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# Sympatric Invasive Rats Show Different Diets in a Tropical Rainforest of an Island Biodiversity Hotspot<sup>1</sup>

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**Abstract:** Invasive rats (*Rattus rattus*, *R. norvegicus*, *R. exulans*) are recognized as a major threat to native island ecosystems and biodiversity. On many islands, two or three invasive rat species co-occur, often sharing the same habitat; however few studies have focused on the effects of coexisting invasive rat species on native biodiversity. We investigated rat population ecology and diet in a New-Caledonian rainforest where black (*Rattus rattus*) and Pacific rats (*R. exulans*) coexist. Black rats dominated Pacific rats in relative abundance with a proportion varying between 80.9 and 88.9%. A total of 374 black rats and 87 Pacific rats were sampled for diet assessment through stomach and caecum analysis. Rat diet was mainly composed of plants, invertebrates and to a lesser extent Squamata, with black rats being more frugivorous and Pacific rats being more omnivorous. Ten of 15 endemic skink and gecko species were consumed, nine species by black rats and six species by Pacific rats. Thus, the presence of both rat species may strengthen the overall predation rate on each native prey species, and/or broaden the total number of native prey species impacted in the New-Caledonian rainforest. These results highlight the importance of preventing new rat species introduction on islands to avoid the strengthening and/or the broadening of negative effects on native biodiversity, and the importance of following the proportion of each rat species during rat control operations. Research to assess the threats generated by various assortments of rodent species on native biodiversity could improve priority setting in conservation actions.

**Keywords:** rodent impacts, sympatric species diet, food preference, trophic niche partitioning, endemic Squamata, island conservation

ALIEN SPECIES INVASIONS ARE recognized as a main cause of species extinction and ecosystem degradation on islands (Blackburn et al. 2004, Tershy et al. 2015). The overall impact of invasive species on islands increases with invasive species richness and native species endemism (Blackburn et al. 2004, Walsh et al.

2012a). Consequently, island communities facing multiple invasive species may be particularly endangered (Bellard et al. 2014). The presence of multiple invasive predator species can strengthen the overall predation rate on each native prey species, and/or broaden the total number of native prey species impacted

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(Blackburn et al. 2004, 2005). The strengthening and the broadening of invasive predator effects on native prey species caused by multiple invasions seems obvious in the case of invasive predators of very different functional types and with different ecological niches. However, it is still unclear whether phylogenetically closely-related invasive species (with potentially quite similar ecological niches and impacts) will show sufficient niche complementarity for the multiple invasion to be functionally different than an invasion by only one of these species (Kumschick et al. 2015).

Several closely-related species of rats (*Rattus rattus*, *R. norvegicus*, *R. exulans*) are highly invasive and have been introduced on most of the world's island groups (Atkinson 1985, Towns et al. 2006, Russell et al. 2014). *Rattus* spp., in the order of impact strength: *R. rattus*, *R. norvegicus* and *R. exulans*, are recognized as major threats for native island ecosystems and biodiversity (Towns et al. 2006, Capizzi et al. 2014, Harper and Burbury 2015). On many islands, two or three species of invasive rats co-occur, sharing generally the same habitats and the same range of resources (Yom-Tov et al. 1999, Russell et al. 2014, 2015). In tropical islands of the Pacific Ocean, successive human settlements have been responsible for several waves of rat introductions. It is assumed that Pacific rats (*R. exulans*) colonized major island groups during the first Austronesian and Polynesian settlements, from 1500 B.C. to 1000 A.D. (Atkinson 1985, Matisoo-Smith and Robins 2004). More recently, starting from the sixteenth century, black (*R. rattus*) and/or Norway rats (*R. norvegicus*) have been brought by European settlers (Atkinson 1985), which has often led to over-invasion of the islands where Pacific rats were already established (Russell et al. 2014, 2015). Their impacts upon island biodiversity are generally considered to be quite similar (Towns et al. 2006, Jones et al. 2008), but few studies have compared the ecology of sympatric alien rats on islands (Shiels et al. 2013, Russell et al. 2014, 2015), or examined potential differences in their effects on native biodiversity (Jones et al. 2008, St Clair 2011). Although such studies are scarce, they are crucial to evaluate invasive

rat effects on biodiversity, and to make evidence-based decisions about rat management (Ringler et al. 2014, Harper et al. 2015).

Trophic relationships between rats and native biodiversity can be revealed through rat diet studies (e.g. Shiels et al. 2013, Zarzoso-Lacoste et al. 2016). Among 55 studies examined (Supplemental Online Material, Appendix 1), rat diet was highly variable depending on the geographic area and the ecosystem. Most studies (i.e. 36, or 66.7%) dealt with one species of rat only, seven studies (13%) concerned both the Pacific and the black rat, one (1.9%) was on both the black and the Norway rat, and only one considered the three rat species together. This observation highlights a need for more research on the impacts of invasive rats coexisting in different assortments. Most of the time, black rats are reported to be almost exclusively herbivorous (Sweetapple and Nugent 2007, Caut et al. 2008, McQueen and Lawrence 2008, Ruffino et al. 2011), although their diet is sometimes dominated by invertebrates (Clout 1980). The dominance of plants or invertebrates can even switch across seasons (Daniel 1973). Age and sex of black rats may also lead to individual diet differences with higher frequency of occurrence of animal remains in juvenile and female stomachs (Gales 1982). Vertebrates, and particularly birds, which are often considered to be highly threatened by invasive rats (Jones et al. 2008, O'Donnell and Hoare 2012), are sparsely represented in the black rat diet (Innes 1979, Harper 2007) except in some coastal areas (Yabe et al. 2009, Rodríguez and Herrera 2013, Ringler et al. 2015). Conversely, Pacific rats are reported to be more omnivorous, with a high consumption of both plants and invertebrates (Bettesworth 1972, Ferreira et al. 2001). When black and Pacific rats coexist, their diets are often reported to be similar (Fall et al. 1971, Robinet et al. 1998, Beard and Pitt 2006). However, Sugihara (1997) and Shiels et al. (2013) suggested a dietary niche differentiation among introduced rodents in Hawaiian forests, with black rats being more herbivorous and Pacific rats being more omnivorous. These results suggest that invasive rats may show both trophic niche

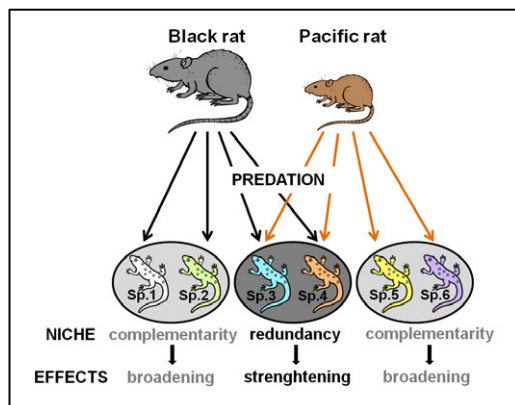


FIGURE 1. Niche complementarity and redundancy for black and Pacific rat respectively induce a broadening and a strengthening of the negative effects on biodiversity. The species 1 (Sp.1) and the Sp.2 are only preyed upon by Black rats whereas the Sp.5 and the Sp.6 are only preyed upon by Pacific rats when both rat species coexist. Black rat and Pacific rat niches are complementary and more prey species can be affected. Conversely, Sp.3 and Sp.4 are concurrently preyed upon by both rat species: rat niches are redundant and effects observed on these species can be stronger.

redundancy and complementarity (Figure 1). Consequently, they may have different effects on native biodiversity, and the arrival of another rat species may both strengthen and broaden the overall rat effects on biodiversity (Figure 1).

A better knowledge of the ecology of invasive rat communities is needed in order to understand the need for and implications of management operations in sensitive areas such as biodiversity hotspots. The New Caledonia archipelago (South Pacific) is one of the world's 36 biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2011, Critical Ecosystem Partnership Fund 2017), with exceptional endemism rates for fauna and flora (e.g. endemism rates of rainforest flora: 83.2% (Morat et al. 2012); Squamata 92% (Bauer and Jackman 2006); and cicadas 100% (Delorme et al. 2016)). Rodents were absent from New Caledonia prior to human arrival 3,000 years ago, but now two invasive rat species, the Pacific rat (which arrived with first human settlers) and the black rat (which arrived with Europeans settlers around

150 years ago), coexist throughout the natural areas of New Caledonia (Beauvais et al. 2006).

In this context, the aim of this work was to explore the respective trophic niches of black and Pacific rats, and to use this information along with population demographic data for each species to predict their respective effects on native biodiversity in a New Caledonian rainforest. This was done by assessing rat diet and by measuring rat community parameters and individual characteristics. Specifically, we addressed the following questions: (i) What are the relative abundances, weights, sex ratios, and proportions of juveniles of black and Pacific rats in our study area? (ii) How do the identities and proportions of organisms consumed by black and Pacific rats differ? (iii) How does rat diet change with age, sex, and capture sessions for each species? and, (iv) Integrating this information with the conservation statuses of local endemic species, what can we predict about the respective and combined effects of invasive rats on native flora and fauna in New Caledonian rainforest, and what recommendations can we therefore make for rat population management?

## MATERIALS AND METHODS

### Study Site

This study was conducted in a dense evergreen rainforest located between 550 and 950 m a.s.l. in the wilderness reserve of Mont Panié (20° 37' 30" S, 164° 46' 56" E, 5400 ha) in the northern province of New Caledonia (Figure 2A–C). Mont Panié reserve has been protected since 1950 because of its cultural importance and high micro-endemism rates observed for most taxa (plants, insects, Squamata) (Tron et al. 2013). The climate is moist subtropical with a hot season between December and mid-April and a cool season between mid-May and September. The area is mainly covered by primary rainforest lying on a metamorphic substrate. In 2010, a rapid assessment survey evaluated the fauna and flora biodiversity of the Mont Panié region, listing 617 species of plants, 29 of birds, 18 of

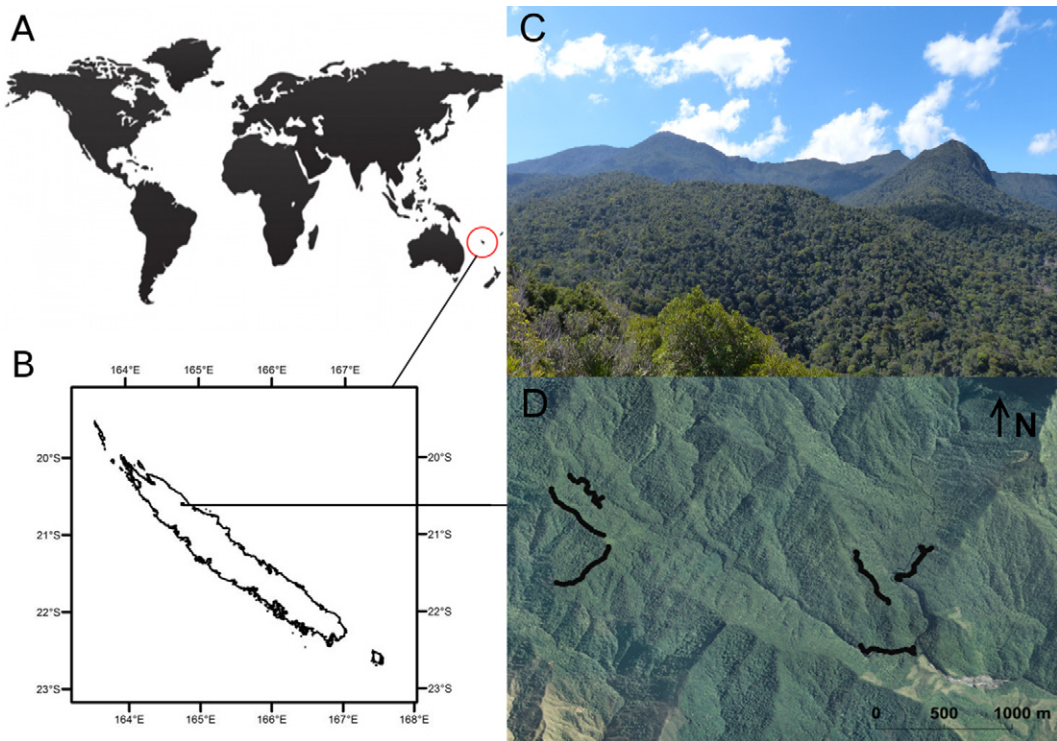


FIGURE 2. Location of the study in the wilderness reserve of Mont Panié, northern New Caledonia. (A) Location in the world. (B) Location in New Caledonia. (C) Mountain rainforest of Mont Panié. (D) Location of the 6 rat transects (black lines) in Mont Panié study area.

Squamata, 19 of freshwater fishes and crustaceans, and 23 odonates (Tron et al. 2013).

### Rat Sampling

In order to determine rat population parameters and to collect individuals for the diet analysis, we worked on six line-transects of 600 m length (Figure 2D). Thirty traps were set up along each transect, spaced by 20 m. Rats were caught at each site using the “Snap E Rat Trap” (Kness Mfg. Co., Albia, IA, USA). Four capture sessions of five consecutive nights took place in April–May 2013 (end of hot season), November–December 2013 (hot season), September 2014 (end of cool season) and April 2015 (end of hot season). Each day, traps were baited with coconut chunks at sunset and checked at sunrise. All rats caught were identified to species level (black rat *R. rattus* versus Pacific rat

*R. exulans*), sexed, weighed to the nearest 2.5 g, and checked for sexual maturity (females: perforate vagina and teat development status, males: presence of a scrotal sac). Because most black rat individuals weighing more than 120 g and most of Pacific rat individuals weighing more than 55 g were sexually mature (respectively 95% and 96%), we used the weight as a proxy of rat sexual maturity.

### Rat Community and Population Parameters

In order to compare relative abundances of the two rat species across seasons and years, we calculated an index of abundance (IA) as the number of trapped rats per 100 trap-nights, adjusted for the corrected number of trap-nights (CTN), that is, by subtracting half a trap night for each sprung trap (Nelson and Clark 1973). IA were estimated for each transect on

each night of trapping and these were used for calculating mean IA and IA standard deviation ( $\pm$ SD). To test whether the number of trapped rats changed between capture sessions for all rats or for each species separately, we used three binomial Generalized Linear Models (GLMs). The proportions of total rats, black rats, and Pacific rats trapped on the total number of traps available for each transect on each night of trapping were respectively the three response variables. In each model, ‘capture session’ was the predictor variable, and we used a chi-square test to assess the significance of the deviance change between the null model and the model with the variable (Note that the variable ‘capture session’ encompasses tests of both the effects of season and year, since the first two capture sessions were different seasons within one year, the third capture session was a different season again, but also a different year, and the fourth capture session repeated the April capture session in a different year.). Then, to test whether the proportion of trapped Pacific rats may vary with trapped black rats, we used a binomial GLM model with ‘proportion of Pacific rats’ as the response variable and ‘number of black rats’ as the predictor variable. Finally, to test whether sex-ratio or proportion of juveniles changed with capture session for each rat species, we used four GLM models. In models for each species separately, either ‘sex-ratio’ or ‘proportion of juveniles’ was the response variable and ‘capture session’ was the predictor variable. All analyses were conducted with R 2.15.3.

#### *Rat Diet Analysis*

Stomachs and caeca of trapped rats were collected and preserved in 95% ethanol (Clark 1982). For both rat species, diets were assessed by morphological analysis of food items from stomach and caecum contents. Although the majority of diet studies are based on stomach contents alone (Sugihara 1997, Shiels et al. 2013), a recent study has shown that combined analysis of stomach and caecum contents provides much more information on taxon richness in rat diet, particularly for Squamata (Thibault et al. 2017). Each sample, that is, stomach or caecum, was rinsed with

tap water and sieved through a 500  $\mu$ m mesh (Sugihara 1997). Macroremains from each sample were placed in a Petri dish, examined and identified under a dissecting microscope (10–40 $\times$  magnification). Each item was identified to the lowest taxonomic level possible using a reference collection. A determination key based on morphology of scales was used to determine skink remains to species level (IMBE, unpublished data). Frequency of occurrence (percent) for each food item and each food type (plants, invertebrates, Squamata, birds) was determined by dividing the number of samples (i.e. rat individuals) containing the food item or food type by the total number of analyzed samples. Based on the volume occupied by remains in the Petri dish (Sugihara 1997), a score ranging from 0 to 5 was given for each food type (plants, invertebrates, Squamata, and birds) as follows: 0 (absent), 1 (<0.5%), 2 (>0.5 to 5%), 3 (>5 to 25%), 4 (>25 to 50%), and 5 (>50%).

Due to an estimated mean transit time of 12 h in rats (Platel and Srinivasan 2001), stomach contents include consumed items for only a few food intakes. By contrast, the caecum can stock remains that are difficult to digest from multiple food intakes (Perrin and Curtis 1980). For example, items with cellulose (e.g. plant seeds), chitin (e.g. insect cuticle) or keratin (e.g. Squamata scales, bird feathers) need a longer time to be digested than fruit pulp or animal flesh, and may be retained during several food intakes. Consequently, stomach contents may better reflect the relative proportions of consumed items than caecum contents. Therefore, we chose to estimate frequencies of occurrence and volume scores based on stomach contents data only. By contrast, we used both stomach and caecum data in order to get the maximum resolution on Squamata diversity in rat diet (Thibault et al. 2017).

First, to test whether the frequency of occurrence for each food type changed with rat species, we used four binomial GLMs, with ‘plant frequency of occurrence (FO)’, ‘invertebrate FO’, ‘Squamata FO’, or ‘bird FO’ as the response variables. In each model, ‘rat species’ was the predictor variable, and we used chi-square tests to assess the significance

of the deviance change between the null model and the model with the ‘rat species’ variable. Next, for each species considered independently, we checked whether the frequency of occurrence (FO) for each food type varied with sex, age, or capture session using binomial GLMs. In each model, ‘plant FO’, ‘invertebrates FO’, ‘Squamata FO’ or ‘bird FO’ were the response variables and ‘sex’, ‘age’, or ‘capture session’ were the predictor variables. We also used chi-square tests to assess the significance of the deviance change between the null model and the models with ‘sex’, ‘age’, or ‘capture session’ variables.

Second, the effect of rat species on relative volume scores of each food type were assessed with a PERMANOVA, that is permutational multivariate analysis of variance for non parametric data (Anderson 2001). The PERMANOVA test uses the distances between samples to partition variance, and uses randomizations or permutations of the data to produce the p-value for the hypothesis test. As volume scores corresponded to categories with unequal class intervals, distances between each individual were calculated with Gower’s method which considers non-numeric ordinal data (Gower 1971). The number of permutations was set at 999. The distance matrix of relative volume scores of each food type was used as the response variable and ‘rat species’ as the predictor variable. We also ran PERMANOVA for each rat species to assess if relative volume scores changed with sex, age and capture session. The distance matrix of relative volume scores was used as the response variable and ‘sex’, ‘age’ or ‘capture session’ were the predictor variables. For the four levels of the ‘capture session’ variable, we performed post-hoc tests, that is, pairwise comparisons for PERMANOVA.

Last, we described in detail the diets of black rats and Pacific rats, according to stomach contents, and focused on endemic Squamata species which were found either or both in stomachs and caeca. All the analyses described above were performed with the R packages ‘vegan’ (Oksanen et al. 2016), ‘cluster’ (Maechler et al. 2016) and ‘ade4’ (Dray et al. 2016) in the R version 2.15.3.

## RESULTS

### *Rat Community and Population Parameters*

Mean rat IA ranged between  $8.33 \pm 9.21$  ( $\pm$ SD, September 2014) and  $46.83 \pm 16.17$  ( $\pm$ SD, April 2015) per 100 corrected trap-nights (100 CTN). The mean IA for black rats was  $20.02 \pm 11.37$  and mean IA for Pacific rats was  $3.19 \pm 3.42$  per 100 CTN (Figure 3). The chi-square test conducted in the GLM results showed the existence of a significant effect of capture session on the total number of trapped rats (deviance explained by the variable (dev) = 46.49%,  $P < .001$ , Figure 3). The number of black rat captures varied with capture session (dev = 44.68%,  $P < .001$ ) as did the number of Pacific rat captures (dev = 15.51%,  $P < .001$ , Figure 3). Although we did not statistically test year and season effects separately, the capture session effect seems to be due to strong changes in abundance between years, rather than between seasons (Figure 3). For black rat, IA in April 2015 was three times higher than at approximately the same period in April–May 2013. For Pacific rat, IA in April 2015 was two times higher than in April–May 2013 (Figure 3). Black rats were consistently more often trapped than Pacific rats (Figure 3), with a proportion varying between 80.88 and 88.89% according to the capture session. The proportion of Pacific rats decreased with black rat relative abundance

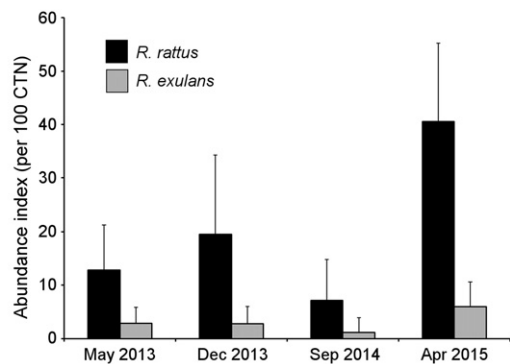


FIGURE 3. Mean ( $\pm$ SD) of index of abundance (per 100 CTN) for black rat (*R. rattus*) and Pacific rat (*R. exulans*) recorded during the first five days of trapping by snap trapping line captures in Mont Panié study area.

(dev = 8.84%,  $P = .007$ ) but did not vary with capture session (dev = 2.24%,  $P = .601$ ).

Sex-ratio varied, but was not significantly different between rat species (dev = 0.2%,  $P = .473$ ) nor between capture sessions (dev = 1.76%,  $P = .246$ ) (Supplemental Online Material, Appendix S2). The proportion of juveniles in the population did not vary with species (dev = 0.17%,  $P = .772$ , Supplemental Online Material, Appendix 2). However, the proportion of juveniles changed significantly across capture sessions (dev = 53.9%,  $P < .001$ , Supplemental Online Material, Appendix 2). In September 2014, the proportion of juveniles was very low and significantly lower than in May 2013 ( $P = .011$ ), December 2013 ( $P < .001$ ) and April 2015 ( $P = .007$ ). The highest proportion of juveniles was recorded in December 2013: 42.3% for the black rat and 65% for the Pacific rat (Supplemental Online Material, Appendix 2).

The mean black adult rat weight was  $177.40 \pm 30.09$  g ( $\pm$ SD) and the mean Pacific adult rat weight was  $71.58 \pm 11.77$  g ( $\pm$ SD).

### Rat Diet

Rat stomachs and caeca were collected during each capture session (April–May 2013:  $n = 112$ ; November–December 2013:  $n = 150$ ; September 2014:  $n = 68$ ; and April 2015:  $n = 131$ ) for a total of 374 black rat and 87 Pacific rat samples (Supplemental Online Material, Appendix 3). We found rat diet in Mont Panié forest to be mainly composed of plants and invertebrates (Figure 4a). For plants, the frequency of occurrence (FO) was higher in black rat stomachs than in those of Pacific rats (deviance explained by the model (dev): 21.41%,  $P < .001$ ). Conversely, Pacific rat stomachs contained invertebrates significantly more frequently than those of black rats (dev: 25.17%,  $P < .001$ ). We did not find differences for the FO of Squamata or bird remains among the two rat species (respectively dev: 2.61%,  $P = .106$  and dev: 1.68%,  $P = .195$ ). Nonetheless, 9.20% of Pacific rat stomachs and 4.55% of black rat stomachs contained Squamata remains. No bird remains were found in Pacific rat stomachs and only 1.07%

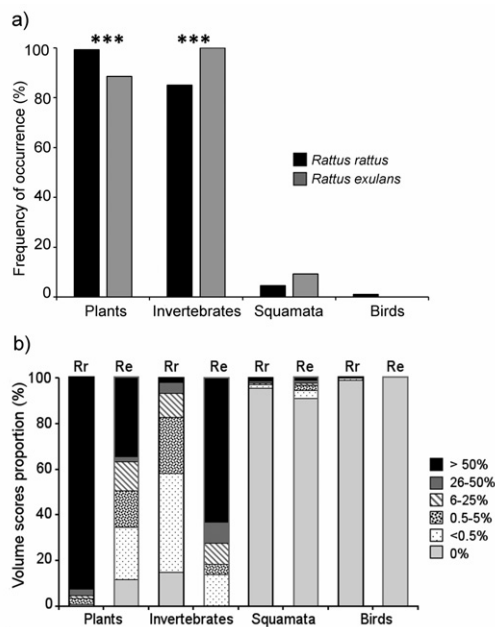


FIGURE 4. (a) Frequency of occurrence and (b) volume scores proportion for major prey groups found in black rat (*R. rattus*) and Pacific rat (*R. exulans*) stomachs. The number of \* indicates the degree of significance (\*  $P < .05$ , \*\*  $P < .01$ , \*\*\*  $P < .001$ ). Rr: *R. rattus* and Re: *R. exulans*.

of black rat stomachs contained bird feathers (Figure 4a).

For each rat species, we examined if the FO for each food type varied with sex, age, or capture session. For black rats, we found that plant, invertebrate, and bird FO did not vary with sex, age, or capture session. However, Squamata FO varied with age (dev = 4.52%,  $P = .012$ ) and capture session (dev = 12.48%,  $P < .001$ ). Squamata remains were more often present in stomachs from juvenile than from adult individuals. The rate of stomachs with Squamata remains was the highest for April 2015 sampling compared with all other sessions.

For the Pacific rat, we found that plant FO varied with capture session (dev = 17.91%,  $P = .01$ ). We observed significantly more plants in stomachs collected in May 2013 and December 2013 compared to September 2014 (respectively  $P = .018$  and  $P = .007$ ). Invertebrate FO and Squamata FO did not



show any significant variation according to sex, age, or capture session.

Relative volumes of the different item categories were significantly different according to rat species ( $R^2 = .39$ ,  $P = .001$ , Figure 4b, Supplemental Online Material, Appendix 4). Black rats ate a higher volume of plants whereas Pacific rat ate more invertebrates (Figure 4b). For the black rat, the relative volumes did not vary significantly with age ( $R^2 = 0.45$ ,  $P = .228$ ), or sex ( $R^2 = 0.01$ ,  $P = .828$ ) but did vary significantly with capture session ( $R^2 = 6.04$ ,  $P = .001$ ). Post-hoc tests revealed that the relative volume of insects and Squamata in black rat stomachs were significantly higher in September 2014 and April 2015 than in April–May and December 2013. For the Pacific rat, the relative volumes did not vary with age ( $R^2 = 1.11$ ,  $P = .358$ ) or sex ( $R^2 = 3.57$ ,  $P = .067$ ), nor with capture session ( $R^2 = 7.85$ ,  $P = .058$ ).

Regarding plant material, we found that 35.0% of black rat stomachs contained seeds and 96.8% contained fruit pulp (Table 1). However, plant remains in stomachs were difficult to identify at high taxonomic resolution. Regarding seeds, we were able to identify seeds of *Freycinetia sulcata* and *Ficus* spp. For the Pacific rat, 27.6% of stomachs contained seeds and 77.0% contained fruit pulps. The invertebrates found were Arachnida, Chilopoda, Crustaceae, Insecta, Gastropoda and Oligochaeta. Pacific rats ate more Arachnida, Chilopoda, Crustaceae, Coleoptera (Carabidae and Curculionidae), Orthoptera, Dictyoptera, Lepidoptera larvae, Gastropoda and Oligochaeta than black rats. By contrast, black rats ate more Formicidae than Pacific rats.

Squamata identifications were conducted for remains from both stomach and caecum contents. Studying both organs provided more scale remains and information about Squamata species preyed upon by rats (Tables 1 and 2). The frequency of occurrence of Squamata in black rat stomachs was 4.55%, compared to 6.17% in both stomachs and caeca, and 9.20% compared to 23.26% for Pacific rats (Table 2). Regarding prey diversity, black rats preyed upon more species than Pacific rats, with seven species of diurnal skinks (Scincidae) and two species of geckos (Diplodactylidae). Conversely, Pacific rats

preyed upon six species of diurnal skinks, mostly *Celatiscincus similis* and *Caledoniscincus aquilonius* (Table 2). Among the 15 Squamata species present at the Mont Panié study site, our sampling detected 10 species eaten by rats. Among these species, five were eaten by both rat species, and five were eaten by one rat species only. Concerning birds, only five black rat stomachs contained bird remains, and of these, only feathers of the native Coconut Lorikeet *Trichoglossus haematodus* in one stomach were identifiable.

## DISCUSSION

Black and Pacific rats have coexisted for more than a century in New-Caledonian rainforests (Beauvais et al. 2006). In our study, black rats were considerably more frequently trapped than Pacific rats and both rat species were omnivorous, eating mainly plants, invertebrates and to a lesser extent, Squamata. However, frequencies of occurrence of each food type were different depending on the rat species: black rats were more frugivorous whereas Pacific rats were more omnivorous, eating a greater proportion of invertebrates and Squamata. Some prey taxa were preyed upon by both black and Pacific rats, whereas other taxa were preyed upon by one rat species only. These results seem to show that black and Pacific rat trophic niches are both partially redundant and complementary when coexisting. However, the fact that the sample of black rats is larger than that of Pacific rats may have partially influenced the width of the trophic niche found. Rat relative abundance fluctuated across sessions, and demographic parameters (sex-ratio and proportion of juveniles) fluctuated across sessions. In our study, relative volume of each food type changed with maturity as well as sessions for black rats. Therefore invasive rat diet and overall effects on biodiversity may also vary greatly along with seasons and years, and relative abundances of plants and animals available (Caut et al. 2008, Ruffino et al. 2011).

The magnitude of a rat populations' effects on native species may depend on the abundance and population structure of each rat species. In our study site, the rat relative abundance seems high for tropical island

TABLE 1

Frequency of Occurrence (%) for Plants, Invertebrates, Squamata and Bird Taxa Identified in Black Rat and Pacific Rat Stomach Contents

Group	Order/Family	Species or Taxa Identified	Black Rat (n = 374)	Pacific Rat (n = 87)
<b>PLANTS</b>			<b>99.20</b>	<b>88.50</b>
<b>Seeds</b>			35.29	27.59
	Pandanaceae	<i>Freycinetia sulcata</i>	14.97	2.3
	Moraceae	<i>Ficus</i> spp	1.34	0.00
	undefined seeds		23.8	25.29
<b>Fruit pulp</b>			96.79	77.01
<b>Other plant material</b>			32.62	32.18
<b>INVERTEBRATES</b>			<b>85.00</b>	<b>100.00</b>
<b>Arachnida</b>			14.17	45.98
	Araneae		13.64	45.98
	Opiliones		2.06	0.00
<b>Chilopoda</b>			7.49	62.07
<b>Crustaceae</b>		Amphipods and isopods	0.00	5.88
<b>Insecta</b>			81.82	97.7
	Coleoptera Scarabidae		5.88	16.09
	Coleoptera Curculionidae		0.27	5.75
	Coleoptera others	Cucujoidae, Staphilinidae and undefined species	17.65	20.69
	Blattodea	Cockroaches	7.75	28.74
	Hymenoptera Formicidae	mainly <i>Paraparatrechina</i> sp and <i>Pheidole</i> sp	25.4	10.34
	Hymenoptera others		5.08	3.45
	Orthoptera	Crickets, grasshoppers, wetas	12.03	26.44
	Phasmatodea	Stick insects	8.06	12.64
	Imago others	Dermaptera, Thysanoptera, Diptera, Hemiptera and undefined imago	43.85	41.38
	Larvae Lepidoptera	Caterpillars	17.11	59.77
	Larvae others	Coleoptera, Diptera, Hemiptera and undefined larvae	5.88	24.14
<b>Gastropoda</b>	Pulmonata	Snails and slugs	2.14	24.14
<b>Annelida</b>	Oligochaeta	Earthworms	2.41	18.39
<b>REPTILES</b>			<b>4.55</b>	<b>9.20</b>
<b>Squamata</b>	Scincidae	species specified in <a href="#">Table 2</a>	2.94	11.49
	Diplodactylidae	species specified in <a href="#">Table 2</a>	1.6	0.00
<b>BIRDS</b>			<b>1.07</b>	<b>0.00</b>
<b>Psittaciformes</b>	Psittacidae	<i>Trichoglossus haematodus deplancheii</i>	0.27	0.00
	undefined birds		1.07	0.00

rainforests, compared with other studies (but note that the calculation of rat relative abundances depends on trap type and spacing). In Hawaii, an IA of roughly 8–17 per

100 CTN was recorded in wet forests on Maui ([Sugihara 1997](#)) and of roughly 11–25 per 100 CTN in wet forests on Big Island ([Lindsey et al. 1999](#)). For our sampling site, mean black

TABLE 2

List of Squamata Observed in Mont Panié Rainforest and Their Frequency of Occurrence (%) in Black Rat and Pacific Rat Stomach and Caecum Contents

	Binomen	IUCN Status	Frequency of Occurrence (%) in Stomachs and Caeca	
			Black Rat	Pacific Rat
<b>Scincidae</b>	<i>Caledoniscincus aquilonius</i>	NT	0.00	4.65
	<i>Caledoniscincus festivus</i>	LC	0.54	0.00
	<i>Caledoniscincus haplorhinus</i>	LC	0.54	1.16
	<i>Caledoniscincus orestes</i>	EN	0.00	0.00
	<i>Epibator nigrofasciolum</i>	LC	0.54	1.16
	<i>Caesoris novaecaledoniae</i>	LC	0.27	1.16
	<i>Lioscincus steindachneiri</i>	EN	0.00	0.00
	<i>Celatiscincus similis</i>	EN	1.34	10.47
	<i>Marmorosphax tricolor</i>	LC	1.07	2.33
	<i>Tropidoscincus boreus</i>	LC	0.27	0.00
	<i>Undefined scales</i>		0.27	5.81
<b>Gekkonidae</b>	<i>Bavayia montana</i>	DD	0.54	0.00
	<i>Bavayia sauvagii</i>	DD	no data	no data
	<i>Eurydactylodes agricolae</i>	NT	0.80	0.00
	<i>Paniegekko madjo</i>	NT	0.00	0.00
	<i>Rhacodactylus leachianus</i>	LC	0.00	0.00
	<i>Undefined species</i>		0.54	0.00
Squamata*			6.17	23.26

Squamata\* corresponds to the total frequency of occurrence (%) of Squamata remains in black rat and Pacific rat stomach and caecum contents. IUCN categories: NT (Near Threatened), LC (Least Concern), EN (Endangered), DD (Data Deficient).

rat IA was around 20.0 per 100 CTN and mean Pacific rat IA was around 3.2 per 100 CTN. Shiels et al. (2013) also highlighted the dominance in abundance of black rats over Pacific rats in Hawaii; data from capture-mark-recapture gave IA of 13.5 for black rats and of 0.7 for Pacific rat. This result can come from a lower true abundance of Pacific rats, but may also reflect a lower attractiveness for the bait used (coconut flesh) or even a lower tendency of Pacific rats to explore novel objects. In our case, the proportion of Pacific rats decreased with black rat abundance suggesting that Pacific rats might be less competitive at accessing traps than the larger black rats (Harper and Veitch 2006). Black rats weighed around 149 g and Pacific rats around 61 g which are very close to weights found in other tropical forests, for example, by Sugihara (1997) and Rouys (2008). As rats consume about 10% of their weight each day

(Long 2003), a black rat may eat more than 5 kg of food each year where as a Pacific rat may eat around 2 kg of food. However, even if Pacific rats may be present in lower abundance and are smaller than black rats, their presence likely strengthens the overall rat impact on shared prey species, and broadens the rat overall impact by extending the number of native species impacted.

Our results also suggest that the overall effects of invasive rats in Mont Panié study site are likely high for plants, invertebrates and Squamata. Regarding the high proportion of plant remains in rat diets and the occurrence of fragmented or intact seeds, black rats especially may contribute negatively (as seed destructors) or positively (as seed dispersers) to plant reproduction and dynamics (Williams et al. 2000, Meyer and Butaud 2008, Shiels and Drake 2011, Pender et al. 2013). Precise identification of consumed plants was almost

impossible without molecular analysis as fruit and seed remains were highly fragmented. Among intact seeds, *Freyinetia sulcata* and *Ficus* spp. were the only seeds identified in stomach contents, and are likely part of the set of plant species dispersed by rats (Duron et al. 2017b). Unfortunately, we could not identify other seeds destroyed by rats and so plant species potentially threatened by rats.

All the Pacific rats and 85% of black rat samples contained invertebrate remains. However, the predominant invertebrate prey taxa were different according to rat species. Black rats consumed far fewer invertebrates in general but many Hymenoptera, which may be ingested accidentally while eating fruits. In his review, St Clair (2011) reported that beetles (Coleoptera), Orthoptera, and terrestrial mollusks were the taxa most threatened by invasive rats. Macro-insects like stick insects (Phasmatodea) and wetas (Orthoptera) were present in low abundance in rat stomachs. However, these large-bodied insects with little defensive behavior may also be highly threatened by rats (Gibbs 1998, Carlile et al. 2009, Watts et al. 2011) and some uncommon species may have already disappeared from Mont Panié rainforest.

Valuable information on the identity of the Squamata species potentially threatened by rats was provided in this study by the concurrent analysis of stomach and caecum contents. Mont Panié rainforest hosts at least 15 Squamata species (all endemic), 10 species of skinks and five species of geckos (Tron et al. 2013). Among these species, five were preyed upon by both rat species and five by one rat species only, indicating that the presence of both rat species likely strengthens and broadens the overall impacts on Squamata species. The black rat does not seem to be specialized and may eat Squamata opportunistically whereas Pacific rats seemed to prey preferentially on *Celatiscincus similis* and *Caledoniscincus aquilonius*, two species evaluated as endangered (EN) and near threatened (NT) respectively under IUCN Red List criteria (IUCN 2016). In this context, invasive rat management may help to reduce threats to endemic Squamata species. On islands of New Zealand, the abundances of skinks and geckos

have already shown large increases after rat eradication (Towns and Broome 2003, Monks et al. 2014). At Mont Panié, rat predation rates on Squamata seem relatively high when compared with studies conducted in other tropical forest ecosystems. For example, in two Hawaiian forests (Sugihara 1997, Shiels et al. 2013), no skink or gecko remains were found in black or Pacific rat stomachs. The high incidence of Squamata in our results may also be due to exceptional Squamata fauna richness and abundance in New Caledonia (Bauer and Sadlier 2000).

Despite intensive sampling, we found no evidence that birds or bird eggs are part of Pacific rat diet, and birds only represented a minute part of the black rat diet. Moreover, the possibility that black rats fed in bird carrion instead of live birds cannot be discarded (Zarzoso-Lacoste et al. 2016). Eggs and birds have previously been found to be absent from rat stomach contents in other forests where plants and invertebrates appeared to be their primary food sources (Sugihara 1997, Shiels et al. 2013). Artificial nest experiments conducted in Mont Panié rainforest also suggested a low level of predation on bird eggs but this complements the predation pressure exerted by native predators in this ecosystem (Duron et al. 2017a). However, the few bird remains found in the black rat diet might also be due to the low power of detection of egg predation by diet morphological studies (Zarzoso-Lacoste et al. 2016) and also the rather low abundance of birds in the study area.

Although the management of invasive species in New Caledonia is of primary importance in order to preserve its native and endemic biodiversity (Beauvais et al. 2006, Pascal et al. 2008), very few studies have been conducted on New Caledonia's rat population ecology and diet (Robinet et al. 1998, Rouys 2008, Brescia 2011, Thibault et al. 2017). Our study shows that both *Rattus* spp. play important and different roles in the overall invasive pressures that native island flora and fauna have to cope with. Our results further suggest that secondary invasion by the black rat where the Pacific rat has already been introduced before is likely to result in a

strengthening and broadening of overall rat impacts on native biodiversity. Therefore, preventing new rat species introduction on islands, even if one of them is already present, is a crucial conservation goal to avoid new and enhanced risks for native species (Blackburn et al. 2004, Russell et al. 2008, Walsh et al. 2012b, Simberloff et al. 2013). In the absence of competitors, rats are known to have a wider fundamental niche while in presence of competitors, their realized niche is likely to be much narrower. This was already suggested by the change in relative abundances in favor of the dominant rat species (Harper et al. 2005). Further investigation will determine whether in addition to the above, rat diet is modified according to the absence or presence of congeneric rats.

As many invasive rat control operations (i.e. local reduction of rat abundance) are now being conducted on large islands where eradication is not feasible (Duron et al. 2017c), it is important to ensure, when both rat species are concurrently present, that reduction of Pacific rat abundance operates in parallel with the reduction of the black rat. For instance, their relative abundance can be monitored by trapping transects before, during and after rat control operations. When both species are present in the same habitat, Pacific rat density may be constrained by the dominance of the black rat (Yom-Tov et al. 1999, Russell and Clout 2004). Consequently, a reduction of black rat abundance during rat control may lead to competitor release effects (Caut et al. 2007), which could result in an increase of Pacific rat abundance and Pacific rat effects on threatened endemic invertebrates and Squamata. Invasive rat community impacts on island native biodiversity certainly depend on the assortment of rodent species present, which may include two, three or four species (*R. norvegicus*, *R. rattus*, *R. exulans*, and *M. musculus*). The effects of invasive rodent assortments in various habitats are little known, and thus there is a great necessity for research to assess threats generated by various rodent assortments on native island biodiversity, in order to define action priorities for biodiversity conservation and restoration.

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