



## Review

## The impacts of invasive rodents on island invertebrates

James J.H. St Clair<sup>\*</sup>

Department of Biology &amp; Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK

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## ABSTRACT

The widespread invasive rodents *Rattus norvegicus*, *R. rattus*, *R. exulans* and *Mus musculus* have been implicated in the decline and extinction of hundreds of island endemic vertebrates, but their effects on island invertebrates are less well-known. Here I present the first global review of the subject, which confirms that large-bodied invertebrates are most at risk from these rodents, and that although a disproportionate number of studies (69%) are from New Zealand, rodent-invertebrate impacts are geographically widespread. Mechanisms of impact are both direct (mediated by predation) and indirect (involving intermediary species). Some studies also suggest knock-on effects on ecosystem properties, and given the diverse ecological functions of invertebrates (as detritivores, primary consumers, predators, prey and pollinators), I suggest that an understanding of the interactions between invasive rodents and invertebrates in island ecosystems is essential for effective conservation management. Currently many reported impacts are unquantified, come from uncontrolled and unreplicated designs, or rely on time-series with inadequate baseline data. In addition to basic improvements in study design, this review highlights a need for studies which investigate mechanisms of impact, or impacts across trophic levels.

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<sup>\*</sup> Present address: Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK. Tel.: +44 (0) 7981826660.

E-mail address: [james.st-clair@zoo.ox.ac.uk](mailto:james.st-clair@zoo.ox.ac.uk)

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## 1. Introduction

The arrival of humans on remote islands is usually associated with a wave of extinctions in the native biota (James, 1995; Steadman, 1997; Blackburn and Gaston, 2005). Rodents that accompany human colonisation are a major contributor to this effect, likely accounting for more recent bird extinctions than any other single factor, and implicated in the extirpation of numerous small mammals, reptiles, amphibians and plant species (Johnson and Stattersfield, 1990; Blackburn et al., 2004; Towns et al., 2006; Athens, 2009; Jones et al., 2008; Harris, 2009).

Four rodent species are particularly notorious, having achieved enormous distributions due to their ability to hitch-hike on ships and canoes. Three of these (*Rattus rattus*, *Rattus norvegicus* and *Mus musculus*) have attained near-global distributions and a fourth (*Rattus exulans*) is widely distributed in the Pacific (Atkinson, 1985). Henceforth, 'invasive rodents' refers to these four species. Population-level effects (henceforth 'impacts') of invasive rodents on vertebrate populations have received considerable attention, but evidence from New Zealand also implicates invasive rodents in the decline and extinction of invertebrate populations, with many of New Zealand's endemic invertebrates now confined to rodent-free offshore islands (Ramsay, 1978; Meads, 1990; Gibbs, 2009).

Despite this emergent New Zealand case study, the potentially global impact of invasive rodents on invertebrates has received little attention: a recent review of rat impacts cites only nine examples of rat-invertebrate interactions, which were largely from New Zealand study sites (Towns et al., 2006). This emphasis is consistent with the poor appreciation of invertebrates in conservation research: they comprise over 79% of all described animal and plant species, and yet only 11% of articles in leading conservation journals concern invertebrate taxa (Clark and May, 2002).

There are at least two major reasons to take invertebrate conservation seriously. Not only do island invertebrates often exhibit high levels of endemism and thus form a substantial component of biodiversity, but they can occupy key roles in ecosystems as detritivores, primary consumers, predators, prey, competitors, mutualists, pollinators and disease vectors. Effects at any of these functional levels may have knock-on effects on other ecosystem components (Duthie et al., 2006; Dixon, 2009).

Here, I overview the impacts of invasive rodents on island invertebrate populations across the globe. Using these data, I ask whether such impacts are likely to be a common feature of rodent invasion, and what can be learned from the geographical distribution, methodologies and results of the studies. I searched the literature for studies which investigated population-level effects of invasive rodents on island populations of invertebrates, including both island endemics and species with wider distributions. Within these criteria, I included records from well-controlled and replicated experiments to unquantified observations from single sites. I used ISI Web of Science and Google Scholar with combinations of search terms including "Introduc", "Invasi", "Exotic", "Eradicat", "Extinct", "Island", "Diet", "Rodent", "Rat", "Rattus", "Mouse", "Mus", "Invertebrate", and various high-level taxonomic names including "Mollusc", "Crustacea", "Arthropod" and "Insect" plus grammatical variations of these terms when appropriate. Having identified studies dealing with impacts of invasive rodents on island invertebrates, their reference lists were scoured in turn. To

summarise the diet of invasive rodents on islands with respect to invertebrates, I also sampled rodent-diet literature originating from geographically widespread and largely insular study sites. Systematic data collection was terminated in March 2010.

## 2. The diet of invasive rodents

A comprehensive review of the diet of invasive rodents is beyond the purview of this review. However, my sample of the rodent-diet literature shows three apparent patterns that are relevant to their potential impacts.

Firstly, the invasive rodent species are remarkably catholic in their diets, consuming vegetable matter, vertebrate animals of several different classes, and invertebrates (Landry, 1970). Few studies report no invertebrate dietary component (one being Witmer et al., 2006) whereas most studies report a significant invertebrate component (Drever and Harestad, 1998; Cole et al., 2000; Ruscoe, 2001), and in the majority of these, invertebrates are the most frequently recorded food category (Harrison, 1954; Daniel, 1973; Gales, 1982; Moors, 1985; Copson, 1986; Chown and Smith, 1993; Key et al., 1998; Miller and Webb, 2001; Le Roux et al., 2002; Smith et al., 2002; Caut et al., 2008). The potential for impacts on invertebrate populations is clear.

Secondly, invasive rodent populations frequently exhibit extreme dietary plasticity, with the relative contributions of different food types varying seasonally (Copson, 1986; Bunn and Craig, 1989; Miller and Webb, 2001; Ruscoe, 2001; Le Roux et al., 2002), spatially (Erickson and Halvorson, 1990; Key et al., 1998; Jones et al., 2003) or both (Chown and Smith, 1993; Smith et al., 2002). Facultative plasticity and broad diets may not only facilitate establishment and persistence of invasive rodents in novel habitats, but may also allow predators to drive individual prey species to extinction while avoiding density dependent feedback effects.

Thirdly, a handful of studies report marine littoral invertebrates forming part of invasive rodent diet, particularly in rats (Landry, 1970; Parisi and Gandolfi, 1974; Moors, 1985; Erickson and Halvorson, 1990; Navarrete and Castilla, 1993; Woods and Woods, 1997; reviewed by Carlton and Hodder (2003)). The ability to exploit littoral resources may explain the frequently noted coastal bias in rat distribution and density (Erickson and Halvorson, 1990; Harper, 2006), which may in turn cause particularly strong impacts on vulnerable rat prey populations in coastal areas. Such effects on rat density (and thus their prey populations) may be critical on very small islands, such as those commonly used by breeding seabirds, in which most of the land area is close to the shore. In the Falkland Islands, the distribution of *R. norvegicus* is reported as being heavily biased towards the coast (Peter Carey and Darren Christie, pers. comms.), and studies of passerine bird distribution demonstrate that these rats have their greatest impacts on mainly coastal species such as Cobb's Wren *Troglodytes cobbi* and the Tussacbird *Cinclodes antarcticus* (Hall et al., 2002).

## 3. The impact of invasive rodents

### 3.1. Responses

Forty-five studies reported on population-level effects of invasive rodents on island invertebrates (Table 1). The majority

of studies reported negative impacts of these rodents on island invertebrate populations, although four reported weak or negligible effects (Spurr, 1996; Rufaut and Gibbs, 2003; Van Aarde et al., 2004; King, 2007) and three reported a positive effect of rodent presence (Sinclair et al., 2005; Kurle et al., 2008; Rate, 2009). In some cases, a mixture of positive and negative effects are reported for different invertebrate taxa or size-classes (Palmer and Pons, 1996; Craddock, 1997 – see ‘Indirect mechanisms’ below). Suppression was the most commonly recorded effect of rodent presence, although twelve studies inferred local extinction of invertebrate populations. The extreme declines of two restricted-range endemics following rodent invasion, the Lord Howe stick insect (*Dryocelus australis*) and the Frigate giant tenebrionid beetle (*Polposipes herculeanus*), suggested that the species would have become entirely extinct in the wild without intervention. Several studies investigated effects on species richness or other measures of diversity, with most finding these indices lower when rodents were present (e.g. Bremner et al., 1984; Craddock, 1997; Towns et al., 2009), although the opposite effect also occurred (e.g. Sinclair et al., 2005).

### 3.2. Rodent species

*R. exulans* was the best-represented, being the subject of nine studies; *M. musculus*, *R. norvegicus* and *R. rattus* were the subjects of seven, seven and five studies respectively, and the remainder investigated effects of two or more rodent species concurrently.

### 3.3. Location of studies

The geographical locations of study sites exhibit two apparent patterns. Firstly, the majority (31/45 = 69%) of studies are from New Zealand and its offshore islands (Fig. 1). It is possible that New Zealand has an unusually high proportion of rodent-vulnerable invertebrate taxa (Meads, 1990), but the trend may also be explained by the unusually strong commitment to invasive species research in New Zealand, and to the fact that it lends itself historically and geographically to the conservation interventions that provide the framework for many studies. Australasia (principally New Zealand) has been the site of 54% of the world's 284 successful rodent eradications from islands up to 2006 (Howald et al., 2007), and in keeping with this geographical bias in interventions, a disproportionate number of studies which used rodent eradication to investigate impacts on invertebrates (11/13 = 85%) were from New Zealand.

Secondly, very few studies ( $n = 7$ , most from Hawai'i and the Seychelles, and one – albeit tenuous – from the Caribbean) were from the tropics, despite a clear tropical bias in the distribution of rodent-infested islands (Atkinson, 1985). Apart from those on New Zealand or its nearby offshore islands, most studies were from Southern Ocean Islands (sensu Chown et al., 2008) including the Falkland Islands, the Prince Edward Islands, the Kerguelen archipelago, and the Antipodes archipelago. The median latitude (disregarding hemisphere) of non-NZ study sites in Table 1 is 42°, while the median latitude of rat-infested islands according to published data is 19° ( $n = 120$  islands or island groups; Atkinson, 1985), although the paucity of non-NZ studies in Table 1 ensures the difference is not statistically significant (Mann–Whitney test:  $U = 7679$ ,  $P = 0.116$ ). When NZ sites are included in the analysis, the latitudinal distribution of study sites in this review becomes significantly higher than that of rat-infested islands generally (40° vs 19°, Mann–Whitney test:  $U = 8233$ ,  $P < 0.001$ ). Any latitudinal bias may be due to differences in research effort, or to inherent vulnerability of invertebrate species at higher latitudes, for instance due to slower population growth rates or lower diversity in high-latitude invertebrate communities (Chown et al., 2004; Donlan and Wilcox, 2008). Work by Atkinson (1985) hints at another possibility; he notes bias away from tropical latitudes in the distribution of bird extinctions attributable to invasive rats, and speculates that prior exposure to native terrestrial predators (which are more common in the tropics) may be important in determining vulnerability to invasive rodents – an ‘extinction filter’ sensu Balmford (1996). Consistent with island invertebrates being subject to such extinction filters, only two reports of invasive rodent impacts on invertebrates come from island groups which may once have contained native rodent species (Palmer and Pons, 1996; Pascal et al., 2004), the majority coming from historically mammal-free New Zealand and the remainder from sites such as the South Atlantic Islands which have never contained endemic rodents.

### 3.4. Taxa affected

Arthropods, especially Coleoptera and Orthoptera, account for most of the reported negative impacts, with molluscs (largely terrestrial snails) the next most frequent (Table 1; Fig. 2). As the beetles are a highly speciose group, their substantial representation among the recorded impacts is unsurprising, while the very strong representation of the (relatively species-poor) Orthoptera among impacted taxa is less likely to be due to chance. Much of the

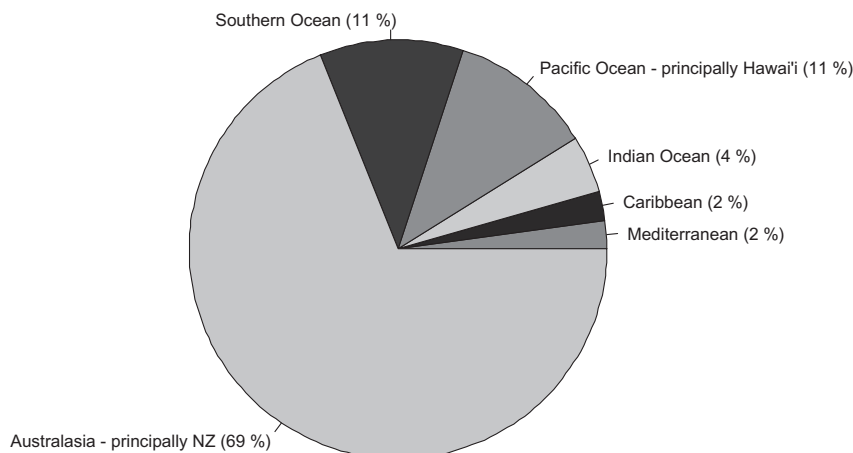


Fig. 1. Proportion of studies dealing with the impact of invasive rodents on invertebrates from different geographical regions.

**Table 1**

Studies investigating population-level impacts of invasive rodents on island invertebrates. Species codes: MM = *Mus musculus*; RR = *Rattus rattus*; RE = *Rattus exulans*; RN = *Rattus norvegicus*; R. spp. – two or more *Rattus* species; FC – feral cats; OC – European rabbit. Sample sizes:  $n_1$  = treatment group,  $n_2$  = control group.

Rodent	Invertebrates	Data source and collection	Impact of rodents, and details	Location	Sample size	Publication
R. spp. and MM	Giant predacious land snail <i>Powelliphanta traversi</i>	Baiting (monitoring and comparison)	Possible suppression; significant treatment effect (increase in snail population) in one of two sites. High temporal variation at all sites. Rat predation estimated to account for at least 20% of snail mortality.	Lake Papaitonga, North Island, NZ	$n_1 = 2$ $n_2 = 2$	Bennett et al. (2002)
RN	Invertebrates >4 mm in length including beetle <i>Dorcus helmsi</i> , excluding amphipods and molluscs	Natural experiment (comparison)	Suppression (densities of most invertebrate taxa much higher on rat-free Gilbert Is. compared to rat-infested Breaksea Is.). On Breaksea, possible local extinction of the beetle <i>Dorcus helmsi</i> , which was not captured at all although fragments were abundant in the leaf litter.	Breaksea Island and Gilbert Island No. 6, NZ	$n_1 = 1$ $n_2 = 1$	Bremner et al. (1984)
RE	Endemic land snails <i>Amborhytida tarngensis</i> and <i>Placostylus hongii</i>	Prehistoric invasion (stratigraphy)	Local extinction (taxa went extinct on the island at approximately the colonisation time of RE. Evidence for an interaction is circumstantial)	Lady Alice Island, NZ	$n_1 = 1$	Brook (1999)
RR and MM	All invertebrate taxa (order or family)	Baiting (comparison)	Suppression (rat density was reduced at the baited site and mouse density increased slightly. The baited site had higher catches of several taxa determined to be particularly important in Rat diets (beetles, cave weta and moths, and also snails which were less important) while some smaller-bodied taxa (ants, woodlice, springtails, flies, millipedes and also crickets) were more abundant at the unbaited site. There were no significant differences for the remaining groups. Taxon diversity was significantly higher at the baited site)	North Island, NZ	$n_1 = 1$ $n_2 = 1$	Craddock (1997)
MM (+FC)	Weevil larvae flightless moths <i>Pringleophaga</i> spp.	Natural experiment (comparison)	Suppression of both groups, described as 'several times more abundant' on mouse-free Prince Edward Is., possible local extinction of <i>P. kerguelensis</i> on Marion Island. Mice estimated to take 21% of the standing crop of moth larvae annually. (NB trophic effect of cat-seabird-nutrient relationship is discussed)	Marion Island and Prince Edward Island, Southern Ocean	$n_1 = 1$ $n_2 = 1$	Crafford and Scholtz (1987), but see Van Aarde et al. (2004)
R. spp.	Soil invertebrates <10 mm identified to order level: nematodes (herbivorous, microbivorous and predacious), land snails, enchytraeid worms, rotifers, springtails, amphipod crustaceans and moth larvae	Natural experiment (comparison)	Indirect suppression of all invertebrate taxa studied, although trend not significant in predacious nematodes. Unclear whether suppression at this taxonomic level results from species loss, reduced density of individuals, or both. Rats strongly affected nutrient levels and soil structure via effects on burrowing seabird abundance; soil invertebrate effects are interpreted as downstream consequences	Various offshore islands, North Island, NZ	$n_1 = 9$ $n_2 = 9$	Fukami et al. (2006)
RE	Middle Island tusked weta ( <i>Motuweta isolata</i> )	Natural experiment (comparison)	Local extinction (species found only on rodent-free Middle Island, not on adjacent islands in the Mercury group which contain <i>R. exulans</i> . However, there is no evidence that its distribution was once broader)	Middle Island, Mercury Islands, NZ	$n_1 = 1$	Gibbs (2002)
R. spp.	1 Endemic snail <i>Partulina redfieldi</i>	Local irruption (monitoring)	Suppression (85% decline in three years following appearance of rats at site)	Moloka'I, Hawaii, USA	$n_1 = 1$	Hadfield and Saufler (2009)
R. spp.	Endemic land snail <i>Achatinella mustelina</i>	Baiting (monitoring)	Suppression via selective predation on larger (mature) size-classes. Population decline stopped 'abruptly' after rat poisoning began at the site.	O'ahu, Hawaii, USA	$n_1 = 1$	Hadfield et al. (1993)
R. spp., MM and Possums, Stoats, also	Ground Weta, cave Weta and prowling spiders	Baiting (monitoring and comparison)	No consistent treatment effects: some strong differences between sites, treatments, species and within-	Waitakere Ranges, North Island, NZ	$n_1 = 3$ $n_2 = 6$	King (2007)

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Table 1 (continued)

Rodent	Invertebrates	Data source and collection	Impact of rodents, and details	Location	Sample size	Publication
present			species size-classes. Tracking data suggests treatment (baiting) failed to suppress rodent populations relative to control sites in several cases.			
RN	Various littoral invertebrates including grazing molluscs and barnacles	Natural experiment (comparison)	<i>Increase</i> in abundance of most groups (release from predation by gulls and oystercatchers, both of which were an order of magnitude more abundant on rat-free coastlines)	Aleutian Islands, USA	n1 = 8 n2 = 15	Kurle et al. (2008)
R. spp. and MM	Various large weevil species (including <i>Anagotis stephensis</i> , <i>Anagotis rugosus</i> and <i>Oclandius</i> spp.)	Prehistoric and historical invasion (stratigraphy)	Suppression/local extinction: current distribution determined from museum collections, past distribution by stratigraphical examination of owl middens ( $n = 12$ ). Several large weevil species now confined exclusively ( <i>Anagotis stephensis</i> ) or 'almost exclusively' ( <i>Anagotis rugosus</i> ) to rat-free offshore islands, while pre-invasion strata indicate distributions were once much wider. <i>Oclandius</i> species are mentioned as having been 'common' on the Auckland Islands 'before mice arrived on boats'; mouse nests have been found 'with heaps' of <i>Oclandius</i> remains.	Canturbury, South Island, NZ (also Auckland Islands, $n1 > 1$ )	n1 = 12	Kuschel and Worthy (1996)
RR	Flightless beetles <i>Hadramphus stilbocarpae</i> and <i>Dorcus helmsi</i>	Invasion (monitoring)	Local extinction (both species 'abundant' before rat introduction and apparently absent afterwards. <i>H. stilbocarpae</i> was 'teeming' in 1955; two expeditions in 1968 and 1969, ~20 yrs after <i>R. rattus</i> invasion, failed to find it alive. The weevil's host plant <i>Stilbocarpa lyallii</i> was also strongly impacted)	Big South Cape Island, NZ	n1 = 1	Kuschel and Worthy (1996) and Ramsay (1978)
R. spp. and MM	Seychelles giant millipede ( <i>Seychelleptus seychellarum</i> )	Natural experiment (comparison)	Suppression or local extinction (millipedes superabundant on rodent-free Cousine, but 'extirpated or... very scarce' on mouse- and rat-infested islands including Praslin Island and Silhouette Island)	Cousine Island Seychelles	n1 = 1 n2 = 2+	Lawrence and Samways (2003)
MM	Various inc. new carabid beetle <i>Loxomerus</i> sp.; four other beetle species were recorded more frequently on Bollons Island than nearby mouse-infested Antipodes Island;	Natural experiment (comparison)	Suppression of most species on Bollons relative to mouse-free Antipodes; possible local extinction of <i>Loxomerus</i> spp. which was last seen as fragmentary remains in 1969	Bollons and Antipodes Islands, NZ Southern Ocean	n1 = 1 n2 = 1	Marris (2000)
RE	Stag beetles ( <i>Hemidorcus</i> spp.), Weta, and other unspecified invertebrates	Eradication (monitoring)	Suppression ('major increases in... numbers of invertebrates' and discovery of species not known before eradication)	Rarotoka and Putauhinu Islands, NZ	n1 = 2	McClelland (2002)
RR	2 invasive snails ( <i>Achatina fulica</i> and <i>Euglandina rosea</i> )	Variation in rat abundance between sites (comparison)	Suppression (estimated minimum 7–20% of snail mortality) based on quantity of predation sign, correlated with rat abundance at different sites	Wai'anae mountains, Oahu, Hawaii, USA	n1 = 2	Meyer and Shiels (2009)
RN	2 Beetles <i>Mimopeus elongatus</i> and <i>Ctenognathus novaezealandiae</i> 1 Centipede <i>Cormocephalus rubriceps</i>	Natural experiment (comparison)	Suppression of <i>M. elongatus</i> and <i>C. novaezealandiae</i> and local extinction of <i>C. rubriceps</i> on rat-infested Otata and Motohoropapa (inferred from their abundant presence on nearby rat-free David Rocks and Maria Island)	Otata and Motohoropapa Islands, NZ	n1 = 2 n2 = 2	Watt (1983) and Moors (1985)
RN	1 Land snail <i>Placostylus hongii</i>	Invasion (monitoring)	Suppressed (thrived before rat introduction and 'declined' afterwards – situation described as 'near-loss')	Motuhoropapa Island, NZ	n1 = 1	Moors (1985)
MM	Cook's Strait giant weta ( <i>Deinacrida rugosa</i> ) and exotic land snail <i>Helix aspersa</i> ; also various 'other invertebrates'	Eradication (monitoring)	Suppression; although definitely present, snail catches were zero in all years prior to eradication and consistently high afterwards, based on 4 yrs pre- and 4 yrs post-eradication. Numbers of <i>D. rugosa</i> increased from <1 to >10 per 1000 trap nights. 'Other invertebrates' are	Mana Island, NZ	n1 = 1	Newman (1994) expanded results for <i>D. rugosa</i> in McIntyre (2001)



Table 1 (continued)

Rodent	Invertebrates	Data source and collection	Impact of rodents, and details	Location	Sample size	Publication
RR	5 endemic tenebrionid beetle spp.	Natural experiment (comparison)	mentioned as increasing in abundance and diversity after eradication, although not quantified. Suppression or local extinction of five endemic species; two non-endemic species more likely to occur on rat-infested than rat-free islands	Various Islands, Mediterranean, Spain	n1 = 25 n2 = 26	Palmer and Pons (1996)
RR	Land crab <i>Gecarcinus ruricola</i>	Attempted eradication (monitoring)	Unclear; after attempted eradication and decrease in rat abundance, crab catches increased from 0.85 to 1.36 per 100 trap nights, following an initial decrease to 0.46.	Hardy Islet, Caribbean, Martinique	n1 = 1	Pascal et al. (2004)
MM	'Medium-sized flightless invertebrates'	Natural experiment (comparison)	Suppression or local extinction (unspecified 'medium-sized flightless invertebrates' are lacking on Antipodes Island, but present on Bounty Island, which lacks mice, ~200 km to the North)	Antipodes Island, NZ	n1 = 1 n2 = 1	Patrick (1994)
RR and MM	Endemic Lord Howe Island stick insect ( <i>Dryocelus australis</i> )	Invasion (monitoring)	Extirpation (insect disappeared from Lord Howe Is. following rat introduction in 1918. Population now relict (9–35 individuals) on a tiny rat-free offshore islet (Carlisle et al., 2009)	Lord Howe Island, Australia	n1 = 1 n2 = 1	Priddel et al. (2003)
R. spp.	Morphotaxa >3 mm length	Baiting (monitoring)	No discernible treatment effect; ant abundance increased	Moehau, North Island, NZ	n1 = 2 n2 = 2	Rate (2009)
RR and MM	2 large land snails <i>Placostylus bivaricosus</i> and <i>Gudeococha sophiae</i>	Invasion (monitoring)	Suppression (both species were 'common' before the wreck of the SS Makembo which introduced rats; subsequently they became 'rare, confined to a few small colonies')	Lord Howe Island, Australia	n1 = 1	Recher and Clark (1974)
MM	Various arthropods, particularly the flightless moth <i>Pringleophaga marioni</i>	(Estimated from diet)	Suppression (estimated consumption of 0.7% of 'standing crop' of arthropods per day, and 1% of <i>P. marioni</i> population per day leading to population decline)	Marion Island, Southern Ocean, SA	–	Rowe-rowe et al. (1989)
RE	Arboreal Weta <i>Hemideina crassidens</i>	Eradication (monitoring)	No clear population effect (Overall index of Weta abundance showed an increase for three years following eradication and a decrease in the fourth, possibly due to weather or density effects following rapid population growth. No pre-eradication data presented.)	Nukuwaiata Island, NZ	n1 = 1	Rufaut and Gibbs (2003)
RE (+ RR?)	2 land snails: the endemic <i>Placostylus ambagiosus</i> and introduced <i>Helix aspersa</i>	Baiting (monitoring and comparison)	Suppression via reduced recruitment due to selective predation on medium-sized individuals. Population changes correlated with rat predation both through time at the study site, and spatially between the study and unbaited control site	North Island, NZ	n1 = 1 n2 = 1	Sherley et al. (1998). Prehistoric rat predation of <i>P. ambagiosus</i> is also discussed by Brook (2000)
RN and RE	All morphospecies >5 mm in length	Eradication (monitoring)	Overall decrease in invertebrate diversity through time following eradication; site monitored for 2 yrs before and 3 yrs after eradication. Results highly variable and not consistent between taxa	Kapiti Island, NZ	n1 = 1	Sinclair et al. (2005)
RR	2 littoral molluscs <i>Nerita picea</i> and <i>Littoraria pintado</i> 1 crustacean <i>Grapsus tenuicrustatus</i>	Eradication (monitoring)	Suppression (increase post-eradication, leading to "an abundance... where they were previously scarce")	Mokoli'i, Oahu, Hawaii, USA	n1 = 1	Smith et al. (2006)
R. spp.	All families of arthropods	Baiting (monitoring and comparison)	No consistent trends; results variable.	Nelson, South Island, NZ	n1 = 3 n2 = 1	Spurr (1996)
RE	3 Cockroaches <i>Celatoblatta</i> sp., <i>Parellipsidion latipennis</i> , <i>Platyzosteria novaezealandiae</i> 4 beetles <i>Mimopeus elongatus</i> *, <i>Mimopeus opaculus</i> *, <i>Holocaspis mucronata</i> , <i>Ctenognathus novaezealandiae</i> * 1 earwig <i>Anisolabis littorea</i> *	Eradication and Natural experiment (monitoring and comparison)	Suppression or local extinction (on Korapuki island one pre- and one post-eradication survey completed; with the exception of the Orthoptera and <i>M. opaculus</i> , of taxa listed, all were found in the second survey, but only <i>H. mucronata</i> was present in the first. This species increased in abundance	Korapuki Island and Middle Island	n1 = 1	Towns et al. (1997)
OC	1 woodlouse* 1 centipede <i>Cormocephalus rubriceps</i> *		Natural experiment data: taxa marked with an asterisk were all	Mercury Islands, NZ	n2 = 1	

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Table 1 (continued)

Rodent	Invertebrates	Data source and collection	Impact of rodents, and details	Location	Sample size	Publication
	1 + weta (Rhaphidophoridae)* 2 Jerusalem crickets <i>Hemidrius</i> sp., undescribed sp.*		found on rat-free Middle island, but not on Korapuki prior to eradication, while no species found on Korapuki were absent from Middle island (except possibly the cockroaches and beetle <i>H. mucronata</i> )			
R. spp	18 soil macro-invertebrate orders and 3 micro-invertebrate taxa (Rotifera, Enchytraeidae and Nematoda)	Natural experiment (comparison)	Indirect suppression of most invertebrate taxa studied; 16/18 macro-invertebrate orders were less abundant (per m <sup>2</sup> ) on rat-invaded islands (8 of these statistically significant), and 3/3 micro-invertebrate taxa also significantly less abundant. Taxon diversity of soil invertebrates was reduced. Differences associated in part with changes in soil chemistry and structure, due to reduction of burrowing seabirds by rat predation.	Various offshore islands, North Island, NZ	n1 = 9 n2 = 9	Towns et al. (2009)
RE (+OC)	1 scale insect <i>Coelostoma zealandica</i>	Eradication (comparison and monitoring)	Suppression via prevention of host plant recruitment pre-eradication on rat-infested Korapuki Is, compared to rat-free Green and Middle Islands. Abundance of host plant and scale insects increased following rat (and rabbit) eradication	Korapuki, Green and Middle Islands Mercury Islands, NZ	n1 = 1 n2 = 2	Towns (2002)
MM	Various soil invertebrates including <i>Pringleophaga</i> moths, weevils, lumbricids worms, spiders and terrestrial molluscs	Exclosure (comparison and monitoring)	Suppression of <i>Pringleophaga</i> larvae (43% greater biomass in exclosures by 3rd year) compared to paired control plots, although marginally nonsignificant. Other invertebrate groups did not differ significantly in abundance or biomass. The manipulation did not exclude mice but only reduced abundance; low power may explain weak results. Not enough moth adults were found in either treatment to allow comparison	Marion Island, Southern Ocean, SA	n1 = 5 n2 = 5	Van Aarde et al. (2004)
RN	Intertidal molluscs, small crabs, large shore crab <i>Leptograpsus variegatus</i>	Eradication (monitoring)	Possible suppression; unquantified, although numbers of these intertidal groups were 'considerably' greater after eradication. Terrestrial pitfall trapping was attempted, but was poorly controlled, with no baseline (pre-eradication) sample.	Motu-o-kura Island, NZ	n1 = 1	Walls (1998)
R. spp	Mahoenui Giant Weta <i>Deinacrida mahoenui</i>	Reintroduction (monitoring and comparison)	Suppression or local extinction (populations introduced to rat-free sites flourished; those at rat-present sites persisted 'in proportion to' the amount of rodent control, and those at sites with little or no rodent control went extinct)	North Island, Mahurangi Island and Motutapere Island, NZ	n1 = 6	Watts and Thornburrow (2009)
RE	Giant wetapunga <i>Deinacrida heteracantha</i>	Eradication (monitoring)	Suppression (capture rates have increased over 5 years, to twice the rate immediately following eradication. No baseline data)	Little Barrier Island, NZ	n1 = 1	Chris Green, Pers. Comm
RE	Most insect taxa >5 mm in length, including ground weta <i>Hemidrius pallitarsus</i> , 'several' prowling spider species (Araneae: Zoropsidae), various other spiders, beetles, and other arthropods including the giant centipede <i>Cormocephalus rubriceps</i>	Eradication (monitoring)	Suppression (capture rates of many taxa increased over the long term post-eradication; average increase in capture rates over 15 years since rat eradication are: ground Weta 1.7×, prowling spider >2.0×, all spiders over 5 mm 1.6×, all beetles over 5 mm 2.8×, all insects over 5 mm pooled together 1.4×. Apparent species richness has also increased, with species such as a giant centipede <i>Cormocephalus rubriceps</i> only appearing in traps several years after rat eradication. No baseline data)	Tiritiri Matangi Island, NZ	n1 = 1	Chris Green, Pers. Comm and Green (2002)
MM	2 Spider species <i>Uliodon</i> sp., (Zoropsidae) and <i>Meringa</i> sp. (Synotaxidae)	Eradication and natural experiment	Suppression; 8 beetle species increased in abundance after mouse eradication on Allports Is., one of	Allports Island and South Island, NZ	n1 = 1	Mike Fitzgerald pers. comm.; data also mentioned in Ruscoe

Table 1 (continued)

Rodent	Invertebrates	Data source and collection	Impact of rodents, and details	Location	Sample size	Publication
	2 Moth larvae <i>Mallobathra</i> sp. and <i>Grypotherca</i> sp. Various beetles <i>Agaricalodes</i> sp., <i>Colon hirtale</i> and <i>Isocolon</i> sp. (Leiodidae); <i>Holcaspis oediceuma</i> and <i>Zeopoecilus calcaratus</i> (Carabidae); various others: Staphylinidae spp., <i>Carpophilus gaveni</i> (Nitidulidae) and <i>Melanophthalma variegata</i> (Corticariidae)	(comparison and monitoring)	which was absent from the baseline pre-eradication survey and 'common' afterwards. Although 5 beetle species also increased at the mainland control sites, the increases were 'much smaller' than on the island. The 2 spiders and 2 moths increased significantly after mouse eradication, but only 1 of these (the moth <i>Mallobathra</i> sp.) also increased on the mainland		n2 = 2	(2001)
RN	1 Giant endemic tenebrionid <i>Polposipes herculeanus</i>	Invasion (monitoring)	Rapid suppression (80% decline after 5 years post-invasion). Thorsen et al. also list a land snail and giant scorpion as being at 'high risk' from rat predation	Fregate Island, Seychelles	n1 = 1	Parr (2000), cited in Merton et al. (2002). Also see Thorsen et al. (2000)
RE	Ground weta 1 Beetle <i>Mimopeus opaculus</i>	Eradication (monitoring)	Probable suppression ('increases in capture frequency' of these species occurred after rat eradication)	Lady Alice Island, Chicken Islands, NZ	n1 = 1	Parrish and Towns, unpublished data cited in Atkinson and Towns (2002)
RN	Endemic Falkland camel cricket ( <i>Parudenus falklandicus</i> )  Various large-bodied beetle species including <i>Lissopterus</i> spp., <i>Caneorhinus biangulatus</i> , <i>Cylydrorhinus lemniscatus</i>	Natural experiment and eradication (comparison)	Suppression of beetles and crickets; lower relative abundance of large-bodied beetles and camel crickets on rat-infested islands (n = 18) than rat-free islands (n = 13). Camel cricket abundance on rat-eradicated islands (n = 6) increases significantly with time elapsed since rat eradication.	Falkland Islands, Southern Ocean UK	n1 = 18 + 6 n2 = 13	St Clair et al. (in press, unpublished data)
RE, RR, RN, MM	Various Weta species <i>Deinacrida heteracantha</i> , <i>D. rugosa</i> , <i>D. carinata</i> , 2 unknown <i>Deinacrida</i> sp. <i>Hemianthus</i> sp. 3 Click-beetles <i>Amychus</i> spp. Campbell Island Ribbed Weevil ( <i>Heterexis seticosatus</i> ) Weevils <i>Anagotus fairburni</i> , <i>A. turboti</i> Speargrass Weevil <i>Lyperobius huttoni</i> Knobbed Weevil <i>Hadramphus stilbocarpae</i> 3 Moth species (1 Noctuidae, 2 Oecophoridae) Giant centipede <i>Cormocephalus rubriceps</i> Giant pill millipede <i>Procyliosoma tuberculata</i> Various unnamed beetle species including stag beetles	Various sources: Natural experiment, local irruptions, subfossil evidence	Suppression and/or local extinction (species absent or suppressed at sites/islands where rodents are present)	Various Islands, NZ	–	Ramsay (1978) and Meads (1990) <sup>a</sup>

<sup>a</sup> A review by Ramsay (1978) and a book by Meads (1990) both contribute accounts of rodent impacts on dozens of New Zealand endemic invertebrates, although the sources of most data are not referenced; as there is likely to be considerable replication in their sources, I have pooled these data into a single row.

variation among taxa may be explained by body-size effects (discussed in Section 4.1).

#### 4. Mechanisms of impact

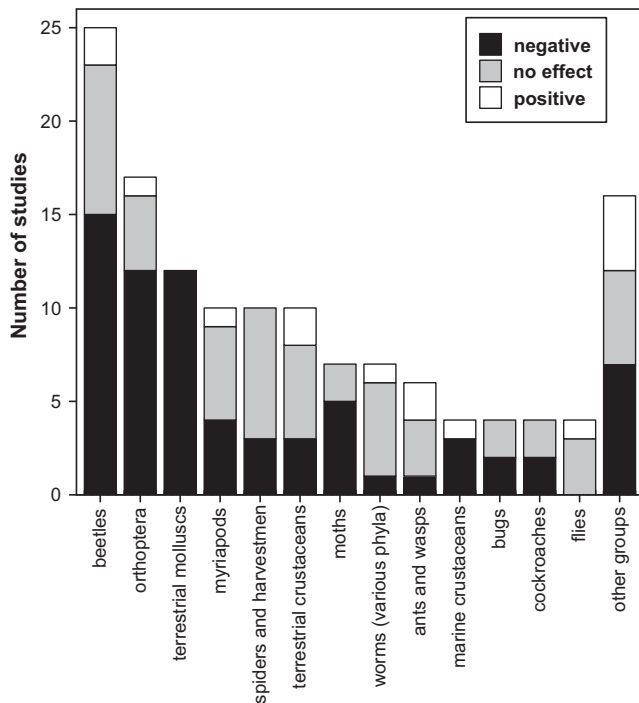
##### 4.1. Direct effects

Rodents may affect invertebrates directly (via predation) or indirectly via effects on the predators, competitors, prey, hosts or ecosystem engineers that regulate invertebrate abundance. Most studies do not attempt to distinguish direct from indirect mechanisms of impact, although inferences can be drawn from the patterns of impact across taxa. This is because rodents are predicted to prey selectively on particular types of invertebrate; in particular, those with a body size large enough to make them profitable food items (Pyke et al., 1977). The direct impact hypothesis predicts that negative effects will occur more frequently among rodent prey taxa than non-prey taxa. Given that large-bodied taxa form a tiny

minority of invertebrates, they are indeed disproportionately well-represented in the studies collected here, with impacts on various Weta species (Orthoptera: Anostomatidae), giant land snails and other exceptionally large taxa including a giant centipede and giant millipedes in New Zealand, a giant beetle in the Seychelles, and a giant stick insect on Lord Howe Island, Australia. Moreover, studies that measure differences in invertebrate abundance across a number of size-categories often find that larger-bodied invertebrates are negatively affected by invasive rodents more frequently than smaller-bodied taxa (Bremner et al., 1984; Chown and Smith, 1993; Craddock, 1997; Chris Green, pers. comm.).

When data on named invertebrate taxa of known body size are collated from all studies reviewed here (on effects of *Rattus* species, mice and both in combination), it is apparent that invertebrate taxa that may be extirpated (locally driven to extinction) by rodents tend to be larger-bodied than those that are merely suppressed, and that rodent-suppressed taxa have over twice the body length, on average, of those which are unaffected (Table 2,





**Fig. 2.** Number of studies reporting negative, positive or no impact of invasive rodents on different invertebrate groups. Thus negative impacts on 1 or more beetle taxa were reported by 15 studies, while no impact was reported by 8 studies, and so on. Note that some studies contributed to more than one column or impact category. When effects on the same species were reported by two or more studies, only one was counted. Groups investigated fewer than four times (such as stick insects, order Phasmatodea) were pooled into the 'other groups' column.

**Fig. 3.** There is no significant difference in the lengths of invertebrates that were reported to increase under rodent presence and those that were unaffected. The data are not numerous enough to investigate the effects of each rat species individually. However, when data for the three rat species are pooled they show that extirpated invertebrates are on average larger than suppressed ones, which are larger in turn than taxa which are unaffected or respond positively to rat presence. Data for mouse effects in isolation are sparse, but they suggest that suppressed invertebrates are larger-bodied on average than those which are unaffected, although the difference is not statistically significant. Data from studies reporting effects of co-invasive rats and mice suggest that the relationship between invertebrate body size and vulnerability is less clear, with extirpated invertebrates being on average smaller-bodied than those which are simply suppressed (although sample sizes are small and the difference is not statistically significant; Table 2).

Overall, these results suggest that large invertebrate body size is a strong predictor of risk from invasive rodents, consistent with a direct mechanism of impact (predation) in many cases.

#### 4.2. Indirect effects

Here I use 'indirect effects' to refer to interactions between two species which require the presence of a third (intermediary) species, as opposed to direct pairwise interactions such as predation (Wootton, 1994). Indirect effects are frequently found to be important in population regulation, and are the subject of a growing genre of studies (Pace et al., 1999; Van Bael et al., 2003). The 'rampant trophic opportunism' (Paine, 1980, see Section 2) typical of the invasive rodents suggests a particularly wide range of potential indirect effects, due to direct impacts on groups occupying a diverse range of trophic levels, from primary producers (plants) through primary consumers and mesopredators (such as other invertebrates) to top predators (often birds) and ecosystem engineers (including burrowing seabirds).

One of the first descriptions of a complex indirect effect involved rodents and invertebrates: Charles Darwin wrote that field mice (*Apodemus sylvaticus*) destroyed the combs and nests of bumble-bees (*Bombus* sp.), and that this particular bee alone pollinated red clover (*Trifolium pratense*). Darwin speculated that a local increase in cat abundance "might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!" (Darwin, 1859). Logic dictates that such indirect effects must occur frequently – for example, thousands of feather- and nest parasites must have been extirpated when rats drove their avian hosts to extinction (Ramsay, 1978; Steadman, 1997). It should be noted that although perturbation of native host-parasite systems following rodent invasion is a little-studied subject, when it occurs it may have major implications for the population dynamics of both primary and intermediate host species, and of the parasites themselves (Prenter et al., 2004; Torchin and Mitchell, 2004).

It can be notoriously difficult to demonstrate indirect mechanisms of impact (White et al., 2006), but a number of studies, discussed below, indicate that invasive rodents can affect island invertebrates via indirect mechanisms.

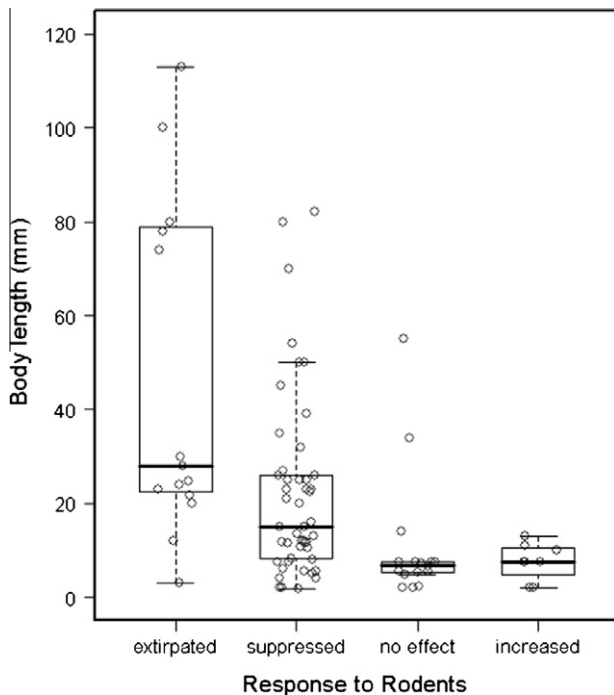
#### 4.3. Effects on invertebrates via their hosts

A powerful mechanism of invertebrate extinction is thought to be the extinction or suppression of host organisms, particularly when the relationship is highly specific (Dunn et al., 2009). When plant populations decline, there is clearly potential for parallel effects on dependent invertebrates including parasitoids, herbivores, frugivores and nectarivores, and species for which plants provide

**Table 2**

Median body lengths (mm) of invertebrate taxa of known size, according to their population responses to the presence of invasive rats and mice (singly, in combination, and overall). Also presented are test statistics and *P*-values of Mann–Whitney U-tests of differences in body length between population-response categories. Data sources are tabulated in Appendix A.

	Extirpated, mm (n)	Comparison – extirpated vs suppressed	Suppressed, mm (n)	Comparison – suppressed vs no effect	No Effect, mm (n)	Comparison – no effect vs increased	Increased, mm (n)
<i>Rattus</i> spp. only	76.0 (8)	$\left\{ \begin{array}{l} P = 0.002 \\ U = 222.0 \end{array} \right\}$	18.0 (30)	$\left\{ \begin{array}{l} P = 0.001 \\ U = 675.0 \end{array} \right\}$	7.5 (8)	$\left\{ \begin{array}{l} P = 0.294 \\ U = 57.50 \end{array} \right\}$	7.5 (8)
<i>M. musculus</i> only	–	–	11.2 (14)	$\left\{ \begin{array}{l} P = 0.432 \\ U = 173.0 \end{array} \right\}$	6.0 (8)	–	–
Rats + mice	23.0 (7)	$\left\{ \begin{array}{l} P = 1.000 \\ U = 45.00 \end{array} \right\}$	45.0 (5)	–	9.8 (2)	–	–
All studies	28.0 (15)	$\left\{ \begin{array}{l} P = 0.009 \\ U = 654.8 \end{array} \right\}$	15.0 (49)	$\left\{ \begin{array}{l} P = 0.001 \\ U = 1897 \end{array} \right\}$	6.8 (18)	$\left\{ \begin{array}{l} P = 0.505 \\ U = 230.5 \end{array} \right\}$	7.5 (8)



**Fig. 3.** Effect of body length (mm) on the response of island invertebrate species (or within-taxon size-classes) to rodent presence, derived from all reports in the literature for which body length data were available (see Appendix A for sources). Actual data (with jitter, and excluding a single datum at 200 mm) shown in grey, box and whisker plots superimposed. Boxes show the positions of 1st, 2nd and 3rd quartiles; whiskers extend to 1.5 times the inter-quartile range, or min/max values, depending on which is smaller (Crawley, 2007).

essential habitat. A number of studies have demonstrated effects of introduced rodents (particularly *R. rattus* and *R. exulans*) on the distribution, germination or recruitment of plant species (Campbell, 1978; Campbell and Atkinson, 2002; Wilson et al., 2003; Shaw et al., 2005; Wardle et al., 2007; Phiri et al., 2009), although only a few studies have addressed rodent impacts on invertebrate populations via effects on plants. The cushion plant *Azorella selago* is an important habitat for invertebrates on Marion Island, and its destructive use as a nesting habitat by mice is thus likely to affect invertebrate populations (Barendse and Chown, 2001; Phiri et al., 2009). In New Zealand, regeneration of Karo (*Pittosporum crassifolium*) plants is strongly inhibited by *R. exulans*, and when this plant species recovered following eradication of rabbits and *R. exulans* from Korapuki Island, populations of the New Zealand endemic scale insect (*Coelostomidia zealandica*) also recovered (Campbell and Atkinson, 2002; Towns, 2002); direct interaction between rats and scale insects could be excluded as the mechanism of impact because prior to rat eradication the insects remained abundant on the few surviving host plant individuals (Towns, 2002). Finally, the local extinction of the large weevil *Hadramphus stilborcarpae* occurred at the same time as the severe reduction of its host plant *Stilbocarpa lyelli* by *R. rattus* shortly after the invasion of Big South Cape Island in New Zealand (Kuschel and Worthy, 1996). In each of the latter examples it was not possible to demonstrate a rodent-plant-invertebrate pathway due to potentially confounding variables, although it seems likely that such a mechanism at least contributed to the observed impacts.

#### 4.4. Effects on invertebrates via their predators

Impacts of introduced rodents on many native predator populations are known, including birds, mammals and reptiles as well as

predacious invertebrates (Towns et al., 2006; Harris, 2009). Given these impacts, it is perhaps surprising that there are relatively few recorded examples of subsequent prey release. Perhaps the best example is from the Aleutian islands, where invasive rats have caused severe local reductions in the density of shorebirds such as oystercatchers, and populations of invertebrates (on which these shorebirds prey) in the intertidal zone have increased substantially relative to those around rat-free islands (Kurle et al., 2008). Such trophic cascades are currently receiving considerable attention, and more examples of rodent-mediated mesopredator suppression and prey release may emerge in the coming years. Trophic cascades within invertebrate communities are seldom studied, but given that taxa with an important predatory role such as carabid beetles may be particularly susceptible to rodent predation (Parmenter and Macmahon, 1988; Ernsting et al., 1995; McGuinness, 2007), it seems likely that rodent-initiated trophic cascades are a common but under-recorded post-invasion event. It may not be coincidental that rodent-caused suppression of large-bodied (predacious) invertebrate taxa is sometimes accompanied by an increase in smaller-bodied (prey) groups (e.g. Craddock, 1997).

#### 4.5. Effects on invertebrates via their competitors

When a species is removed from a community, the vacated ecological space can benefit its competitors (Schoener, 1983). Introduced rodents clearly have population-level impacts on various species, and competitive release of their competitors might be expected. A prerequisite for this effect is a differential impact of rodents on species within competing pairs; in nature, competing species are likely to be vulnerable to the same predators and thus competitive release will frequently not arise. Exceptions may occur when one competitor has superior anti-predator adaptations, an advantage that invasive invertebrates may have over native species (Lovei and Sunderland, 1996; Blumstein and Daniel, 2005); this is thus a candidate mechanism for rodent-mediated facilitation (*sensu* Simberloff and Van Holle, 1999) of invertebrate invasions. This is a possible explanation (albeit one of several) for Palmer and Pons' (1996) finding from 51 Balearic Islets, on which five endemic tenebrionid beetles were significantly less likely to occur on rat-infested islands, while two non-endemic species (with well-developed chemical anti-predator defenses) were more likely to occur on rat-infested than rat-free islands.

#### 4.6. Effects on invertebrates via ecosystem engineers

A series of studies from New Zealand have demonstrated cascading effects of invasive rats on invertebrates; predation by introduced rats severely reduced the density of burrowing seabirds compared to that on uninvaded islands, causing a marked reduction in the marine nutrient subsidy (Fukami et al., 2006), increased tree recruitment, atmospheric carbon sequestration and plant biomass (Wardle et al., 2007), reduced nitrogen content in the soil and some plant species (Mulder et al., 2008; Wardle et al., 2009), a reduced rate of litter decomposition and nitrogen release (Wardle et al., 2009), and reduced abundance of many below- and above-ground invertebrate groups (including minute land snails, springtails, rotifers, centipedes, ants, moths, amphipods and various vermiform taxa) attributable to the effects of rat-mediated seabird declines on soil characteristics (Fukami et al., 2006; Towns et al., 2009). Reductions of breeding seabird density, and concomitant reductions of marine nutrient inputs, are common consequences of rodent invasion of 'seabird' islands (Towns et al., 2006) and although nutrient and plant-related effects on invertebrate communities may commonly occur they are seldom investigated.

#### 4.7. Evolutionary impact

Island species often lack adaptations to non-native predators, and invasive rodents have clear potential to cause rapid evolutionary change in these species. Insular invertebrates often have remarkable morphologies such as gigantism, which likely result in part from a rodent-free evolutionary history (Meads, 1990; Gibbs, 2009). Novel predators such as rodents are likely to impose strong selection on heritable traits which affect the vulnerability of native prey, which may include body size, anti-predator defences, fecundity and age-at-maturity and other morphological and life-history traits (Strauss et al., 2006; Fisk et al., 2007). Evolution in response to such pressures will not only alter native gene pools, but changes to life-histories also have the potential to affect population dynamics and, in turn, ecosystem properties (Pelletier et al., 2009). Rapid evolutionary responses among island invertebrates are likely to occur following rodent introduction for a combination of reasons: firstly, the widespread ability of invertebrate prey to co-exist with rodents at reduced densities and the typically short generation time of invertebrates are both conditions necessary for rapid evolutionary responses; secondly, because insular invertebrate species will already possess adaptations to native (usually avian or reptilian) predators there is likely to be existing variation in life-history and anti-predator traits upon which selection can act; and finally, the selection pressures imposed on these traits by efficient and functionally alien predators such as rodents are likely to be intense. Despite this, I am aware of no convincing demonstrations of rapid evolutionary responses following rodent invasion of islands, although one study records that three invertebrate species sampled from rat-infested islands showed much greater predator-escape responses than the same species from rat-free sites (Bremner et al., 1989), and Meads (1990) mentions two New Zealand giant myriapod species and a stag beetle (*Dorcus helmesii*) which only reach their largest sizes on rodent-free islands; this may be due to selection of large prey by rodents, or (more likely) to generally increased predation pressure that shortens average and maximum lifespans and prevents recruitment to old (large) size-classes. Either way, the potential for directional selection and evolutionary change is clear.

#### 5. Study design and limitations

Most studies relied on natural or experimental variation in rodent presence or abundance across sites, time periods or both. Response variables included presence/absence of focal invertebrate taxa or size-classes determined by trapping or searching, and indices of relative abundance or species richness estimated using pitfall captures, tracking tunnels or capture/recapture methodologies. A second study type used quantification of rodent diet together with estimates of invertebrate demography to infer a population-level impact (Rowe-rowe et al., 1989; also see Navarrete and Castilla, 1993). Other studies used predation sign (characteristic shell breakage in snails) to correlate invertebrate population declines with rodent predation levels (Hadfield et al., 1993; Hadfield and Saufler, 2009; Meyer and Shiels, 2009). This forensic approach has also proved valuable in studies of prehistoric impact, with shell-breakage patterns implicating *R. exulans* in the extinction of several NZ endemic land snail populations (Brook, 1999; Brook and McArdle, 1999). A distinct and powerful study type uses the deliberate introduction of putatively vulnerable invertebrate populations to sites of varying rodent status – persistence time and population trajectories can then be used to infer impact (Watts and Thornburrow, 2009).

Varying levels of control and replication were used in different study types. All studies of rodent invasion were unreplicated,

reflecting the accidental nature of the variation and the opportunistic nature of the studies. More striking is the finding that the majority (7/13 = 54%) of studies which used deliberate rodent eradication as the source of variation also lacked any replication or spatial control, relying on repeated measurement of invertebrate abundance at a single manipulated site. Furthermore, many of these time-series studies lacked baseline (pre-manipulation) data, or relied on a single pre-manipulation sampling event (e.g. Green, 2002).

Questions of replication and control aside, the choice of method has important implications for the results. It is interesting to note that of the four studies that found no population-level treatment effect, three used methods which merely reduced rodent abundance rather than removing them completely, which perhaps suggests that even low rodent densities serve to suppress the recovery of invertebrate populations (the fourth found population impacts were probably precluded by changes in anti-predator behaviour when rats were present – Rufaut and Gibbs, 2003). Furthermore, a key feature of manipulative designs (eradication, control and enclosure) is that they can only test responses to rodent removal among the subset of species which were able to persist after the initial rodent invasion – in other words, the approach can not detect responses among species which are locally driven to extinction by rodents unless there is rapid recolonisation from nearby healthy populations (Townes, 2009). Designs that record the response of invertebrate populations to manipulation of rodent presence or abundance are thus inherently subject to Type 2 error. On the other hand, natural experiments can be used to infer local extinction of invertebrate populations, but care must be taken to account for confounding variables, such as accessibility or the level of anthropogenic disturbance, which might simultaneously favour rodent presence and negative effects on invertebrate populations. Such confounds raise the probability of Type 1 error in natural experiments.

Such problems may be satisfactorily addressed by the use of combinatorial designs, which consider two or more mutually supporting lines of evidence. Such combinations may include the incorporation of manipulated (rodent-eradicated) sites into natural experiments, or other methods (discussed above) such as subfossil chronology, dietary studies and invertebrate reintroduction.

#### 6. Conclusions and future directions

##### 6.1. Summary

Taken together, the studies collected here suggest that impacts of invasive rodents on island invertebrates are globally widespread, although they have been investigated largely in New Zealand. These impacts involve direct and indirect mechanisms, and are phylogenetically diverse, with effects on several invertebrate phyla documented for each of the four invasive rodent species. In several cases invertebrate populations have been driven to extinction by invasive rodents, but the most commonly recorded impact is population suppression. Negatively affected invertebrates tend to be larger-bodied than those which are unaffected by rodents, a trend which may be driven by rodent dietary preferences and/or life-history correlates of large body size that confer vulnerability (at the population level) to increased predation. Further research is urgently needed to investigate, for each rodent in turn, the distribution, severity, mechanisms and population and ecosystem consequences of these rodent-invertebrate interactions. I also hope that opportunistic, incidental and small-scale studies which make up the bulk of the literature reviewed here, and which are often conducted alongside or as part of conservation management programmes, will in future be supplemented by more dedicated research projects

which are not limited by the need to divide valuable resources between research and conservation action. Some areas in which this effort could profitably be focussed are outlined below.

### 6.2. Differences and interactions between rodent species

The effects of the three *Rattus* species and *M. musculus* on prey populations may or may not be broadly equivalent (Angel et al., 2009), and largely for reasons of data availability I have not attempted to distinguish between their impacts in this review. However, these rodent species have different distributions and foraging ecologies, which may lead to differences in their impacts on prey species including invertebrates (Atkinson, 1985; Amarasekare, 1994; Harper, 2006). There is thus a clear need to know about their relative impacts when prioritising eradications, or when planning conservation management of sites at which two or more (potentially interacting) invasive rodent species are present (Clout and Russell, 2007). Further research into the impacts and demographic interactions of different invasive rodents (and other common invasives including stoats, cats and foxes) would also be of considerable value, allowing the consequences of step-wise or partial eradications of alien communities to be modelled in advance, and 'surprise effects' to be avoided (Caut et al., 2009).

### 6.3. Indirect effects

It is clear that indirect effects of rodents on invertebrates are often mediated by direct impacts on keystone vertebrates (Kurler et al., 2008; Towns et al., 2009). However, this review would not be complete without encouraging greater consideration of the potential consequences of rodent-invertebrate interactions for other ecosystem components. Although invertebrates are vital for ecosystem functioning, relatively few studies have yet investigated the knock-on effects of the suppression of invertebrate species on other ecosystem properties such as native predator guilds, soil processes, invertebrate community structure and resilience to further invasions (Simberloff and Van Holle, 1999; Huyser et al., 2000; Lawrence and Samways, 2003; Pisanu et al., 2005). Effects such as these may be important mechanisms of change in invaded ecosystems, and are pertinent both to conservation biology and to basic research in ecology and biogeography.

### 6.4. Towards a predictive framework of vulnerability

Among vertebrate taxa, considerable effort has gone into identifying the phenotypic and phylogenetic correlates of extinction risk, ostensibly to generate predictive frameworks to inform conservation management (Fisher and Owens, 2004; Reynolds et al., 2005). However, the question of correlates of extinction risk in invertebrates has seldom been addressed (Krushelnysky and Gillespie, 2010). I suggest that such studies, which can lead to the identification of particularly vulnerable guilds or taxa, may be of considerable use in the prioritisation of conservation interventions such as rodent eradications. A clear correlate of vulnerability to invasive rodents highlighted in this review is large body size, and a knowledge of threshold body sizes – above which the risk from a given invasive rodent species is substantially increased – may prove to be a valuable tool for conservation managers. In addition to large body size, other risk factors have been proposed – flightlessness, ground-dwelling habits, strong odours, and a lack of anti-predator adaptations such as escape responses and distasteful compounds may all increase vulnerability (Gibbs, 2009), and to this list of candidate traits we can add life-history traits such as delayed reproductive maturity and low reproductive output which often confer vulnerability at the population level (Fisher and Owens, 2004). Studies that record variation in such phenotypic

traits across a spectrum of rodent-affected and -unaffected invertebrate species may thus prove invaluable in constructing a predictive framework of risk.

### 6.5. Evolutionary responses to rodent invasion

As discussed in Section 4.7, the suppression of invertebrate populations by invasive rodents provides the conditions necessary for rapid evolutionary change. To date, there has been little investigation of evolutionary responses of native species to invasives in any system (Strauss et al., 2006). Given that rapid evolutionary change can reduce ecological effect sizes and facilitate persistence of native species in the presence of invasives (Pelletier et al., 2009), the phenomenon is likely to structure disturbed communities and merits further attention. Furthermore, rapid evolutionary change may also represent a mechanism for the cryptic loss of biodiversity, reducing genetic variance and eroding the very characteristics that make many island endemics 'special' or phenotypically distinct from their continental relatives – in the case of New Zealand's invertebrates, such characteristics may include gigantism (Meads, 1990). In invertebrates, evolved differences are relatively easy to detect using common-garden experiments, in which phenotypic assays are conducted on cultured populations originating from different sites (e.g. those with and without invasive rodents), and I suggest that such studies may provide fascinating insights into a cryptic and neglected aspect of species invasions.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2010.10.006](https://doi.org/10.1016/j.biocon.2010.10.006).

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