos and 5 skinks) (Hervé Jourdan, personal communication), 15 species of birds (Barré and Dutson 2000; Tassin et al. 2010), and four species of flying foxes (Flannery 1995), and may have been more diversified before human and rat colonization (Balouet and Olson 1989; Balouet 1991).

Few comparisons of the effects of passage through invasive versus native species' digestive tracts on seed germination have been conducted (Nogales et al. 2005). To the best of our knowledge, only one study conducted in the Cook Islands, on *Ficus prolixa*, compared the differences in native seed germination after passage through native frugivorous (bird and flying foxes) and invasive rat species digestive tracts (Staddon et al. 2010). Therefore, the presence of both native frugivores (birds and flying foxes) and invasive rats in New-Caledonian rainforest represented a unique opportunity to test their relative effects on seed germination. In this study, we focused on the first steps of dispersal by endozoochory i.e. seed survival and germination after passing through the digestive tract, and compared these in native frugivores and invasive rats. Our aims were to evaluate whether seeds can survive and germinate after passing through the invasive rat digestive tract and to compare seed germination effectiveness (germinability and germination time), between non ingested seeds and seeds ingested by native frugivores or invasive rats.

Methods

Fruits and seeds characteristics

Two native plant species were selected based on morphological, ecological, and phenological criteria and their accessibility: *Ficus racemigera* (Bureau, Moraceae) and *Freycinetia sulcata* (Warb., Pandanaceae). Their fruits are known to be eaten by both native frugivorous birds and flying foxes, as well as by invasive rats in New Caledonia (M. Boissenin and H.Vandrot, personal communication). Moreover, species of the genera *Ficus* and *Freycinetia* are known to be eaten by flying foxes (Parsons et al. 2006; Nakamoto et al. 2009; Heer et al. 2010) and bats (Burrows 1996) in other parts of the world. *Ficus* species were also noted as the most common food source for *Ducula galeata* in the Marquesas archipelago (Blanvillain and Thorsen 2003) and are consumed by *Ducula pacifica* in Tonga (McConkey et al. 2005). *Ducula goliath* was observed feeding on *Freycinetia arborea*, a species closely related to *Freycinetia sulcata*, in Mont Panié, New Caledonia (personal observation). Seeds of both the genera *Ficus* and *Freycinetia* were found in *R. rattus* and *R. exulans* stomach and caecum contents for specimens collected in Mont Panié rainforest area, and these results oriented our choice to study germination of these two plant species. *Ficus* and *Freycinetia* have small seeds (<1.5 mm) which may allow dispersal by endozoochory by both native frugivores and invasive rats (Williams et al. 2000; Shiels 2011; Shiels and Drake 2011). For both species, a sample of fruits and seeds was weighed with a precision balance Mettler AE 240 (precision 0.1 mg), fruits were measured using a digital caliper (precision 0.001 mm) and seeds from binocular photography with "Image J" software (Table 1).

Ficus racemigera (hereafter *Ficus*) is a species of tree endemic to New Caledonia and Vanuatu, found in dense rainforests at various elevations. The fig "fruit", called a syconium, is a multiple pseudocarp, which includes several achene fruits. Each achene is made up of a seed surrounded by its calyx and fixed by a pedicel to the syconium fleshy receptacle. Each fig contains more than 300 small brown and rounded seeds (length 1.03 ± 0.89 mm; width 0.72 ± 0.84 mm). Mature fruits, selected for their reddish color and smooth texture, were collected in rainforest areas on Mont Koghi (22°10′38″S, 166°30′30″E, 450 m a.s.l.) in February and March 2015. *Freycinetia sulcata* (hereafter *Freycinetia*) is a hemiepiphyte native liana. Their fruits, or berries, are gathered in a yellow scented infructescence. Each infructescence contains more than 1000 seeds (length 1.15 ± 0.08 mm; width 0.28 ± 0.03 mm), which are covered by a thick mucilaginous flesh. Seeds are slightly curved with hyaline membrane margins on each side (Stone et al. 1998). Mature fruits, distinguished by their yellow color and their strong scent, were collected on Mont Panié (20°37′30″S, 164°46′56″E, 650 m a.s.l.) in March and May 2015.

Table 1 Summary of fruit and seed color, size, weight, and numbers for *Ficus racemigera* and *Freycinetia sulcata*. Fruits measures for *Freycinetia* were made on the whole inflorescence

	Ficus racemigera	*Freycinetia sulcata*
Family	MORACEAE	PANDANACEAE
Life form	Shrub or tree	Secondary hemiepiphyte
Fruit color	Red	Yellow
Fruit length (mm)	14.42 ± 1.47 ($n = 33$)	81.28 ± 11.1 ($n = 21$)
Fruit width (mm)	16.09 ± 1.85 ($n = 33$)	46.57 ± 7.03 ($n = 21$)
Fruit fresh mass (mg)	2.00 ± 0.22 ($n = 25$)	70.45 ± 8.6 ($n = 6$)
Number of seeds per fruit	329 ± 15	>1000
Seed color	Brown	Yellow
Seed length (mm)	1.03 ± 0.90 ($n = 31$)	1.15 ± 0.08 ($n = 36$)
Seed width (mm)	0.72 ± 0.85 ($n = 31$)	0.28 ± 0.04 ($n = 36$)
Seed mass (mg)	0.21 ± 0.04 ($n = 100$)	0.31 ± 0.00 ($n = 90$)
Seed shape	Reniform	Curved

Frugivorous vertebrate species tested

We tested two groups of vertebrate disperser species i.e. native frugivores (three species of flying foxes, *Pteropus ornatus, P. tonganus* and *P. vetulus*, and the imperial pigeon, or Notou, *Ducula goliath*), and introduced omnivorous rodents (two invasive rat species, *R. rattus* and *R. exulans*). *P. ornatus* is endemic to New Caledonia. Adult males can weigh 570 g with body size of 23 cm (Flannery 1995). *P. tonganus* is native to New Caledonia and has a large distribution in the Pacific. Adults weigh between 530 and 710 g (Flannery 1995). *P. vetulus* is endemic to New Caledonia and it is the smallest species of flying fox of the genus *Pteropus* in New Caledonia, weighing between 180 and 220 g (Flannery 1995; Brescia 2007). *D. goliath* is reputedly the largest arboreal pigeon in the world and its exclusively frugivorous regime confers an essential role as dispersal agent for many fruit species in rainforests (Barré et al. 2003). The feeding experiments were done on animals held in captivity in a zoological park. For *P. ornatus*, we worked with a group of five males held in a 3.4 m × 3.1 m × 6.2 m aviary; for *P. tonganus*, we worked with one male and two females held in a 3 m × 2.5 m × 4.6 m aviary; and, for *P. vetulus* we worked with two males and four females held in a 3 m × 2.5 m × 7 m aviary. For *D. goliath*, we did the experiments with two males and three females, each one being held in an individual cage of 4.9 m × 2 m × 1.5 m. All the animals were fed daily in the morning by zookeepers, with fresh fruits and water was provided ad libitum.

The two invasive rats, *R. rattus* and *R. exulans*, were also considered. In Mont Panié area, adult *R. rattus* usually weigh around 177.4 ± 30.1 g (±SD, min = 120 g, max = 263 g) whereas adult *R. exulans* weigh around 69.5 ± 12.8 g (±SD, min = 50 g and max = 95 g). Ten adult *R. rattus* and four *R. exulans* were live trapped from two locations in forests near Nouméa (Ouen Toro dry forest, 22°18′36″S, 166°27′16″E and Koghi rainforest, 22°10′38″S, 166°30′30″E). Each rat was held in an 40 cm × 33 cm × 28 cm or 60 cm × 41 cm × 37 cm individual metal mesh cage with bedding material and shelter. They were fed daily with mixed seeds and water was provided ad libitum.

Fruit consumption trials

All the feeding trials were performed from February through May 2015 with fresh fruits of *Ficus* and *Freycinetia* collected the day before. Before each feeding trial, all the cages were cleaned entirely to remove all remains of old faeces and uneaten food, in order to facilitate faeces collection. For native frugivores, the fruits were offered at the same time as their usual diet during their morning meal for one or 2 days depending on the species. Fruits were offered to five *D. goliath*, five *P. ornatus*, three *P. tonganus*, and six *P. vetulus*. Rats were deprived of their usual food (mixed seeds) 24 h before feeding trials to ensure that they consumed the tested fruits. The fruits were offered to four *R. rattus* and four *R. exulans* by offering fruits in each cage for 2 days. Rats were returned to their regular diet for at least 48 h between

feeding trials. The faecal material was collected 24 and/or 36 h after consumption tests. In order to avoid any influence on germination induction or a hypothetical dormancy, faeces were stored at room temperature and were rapidly processed for germination tests in the 24 h following collection.

Assessment of seed percent survival

Visual inspection of faeces showed us that passage through native species digestive tracts did not destroy seeds. Moreover, *D. pacifica*, a species closely related to *D. goliath*, was observed defecating seeds up to at least 26 mm in diameter (McConkey et al. 2005), which is 20 times greater than the size of our tested seeds. Similarly, *Pteropus conspicillatus* can defecate seeds of at least 3.7 mm (Richards 1990). Consequently, we assumed that 100 % of seeds ingested by native frugivores survived. However, flying foxes also spit out fruit pulp and some seeds after squeezing the juice from the fruits (Banack 1998; Shilton et al. 1999). Consequently a portion of the seeds may be not dispersed as far as the others. For invasive rats, in parallel to the consumption trials described above, a parallel experiment was set up to estimate the percentage of seed survival when seeds were ingested by the two species of rats (Williams et al. 2000; Shiels and Drake 2011). The number of seeds offered to rats was controlled by placing a precise number of seeds (100 seeds for *Ficus* and 50 seeds for *Freycinetia),* into a highly palatable bait composed of a mixture of crushed kibbles and peanut butter. This bait was offered individually to six *R. rattus* and four *R. exulans* but faeces could only be collected from five *R. rattus* and two *R. exulans*. All the droppings were carefully collected and inspected under a binocular microscope Leica MZ75 (4× magnification) in order to determine the percentages of damaged and undamaged seeds passing through the rat digestive tract. Seeds were considered undamaged when there was no visible change in the seed coat after passage through the digestive tract (Nogales et al. 2005). The removal of the calyx for the *Ficus* seeds was not considered to be damage.

Germination trials

Undamaged seeds were removed from native and invasive species faeces and were cleaned with tap water in order to avoid the potential effects of nutrients coming from faeces. Then seeds were quickly placed on water-wet cotton (humidity 100 %) in transparent Petri dishes. Four replicates of 25 seeds each (pooled from different individual plants and different individual animals) were tested for each treatment (Tassin et al. 2010; De Carvalho-Ricardo et al. 2014) except for *R. exulans,* for which very few seeds were obtained from the faeces ($n = 12$ for *Ficus* and $n = 9$ for *Freycinetia*). There were six ingested seed treatments: *R. rattus*, *R. exulans*, *P. ornatus*, *P. tonganus*, *P. vetulus*, and *D. goliath*. Non ingested seeds, used as a control treatment, were manipulated in the same manner as ingested seeds. In the case of *Ficus,* two sets of control treatments were carried out: seeds without calyx ("no calyx" treatment) and seeds with calyx ("calyx" treatment). The reason for this was that when non-ingested seeds were hand-extracted, the seeds came with the calyx, though ingested seeds were found without the calyx. *Freycinetia* seeds do not have an individual calyx, so the second control group was not necessary in this case. The Petri dishes were placed in an incubator at 26.5 °C with a natural photoperiod. Germination, defined as the emergence of 2 mm of the primary root (De Carvalho-Ricardo et al. 2014), was checked daily with a binocular microscope Leica MZ75 (4x magnification). Germination was monitored 15 days after sowing for *Ficus* and after 49 days for *Freycinetia*.

Statistical analysis

Seed percent survival was compared between rat and seed species with Chi-square tests for homogeneity with Yates' continuity correction. Concerning germination data analysis, for each Petri dish, the percentage of seeds that had germinated ("germinability") at the end of germination monitoring was calculated. Germination times were also measured. The "date of germination start" was noted as the day when the first seed had germinated in a Petri dish, and "T50″ corresponded to the number of days required to reach 50 % germination of the total number of sown seeds.

We assessed whether the germinability varied according to the different treatments using Generalized Linear Models (GLMs, quasibinomial family to account for over- or under-dispersion). We used a Chi-square test to assess the significance of the deviance change between the null model and the model with the

"treatment" variable. GLMs were performed initially on data when grouped into four categories of treatments: controls (with and without calyx), invasive rats (*R. rattus* and *R. exulans*), native pigeons (*D. goliath*) and native flying foxes (*P. ornatus*, *P. tonganus*, and *P. vetulus*). Secondly, all treatments were compared by pairs using post hoc Tukey's tests, with the Holm correction (Aickin and Gensler 1996).

The germination times for each treatment were analyzed using Generalized Additive Models (GAMs) with the proportion of seed germinated as a response variable and quasibinomial errors to account for over- or under-dispersion. Seed germination is not a linear function of time so we fitted change in number of seeds germinated with time using a thin plate regression spline (Wood 2006). We set the spline basis dimension '*k*' to 6 to limit the complexity of the splines and prevent overfitting. GAM model predictions were then used to calculate the T50 of each treatment. All analyzes were performed under R Version 3.1.2 with packages multcomp and mgcv.

Results

Assessment of seed percent survival

Visual inspections of faeces showed that 100 % of seeds were undamaged after passing through native frugivore guts. By contrast, the seed survival results showed that the invasive rats destroyed a large proportion of the seeds that they ingested. For *Ficus*, the percentage of intact seeds passed through the *R. rattus'* digestive tract averaged 30.6 ± 13.5 % (±SD, $n = 5$) and was significantly higher than the percentage of intact seeds that passed through *R. exulans*: 14 ± 1.4 % (±SD, $n = 2$, $\chi^2 = 7.02$, $df = 1$, $p = 0.008$). For *Freycinetia*, 30 ± 19.0 % (±SD, $n = 5$) of seeds were found intact in *R. rattus* faeces and only 16 ± 2.8 % (±SD, $n = 2$; $\chi^2 = 4.77$, $df = 1, p = 0.029$) in *R. exulans* faeces. No difference in survival rates was recorded between *Ficus* and *Freycinetia* species ($\chi^2 = 0.014$, $df = 1$, $p = 0.905$).

Germinability

The low number of seeds ($n = 12$ for *Ficus* and $n = 9$ for *Freycinetia*) found in *R. exulans* faeces did not allow comparison of germinability and germination time with other treatments, so the *R. exulans* data were excluded from the statistical analysis of separate species. When analyzes were performed on treatment category, *R. exulans* data were grouped with *R. rattus* data in the "invasive rats" group.

For *Ficus*, the Chi-square test conducted in GLM results showed the existence of a significant effect of the treatment category, i.e. a difference in germinability among controls, native pigeons, native flying foxes and invasive rats (deviance explained by the model: 6.69 %, $p < 0.001$). Seeds passing through native flying foxes (*Pteropus* spp.) had a higher germinability than those passing through invasive rats ($p = 0.012$). However, no difference in germinability was recorded between invasive rats and the control treatments ($p = 1$) nor with native pigeons (*D. goliath*, $p = 0.140$). When all treatments were compared (Table 1a; Fig. 1), control seeds with calyx had lower germinability than control seeds without calyx ($p = 0.013$). Control seeds with calyx also had lower germinability than seeds ingested by *Ducula goliath* ($p = 0.004$), *Pteropus ornatus* ($p = 0.005$), *P. tonganus* ($p = 0.005$) and *P. vetulus* ($p = 0.005$). However, no significant difference was registered between control seeds with calyx and *R. rattus* ($p = 0.355$). For *R. rattus*, if we take into account the seed percent survival after gut passage, only 27 % of ingested seeds are likely able to germinate.

For *Freycinetia*, the Chi-square test conducted in GLM results also showed the existence of a significant effect of the treatment category on the germinability (deviance explained by the model: 24.8 %, $p < 0.001$). Seeds ingested by invasive species (i.e. *Rattus* spp.) had a 50 % lower germinability than those ingested by native pigeons ($p < 0.001$), native flying foxes ($p < 0.001$) and the control seeds ($p < 0.001$). However, there was no difference between seeds ingested by native pigeons or native flying foxes and the control ($p = 0.191$ and $p = 0.086$ respectively). When regarding native species, seeds ingested by *D. goliath* had a higher germinability followed by *P. vetulus* and *P. tonganus*. In contrast, *P. ornatus* treatment had the lowest germinability among native species (Table 1b; Fig. 1). Seeds ingested by *R. rattus* and *P. ornatus* had lower germinability than control seeds ($p < 0.001$ and $p = 0.006$ respectively). Seeds subjected to *R. rattus* treatment had lower germinability than those subjected to *D. goliath* ($p < 0.001$), *P. tonganus* ($p < 0.001$) and *P. vetulus* treatments

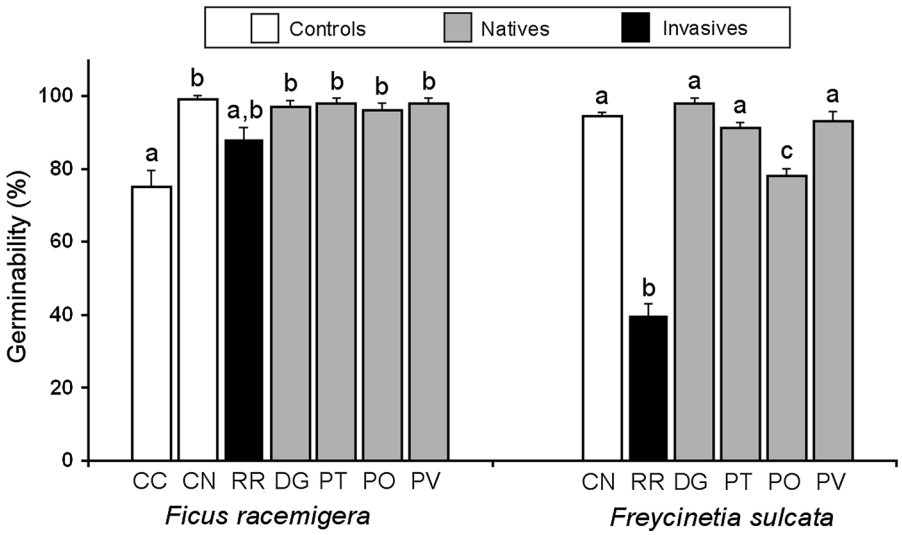

Fig. 1 Germinability (% mean ± 1SD) of *Ficus racemigera* and *Freycinetia sulcata* seeds according to the following treatments: controls (i.e. non-ingested seeds: *CN* control without calyx, and *CC* control with calyx), introduced omnivorous rodents: *RR R. rattus,* and native frugivorous species (*DG Ducula goliath*, *PT Pteropus tonganus, PO P. ornatus* and *PV P. vetulus)*. Within a plant species, means sharing the same letter are not significantly different ($p > 0.05$)

($p < 0.001$). For *R. rattus*, if we take into account the seed percent survival after gut passage, only 12 % of ingested seeds are likely able to germinate.

Germination time

First germinations of *Ficus* seeds were registered 2 days after sowing for seeds subjected to passage through *D. goliath* whereas seeds subjected to *R. rattus* treatment began to germinate 5 days after sowing (Table 2a; Fig. 2). The last germination was recorded on day 13 for the control without calyx treatment. T50 (number of days required to reach 50 % of the total number of sown seeds) differed for all treatments (Table 2a; Fig. 2). Whereas seeds ingested by native species germinated quickly ($4.35 < T50 < 5.65$ days), seeds ingested by *R. rattus* reached T50 about 3 days later (T50 = 8.25 days, Table 2a).

First germinations of *Freycinetia* seeds were registered 15 days after sowing for seeds ingested by *D. goliath, P. ornatus* and *P. vetulus*, whereas seeds ingested by *R. rattus* began to germinate on day 20 (Table 2b; Fig. 3). The last germinations were recorded on day 40 for *R. rattus* and *Pteropus* spp. treatments (Table 2b; Fig. 3). For the native species treatments, the smaller T50 s were recorded for *P. vetulus* (T50 = 19.95 days), followed by *D. goliath* (T50 = 20.22 days), and the control treatment (T50 = 22.36 days, Table 2b). As only 39.7 % of seeds have germinated with *R. rattus* treatment, the T50 was not estimated.

Discussion

Our results suggest that both native frugivorous vertebrates (*D. goliath* and *Pteropus* spp.) and introduced rodents (*Rattus* spp.) are potential dispersers of *Ficus racemigera* and *Freycinetia sulcata* seeds. However, seed dispersal by invasive rats is likely less efficient than by native frugivores as (1) more seeds were destroyed when passing through rats' digestive tracts than native frugivores', (2) germinability was lower for seeds passing through rat digestive tracts than native frugivores' and (3) T50 was longer when seeds were eaten by rats than by native frugivores. These results are consistent with other studies, which showed that invasive dispersers may be not as effective as native dispersers. For example, in the Canary Islands, invasive vertebrate frugivores defecated more damaged seeds of *Rubia fruticosa* than natives and fewer seeds germinated (Nogales et al. 2005). Invasive rats were found to be less effective than native species in dispersing *Ficus prolixa* in the Cook Islands (Staddon et al. 2010). This may be explained by the fact that, especially on islands, non-native seed dispersers generally have a more generalist and opportunistic diet than many native species, which are more specialized and so adapted to disperse native plant species (Aslan et al. 2012).

Differences in seed percent survival, germinability and germination time, may occur because of frugivore morphology and behavior, or from fruit and seed characteristics (Traveset 1998). First, vertebrate's body size determines the size of seeds that can pass

Table 2 Germinability (%, mean ± SE) for each treatment and significant differences between treatments, day of first germination, and T50, i.e. number of days required to reach 50 % of the total number of sown seeds; for a) *Ficus racemigera* and b) *Freycinetia sulcata*

Treatment	Germinability (%)	Day of first germination	T50 (days)
(*a*)			
ControlN (CN, $n = 6$)	99.0 ± 0.01/CC*	4	6.04
ControlC (CC, $n = 5$)	75.0 ± 4.6/CN*, DG**, PO**,PT**, PV**	4	7.58
R. rattus (RR, $n = 4$)	88.0 ± 3.4	5	8.25
P. ornatus (PO, $n = 4$)	96.0 ± 2.0/CC**	2	5.65
P. tonganus (PT, $n = 4$)	98.0 ± 1.4/CC**	3	4.06
P. vetulus (PV, $n = 4$)	98.0 ± 1.4/CC**	3	4.10
D. goliath (DG, $n = 4$)	97.0 ± 1.7/CC**	4	4.56
(*b*)			
Control (CN, n = 5)	94.4 ± 2.1/PO**, RR***	17	22.36
R. rattus (RR, n = 5)	39.7 ± 4.6/DG***, PT***, PV***, PO***,CN***	20	70
P. ornatus (PO, n = 4)	78.0 ± 4.2/DG**, RR***, PT., PV*, CN**	15	23.16
P. tonganus (PT, n = 5)	91.2 ± 2.5/PO., RR***	18	26.21
P. vetulus (PV, n = 4)	93.0 ± 2.6/PO*, RR***	15	19.95
D. goliath (DG, n = 4)	98.0 ±1.4/PO**, RR**	15	20.22

Treatment initials are used to indicate when a significant difference exists between treatments and the number of * indicates the degree of significance (.: $p = 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Controls (non-ingested seeds) are denoted as ControlN when calyx was removed and ControlC when calyx was left

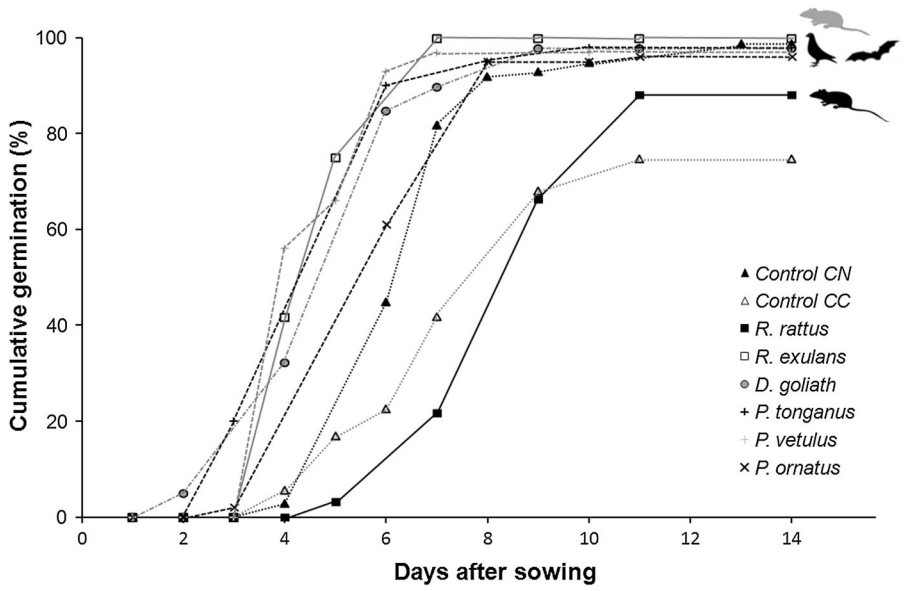

Fig. 2 Cumulative proportion of seeds (%) germinated of *Ficus racemigera* according to the treatment. *Control CN* control without calyx and *Control CC* Control with Calyx

intact through its digestive tract (Traveset 1998; Pérez-Méndez et al. 2015). Rats are smaller than flying foxes or imperial pigeons, and this difference may partly explain the lower percent survival for seeds in the rat treatment. The size limit for seeds passing intact through the digestive tract is reported to be 2.0–2.5 mm for *R. rattus* and 0.11 mm for *R. exulans* (Williams et al. 2000; Shiels 2011) whereas a limit of

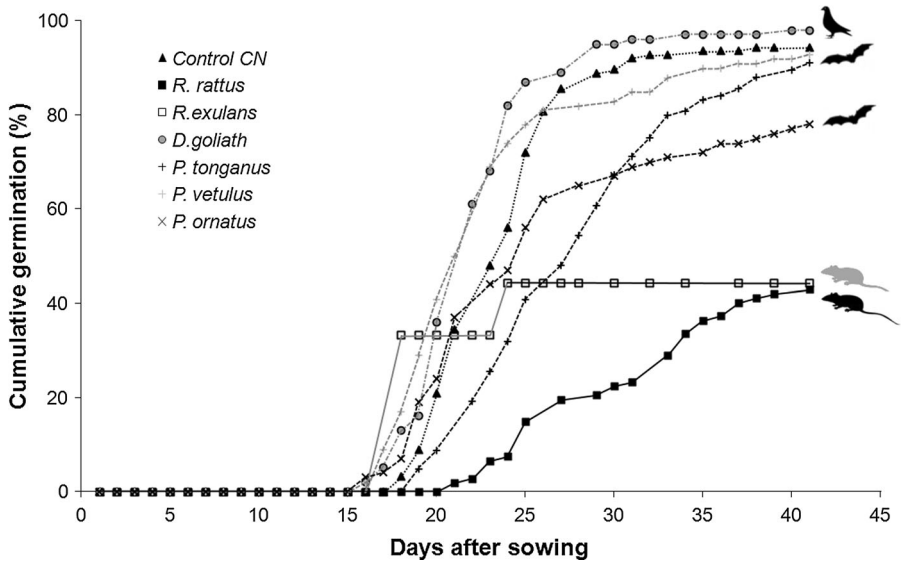

Fig. 3 Cumulative proportion of seeds (%) germinated of *Freycinetia sulcata* according to the treatment

3.7 mm has been noted for a species of flying fox (*Pteropus conspicillatus*) (Richards 1990). In our case, *Ficus* and *Freycinetia* seeds were about 1.0–1.15 mm which might explain the lower survival of seeds from rat treatment, particularly for *R. exulans*. Second, small ground-dwelling mammals, flying foxes, and birds differ in the structure of their digestive tracts, and seed survival and germination may be affected differently throughout the digestive process, from ingestion to excretion (Traveset 1998). For example, invasive rats can destroy seeds by chewing them with their teeth before swallowing fruit fragments, whereas birds do not have teeth and usually swallow the whole fruit without mastication. Moreover, seed retention time in the digestive tract can influence the seed coat because the greater the retention time, the greater the mechanical and chemical abrasion to the seed coat which can lead to variable germination efficiency (Barnea et al. 1991; Traveset 1998). Seed retention times were noted to range from 12 to 45 min to several hours for some other species of the genus *Pteropus* (Funakoshi et al. 1993; Shilton et al. 1999; De Carvalho-Ricardo et al. 2014). According to the fruit species ingested seed retention time went from 37 to 181 min in a New Zealand frugivorous pigeon, *Hemiphaga novaeseelandiae,* (Clout and Tilley 1992; Wotton et al. 2008), and would be about 30 min for a New-Caledonian dove, *Ptinolopus greyii,* when eating *Ficus* spp. (Boissenin et al. 2006). By contrast, it is reported to range from 12 to 48 h for rats (Perrin and Maddock 1983; Sakaguchi et al. 1987). The longer time passed in the rat digestive tract may lead to an excessive seed chemical abrasion, which may explain the lower seed germinability (Traveset 1998).

In our experimentation, germinability differences between native and invasive treatments were higher for *Freycinetia sulcata* than for *Ficus racemigera*. As noted by Traveset (1998), a frugivorous species can have different effects on seed germination depending on fruit and seed traits, such as size, shape, pulp consistency, seed coat thickness, etc. Seeds with high permeability and a thin coat may germinate more rapidly thanks to faster water absorption (Traveset et al. 2008). *Freycinetia* seeds have thicker coats than *Ficus* (personal observation) which may explain why the first germination was on day 15 for *Freycinetia* and on day 2 for *Ficus*. For *Ficus*, a higher germinability was observed when seeds were ingested or when the calyx was removed. In other *Ficus* species, the effect of seed passage through various vertebrates (primates, bats and birds) has also generally been enhancement of germination (Traveset 1998). Likewise, regarding morphological features of *Freycinetia* fruits, the hypothesis that seeds need to be released from the mucus sheath through ingestion by frugivores is a possibility, but, to the best of our knowledge, it has never been experimentally demonstrated before.

When compared with non-ingestion of seeds and ingestion by flying foxes, ingestion by the native imperial pigeon (*Ducula goliath*) seemed to better

enhance germination for *Freycinetia*. By contrast, for *Ficus*, the native pigeons did not have a greater facilitative effect than when no ingestion or ingestion by flying foxes occurred. The effects of birds on germination are variable according to seed species, sometimes enhancing and other times inhibiting germination, whereas no influence of ingestion by flying foxes on seed germinability has been reported (Traveset 1998). However, flying foxes and frugivorous pigeons are recognized to play an important role in seed dispersal, as they can allow seeds to germinate far from the mother plant (Galindo-Gonzalez et al. 2000; Olesen and Valido 2004; Nakamoto et al. 2009). *Ficus* is a key genus for flying foxes; for example, *Pteropus dasymallus* in Japan consumed nine different species of *Ficus* (Nakamoto et al. 2009), and *Pteropus conspicillatus* in Australia ate 13 different species of *Ficus* (Parsons et al. 2006). *Ficus* species were frequently eaten by *Pteropus conspicillatus* in a study conducted in the Australian wet tropics (Parsons et al. 2006). In the Cook Islands, native pigeons and doves appeared to be the most effective native dispersers of *Ficus prolixa* (Staddon et al. 2010) and *Ducula galeata* fed principally on fruits of *Ficus* in the Marquesas archipelago (Blanvillain and Thorsen 2003). Likewise, *Ficus racemigera* may be well dispersed by native *Pteropus* spp. and *Ducula goliath* in New Caledonia. Almost no information on *Freycinetia* germination or dispersal is known except that *Freycinetia* spp. can be dispersed by bats (Van Der Pijl 1957; Lord 1991) and that *Ducula goliath* was observed feeding on *Freycinetia arborea* in Mont Panié (personal observation), a *Freycinetia sulcata* closely related species.

Seed survival and germination are just two of many required steps for the development of a new plant individual. Another important condition is that animals have to defecate in suitable sites for germination (Calviño-Cancela 2004). To avoid competition, it is better for seeds to be taken away from the mother tree. *Ducula* pigeons and flying foxes help fulfill this condition by travelling long distances. In New Caledonia, Boissenin and Brescia (2014) showed that by night *P. ornatus* and *P. tonganus* equipped with satellite transmitters can fly distances between 8 to 15 km, from their day roosts to feeding areas. In contrast, rats are territorial and do not travel long distances (Bramley 2014; Ringler et al. 2014). On an island in the Indian Ocean, spool-line experiments showed that *R. rattus* made trips from 63 to 192 m inside the forest (Ringler et al. 2014). In a New-Caledonian rainforest, spatially explicit capture-recapture analyzes showed that *R. rattus* and *R. exulans* home ranges vary from 0.41 to 1.34 ha (Duron et al. unpublished results). These results suggest that invasive rats are not able to disperse seeds as far as native species. However, small movements may still help plants to avoid competition with siblings and, spread of pathogens and may allow colonization of treefall gaps (Traveset et al. 2014).

In view of these elements, invasive rats do not seem to be efficient dispersers when native pigeons and flying foxes are still present. Moreover, some species of passerines and Squamata are frugivorous or partly frugivorous and may play a disperser role in the rainforest, but very little is actually known. Nonetheless, the question of the importance of rats in the dispersal process is crucial as invasive rat populations are more and more subject to management operations i.e. eradication (complete removal) or control (rat population reduction). In New Caledonian rainforest, dispersal services for both species studied seem well-fulfilled by native flying foxes and imperial pigeons. However, flying foxes and imperial pigeons are popular game species in New Caledonia, and their populations are globally considered as decreasing (Mickelburgh et al. 1992; Barré and Dutson 2000; Brescia 2007). Low population densities i.e. less competition between individuals can lead to a cessation of dispersal function (McConkey and Drake 2006). If native dispersers' populations become small or disappear entirely, the role of invasive rats in seed dispersal may become more important (Staddon et al. 2010).

In New Caledonia, an assessment has been undertaken to determine whether controlling invasive rats would be beneficial for native biodiversity. Studying the trophic interactions and functional roles of invasive rats before making decisions about their management is crucial in order to avoid causing undesirable changes in the ecosystem (Zavaleta et al. 2001). Today, controlling rats in New Caledonia does not seem to pose a threat to essential seed dispersal services. Assuming that fruit resources may be limited, controlling rats may reduce competition with native frugivores. In some studies, a decrease in competition was hypothesized to foster seed dispersal (Bourgeois et al. 2005; Chimera and Drake 2010;

Shiels 2011; Jordaan et al. 2011), but to the best of our knowledge, this has not been demonstrated. Moreover, in some cases, competition may reduce seed dispersal by reducing the necessity of longer travels for animals to find food (McConkey and Drake 2006; McConkey and O'Farrill 2016). Consequently, it is difficult to predict the effect of rat control on seed dispersal. Stringent management measures to protect native frugivores should be reinforced in order to maintain frugivore populations at high densities, in order to ensure continuing seed dispersal services.

Acknowledgments This study was funded by the Northern Province of New Caledonia to REFCOR project (Réponses des Ecosystèmes Forestiers au COntrôle des Rongeurs, Convention No 12C240). We are grateful to Mélanie Boissenin, Bruno Fogliani, Charly Zongo from IAC (Institut Agronomique Néo-Calédonien) and Philippe Marmey from IRD (Institut de Recherche pour le Développement) for the valuable discussions about the experiment. We thank Almudena Lorenzo, Oriane Lallemand and Marianne Bonzon from Michel Corbasson Zoological and Forest Park of Noumea, "Direction de l'Environnement" of the Southern Province of New Caledonia, who allowed us to work with imperial pigeons and flying foxes. We also thank Edouard Bourguet and Frédéric Rigault for their help in collecting fruits, Josepho Bahormal for his help in taking care of rats, and Carol Frost for English advice and useful comments on the paper draft.

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