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Special Issue Article: Tropical rat eradication

Invasive rat interactions and over-invasion on a coral atoll

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ABSTRACT

Invasive rats are found on most island groups of the world, and usually more than one species has invaded. On tropical islands populations of different invasive rat species can co-exist on very small islands, but the population dynamics of such co-existing rat species, their impact on each other, and the mechanisms of coexistence are not well known. This lack of knowledge is a barrier to improving the success rate of tropical island rat eradications. Through an exhaustive trapping eradication campaign on a small tropical island, we study the population structure of historically established *Rattus exulans* where *R. rattus* have colonised within the last fifty years and over-invaded. We contrast this *R. exulans* population with a nearby island population where *R. exulans* exist alone. Recently invaded *R. rattus* numerically and morphologically dominate *R. exulans*; however stable isotope analyses show that the trophic position of *R. exulans* remains consistent regardless of the presence of *R. rattus*, once differences in trophic foundations of islands are accounted for. Although the trophic position of both rat species is indistinguishable, *R. rattus* is able to dominate *R. exulans* through interference competition. Our eradication attempt was interrupted by a tropical cyclone and ultimately unsuccessful, but there is some evidence that *R. rattus* reduced control device availability to *R. exulans*, which has important implications for multi-species control operations.

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1. Introduction

Invasions by multiple species with similar functional ecology are becoming more common (Russell et al., 2014). Congeneric invasive rats are one such group of closely related species with a historical checkerboard distribution across islands and continents of the world. Atkinson (1985) records for 123 islands groups, invasive *Rattus rattus* on 50%, *Rattus norvegicus* on 36% and *Rattus exulans* on 24%. The negative impacts of rats on island biota are well documented (Towns et al., 2006) and differ subtly among the three rat species (Jones et al., 2008). Much work has considered the processes by which invasive rat species can co-exist on islands (Yom-Tov et al., 1999; Russell and Clout, 2004; King et al., 2011; Shiels et al., 2013), as well as the related interactions among invasive rats and mice (Caut et al., 2007; Harper and Cabrera, 2010; Bridgman et al., 2013). Subtle differences in competitive ability clearly lead to major differences in the outcome of invasions by multiple rat species.

Eradication campaigns against rats have been successful in temperate regions, but less so in tropical regions, due in part to unique aspects of tropical islands and their rat population dynamics (Holmes et al., 2015), which have resulted in eradication failures and ultimately limited the efficacy of eradication as a conservation tool (Russell and Holmes, 2015). The presence of different crab species on tropical islands, and their complex interactions with invasive rats, is one factor which is considered particularly important (Samaniego-Herrera and Bedolla-Guzmán, 2012). Better understanding of the population structure and dynamics of invasive rats on tropical islands would help conservation managers plan and optimise island eradication campaigns (Keitt et al., 2015). However, the population structure and dynamics of invasive rats differs among island groups depending upon the climatic region, and within island groups depending on the coexistence of other predators and competitors, particularly other introduced mammals (Russell et al., 2011b; Ringler et al., 2015). Aerial eradication campaigns often preclude simultaneous study of the population ecology of the target population. In contrast experimental-type eradications on small islands where the population is first trapped to 'zero density' before remaining survivors are eradicated with poison, have been very powerful for advancing our knowledge on

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the population dynamics of invasive rats (Lorvelec and Pascal, 2005; Russell et al., 2009b).

Our study took place on a small tropical island (Honuea), on an atoll in the Society Islands of French Polynesia, where the history of rat invasion is well-known. *R. exulans* have been historically present for at least a hundred years, probably longer, until *R. rattus* arrived and over-invaded (a process whereby one invasive species displaces another *sensu* Russell et al., 2014), as occurred commonly throughout the Pacific. The study had two main goals. The first goal was to enumerate an entire tropical island population of co-existing invasive *R. exulans* and *R. rattus* by comprehensively trapping rats as part of an eradication campaign. This intensive trapping program was intended to provide data on tropical island rat population structure (e.g. density and morphology) and the differences in trophic ecology of two co-existing invasive rat species. The second goal was to contrast the population structure and trophic ecology of invasive *R. exulans* on our island (Rimatuu) of experimental eradication with a second island where they existed in the absence of *R. rattus*. This comparison was intended to determine whether the arrival of a second congeneric invasive species might substantially alter the population structure and trophic position of the incumbent invasive species.

2. Materials and methods

2.1. Study site

Honuea is a 28 hectare uninhabited island located in the Tetiaroa atoll (Fig. 1). The vegetation of Honuea consists of dry primary succession forest and can be divided into the eastern more open

abandoned coconut plantation (*Cocos nucifera*), and the western area occupied by dense patches of pandanus (*Pandanus tectorius*), both coastally fringed by *Guettarda speciosa* and *Heliotropium foertherianum* (previously *Tournefortia argentea*). *R. exulans* existed alone on Honuea for at least a hundred years until *R. rattus* colonised the island in the early 1970s (Russell et al., 2011a). Rimatuu is an 88 hectare island also located in the Tetiaroa atoll, 2 km from Honuea. The vegetation of Rimatuu is more varied and disturbed, including coconut trees, *G. speciosa*, *Morinda citrifolia* and a range of other species which reflect its history as the main island of Polynesian occupation and modification on Tetiaroa. *R. exulans* have existed alone on Rimatuu for over a hundred years. The recent history of the entire atoll is described elsewhere (Russell et al., 2011a).

2.2. Fieldwork

During 7–9 July 2009 a line of up to 30 kill traps (Victor Professional) placed every 50 m was laid around the coast of Rimatuu for three nights as part of an atoll wide rat survey (Russell et al., 2011a). During 20–27 January 2010 a grid of 118 stations with traps every 50 m was laid across the entirety of Honuea for 7 nights as part of an experimental eradication campaign. This grid alternated live (Manu, France; $n = 59$) and kill (Victor Professional; $n = 59$) traps due to limited availability. All live rats captured were immediately euthanized. All rats caught were identified to species, sexed, weighed (500 g Pesola) and had standard morphological measurements of head–body length and tail length taken (to the nearest millimetre). Tissue samples were taken from all rats captured.

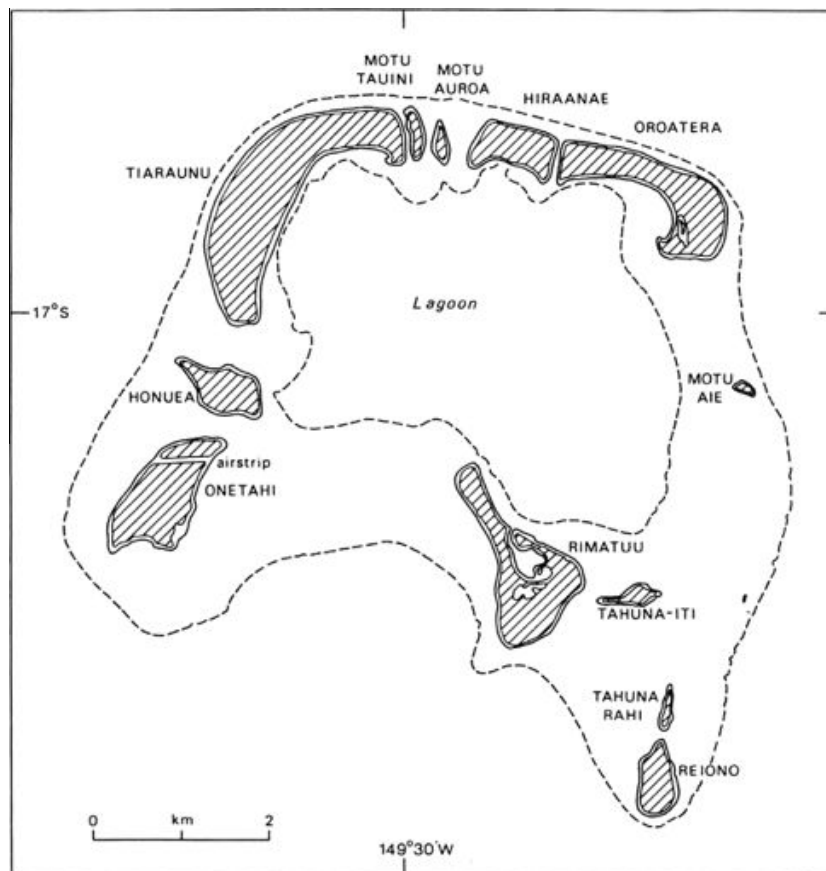


Fig. 1. Tetiaroa atoll (3366 ha; 17°05'S, 149°30'W), lies 50 km north of Moorea and Tahiti in the Society Islands of French Polynesia. The atoll comprises 12 vegetated motu (small islands) and an emerging sandbank (Motu One) east of Tahuna Iti, all circling a large lagoon. Source: David Stoddart.

Five days after trapping had ceased on Honuea, a ground-based poison campaign was initiated using 30 g 'PestOff' chocolate-flavoured rodent blocks with active ingredient 20 ppm brodifacoum (Animal Control Products, Whanganui, N.Z.) at 1 kg/ha (two tethered blocks per station every 50 m to allow monitoring, and two additional blocks between stations every 25 m for coverage). It was intended to monitor bait-take until it was zero, but this monitoring program had to be ceased after one night, and ultimately the eradication campaign abandoned, with the arrival of Tropical Cyclone Oli which inundated the entire atoll and required evacuation of all personnel (Etienne, 2012).

2.3. Stable isotopes analysis

Samples from the muscle and livers of a subset of captured rats representing both sexes and age classes, as well as from potential food items including invertebrates and plants (Supplementary Material), were collected from Honuea and Rimatuu for stable isotope analysis and fixed in 90% ethanol. Although seabirds are not present on Honuea or Rimatuu, they are abundant elsewhere in the atoll and are known to play a major nutrient input role in insular ecosystems (Caut et al., 2012). Seabird samples from elsewhere in the atoll were thus included to contextualize the trophic level of rats. All samples were later dried at 60 °C for at least 48 h and homogenised using a mortar and a pestle. Aliquots of homogenised sample were packed into tin cups. Stable carbon and nitrogen isotope measurements were carried out using a continuous flow isotope ratio mass spectrometer (Optima, Micromass, UK) coupled to a C–N–S elemental analyser (Carlo Erba, Italy). Stable C and N isotope ratios are expressed as: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, respectively. R_{standard} is the ratio of the international references PDB for carbon and AIR for nitrogen. One hundred replicate assays of internal laboratory standards indicate maximum measurement errors (SD) of $\pm 0.2\text{‰}$ and $\pm 0.15\text{‰}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ measurements, respectively.

2.4. Statistical analysis

We estimated captures per 100 Corrected Trap Nights (CTN) for rats and crabs, subtracting half a trap-night for every sprung trap (Nelson and Clark, 1973). The population size of each rat species on Honuea was estimated by fitting a Bayesian removal trapping model with parameters population size N_{RA} and N_{EX} , and nightly individual capture probability, k , in different devices (similar to Mäntyniemi et al., 2005). Species catchability was modeled under two scenarios; the first where k for each species in each trap type is independent, and the second where the catchability of the sub-dominant species *R. exulans* is dependent on the population size of the dominant *R. rattus*. In the second scenario catchability is modeled as a density dependent relationship with a modifying constant, c , on rat catchability ($c \cdot k_{RA}/N_{RA}$), where the constant estimates the population size of *R. rattus* at which the catchability of both rat species is equal. We used diffuse priors drawn from a random uniform distribution between 0 and 1 for catchability, the MNA and $4 \times$ MNA for rat species population size, and 0 and $2 \times$ MNA for the density dependent modifier, where MNA is the minimum number alive of each species (i.e. the number actually captured). We excluded scavenged rats where species could not be reliably identified. These models were fitted in OpenBUGS using four chains with 50,000 iterations burn-in, and a further 200,000 iterations to estimate parameters (Supplementary Material). Model fit was compared using DIC.

Differences in morphological measurements between *R. exulans* populations were tested using linear models of weight and body-length against island and sex. To estimate the difference in isotopic

values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) between the two rat species on Honuea, we used linear models in which species (*R. rattus* and *R. exulans*) and tissue (liver and muscle) were included as fixed effects. To compare the trophic level for the same species (*R. exulans*) between two different islands (Honuea with and Rimatuu without *R. rattus*), we corrected the rat tissue $\delta^{15}\text{N}$ by the isotopic baseline of each island ($\delta^{15}\text{N}_{\text{COR}} = \delta^{15}\text{N} - \text{island isotopic baseline}$ being the mean of the plant compartment) and then used linear models in which island (Honuea and Rimatuu) and tissue (liver and muscle) were included as fixed effects.

3. Results

3.1. Density

On Rimatuu we captured a total of 24 *R. exulans* over 65 trap nights. *R. exulans* captures peaked on the first day and declined thereafter. On Honuea we captured a total of 125 rats over 826 trap nights, comprising 80 *R. rattus*, 36 *R. exulans* and 9 individuals unidentifiable due to scavenging. Adults were *R. exulans* > 40 g and *R. rattus* > 120 g (Russell et al., 2011a). Juveniles made up 0% of *R. exulans* captured on Rimatuu in winter 2009, and 34% of *R. exulans* and 24% of *R. rattus* captured on Honuea in summer 2010.

During our trapping campaign on Honuea we captured 154 crabs, most commonly the hermit crab *Coenobita brevimanus*, as non-target species which were released alive where possible. Crab captures remained constant around 27 crabs per 100CTN (Fig. 2). *R. rattus* captures peaked on the first day, whereas *R. exulans* captures peaked on the third day, with a final ratio of *R. rattus* to *R. exulans* captured of 7:3. On the final day there were more rat captures of both species than would have been expected from the previous decline in captures. Highest rat capture rates were in the island interior, particularly at the interface between coconut and mixed woodland habitat (Fig. 3), but whereas *R. rattus* were caught across the entire island, *R. exulans* were generally caught in the interior. Crabs were caught uniformly across the entire island.

Following distribution of bait, monitoring on the first day indicated rodent sign (gnawing) at 20% of 97 tethered stations. We defined rodent sign as greater than half a block eaten. The number of rats remaining prior to poisoning was estimated between 10 and 15 from the clustering pattern of interference on baits (i.e. neighbouring stations considered likely to be the same individual). The following day all operations ceased with the onset of Tropical Cyclone Oli and all team members were evacuated to Papeete on Tahiti by the French airforce.

Both removal models converged (R-hat approximately 1.0 for all parameters) and estimated a similar sized total rat population on the island (138–148 individuals). These estimates suggest 13–23 rats survived our trapping campaign, similar to our estimate from rodent sign, and that the density of rats on Honuea was about

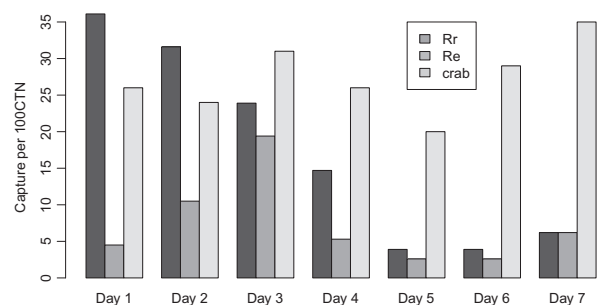


Fig. 2. Daily corrected trapping rates of rats (*R. rattus* RA and *R. exulans* EX) and crabs (*Coenobita brevimanus*) on Honuea.

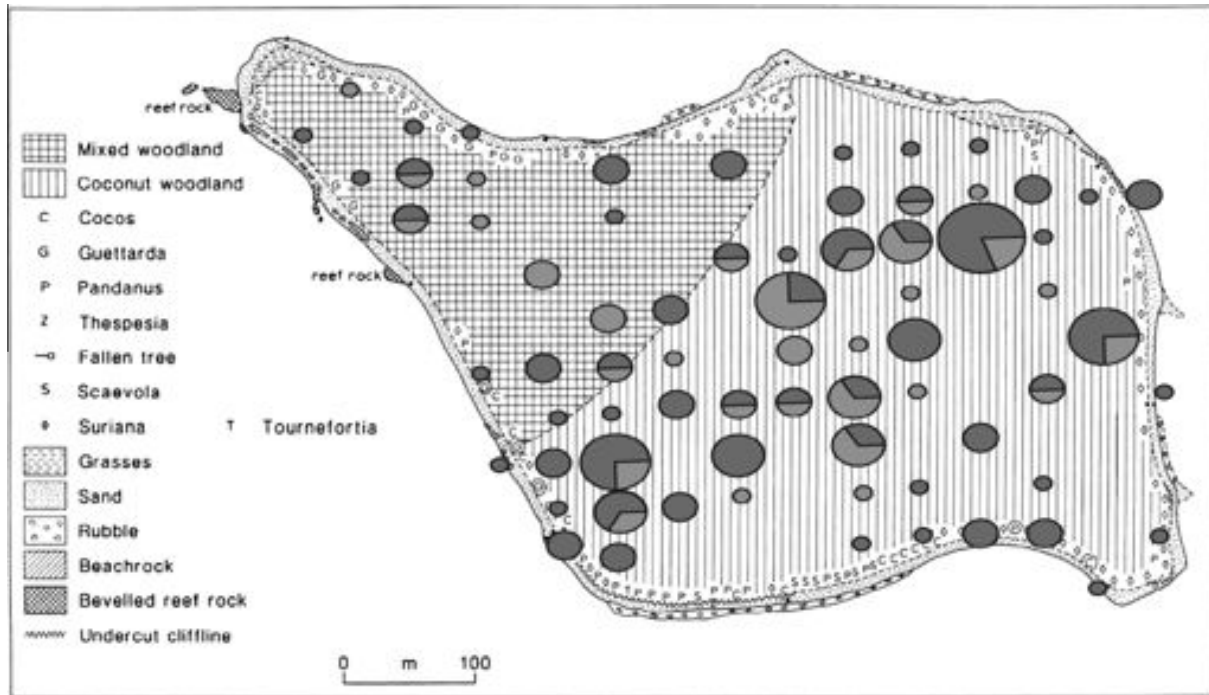


Fig. 3. Number of rats caught per trap by species. Radius of bubble is proportional to the number of rats caught. RA = black, EX = grey.

5 ha⁻¹ (Table 1). However, whereas the model with independent species catchability coefficients suggested most survivors were *R. exulans* (DIC = 120.1), the model where *R. exulans* catchability depended on *R. rattus* population size suggested most survivors were *R. rattus* (DIC = 122.7). DIC comparison suggested very slightly more support for the density independent model. *R. rattus* had a higher capture probability than *R. exulans* when catchability coefficients were independent, but a density dependent catchability coefficient for *R. exulans* was estimated at 56, or about half of the original estimated *R. rattus* population size. In both models snap traps had a higher probability of catching either rat species compared to live traps, but this result was not significant (95% credible interval overlaps zero).

3.2. Morphology

Adult *R. exulans* on Honuea were significantly lighter and smaller (weight: $t = 2.11$, $P = 0.042$; body length, $t = 2.45$, $P = 0.019$), than *R. exulans* on Rimatuu, and males were significantly heavier and slightly larger than females (weight: $t = 3.60$, $P < 0.001$; body

Table 1

Bayesian removal model estimates of population sizes and individual capture probabilities for models where k is independent for each species (left column), and where *R. exulans* catchability depends on the population size of *R. rattus* (right column).

Parameter	Estimate (95%CI)	
	k Independent	k Density dependent
\hat{N}	148 (123–208)	138 (124–164)
\hat{D}	5.3 (4.4–7.4)	4.9 (4.4–5.8)
\hat{N}_{RA}	88 (81–101)	99 (87–121)
\hat{N}_{EX}	60 (39–120)	39 (37–49)
c	NA	56.4 (24.3–119.1)
\hat{k}_{RA}	0.12 (0.08–0.17)	0.11 (0.06–0.15)
\hat{k}_{spp}	–0.08 (–0.15–0.00)	Dependent
\hat{k}_{snap}	0.06 (–0.02–0.14)	0.04 (–0.01–0.09)

length, $t = 1.97$, $P = 0.057$). Adult *R. exulans* on Rimatuu were intermediate in size to adult *R. exulans* and adult *R. rattus* on Honuea (Table 2), occupying the body-size space of juvenile *R. rattus* on Honuea.

3.3. Stable isotopes analysis

Seabird $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were both high, characteristic of a marine diet including fish, and $\delta^{13}\text{C}$ of eggshells amplified the ^{13}C enrichment compared to muscle. However, seabirds are not commonly found on either Honuea or Rimatuu, probably due to local extinction following rat invasion, and are clearly no longer a common prey item of rats. At the base of the terrestrial ecosystems, plants on Honuea showed lower $\delta^{15}\text{N}$ values than Rimatuu, characterizing the different edaphic conditions between the islands. This ^{15}N enrichment accumulated in the trophic web, explaining the higher $\delta^{15}\text{N}$ value of ants and rats on Rimatuu (Fig. 4), which we subsequently corrected for (Supplementary Material Figure). Even accounting for this edaphic difference, crabs on Rimatuu occupied a significantly higher trophic position, both for the same hermit crab species on each island (*C. brevimanus*) and a land crab species only collected on Rimatuu (*Cardisoma carnifex*).

There were no significant differences between tissue type nor trophic position of either rat species on Honuea for $\delta^{15}\text{N}$ (species, $F_{1,52} = 1.29$, $P = 0.262$; tissues: $F_{1,52} = 1.00$, $P = 0.323$; interaction: $F_{1,52} = 0.01$, $P = 0.937$) and $\delta^{13}\text{C}$ values (species, $F_{1,52} = 3.04$, $P = 0.087$; tissues: $F_{1,52} = 1.67$, $P = 0.202$; interaction: $F_{1,52} = 0.03$, $P = 0.861$). There were also no significant differences between Honuea and Rimatuu, nor tissue type, for $\delta^{15}\text{N}$ corrected values (island, $F_{1,64} = 0.01$, $P = 0.937$; tissues: $F_{1,64} = 1.76$, $P = 0.190$; interaction: $F_{1,64} = 0.24$, $P = 0.627$).

4. Discussion

Invasive rat species coexist on many islands of the world, but the mechanisms and outcomes of their coexistence, or exclusion, remain under-studied. The opportunity to enumerate almost

Table 2
Morphology of adult *R. rattus* and *R. exulans* on Honuea and Rimatuu (\pm SD).

Island	Species	Sex	n	Weight (g)	HBL (mm)	TL (mm)
Honuea	<i>R. rattus</i>	M	31	170 (33.2)	191 (10.1)	220 (10.4) ^a
		F	28	162 (20.7)	190 (10.7)	217 (12.6)
	<i>R. exulans</i>	M	10	67 (7.8)	137 (8.3)	143 (6.4)
		F	11	50 (5.6)	128 (10.3)	138 (5.5)
Rimatuu	<i>R. exulans</i>	M	9	74 (17.5)	146 (12.3)	166 (6.2) ^a
		F	11	60 (6.5)	139 (10.1)	147 (12.1)

^a Some individuals excluded due to missing tail tips.

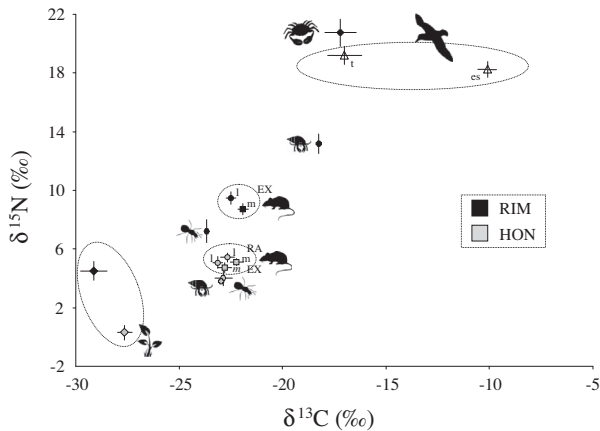


Fig. 4. Carbon and nitrogen stable isotope ratios (\pm SE) for rats (*Rattus rattus* (RA) and *Rattus exulans* (EX); *l* = liver and *m* = muscle) and different species sampled (seabird; *t* = tissue (muscle, yolk egg, feather) and *es* = egg shell; crabs; 1 = *Cardisoma carnifex*, and 2 = *Coenobita brevipanensis*) in the two different islands (Honuea in grey and Rimatuu in black).

completely the populations of two co-existing species on a small tropical island allowed us to investigate the changes in population structure and ecology which occur to one rat species (*R. exulans*) when a second rat species (*R. rattus*) invades. The theoretical outcomes of this type of over-invasion have previously been modeled (Russell et al., 2014), but have not been empirically investigated for rats. The invasion of a second rat species with very similar functional ecology to an incumbent species would be expected to cause changes in the population structure (density, age structure, body-size) and ecology (diet and space-use) of both species. These changes would be driven by interference or exploitative competition, or both. Both species would need to immediately adapt their behaviour, particularly the sub-dominant competitor, and would eventually either co-exist as a result, or completely exclude one or other species. Such adaptations in rat population structure and dynamics have been observed inter-trophically via predator-prey mediation where invasive rats co-exist with introduced cats on tropical islands (Russell et al., 2011b), and might be expected immediately following the introduction (either accidentally or intentionally) of *R. rattus* to an island where only *R. exulans* are currently present.

We found differences in most aspects of *R. exulans* population structure and ecology on Honuea where they co-existed with *R. rattus*, compared to nearby Rimatuu where *R. exulans* exist alone. We propose that the observed differences between the *R. exulans* populations are due to *R. rattus* over-invasion, although a before and after over-invasion comparison would strengthen this case. Pre-existing differences between the islands (e.g. edaphic conditions and plant nitrogen signature) and the seasons of our comparisons (summer for Honuea and winter for Rimatuu) cannot be excluded as possible explanations for the observed differences.

We account for these in our trophic analyses by correcting our stable isotope signatures relative to island baselines and analysing rat tissues of different turn-over (liver for weeks and muscle for months). For morphological analyses we only analyse adult rats, and suggest that substantial body-size differences are more likely explained by species interactions than differing food resources between islands (Russell et al., 2011b). Juveniles of both species were abundant in summer 2010 on Honuea but less common throughout Tetiaroa overall in winter 2009 (0% *R. exulans* and 15% *R. rattus*; Russell et al., 2011a), suggesting a cessation of breeding over the dry tropical winter in French Polynesia, particularly for *R. exulans*. *R. exulans* on Honuea were at a lower density than *R. rattus*, and apparently a lower density than found on Rimatuu (although we only have comparable index data from coastal Rimatuu), and a smaller body-size. Although Honuea is only a small island, *R. exulans* were generally caught in the interior, whereas on Rimatuu *R. exulans* were caught (though also only targeted) around the coast (Russell et al., 2011a), which may reflect a partitioning of space-use between the two invasive rat species, as found on temperate islands (Harper et al., 2005; Harper, 2006; Bramley, 2014). On both Honuea and Rimatuu rat diet was typically dominated by plants and invertebrates, as found elsewhere (Russell et al., 2011b; St Clair, 2011; Shiels et al., 2013). The trophic position of *R. exulans* on Honuea was similar to *R. rattus*, and did not appear to have changed following invasion by *R. rattus*. This has also been observed on a temperate island (Harper, 2006), but not on a tropical high island where niche partitioning of two rat species also coexisting with mice occurred (Shiels et al., 2013). Overall the results suggest *R. exulans* have a consistent diet both in the presence or absence of *R. rattus*, but that their size, population structure and habitat use, and to a lesser extent behaviour, may change as a result of over-invasion by *R. rattus*.

From the results of this study it appears the mode of competition between invasive rat species is predominantly interference and not exploitation. *R. exulans* were able to maintain a similar trophic position to *R. rattus* without diet niche differentiation, which might be expected to occur if there had been exploitative competition by *R. rattus*. On sub-tropical Raoul Island and mid-temperate Kapiti Island *R. norvegicus* also dominated *R. exulans* by interference competition (Harper and Veitch, 2006; Bramley, 2014), and on cold temperate New Zealand islands *R. rattus* dominates and *R. exulans* exists at lower densities, in restricted habitats (especially when co-existing with introduced mammalian predators), and with potentially delayed breeding (Harper et al., 2005; Harper, 2006). Limited resources may lead to exploitative competition between rat species, particularly *R. rattus* and *R. norvegicus*, and explain the lack of rat species co-existing on some temperate islands (Russell and Clout, 2004), but on highly productive and diverse tropical islands invasive rats can co-exist on even very small islands (such as throughout the Tetiaroa atoll). On tropical islands, interference competition between invasive rat species appears prevalent. This interference competition probably results from directly aggressive behaviour between the two rat species, where *R. rattus* is superior, if only for its larger body-size. Such

strong aggressive interference competition has also been observed by *R. rattus* on introduced mice (*Mus musculus*), which are smaller than *R. exulans* (Bridgman et al., 2013). Similarly the larger *R. norvegicus* probably dominates *R. rattus* by interference competition, except on forested islands where *R. rattus* has an arboreal exploitative competition advantage (King et al., 2011). Through a combination of interference competition over small rodent species (*R. exulans* and *M. musculus*) and exploitative competition advantage over larger rodent species (*R. norvegicus*) *R. rattus* thus becomes the dominant rat species on most islands of the world (Atkinson, 1985) except where other rodent species have either propagule pressure or incumbent advantage effects (Russell et al., 2014). However, a benefit of *R. rattus* invasion to other rodent species in tropical systems is its ability to open coconuts, which smaller rodents cannot do, thus engineering tropical coconut forest ecosystems and providing both themselves and other rat species with an abundant highly nutritious food resource.

These interactions among invasive rat species have important implications for the impact, monitoring, control and eradication of invasive rats on tropical islands. Although invasion by *R. rattus* did not alter the trophic position of *R. exulans*, it may have downgraded the trophic position of other species such as crabs, probably through successful exploitative competition and possible predation leading to local extinction of some land crab species (Samaniego-Herrera and Bedolla-Guzmán, 2012). Seabirds were locally extinct on Honuea except a few pairs of white terns (*Gygis alba*) nesting in pandanus tops and a roosting site for a few dozen greater crested terns (*Thalasseus bergii*) on the beach. In other words, the impact of rat invasion depends on the species, and even if one invasive rat species is already present, ongoing biosecurity to prevent other invasive rat species colonising should be enforced. However, the density of both rat species on Honuea was relatively low for tropical islands (c.f. Caut et al., 2008; Russell et al., 2011b), and so community impacts may not have been as strong as elsewhere. Although eradication of all three invasive rat species has been achieved on temperate islands (Russell et al., 2010), on tropical islands the failure rate of rat eradications remains high (Russell and Holmes, 2015). On Honuea the peak of *R. exulans* rat-trapping did not occur until three days after trapping began. Other studies confirm that for rodent presence surveying purposes, trapping should occur for a minimum of three nights to maximise the probability of detecting more than one rat species (Weihong et al., 1999; Harper and Veitch, 2006). When eradicating multiple invasive rat species from an island, managers may wish to extend the period bait is available and the volume of bait used. Furthermore, although our indices of captures per 100 corrected trap nights were relatively high, the density of rats on the island was relatively low, suggesting the index actually reflected a high capture probability of rats on the tropical island. As well known, indices of rat capture should be cautiously interpreted, particularly when comparing different sites.

The failure of our rat eradication on Honuea was confirmed when both species were recorded as present and abundant on the island 20 months later using a 100 m coastal perimeter grid alternating ten tracking tunnels and ten waxtags, and visual observation of rats and their sign (coconut gnawing, footprints). The eradication failure was attributable to the eradication campaign ending prematurely due to the onset of a tropical cyclone. Our trapping programme substantially reduced rat numbers and models of subsequent poison interference monitoring as well as removal trapping both suggested only a small number of remaining rats. Evidently breeding populations of both species survived, although rapid reinvasion of *R. rattus* from nearby islands cannot be ruled out, especially as the gap between Honuea and Onetahi is only 200 m. Removal models perform better with a monotonic decline in numbers of animals caught, although this assumption

can be relaxed with variation in catchability. *R. rattus* followed this trend, but *R. exulans* captures did not peak until the middle of the trapping programme, suggesting either device competition with *R. rattus* or neophobia. Should the former be the case, our model suggested *R. exulans* did not become as catchable as *R. rattus* until the population size of the latter was halved, but such inverse capture probabilities have not been found in other studies of co-existing rat species (e.g. Bramley, 2014). Neophobia is an unlikely explanation as it was not observed on neighbouring *R. exulans* only islands (Russell et al., 2011a). Unfortunately, it is difficult to make any more inference on the population interactions from our trapping campaign as removal models are notoriously unreliable for estimating population size without auxiliary data, and our present models may already be over-fitting the sparse data (Russell et al., 2009a). On the similarly-sized coral atoll island Surprise Island (24 ha) in New Caledonia *R. rattus* and *M. musculus* eradication was successful using hand bait broadcast (Caut et al., 2009), but New Caledonia in general has a higher rat eradication success rate than French Polynesia. This may in part be related to the population dynamics of land crabs in Eastern Pacific Ocean countries such as French Polynesia and the Mexican Pacific (Samaniego-Herrera and Bedolla-Guzmán, 2012). The dry winter period in French Polynesia appears to reduce breeding in rat populations and should be preferred for eradication operations, particularly for *R. exulans* (Harper et al., 2015).

We expected rapid reinvasion by *R. rattus* across the short channels separating Honuea from other islands in the Tetiaroa atoll, over which *R. rattus* forms a single meta-population (Russell et al., 2011a), but not reinvasion by *R. exulans*. Eradication of both rat species from nearby Onetahi by private operators also failed due to bait distribution gaps, and *R. exulans* survived this eradication attempt and became the most abundant rat species immediately following the failed eradication. During control and eradication operations, interference competition will lead to priority effects in capture probabilities and bait consumption (Harper and Veitch, 2006), and may explain the survival of *R. exulans* in mixed species campaigns on Tetiaroa and other tropical islands. We were unable to revisit Honuea for some time following our eradication attempt to confirm success, and immediate post-operation monitoring would have allowed us both to be better prepared for possible failure and to understand why failure may have occurred, or to rapidly confirm the success of the eradication (Samaniego-Herrera et al., 2013). However, in total our work on Tetiaroa suggests eradication of all rats from the entirety of Tetiaroa atoll at one time is the recommended invasive rat management strategy.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.10.001>.

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