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Rodent management issues in South Pacific islands: a review with case studies from Papua New Guinea and Vanuatu

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Abstract Rodents are a key pest to agricultural and rural island communities of the South Pacific, but there is limited information of their impact on the crops and livelihoods of small-scale farmers. The rodent pest community is known, but the type and scales of damage to different crops on different islands are unknown. Knowledge about rodent pest management in other geographical regions may not be directly transferable to the Pacific region. Many studies on islands have largely focussed on the eradication of rodents from uninhabited islands for conservation benefits. These broadscale eradication efforts are unlikely to translate to inhabited islands because of complex social and agricultural issues. The livelihoods, culture and customs of poor small-scale farmers in the South Pacific have a large bearing on the current management of rodents. The aim of the present review was to describe the rodent problems, impacts and management of rodents on South Pacific islands, and identify gaps for further research. We compared and contrasted two case studies. The situation in Papua New Guinea is emergent as several introduced rodent species are actively invading new areas with wide-ranging implications for human livelihoods and conservation. In Vanuatu, we show how rodent damage on cocoa plantations can be reduced by good orchard hygiene through pruning and weeding, which also has benefits for the management of black pod disease. We conclude that (1) damage levels are unknown and unreported, (2) the impacts on human health are unknown, (3) the relationships between the pest species and their food sources, breeding and movements are not known, and (4) the situation in Papua New Guinea may represent an emergent crisis that warrants further investigation. In addition, there is a need for greater understanding of the invasive history of pest rodents, so as to integrate biological information with management strategies. Ecologically based rodent management can be achieved on Pacific Islands, but only after significant well funded large-scale projects are established and rodent ecologists are trained. We can learn from experiences from other locations such as Southeast Asia to guide the way.

Additional keywords: agricultural production, black pod disease, cocoa, small-scale farmer livelihoods.

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Introduction

Almost 30 years have elapsed since Hoque *et al.* (1988) last reviewed the impacts of rodents in the Pacific Island region. Since that time, little action has been taken in response to their conclusion that rodents represent one of the main constraints to agricultural production across this large and diverse region. By contrast, over the same period, there have been major advances in understanding of the ecology, impacts and management options for rodent pests in agricultural systems in Southeast Asia (Singleton *et al.* 2004; Huan *et al.* 2010; Sudarmaji *et al.* 2010) and Africa (Mulungu 2017; Swanepoel *et al.* 2017). Accordingly, it is timely to look again at the situation in the Pacific region and to ask whether or not lessons learned elsewhere can be usefully applied, either in general or in particular cases.

There are four key issues that need to be considered in any assessment of rodent pest problems across such a broad geographic area. The first is the fact that the proportion of native versus introduced rodents varies enormously among the various islands, being from overwhelmingly native (>95%) on the main island of New Guinea, to entirely introduced on all of the more remote islands. The second is the extreme disparity in the scale of agricultural production systems across the region, ranging from entirely subsistence-based systems in the most remote areas, to systems with combined subsistence and small-scale

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cash cropping, through to commercial-scale production for local and export markets. The third is the enormous human cultural diversity that exists across the region and which remains essentially intact in many areas in terms of lifestyles, socio-political organisation, and belief systems, despite several centuries of Christian missionary influence. Last, and with a few notable exceptions, the entire region is characterised by poor physical infrastructure, a low educational base, and a degree of remoteness that elevates the difficulty and cost of almost everything. The major exception in respect to this last factor is New Zealand, which also differs from all other regional nations in having had a long history of pest rodent research and several active research programs (Parkes and Murphy 2003; Russell and Broome 2016; Parkes *et al*. 2017). For these reasons, we exclude New Zealand from this review.

Rodent impacts are commonly considered from one of three main perspectives, namely, agricultural production (e.g. John 2014), human and livestock health (e.g. Meerburg *et al*. 2009) and nature conservation (e.g. Howald *et al*. 2007; Harris 2009). We will touch on all three aspects in the present review, but will devote more attention to potential impacts on agricultural production and nature conservation than on health. In so doing, it is not our intention to downplay the undoubted significance of rodent impacts on human and livestock health across the entire region; rather, it reflects the even more limited data available on this topic compared with the other two.

The present paper describes the current situation on islands across the South Pacific, identifies constraints and opportunities, similarities and differences. We compare and contrast two case studies on native rodents in Papua New Guinea and rodents in cocoa plantations in Vanuatu, and draw on a range of published literature, grey literature and unpublished reports to reflect on the current status of knowledge about rodent management and identify gaps for further research.

Background and context

The Pacific Island region is characterised by up to 30 000 small islands, made from two broad island geomorphologies (after Park *et al*. 2012) of (1) volcanic (larger high islands with more fertile soil) and (2) coral atolls (smaller low islands with reefs and infertile soils; Fig. 1, Table 1).

Politically, the region comprises a mix of sovereign states or dependencies within the following three geographic realms: Micronesia (Federated States of Micronesia, Guam, Kiribati, Marshall Islands, Nauru, Northern Mariana Islands and Palau), Melanesia (the Indonesian Province of Papua, Papua New Guinea, Fiji, New Caledonia, Solomon Islands and Vanuatu) and Polynesia (America Samoa, Cook Islands, French Polynesia, Hawaii, New Zealand, Niue, Pitcairn Islands, Samoa, Tokelau, Tonga, Tuvalu, and Wallis and Futuna; Table 1). The total estimated population is ~20 million on a land area of 1 308 000 km^2, with an average density of 15 people per km^2 (includes New Zealand and Hawaii). The most populous countries are Papua New Guinea with 6.7 million, Indonesian Provinces of West Papua and Papua with 4.4 million people, and New Zealand with 4 million.

Humans first entered Melanesia more than 40 000 years ago (Spriggs 1997) but deeper penetration of the Pacific Island region commenced much later, with the earliest evidence of human

Fig. 1. Map of the Pacific islands region, showing general areas of Micronesia, Melanesia and Polynesia. Source: Areas based on Campbell (2010); base map from www.freeworldmaps.net.

Table 1. Summary of key physical and economic attributes relevant for agricultural production on selected Pacific Islands

All are Sovereign states, except for New Caledonia, which is a dependency of France. Source: Park *et al.* (2012), CIA (2014)

Name	Geographic location	Geographic configuration	Island geomorphology	Population	Area (km^2)	Density (per km^2)	Agricultural labour (%)	GDP agriculture (%)
Cook Islands	Polynesia	Archipelago	Predominantly atolls, with a volcanic island	10 777	236	46	29	5
Federated States of Micronesia	Micronesia	Archipelago	Volcanic and atolls	111 000	702	158	1	14
Fiji	Melanesia	Archipelago	Predominantly volcanic, some coral islands	849 000	18274	46	70	12
Indonesian Province of Papua	Melanesia	Part of a larger island	Predominantly volcanic, some coral islands and atolls	3 486 432	319 036	11	Large^A	Small^A
Indonesian Province of West Papua	Melanesia	Part of a larger island	Predominantly volcanic, some coral islands and atolls	877 437	140 375	6.3	Large^A	Small^A
Kiribati	Micronesia	Archipelago	Atolls	98 000	811	135	3	24
Marshall Islands	Micronesia	Archipelago	Atolls	62 000	181	343	11	14
Nauru	Micronesia	One island	Coral and raised atolls	13 635	21	649	Small	6
New Caledonia	Melanesia	One main island	Predominantly volcanic, some coral islands and atolls	260 166	18275	14	20	2
Niue	Polynesia	Single island	Coral	1269	260	5	Small	24
Palau	Micronesia	Archipelago	Volcanic and coral	20 000	459	44	20	3
Papua New Guinea	Melanesia	Part of a larger island	Predominantly volcanic, some coral islands and atolls	6 732 000	462 840	15	85	28
Samoa	Polynesia	Archipelago	Volcanic	179 000	2831	63	65	10
Solomon Islands	Melanesia	Archipelago	Predominantly volcanic, some coral islands and atolls	523 000	28 400	18	75	50
Tonga	Polynesia	Archipelago	Volcanic	104 000	748	139	32	21
Tuvalu	Polynesia	Archipelago	Atoll	12 373	26	476	Small	17
Vanuatu	Melanesia	Archipelago	Predominantly volcanic, some coral islands and atolls	243 304	12 190	20	65	22

[A] Unable to obtain specific agricultural statistics for these Provinces of Indonesia.

voyaging into Micronesia, and Polynesia dating to within the past 3000–4000 years (Bellwood 1997; Kirch 1997, 2010; Kayser *et al*. 2000). This can be closely linked to the rodent fauna expansion (particularly for *Rattus exulans*; Thomson *et al*. 2014) through accidental or deliberate introductions. The invasion and expansion of the *R. rattus* complex is likely to have occurred only within the past few hundred years as Europeans have been exploring the Pacific region.

The livelihoods, culture and customs have a large bearing on the agricultural systems, but also on management of other resources. Most agriculture across the region is practiced by smallholders in small gardens with few inputs and relying almost entirely on rainfall. Smallholders account for ~95% of agriculture output. The agricultural labour force is reasonably large for the bigger islands with higher populations and a reliance on subsistence and agriculture, with 85% of people being involved in agriculture in Papua New Guinea, 75% in Solomon Islands, 70% in Fiji, 65% in both Samoa and Vanuatu, reducing to 32% for Tonga and much lower for other islands (Table 1). The contribution of agriculture to GDP for these countries is low (~20% or less), but these countries are predominantly smallholder subsistence or cash-crop oriented. A wide range of tropical crops is grown for subsistence or as cash crops and include root crops (cassava (*Manihot esculenta*), taro (*Colocasia esculenta*), potatoes (*Solanum tuberosum*), sweet potatoes (*Ipomoea batatas*), yams (*Dioscorea* spp.)), fruits (bananas (*Musa* spp.), breadfruit (*Artocarpus altilis*), citrus (*Citrus* spp.), melons various species (*Cucumis* spp.), papayas/pawpaw (*Carica papaya*), passion fruit (*Passiflora edulis*), pineapples (*Ananas comosus*), tomatoes (*Solanum lycopersicum*)), other cash crops (betel nuts (*Areca catechu*), black pepper (*Piper nigrum*), cocoa (*Theobroma cacao*), coconut/copra (*Cocos nucifera*), coffee (*Coffea canephora* and *Coffea arabica*), ginger (*Zingiber officinale*), honey, kava (*Piper methysticum*), vanilla (*Vanilla planifolia*)), livestock products (beef and dairy products (*Bos taurus*), chicken and eggs (*Gallus gallus domesticus*), pigs (*Sus scrofa*)) and fish products (CIA 2014).

New Guinea (including Papua New Guinea (PNG) and the Indonesian Provinces of Papua and West Papua) is very different from the rest of the Pacific island region. New Guinea is a large and diverse island in its own right, with a wide range of natural environments because of variations in landform, rainfall and altitude, with land stretching from lowland swampy regions (0–1200 m) to highlands (1200–2800 m), with peaks over 4000 m (Hansen *et al*. 2001). Much of the land is not suitable for agriculture. There are also highly diverse human cultures in PNG (>800 distinctive local cultures and languages have been identified, Aikhenvald and Stebbins 2007), which are thought to have been present for at least 40 000 years. Most people live on their own land, which is owned through customary title, and most are semi-subsistence farmers who produce food and cash crops from their own gardens. Sweet potato is the most important crop grown and is the staple food for 60% of the rural population (Hanson *et al*. 2001). The agricultural sector provides incomes to ~80% of the population mainly through coffee, cocoa, oil palm and copra production by smallholders (Hanson *et al*. 2001). Resource extraction and development are becoming important for PNG, and this is becoming associated with infrastructure and road developments (Hanson *et al*. 2001).

Pacific Island rodents: distribution and ecology

The Pacific Island region as a whole supports more than 80 rodent species (Flannery 1995*a*, 1995*b*; Musser and Carleton 2005). All belong to the rodent family Muridae, and, within this diverse group, to the subfamily Murinae, which is the group that contains the commensal rats and mice. Most of the region's rodents are endemic to the island of New Guinea, which was probably first colonised by overwater dispersal from island Southeast Asia ~6 million years ago (Rowe *et al*. 2008; Aplin and Ford 2013). Native rodents also occur on many of New Guinea's satellite islands, both to the north as far as Manus Island (Timm *et al*. 2016) and to the east as far as the Solomon Islands. Two major evolutionary lineages are represented among the region's native rodents, including members of the tribe Hydromyini (otherwise found only in the Philippine Archipelago) and members of the tribe Rattini (with a broad Eurasian distribution). The 17 native members of the Rattini all are currently included in the genus *Rattus*, although molecular studies have shown them to be somewhat distantly related to the core members of *Rattus* (Rowe *et al*. 2011; Fabre *et al*. 2013).

Aside from these native rodents, the Pacific Island region supports populations of six or more introduced rodents belonging to the genera *Rattus* and *Mus* (Table 2). These are of varied origin and have diverse histories, which is important background to understanding their current status and ecology.

Mus musculus *complex*

House mice of the *Mus musculus* complex (we follow Macholan *et al*. (2012) in treating the various genetic subgroups as well differentiated subspecies) are recorded from scattered localities across the Pacific Island region, including islands in the Society, Tuamotu and Marquesas groups (Tate 1935), in the Mariana Islands (Stinson 1994), on Hawaii (Tomich 1986) and in PNG (Flannery 1995*a*). In all likelihood, this group is far more widely distributed than these few records might indicate. Certainly, in PNG, it appears to be actively expanding its geographic coverage, with confirmed recent arrival in various parts of Eastern Highlands, Gulf and Hela Provinces (K. P. Aplin, unpubl. data). Most of the records come from the larger towns, but some are from mining and/or petrochemical project sites. The only record from a more rural site comes from a small bush hut beside the Tagari River in Hela Province, from a garden surrounded by relatively undisturbed forest (K. P. Aplin, unpubl. data, 2014). There are no published ecological studies of the house mouse species on any Pacific Island.

The identity of these Pacific Island house mice has not yet been established. There are several possible candidates, including *Mus m. domesticus*, which is widely established in Australia and New Zealand (Gabriel *et al*. 2011), *M. m. castaneus*, which is widely distributed in island Southeast Asia (Suzuki *et al*. 2013) and is also represented in the New Zealand house mouse gene pool (Searle *et al*. 2009), and *M. m. musculus* of eastern European origin, which has also contributed to the New Zealand gene pool (Searle *et al*. 2009) and is well represented in eastern Asia, including Japan (Suzuki *et al*. 2013). In all likelihood,

Table 2. Occurrence of rodent species for selected islands
Source: Hinds and Aplin (2004)

Country	*Mus musculus*	*Rattus argentiventer*	*R. exulans*	*R. nitidus*	*R. norvegicus*	*R. rattus* complex
Cook Islands	✓		✓		✓	✓
Federated States of Micronesia	✓		✓		✓	✓
Fiji	✓		✓		✓	✓
Kiribati	✓		✓		?	✓
Marshall Islands	✓		✓		✓	✓
Nauru	✓		✓			✓
New Caledonia	✓		✓		✓	✓
New Guinea	✓	✓	✓	✓	✓	✓
Niue	✓		✓		✓	✓
Palau	✓		✓		✓	✓
Samoa			✓		✓	✓
Solomon Islands	✓		✓		✓	✓
Tonga	✓		✓		✓	✓
Tuvalu	✓		✓		✓	✓
Vanuatu	✓		✓		✓	✓

the Pacific Island populations will be found to contain multiple genetic components reflecting diverse origins, including some that have already been characterised by genetic admixture (e.g. Nunome *et al*. 2010).

Rattus argentiventer

Rattus argentiventer is the dominant rodent pest of lowland irrigated rice systems in Indonesia, Malaysia and Vietnam (Aplin *et al*. 2003) and it has been the subject of numerous ecological studies in these areas (Lam 1983; Tristiani *et al*. 1998; Brown *et al*. 1999, 2001, 2006; Jacob *et al*. 2010). Within the Pacific Island region, it has been recorded only once, namely in 1910 from a locality called Tanah Merah that Taylor *et al*. (1982, pp. 288, 289) convincingly situated on the coast to the west of modern-day Jayapura, Papua Province, Indonesia. Given the emphasis in the past decades on the establishment of rice-cropping systems in Papua Province, it is possible that this species is now more widely established across the island of New Guinea, although there is no evidence that it has spread to PNG.

Rattus exulans

The Pacific rat (*Rattus exulans*) occurs on virtually every island group, even into the most remote parts of Polynesia and Micronesia (Tate 1935; Flannery 1995*b*; Musser and Carleton 2005). The place of origin of this species was recently narrowed down by molecular sequence data to Flores Island in the Lesser Sunda group, Nusa Tenggara Province, Indonesia (Thomson *et al*. 2014). Its dispersal across the region probably started ~4000 years ago, but was given a major boost by joining forces of Austronesian-speaking seafarers who, during the third and second millennia BCE, rapidly colonised the entire western Pacific region (Bellwood 1997; Kirch 1997, 2010). Debate continues over whether the dispersal of Pacific rats was intentional (as food items) or accidental (as stowaways); however, either way, the Pacific rat established viable feral populations throughout the region. In the case of New Zealand, Pacific rats probably were introduced during early exploratory visits ~1800 years ago and they were already established when the islands were finally settled by ancestral Maori people ~800 years ago (Holdaway 1996). The pattern of genetic relationships among *R. exulans* populations has been used as a proxy for human dispersal across the Pacific (Matisoo-Smith and Robins 2004).

In PNG, it is still possible to find remote human settlements that do not host populations of *R. exulans* (K. P. Aplin, unpubl. data). However, the species is almost certainly expanding its coverage as a consequence of the increasing volume of local commercial traffic by boat and air, as well as the larger-scale activities of the forestry, mining and petrochemical sectors. In areas where forestry activities are ongoing or of recent occurrence, *R. exulans* can usually be found living in the grassy and weedy road-verge habitats, although it rarely seems to venture far into flanking habitats (K. P. Aplin, unpubl. data). The same observation was made by Dwyer (1978) in relation to populations of *R. exulans* in Eastern Highlands Province of PNG, where they occur in active gardens and early regrowth, but not in advanced regrowth or primary forest habitats. By contrast, on some of the islands of eastern Indonesia, *R. exulans* can be found in any habitat, including remnant patches of primary forest (Kitchener *et al*. 1991; K. P. Aplin, unpubl. data). In these contexts, the expanded ecological scope of *R. exulans* may be due to (and may also have contributed to) the extinction of native rodent faunas.

The population ecology of the Pacific rat (*R. exulans*) has been studied in Papua New Guinea (Dwyer 1978), on Ponape in Micronesia, and on Hawaii (Tamarin and Malecha 1971, 1972; Wirtz 1973), and, extralimitally, in Malaysia (Marshall 1977). In Eastern Highlands Province of PNG, this species breeds year round, but with a reduced reproductive output during the cooler months (Dwyer 1978). In Hawaii, where the climate is more strongly seasonal, breeding occurs only during the wetter months. Population-density estimates are available for various Pacific islands and habitats, as follows: 1–3 ha^{-1} in coconut plantation on Guam; 7–12 ha^{-1} in grassland and 11–24 ha^{-1} in a coconut plantation on Ponape; and 7–30 ha^{-1} for various habitats on Tokelau.

Rattus nitidus

Rattus nitidus is recorded regionally only on the Bird's Head of Papua Province of Indonesia where it is known from four historical collecting localities (Taylor *et al*. 1982). This species appears to be native to mainland Asia, with a likely natural range that extends from north-eastern India to southern China and Indochina (Aplin *et al*. 2003). It is also recorded from the Philippines (Benguet Province, Luzon Island) and from several islands of eastern Indonesia (Sulawesi and Seram). In Sichuan Province of China, it is a major pest in both wheat and rice fields (Aplin *et al*. 2003, and references therein). In more southerly areas, it seems to be a minor pest, with records of the species living in rural houses (e.g. northern Thailand: Marshall 1977; Mizoram State, north-eastern India, K. P. Aplin, unpubl. data) and in small, irrigated rice fields within an upland cropping system (northern Laos, Aplin *et al*. 2003). The few specimens from the Bird's Head of New Guinea came from houses and gardens (Taylor *et al*. 1982). The historical circumstances that underlie the widely scattered distribution of *R. nitidus* are not known, but introduction via historical Chinese shipping seems to be a likely mechanism.

Rattus norvegicus

Although *Rattus norvegicus* occurs across most of the Pacific Island region (Table 2), it has a more restricted range of habitats, with confirmed records on New Guinea and on islands in the Society, Samoan and Horne Island groups (Tate 1935). On New Guinea, it is recorded from historical collections at the major sea ports of Port Moresby and Lae in PNG, and Jayapura in Papua Province, Indonesia. A more recent confirmed record of the species comes from Lorengau, the provincial capital on Manus Island to the north of New Guinea (Matisoo-Smith and Robins 2009). Another potential recent record (based on a verbal description only) comes from an industrial site in the vicinity of Lake Kutubu in Hela Province, PNG (K. P. Aplin, unpub. data). As noted above, Atkinson (1973) argued convincingly that before construction of the Suez Canal in 1869, ships sailing from Europe to the Pacific Islands region were more likely to be carrying *R. norvegicus* than *R. rattus* rats. Accordingly, we might expect that some of the earliest introductions into the Pacific Island region might have involved the Norway rat. This can be tested through collection and accurate identification of rat bones and teeth dating from the early colonial period.

The ecology of *R. norvegicus* in tropical areas is essentially unstudied. Taylor *et al*. (1982, p. 287, citing Johnson 1962) stated that this species 'does not spread into tropical forests or to any degree into cultivated areas in the tropics'. However, there are now scattered examples of *R. norvegicus* living as a field pest in both the Mekong River and Red River deltas of Vietnam, and in Thailand, Cambodia and southern China, and in a variety of cropping systems including irrigated rice, wheat and sugarcane (Aplin *et al*. 2003).

Rattus praetor

At least one native rodent species underwent a substantial expansion of its geographic range in late prehistoric times, with a likely connection to human dispersals. This is *R. praetor*, a species found in the lowlands of western and northern New Guinea, but which also occurs on numerous islands to the north and east of New Guinea, including Karkar, Blup Blup and Bat islands in the Admiralty Group, New Britain and New Ireland in the Bismarck Archipelago, and Bougainville and Guadalcanal Islands in the Solomon Island Group. On New Ireland, the species is convincingly absent before the late Holocene and the timing of its arrival is unclear (Summerhayes *et al*. 2009). *Rattus praetor* has also been reported in archaeological assemblages on Nissan and Tikopia Islands in the Solomon Islands (Flannery 1995*b*) and also from Vanuatu and Fiji (White *et al*. 2000). Flannery (1995*b*) suggested a possible link between the spread of *R. praetor* and the dispersal of Austronesian-language speakers across northern Melanesia ~3500 years ago; however, direct dating of archaeological remains is needed before this particular time frame can be accepted.

Rattus rattus *complex*

The black rats (also referred to in Pacific Island literature as house rats, roof rats or ship rats) are a taxonomically complex group and it is not yet clear how many species should be distinguished, or exactly how they are distributed. In some recent literature, a distinction was drawn between *R. rattus* with 38 chromosomes (originally from India and introduced into the Pacific region by Europeans) and *R. tanezumi* with 42 chromosomes (from eastern Asia and introduced into the Pacific region prehistorically; e.g. Yosida 1980; Flannery 1995*b*; Musser and Carleton 2005; Robins *et al*. 2007); however, recent genetic studies have indicated that the '*tanezumi*' group itself probably comprises multiple distinct species (Aplin *et al*. 2011; K. P. Aplin and others, unpubl. data). Following Aplin *et al*. (2011), we use the term *R. rattus* complex (RrC) for this group and refer to the various geographic populations by their mitochondrial DNA-lineage identities (Lineages I–VI in Aplin *et al*. 2011, but now expanded by addition of Lineages VII–X; Aplin *et al*., unpubl. data). Indications are that these lineages diverged in geographically isolated populations across southern, south-eastern and eastern Asia. This background is relevant to the current topic because at least two forms of '*tanezumi*' (mtDNA Lineages II and IV) underwent prehistoric range expansions into the western Pacific region (Aplin *et al*. 2011) and, thus, might be expected to occur within the Pacific Island region. Whether they differ in any significant ways in respect of their ecology, behaviour or reproductive biology remains to be tested. However, as remarked by Aplin *et al*. (2011), the fact that the various lineages within the RrC evolved in different zoogeographic contexts makes it likely that they possess individually contrasting patterns of disease associations; there is some evidence that this might be the case (Aplin *et al*. 2011).

The Pacific Island distribution of black rats includes numerous islands in each of Micronesia, Melanesia and Polynesia (Tate 1935; Flannery 1995*b*). In western Micronesia, bones and teeth of a member of the RrC come from archaeological layers dating to ~3500 years ago, thus predating the earliest evidence of *R. exulans* in this area (Wickler 2004). These prehistoric introductions are most likely to have involved some form of *R.* '*tanezumi*', but the original source area has not been determined through ancient DNA analysis.

Melanesia and Polynesia appear to have been colonised by black rats only during the period of colonial expansion. The sequence and timing of these events has not been mapped out in any detail, and this task cannot be undertaken in any detail here. As outlined above, Atkinson (1973) argued convincingly that, contrary to popular belief, ships departing from English and other European ports during the late 18th century were more likely to be carrying *R. norvegicus* than *R. rattus*, which had declined across Europe by that time, and, furthermore, that this situation may have changed only after construction of the Suez Canal in 1869, which brought European shipping destined for the Pacific Island region into contact with source populations of *R. rattus*. This view is supported by historical accounts from New Zealand but remains untested for any other geographic area. The earliest records of *R. rattus* from the western Pacific region are probably the types of *Mus beccarii* Peters & Doria, 1881, from Sorong on the Bird's Head of New Guinea and *Mus doboensis* de Beaufort, 1911, from the Aru Islands of the southern coast of Papua Province, Indonesia. One significantly earlier record from the wider Pacific region is the type of *Mus jacobiae* Waterhouse, 1838, which was collected by Darwin on the Galapagos Islands. It is possible that this population was introduced by whaling ships that had stopped over in South America, parts of which were colonised by *R. rattus* during the major period of Spanish colonial activity in the 17th century (Armitage 1994).

In Melanesia, black rats are still actively expanding their geographic range, despite having been present in some areas for more than 130 years. Taylor *et al*. (1982) mapped records from 18 localities on the main island of New Guinea, as well as records from the Aru Islands and Waigeo, Japen and Biak islands off the coast of Papua Province, Indonesia, in the west and from Manus Island, New Britain and the Solomon Islands to the north and east. As they observed, most of the historical records came from places with a long history of European colonial activity, including major towns and areas involved in some industrial activity such as gold mining. Away from such contexts, no populations of *R. rattus* were detected on mammal surveys conducted between the 1930s and the 1990s (see Flannery 1995*a*, 1995*b*, for summaries). By contrast, surveys conducted by Aplin and others in PNG over the past decade have detected populations of *R. rattus* in several areas from which they were confirmed absent in the 1980s to 1990s, such as in the upper Ramu Valley in Madang Province, around Goroka in Eastern Highlands Province, around Tari and Komo in Hela Province, at various localities in Gulf Province, and at various sites along the Ok Tedi and Fly rivers in Western Province. This expansion is clearly being facilitated in part by improvements in transport infrastructure (e.g. creation of the Highlands Highway that links Lae on the coast to Goroka and Mount Hagen in the highlands; and of the Tabubil Highway in Western Province) and the increasing volumes of road traffic including freight. However, it is also clear that some local introductions are occurring through transport into remote areas of large equipment or freight associated with commercial agriculture or forestry activities or resource-development projects (e.g. mining and oil and gas sectors). In some cases, the introduced black rats may remain confined to the industry infrastructure sites. However, where these sites are positioned close to rural communities, a more typical outcome is that the rats rapidly invade the village habitat and surrounding gardens. That local people are aware of the link between the invasive rats and the commercial or industry activities is clear from the names that they apply to the new animal, such as *toi rici* (rice rat) used in the Ok Tedi catchment, and 'container rat' used in parts of Gulf and Hela Province. Time frames are sometimes very short; in villages visited during 2016 in Gulf Province, the rats were said to have arrived in 2014 or 2015, but to have rapidly reached high densities.

Impacts of introduced rodents

These pest species cause a wide range of impacts and threats (Table 3). The information in this table is scant; rodent impacts and threats are significant, but there are few reliable assessments or studies to demonstrate or quantify the impacts. The *R. rattus* complex causes the greatest problems across most categories, but *R. exulans* causes significant damage to field crops and moderate damage to stored products and predation of wildlife, whereas *R. norvegicus* and *M. musculus* are seriously implicated in disease transmission to humans and livestock, but also cause moderate damage to stored grain and damage to houses and possessions.

Commensal species pose well known health risks at a global scale (Meerburg *et al*. 2009), but there is a dearth of information about disease impacts by rodents on humans, livestock or other wildlife for the Pacific region. In particular, there is little information about prevalence of zoonoses, despite reports of cases of leptospirosis and angiostrongyliasis. A recent review of rodent-borne diseases and threats to public health demonstrated the significance of *Rattus* spp. in the transmission of a range of pathogens (viruses, bacteria and parasites) to humans

Table 3. Level of threat posed by rodents

–, no threat; +, low threat; ++, moderate threat; +++, high threat; ?, lack of direct evidence. Source: Hinds and Aplin (2004)

Potential impact	*Mus musculus*	*Rattus exulans*	*R. norvegicus*	*R. rattus* complex
Damage to field crops	?	+++	–?	++
Spoilage to stored grain	++?	++?	++?	+++?
Damage to houses and possessions	+++?	+?	++?	++?
Disease transmission: human	–?	+?	+++?	++?
Disease transmission: livestock	–?	+?	++?	+++?
Disease transmission: wildlife	+?	+?	–?	+++?
Predation on wildlife	++?	++	–?	+++
Competition with wildlife	+?	+?	–?	++?
Non-target impacts of control	+?	+?	+?	++?

(Meerburg *et al*. 2009), but there was little mention of the Pacific region in that review.

It is highly likely that there is a significant disease threat to humans in the Pacific, as elsewhere in the world. This is compounded often by the flu-like symptoms and similarities of symptoms of tropical diseases (e.g. malaria) and those of rodent-borne diseases (e.g. leptospirosis; Meerburg *et al*. 2009). In the tropics, episodic outbreaks of rodent populations are becoming more common and may be associated with widespread rodent-borne diseases (such as leptospirosis) that occur in many parts of the world, including the south-eastern Pacific region (Jacob 2002; Berlioz-Arthaud *et al*. 2007). In New Caledonia, >50% of human cases of leptospirosis were associated with serovars of leptospirosis that most likely originated from rodents (Perez and Goarant 2010). Moreover, 85–90% of human-case mortalities were due to these rodent serovars (Tubiana *et al*. 2013). In Fiji, leptospirosis is the number one human infectious disease from animals; ranking higher than dengue fever or HIV–AIDS (Singleton *et al*. 2010). A recent study on Futuna (western Polynesia) suggested that there is an increased risk of leptospirosis when the species composition of rat populations changes (Theuerkauf *et al*. 2013). In 2012, two flood events in Fiji led to an outbreak of leptospirosis and an increase in human deaths (more than 50 people died and many more were seriously ill). Yet, little is known about the epidemiology of the disease with regard to which species are involved and the general epidemiology of the rodent-borne disease. Because of the high relevance of leptospirosis for public health, a national strategic plan was established by the Fiji Ministry of Health and there is a project ‘piloting climate change adaptation to protect human health’ that focuses on general patterns of climate-sensitive infectious diseases in the region (PCCAPHH 2015).

Rodents have been implicated in extinctions of a wide range of plants and animals from islands to such an extent that invasive rodents are considered a threatening process (Harris 2009), including the South Pacific region (reviewed in Ruffino *et al*. 2015). The house mouse (*Mus musculus*) and the black rat (*R. rattus*) are identified as key threatening processes under New South Wales and Australian environmental legislation, for their role in the extinction of at least 20 species of birds, invertebrates and plants on Lord Howe Island (Wilkinson and Priddel 2011). *Rattus exulans* and the *R. rattus* complex are the major culprits for conservation threats. Much of the work to eradicate rodents from islands is for conservation benefits, and there are well established approaches to achieve this (Howald *et al*. 2007). It is obvious what the benefits for conservation are when these invasive rodents have been removed from islands in terms of responses by the threatened flora and fauna, and to the ecosystems in general (Towns *et al*. 2013; Ruffino *et al*. 2015). Unfortunately, it will not always be possible to eradicate rodents from all islands, and particularly from human-inhabited islands. Lord Howe Island is facing some particular challenges because of community issues (Wilkinson and Priddel 2011). Interestingly, the New Zealand Department of Conservation was planning on setting up a sanctuary for kiore (*R. exulans*) on two islands, so as to protect the species that Maori ancestors introduced (Tahana 2010).

Through a case study approach, we now consider impacts of native rodents in New Guinea, then consider what options exist to manage the rodent problems for small-scale farmers on subsistence or cash-crop agricultural systems.

Impacts of native rodents: a case study in New Guinea

At least six of the native New Guinean rodent species might be considered pests on account of the damage they inflict in agricultural systems, particularly for garden crops. This situation is likely to have emerged hand-in-hand with the prehistoric development of agricultural systems, a process that was clearly well underway in the New Guinea highlands by 7000 years ago (Denham 2011).

Everywhere on New Guinea and its major satellite islands, trapping in subsistence gardens is likely to result in captures of a native *Rattus* species (Flannery 1995*a*, 1995*b*), being, in many places, accompanied by captures of *R. exulans* or *R. rattus*. The fact that it is a species of *Rattus* that is involved, rather than a species of other endemic genera, points to something unusual about the fundamental biology of the genus *Rattus* that has enhanced its capacity to adapt to disturbed ecological contexts (see Aplin and Ford 2013 for further discussion of this issue).

In the lowlands, the native *Rattus* species involved in crop damage varies regionally; it is *R. leucopus* in high-rainfall areas of southern New Guinea, *R. sordidus* in areas of southern New Guinea with seasonally dry savanna habitats, *R. mordax* on the south-eastern peninsula and nearby islands, and *R. praetor* in the northern lowlands, the Bismarck Archipelago and the Solomon Islands. At higher elevations (~500–1000 m asl) on New Guinea, these species are usually joined by *R. steini*, which then continues alone to higher elevations (~2000 m asl). These are all moderately large-bodied terrestrial rats (bodyweights up to ≥200 g; although they probably all excavate burrows, none is known to nest communally). Little else is known about the ecology of these species, although Dwyer (1984) described how, in a traditional shifting cultivation system at ~1100 m in Southern Highlands Province, *R. steini* quickly colonises newly planted garden areas and remains through the cropping period, but then declines and is replaced by other native species following garden abandonment and the return of woody plant cover.

One other native rodent that is widely implicated in significant crop damage is the giant white-tailed rat (*Uromys caudimaculatus*). This large-bodied species with bodyweights commonly up to 1000 g is an excellent climber and it is said to be able to gnaw into coconuts as well as destroying other edible tree nuts such as karuka (*Pandanus julianettii*), galip (*Canarium indicum*), okari (*Terminalia kaernbachii*), sea almond (*Terminalia catappa*) and Polynesian chestnut (*Inocarpus fagifer*). This species is most commonly mentioned as a pest animal in lowland New Guinea and it is often said to reside in the crowns of coconut trees within or adjacent to the village environment.

To our knowledge, there are no quantitative data from anywhere on the island of New Guinea or its major satellites on the level of damage inflicted to crops, whether or not these are grown by subsistence agriculturalists or as commercial ventures. However, there is much anecdotal evidence for significant levels of damage to a variety of garden crops, including sweet potato, yams, cassava, beans, corn, sugarcane and peanuts, and little reason to doubt that some of this damage is caused by native species. There is also anecdotal evidence for considerable rodent impacts in commercial-scale cropping of sugarcane and oil palm, but, in these cases, it is more likely that introduced rats (*R. exulans* and *R. rattus*) are responsible (Hinds and Aplin 2004).

The extent to which any of the native Melanesian rodents pose a threat as potential zoonotic disease reservoirs is also unknown. The predictive approach of Han *et al.* (2015) identified only one of the native *Rattus* species (*R. sordidus*) as a potential new rodent reservoir or hyper-reservoir, but the focus on this species is more likely to reflect the more complete biological data available for its Australian populations than any special features of its physiology or life history. More significantly, Han *et al.* (2015) identified two potential predictors of zoonotic disease risk that are of particular relevance to the present topic, namely, synanthropy (see also McFarlane *et al.* 2012; Bordes *et al.* 2013) and a temporally dynamic lifestyle in which there are physiological trade-offs between immunity and reproductive output (see also Martin *et al.* 2008; Ostfeld *et al.* 2014). In our view, these considerations firmly identify all of the native New Guinean *Rattus* species that manifest as agricultural pests as potential zoonotic disease reservoirs or hyper-reserviors. This topic warrants urgent consideration in the New Guinean region where large numbers of people not only live and work in close proximity to these species, but where they are also regularly consumed by many groups.

Case study of managing rats in small-scale cocoa plantations in Vanuatu

Background

The island group that comprises the nation of Vanuatu is situated midway between the Solomon Islands, New Caledonia and Fiji (Fig. 1) and, thus, falls within the region of Melanesia. Prior to the arrival of people ~3000 years ago (Kirch 2010), Vanuatu supported a diverse native vertebrate fauna that included giant turtles, a terrestrial crocodile, and numerous endemic small reptiles and birds (Medway and Marshall 1975). Several bats occur naturally on the islands (Flannery 1995*b*), but it is not known to have had any native rodents or other terrestrial mammals. Extinction of many vertebrate species occurred soon after human arrival. The Pacific rat was probably introduced to Vanuatu with, or soon after, initial human colonisation and black rats and Norway rats probably followed European arrival.

Like for most Pacific Island nations, agriculture provides the livelihoods for ~65% of the population of Vanuatu, but only 22% of GDP (Table 1; CIA 2014). Many small-scale rural households rely on subsistence agriculture, or low-value cash crops or commodities. Vanuatu's agriculture products include copra, coconuts, cocoa, coffee, taro, yams, fruits, vegetables, beef and fish, with exports of copra, beef, cocoa, timber, kava and coffee. Cocoa is an important crop for Vanuatu, with the majority of the production coming from small-scale farms. Vanuatu ranks number 28 in the world for cocoa production, with 1663 t being produced each year (FAOSTAT 2014). Much of Vanuatu's agriculture is organic by default, mainly because of the poor economic situation and the dispersed nature of the islands, both of which make it difficult to access chemical inputs. Because the volcanic soils are generally highly fertile, few fertiliser inputs are required.

The main pre-harvest constraints for cocoa production are rodents and black pod disease, caused by *Phytophthora palmivora* (Acebo-Guerrero *et al.* 2012). In 2010, we conducted preliminary counts of pods on trees (minimum of 25 trees from nine locations), and found that there were 24.2 healthy pods per tree (33.5%), 43.9 diseased pods per tree (58.7%) and 5.5 rat-damaged pods per tree (7.7%; B. J. Ritchie, S. E. Thomas and P. R. Brown, unpubl. data; Fig. 2). Control of black pod disease through removal of infected pods, and good pruning and weeding is thought to be straightforward and practical and these practices are recommended for smallholder farmers (Daniel *et al.* 2011; Acebo-Guerrero *et al.* 2012). Prior to our study, there were no recommendations in regard to the management of rodent damage to cocoa production.

At the outset, it was clear that the problem would need to be addressed using an integrated pest and disease management (IPDM) approach, as was trialled in PNG to manage black pod disease (Daniel *et al.* 2011). Two phases of the development

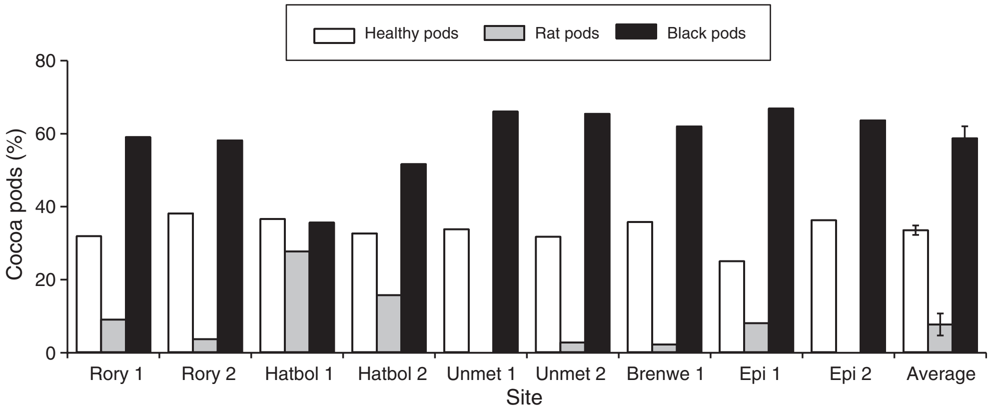

Fig. 2. Percentage of healthy pods, pods damaged by black pod disease and pods damaged by rats in a preliminary survey of cocoa pods from a minimum of 25 trees from nine locations in Vanuatu. Source: B. J. Ritchie, S. E. Thomas and P. R. Brown, unpubl. data.

and testing of practices for IPDM of black pod disease and rodent management in Vanuatu are described below.

Phase 1: intervention for improved livelihoods of small-scale cocoa farmers

A 4-year project was set up to evaluate the benefits of improved IPDM on the livelihoods of small-scale cocoa farmers in Vanuatu. Initially, 10 groups of farmers were trained in IPDM methods for both black pod disease and rodent management. Each group contained ~12 farmers. The aim was for these farmers to share their success with other farmers, in what was called the '12 apostle' approach. Each farmer was provided with some basic written material to show the impacts of black pod disease and rats and the types of management that might potentially control them. Farmers were encouraged to set up three small trial plots in their cocoa plantation over at least 1 year, to evaluate the benefit of improved management themselves, as follows:

- Plot 1: no management; continue undertaking normal practices;
- Plot 2: small-level intervention using light pruning, removal of infected pods and one rodenticide bait station; and
- Plot 3: intensive-level intervention using heavy and light pruning, removal of infected pods, weeding and field hygiene, and five rodenticide bait stations.

Each plot comprised five trees by five trees (total 25 trees), and each plot was placed within close proximity (~10 m away), so that the farmers could make easy comparisons among plots. There are obvious significant problems with this design, given the likely home-range size of rats in the cocoa plantations, but the intention was for farmers to see and compare for themselves what impact a small amount of management might have on cocoa yield per tree. The main focus for the management of black pod disease was removal of infected pods, combined with pruning and weeding, which is the recommended approach for small-holder farmers that do not have access to chemical control methods (Acebo-Guerrero *et al*. 2012). Farmers were asked to fill out a diary to detail the time spent on the different levels of intervention. Farmers were provided with some equipment (including pruning saws and secateurs for heavy and light pruning respectively) and rodenticides. Farmers were encouraged to continue the trial beyond the first year, or to adopt any improvements across their cocoa plantations.

Over the course of the project, a few different types of rodenticides were trialled, but brodifacoum wax blocks appeared to be the most successful and readily available ('PestOff' brand composite cereal and wax block bait containing 0.02 g/kg brodifacoum, manufactured in New Zealand). Individual wax blocks were placed inside small sections of bamboo (~8-cm diameter and ~30 cm long), with one end closed by the wall between compartments and the other end cut so that there was an overhang to reduce entry of rain into the chamber containing the bait. These bait stations were tied onto the jorquette of the cocoa tree using bush vine and held securely to prevent entry of rain but allow entry by rats. Bait stations were checked weekly and replenished if required. Farmers were made aware of the safety precautions for storing, handling and using rodenticides (e.g. potential non-target impacts). Although we used a brodifacoum product in this trial, other types of rodenticides could equally have been used. The use of these needs to be balanced with mitigating the impacts of rodents with the full range of potential costs of using the tool, including non-target impacts or human exposure. Some farmers were also provided with sturdy, plastic kill traps (Kness brand, 'Snap-E' rat traps, manufactured in the USA) to trial an alternative rodent control method. These traps were tied to the jorquette of the cocoa tree in a similar fashion as the bamboo bait stations, and baited with copra. Farmers were asked to check the day after the traps were set.

Pruning of the cocoa trees increases the amount of sunshine in the canopy and allows air flow through the plantation, reducing humidity and the incidence of black pod disease (Acebo-Guerrero *et al*. 2012), and it may also increase predation risk for rats (e.g. snakes, avian predators), thereby reducing damage to cocoa pods. Many cocoa plantations were old (i.e. >30 years), and thus were very tall (i.e. up to 10 m high). It is difficult for farmers to safely harvest cocoa pods high up in these trees, and these pods are effectively accessible only to rats and bats. Although farmers were advised to prune very tall trees, their access to chainsaws to undertake this heavy pruning was limited.

Over the course of the 4-year project, follow-up training was provided and additional farmer groups were trained. In total, there were 14 groups involved, 23 training events and 247 farmers trained. There were two groups on Epi Island, 11 groups on Malekula Island and one group on Efate Island. Some groups ceased operating because of a range of issues (too difficult to fill out diary, poor coordination, ongoing support not maintained). Through observations and general discussions with farmers, we found the following:

- Many farmers saw the benefit of the 'Plot 3' intensive-level management. About half of the farmers expanded their trial plot to their entire plantation of cocoa trees, whereas others did not.
- Farmers reported an increase in yield from one or two bags of green beans (undried fresh cocoa beans) to three or five bags of green beans (effectively a ×2 increase in yield), and were very happy with the increase in yield.
- Farmers confirmed that there was extra effort in undertaking the pruning and weeding, but could see the benefit in terms of increased yields. One farmer commented that yield did not increase until the following harvest season, because it takes time for the tree to produce more pods.
- Cocoa was not the only crop farmers were growing. They also grew coconut for copra, kava, plus other fruits and vegetables. Depending on the fluctuations in prices they receive, farmers switch emphasis from one crop to another.
- Farmers liked using rat poison and wanted more, because they could easily set the bait in bamboo tubes in the jorquette of the cocoa tree, whereas rat traps required more time to set and then check the following day.
- Overall, light pruning (using pruning saws and secateurs) and black pod removal were considered to be highly effective and successful.

A socioeconomic household survey conducted by Martyn (2015) showed that yields increased from 21.4 kg in Plot 1, to

32.3 kg for Plot 2 (150% of Plot 1) to 51.1 kg in Plot 3 (238% of Plot 1). However, more labour was required, with the average wage rate increasing from 292 Vatu h^{-1} for Plot 1, to 318 Vatu h^{-1} for Plot 2 (109% of Plot 1) to 440 Vatu h^{-1} for Plot 3 (150% of Plot 1; Martyn 2015). This demonstrated that more effort was involved in undertaking the management for Plot 3, but returns to labour increased by 150% in Plot 3 compared with Plot 1. Unfortunately, of 72 households participating in the trial, only 26 forms were filled out, of which 13 could be used in the analysis (Martyn 2015).

Phase 2: rodent-management trial

On the basis of the experience gained with the small plots in Phase 1, a larger replicated rodent-management trial was undertaken with four cocoa growers in September 2014, which ran for 4 months to experimentally test the effects of rodent management on the number of healthy pods over time. Each grower randomly identified three areas of cocoa trees, with the following treatments applied:

(a) 'Control' plot: no pruning, no weeding, no rat poison, but with current management,
(b) 'Treatment 1' plot: apply physical management only by using pruning and weeding, and
(c) 'Treatment 2' plot: apply rat bait in bait stations, pruning, weeding, and other physical management. There were 16 rodenticide baits stations set up (4 × 4 grid of bait stations every fifth tree on every fifth row) and monitored and replenished each week if baits had been removed.

Each block was at least an area of 20 × 20 trees (400 trees covering an area of ~0.36 ha) separated by at least 100 m to minimise rodent movements between blocks. The trial was coordinated by one of the growers. All the pods on the central 30 trees near the middle of the block were counted once a month (on the 21st day of the month) and recorded in a note book for

(a) undamaged (healthy) pods per tree (that were left on trees),
(b) rodent-damaged pods per tree (counted and removed),
(c) pods affected by black pod disease per tree (counted and removed), and
(d) number of healthy pods harvested by the grower.

There was a substantial reduction in black pods and rat pods as a consequence of the treatments (Fig. 3). The number of healthy pods harvested over the 3 months from October to December almost doubled on Treatment-1 sites, compared with Control sites (91% increase from 262 pods to 500 pods; Table 4). By contrast, there was only a marginal increase in the number of healthy pods on Treatment-2 sites compared with Control sites (8% increase from 262 to 284 pods). The number of rat-damaged pods decreased dramatically from >4000 pods to four pods in Treatment 1 (99.9% decrease) and to one pod in Treatment 2 (99.9% decrease). The number of black pods decreased dramatically from >14 000 pods to 176 pods in Treatment 1 (98.8% decrease) and to 215 pods in Treatment 2 (98.6% decrease). This clearly shows that a moderate level of rodent management can have a marked impact on rat damage and black pods, leading to increases in the number of healthy pods, although a substantial increase would occur several months after implementation of management because it takes time for the pods to develop.

The number of baits that needed to be replenished declined from 16 at the commencement in 23 September 2015 to 11.25 on 12 November (52 days after implementation; Fig. 4). Therefore, there was evidence that rodents were consuming the baits, but there were progressively fewer rodents to take the baits, thus demonstrating a smaller population size.

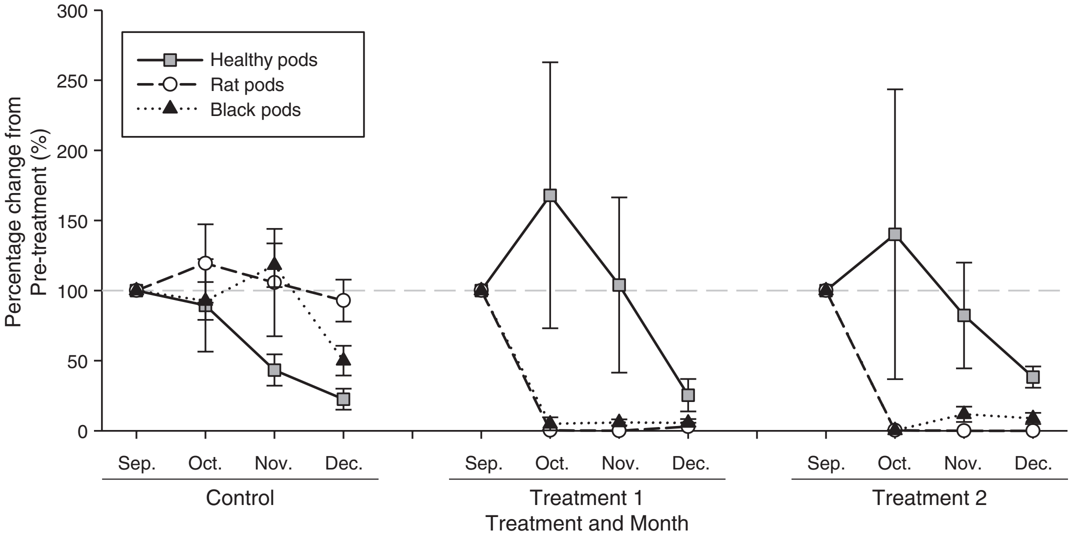

Fig. 3. Relative change in the percentage of healthy pods, rat-damaged pods and black pods counted over 4 months on Control (no treatment), Treatment-1 (pruning and weeding only) and Treatment-2 (rodenticide baits stations, pruning, weeding and other physical management) sites from 30 trees from the centre of each block. All pods were counted and removed from cocoa trees at the time of counting. Treatments were applied in September and counts occurred on the 21st of each month.

Table 4. Mean number (±standard error) of new healthy pods, new rat-damaged pods and new black pods per tree per month across the four replicates, total pods from all sites over 3 months (October–December) and percentage change compared with control sites

Treatments were Control (no treatment), Treatment 1 (pruning and weeding only) and Treatment 2 (rodenticide baits stations, pruning, weeding and other physical management). Counts were conducted on 30 trees per plot. Only post-treatment data are presented (counts from September were excluded)

Treatment	Healthy pods			Rat-damaged pods			Black pods		
	Pods/tree	Total pods	%Change	Pods/tree	Total pods	%Change	Pods/tree	Total pods	%Change
Control	0.24 ± 0.06	262		3.79 ± 0.74	4088		13.74 ± 0.50	14 839	
Treatment 1	0.46 ± 0.16	500	+90.8	0.00 ± 0.00	4	–99.9	0.16 ± 0.05	176	–98.8
Treatment 2	0.26 ± 0.09	284	+8.4	0.00 ± 0.00	1	–99.9	0.20 ± 0.04	215	–98.6

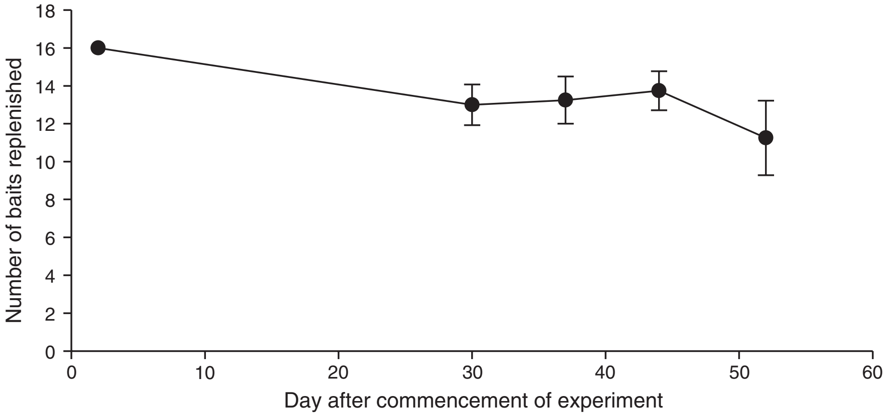

Fig. 4. Number of rodenticide baits replenished on Treatment-2 sites ($n = 4$) for 16 bait stations per plot after implementation of rodent management trial on 23 September 2014. Baits were replenished 2 days, 30 days, 37 days, 44 and 52 days after implementation.

Key findings

These small-scale interventions for managing rats and black pod disease in cocoa plantations in Vanuatu showed benefits within a few months (Treatment 1). Pruning, weeding and removal of black pods appeared to be sufficient to reduce the overall level of rodent damage and the incidence of black pods and led to an increase in healthy (harvestable) pods. The black pod removal and pruning was designed specifically for the management of black pod disease, and it had an additional benefit for managing rodent damage. The use of rodenticides was not necessary to achieve an increase in production. Farmers liked using rodenticides, but it was provided for farmers to trial only through this project, and there were no ongoing plans to provide more. Rodenticides were available in hardware stores and agricultural supply stores in Port Vila (Vanuatu's capital), but they were prohibitively expensive (11 500 vatu, or ~US$150) for a 10-kg bucket and were not available in remote islands or other communities; so, the likelihood of a sustainable baiting program was very low. We trialled the use of sturdy, plastic kill traps (Kness brand, 'Snap-E' rat traps); however, the farmers complained they required too much work. They might be a good method for controlling rodents in houses and villages, similar to the program used in Mozambique, Bangladesh and Myanmar (Belmain *et al.* 2003, 2015).

Discussion

It is clear that rodents are a widespread and significant pest for the Pacific Island region. There is some information available, but there are many gaps in knowledge. We have outlined findings from some recent work through a case-study approach, but these case-studies are few and far between. We now reflect on what needs to be done in the future.

Requirements for developing EBRM for the Pacific Island region

We have outlined key principles and attributes of successful Ecologically Based Rodent Management (EBRM), as found from experiences in Southeast Asia (Table 5). The work conducted in Southeast Asia on the management of ricefield rats, principally in Vietnam and Indonesia, has clearly demonstrated that EBRM is achievable, as independently reviewed by John (2014). The six key principles were modified from those originally coined by Singleton (1997), but it is clear that the work conducted in Southeast Asia meets all the criteria. However, it has taken 10–15 years to reach this point, indicating that the effort involved in gaining this level of knowledge for another region, such as the South Pacific, should not be underestimated. We also take the opportunity to reflect on what we consider as 'attributes' of successful EBRM; that is, what are the preconditions necessary to enable the key principles to be adequately developed and assessed. In terms of the Pacific region, the two main priorities from this exercise are that (1) there needs to be long-term studies of key rodent pests established in key agricultural systems, along with (2) training and support of rodent ecologists within the region. Without these, any efforts to develop effective rodent management will not be successful.

Table 5. Key principles and attributes of ecologically based rodent management (EBRM) for the Pacific island region compared with Southeast Asia
Southeast Asia data are based on Singleton (1997), Singleton and Brown (1999), Singleton *et al*. (1999), Brown *et al*. (2006) and Jacob *et al*. (2010)

Parameter	Southeast Asia (rats in ricefields of Vietnam and Indonesia)	Pacific island region
Principles of EBRM		
(1) The management actions are environmentally sound.	**Yes**. Combination of community trap-barrier system, field sanitation before maximum tillering, reduce bund size, synchronise planting and harvesting, destroy rat burrows, conduct community rat campaigns at key times successful for management rats in ricefields in Vietnam and Indonesia.	**No**. Appropriate management actions not determined yet.
(2) They are cost effective.	**Yes**. Beneficial benefit : cost ratios determined.	**No.** Cost of management not established yet.
(3) The actions are sustainable.	**Yes**. Integrated into government policy.	**No.** Sustainability of management not known.
(4) They are applied at a large scale.	**Yes**. Applied at the community scale; management units >100 ha.	**No.** The scale of application is unknown, but because of the dispersed nature of food production in garden plots it will be difficult establishing 'community' scale management units.
(5) They are politically advantageous.	**Yes**. Integrated into government policy.	**No.** Not known.
(6) They are socially acceptable.	**Yes.** Farmers see the benefit of working together to reduce rat problems.	**No.** Not known.
Attributes of successful EBRM		
Understanding of the taxonomy, biology and ecology (behaviour and life-history characteristics) of the pest species within the agricultural system.	Good understanding of *R. argentiventer* and other species in Vietnam and Indonesia through long-term studies.	Species causing problems are well known, but there is little understanding of biology and ecology of *R. rattus* or *R. exulans* in agricultural situations in Pacific island. **This is a high priority.**
Monitoring systems to determine thresholds for management (linked to socioeconomic thresholds).	Rodent populations and damage monitored routinely.	No monitoring conducted. Little known about thresholds.
Practicing rodent biologists in the region?	Rodent ecologists employed by research and extension agencies.	Some training of individuals in the past, but no extant rodent ecologists in government agencies. **This is a high priority.**
Experimental field studies used to evaluate management strategies and test hypotheses about rodent population dynamics.	Replicated manipulative studies conducted.	Case study presented here, otherwise no studies have been conducted.
Consider a range of management strategies; do not rely on rodenticides alone.	A range of management strategies are recommended and supported by government initiatives.	Little knowledge about successful management techniques available. Rodenticides are expensive, but little knowledge about safe storage or use.

Conclusions and future work

Our aim in the present paper was to reflect on the current situation on islands across the South Pacific and identify the constraints and opportunities for each, their similarities and differences, and identify gaps for further research. We have demonstrated some advancements since the review by Hoque *et al*. (1988), but much more is required. We found that there are many similarities in terms of the rodent taxa across the islands, but there are many differences in the agricultural systems within each country and the extent to which agriculture is important for small-holder livelihoods or for GDP. There is no simple answer, and no 'one-size fits all' approach that can be taken in the South Pacific and PNG. What might work in the context of the management of rodents in cocoa plantations in Vanuatu may not be relevant to the management of rodents for sweet potato production in PNG. There are some broad findings though, that are universal across all islands, and include the following:

1. The rodent pest community is known, but the type and scales of damage to different crops on different islands is unknown.
2. The relationship between the pest species and their food sources, breeding and movements is not known.
3. There are few well trained rodent ecologists actively working in these areas and few well funded research projects. This needs to be supported by a network of practitioners in the Pacific to enable cross-country learning and to provide support at a regional level.
4. The impact of rodent-borne diseases on human health is unknown.

The future priorities for the Pacific Island regions are as follows:

1. Train and support rodent ecologists who can contribute to monitoring and management activities and create a network of practitioners.
2. Design and implement long-term ecological studies to look at rodent population dynamics in key agricultural systems and other habitats, and link this to rodent damage in different situations over time to develop effective management practices.

(3) Undertake a livelihoods and disease study to determine the relative impact of rodents on small-scale farmers in the South Pacific.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Acebo-Guerrero, Y., Hernandez-Rodriguez, A., Heydrich-Perez, M., El Jaziri, M., and Hernandez-Lauzardo, A. N. (2012). Management of black pod rot in cacao (*Theobroma cacao* L.): a review. *Fruits* **67**, 41–48. doi:10.1051/fruits/2011065

Aikhenvald, A., and Stebbins, T. N. (2007). Languages of New Guinea. In 'Vanishing Languages of the Pacific Rim'. (Eds O. Miyaoka, O. Sakiyama, and M. E. Krauss.) pp. 239–266. (Oxford University Press: Oxford, UK)

Aplin, K., and Ford, F. (2013). Murine rodents: late but highly successful invaders. In 'Invasion Biology and Ecological Theory: Insights from a Continent in Transformation'. (Eds H. H. T. Prins and I. J. Gordon.) pp. 196–240. (Cambridge University Press: UK)

Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J., and Singleton, G. R. (2003). 'Field Methods for Rodent Studies in Asia and the Indo-Pacific.' (Australian Centre for International Agricultural Research: Canberra.)

Aplin, K. P., Suzuki, H., Chinen, A. A., Chesser, R. T., ten Have, J., Donnellan, S. C., Austin, J., Frost, A., Gonzalez, J. P., Herbreteau, V., Catzeflis, F., Soubrier, J., Fang, Y.-P., Robins, J., Matisoo-Smith, E., Bastos, A. D. S., Maryanto, I., Sinaga, M. H., Denys, C., Van Den Bussche, R. A., Conroy, C., Rowe, K., and Cooper, A. (2011). Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS One* **6**, e26357. doi:10.1371/journal.pone.0026357

Armitage, P. L. (1994). Unwelcome companions: ancient rats reviewed. *Antiquity* **68**, 231–240. doi:10.1017/S0003598X00046548

Atkinson, U. A. E. (1973). Spread of the ship rat (*Rattus r. rattus* L.) in New Zealand. *Journal of the Royal Society of New Zealand* **3**, 457–472. doi:10.1080/03036758.1973.10421869

Bellwood, P. (1997). 'Prehistory of the Indo-Malaysian Archipelago.' 2nd edn. (University of Hawaii Press: Honolulu, HI.)

Belmain, S. R., Meyer, A. N., Timbrine, R., and Penicela, L. (2003). Managing rodent pests in households and food stores through intensive trapping. In 'Rats, Mice and People: Rodent Biology and Management'. Vol. ACIAR Monograph 96. (Eds G. R. Singleton, L. A. Hinds, C. J. Krebs, and D. M. Spratt.) pp. 440–445. (ACIAR: Canberra.)

Belmain, S. R., Htwe, N. M., Kamal, N. Q., and Singleton, G. R. (2015). Estimating rodent losses to stored rice as a means to assess efficacy of rodent management. *Wildlife Research* **42**, 132–142. doi:10.1071/WR14189

Berlioz-Arthaud, A., Kiedrzynski, T., Singh, N., Yvon, J.-F., Roualen, G., Coudert, C., and Uluiviti, V. (2007). Multicentre survey of incidence and public health impact of leptospirosis in the Western Pacific. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **101**, 714–721. doi:10.1016/j.trstmh.2007.02.022

Bordes, F., Herbreteau, V., Dupuy, S., Chaval, Y., Tran, A., and Morand, S. (2013). The diversity of microparasites of rodents: a comparative analysis that helps in identifying rodent-borne rich habitats in Southeast Asia. *Infection Ecology & Epidemiology* **3**, doi:10.3402/iee.v3i0.2017820178

Brown, P. R., Hung, N. Q., Hung, N. M., and van Wensveen, M. (1999). Population ecology and management of rodent pests in the Mekong River Delta, Vietnam. In 'Ecologically-based Management of Rodent Pests'. Vol. ACIAR Monograph No. 59. (Eds G. R. Singleton, L. A. Hinds, H. Leirs, and Z. Zhang.) pp. 319–337. (Australian Centre for International Agricultural Research: Canberra.)

Brown, P. R., Singleton, G. R., and Sudarmaji, (2001). Habitat use and movements of the rice-field rat, *Rattus argentiventer*, in West Java, Indonesia. *Mammalia* **65**, 151–166. doi:10.1515/mamm.2001.65.2.151

Brown, P. R., Tuan, N. P., Singleton, G. R., Ha, P. T. T., Hoa, P. T., Hue, D. T., Tan, T. Q., Tuat, N. V., Jacob, J., and Muller, W. J. (2006). Ecologically-based management of rodents in the real world: application to a mixed agro-ecosystem in Vietnam. *Ecological Applications* **16**, 2000–2010. doi:10.1890/1051-0761(2006)016[2000:EBMORI]2.0.CO;2

Campbell, J. (2010). An overview of natural hazard planning in the Pacific island region. *Australasian Journal of Disaster and Trauma Studies* **2010-1**, 1–9.

CIA (2014). 'The World Factbook.' (US Central Intelligence Agency.) Available at https://www.cia.gov/library/publications/the-world-factbook. [Accessed 1 October 2014]

Daniel, R., Konam, J. K., Saul-Maora, J. Y., Kamuso, A., Namaliu, Y., Vano, J.-T., Wenani, R., N'nelau, P., Palinrungi, R., and Guest, D. I. (2011). Knowledge through participation: the triumphs and challenges of transferring integrated pest and disease management (IPDM) technology to cocoa farmers in Papua New Guinea. *Food Security* **3**, 65–79. doi:10.1007/s12571-011-0115-6

Denham, T. (2011). Early agriculture and plant domestication in New Guinea and Island Southeast Asia. *Current Anthropology* **52**, S379–S395. doi:10.1086/658682

Dwyer, P. D. (1978). A study of *Rattus exulans* (Peale) (Rodentia: Muridae) in the New Guinea Highlands. *Wildlife Research* **5**, 221–248. doi:10.1071/WR9780221

Dwyer, P. D. (1984). From garden to forest: small rodents and plant succession in Papua New Guinea. *Australian Mammalogy* **7**, 29–36.

Fabre, P. H., Pagès, M., Musser, G. G., Fitriana, Y. S., Fjeldsa, J., Jennings, A., Jonsson, K. A., Kennedy, J., Michaux, J., Semiadi, G., Supriatna, N., and Helgen, K. M. (2013). A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini) and its implication for biogeography and Indo-Pacific Rattini systematics. *Zoological Journal of the Linnean Society* **169**, 408–447. doi:10.1111/zoj.12061

FAOSTAT (2014). 'World-wide Cocoa Production Statistics.' Available at http://www.fao.org/faostat/en/. [Accessed 1 October 2014]

Flannery, T. F. (1995a). 'Mammals of New Guinea.' 2nd edn. (Reed Books: Sydney.)

Flannery, T. F. (1995b). 'Mammals of the South-west Pacific and Moluccan Islands.' (Reed Books: Sydney.)

Gabriel, S. I., Stevens, M. I., da Luz Mathias, M., and Searle, J. B. (2011). Of mice and 'convicts': origin of the Australian house mouse, *Mus musculus*. *PLoS One* **6**(12), e28622. doi:10.1371/journal.pone.0028622

Han, B. A., Schmidt, J. P., Bowden, S. E., and Drake, J. M. (2015). Rodent reservoirs of future zoonotic diseases. *Proceedings of the National Academy of Sciences, USA* **112**, 7039–7044. doi:10.1073/pnas.1501598112

Hanson, L. W., Allen, B. J., Bourke, R. M., and McCarthy, T. J. (2001). 'Papua New Guinea Rural Development Handbook.' (The Australian National University: Canberra.)

Harris, D. B. (2009). Review of negative effects of introduced rodents on small mammals on islands. *Biological Invasions* **11**, 1611–1630. doi:10.1007/s10530-008-9393-0

Hinds, L. A., and Aplin, K. P. (2004). The impacts of mammal pests, particularly rodents, affecting agriculture/livestock production in the

Pacific Region. Scoping study report to ACIAR. CSIRO Sustainable Ecosystems, Canberra.

Holdaway, S. N. (1996). Arrival of rats in New Zealand. *Nature* **384**, 225–226. doi:10.1038/384225b0

Hoque, M. M., Sanchez, F. F., and Benigno, E. A. (1988). Rodent problems in selected countries in Southeast Asia and islands in the Pacific. In 'Rodent Pest Management'. (Ed. I. Prakash.) pp. 85–99. (CRC Press: Boca Raton, FL.)

Howald, G., Donlan, C. J., Galvan, J. P., Russell, J. C., Parkes, J., Samaniego, A., Wang, Y. W., Veitch, D., Genovesi, P., Pascal, M., Saunders, A., and Tershy, B. (2007). Invasive rodent eradication on islands. *Conservation Biology* **21**, 1258–1268. doi:10.1111/j.1523-1739.2007.00755.x

Huan, N. H., Nga, V. T. Q., Brown, P. R., My Phung, N. T., and Singleton, G. R. (2010). Rodent impacts in lowland irrigated intensive rice systems in Vietnam. In 'Rodent Outbreaks: Ecology and Impacts'. (Eds G. R. Singleton, S. R. Belmain, P. R. Brown, and B. Hardy.) pp. 139–152. (International Rice Research Institute: Los Baños, Philippines)

Jacob, J. (2002) Assessment of rodent damage to food crops in the Kingdom of Tonga. Technical report to FAO. 22 p. CSIRO Sustainable Ecosystems, Canberra.

Jacob, J., Sudarmaji, R., Rahmini, S. G., Herawati, N. A., and Brown, P. R. (2010). Ecologically based management of rodents in lowland irrigated rice fields in Indonesia. *Wildlife Research* **37**, 418–427. doi:10.1071/WR10030

John, A. (2014). Rodent outbreaks and rice pre-harvest losses in Southeast Asia. *Food Security* **6**, 249–260. doi:10.1007/s12571-014-0338-4

Johnson, D. H. (1962). Rodents and other Micronesian mammals collected. In 'Pacific Island Rat Ecology: Report of a Study Made on Ponape and Adjacent Islands, 1955–1958. Volume 225 of Bernice P. Bishop Museum Bulletin'. (Ed. I. I. Storer.) pp. 21–38. (Bernice P. Bishop Museum Bulletin: Honolulu, HI.)

Kayser, M., Brauer, S., Weiss, G., Underhill, P. A., Roewer, L., Schiefenhövel, W., and Stoneking, M. (2000). Melanesian origin of Polynesian Y chromosomes. *Current Biology* **10**, 1237–1246. doi:10.1016/S0960-9822(00)00734-X

Kirch, P. V. (1997). 'The Lapita Peoples: Ancestors of the Oceanic World.' (Blackwells: Cambridge, MA.)

Kirch, P. V. (2010). Peopling of the Pacific: a holistic anthropological perspective. *Annual Review of Anthropology* **39**, 131–148. doi:10.1146/annurev.anthro.012809.104936

Kitchener, D. J., Aplin, K. P., and Boeadi, (1991). A new species of *Rattus* from Gunung Mutis, south west Timor Island, Indonesia. *Records of the Western Australian Museum* **15**, 445–465.

Lam, Y. M. (1983). Reproduction in the rice field rat *Rattus argentiventer*. *Malayan Nature Journal* **36**, 249–282.

Macholán, M., Vyskocilova, M. M., Bejcek, V., and Stastny, K. (2012). Mitochondrial DNA sequence variation and evolution of Old World house mice (*Mus musculus*). *Folia Zoologica* **61**, 284–307. doi:10.25225/fozo.v61.i3.a12.2012

Marshall, J. T. (1977). Family Muridae: rats and mice. In 'Mammals of Thailand'. (Eds B. Lekagul, and J. A. McNeely.) pp. 397–487. (Association of Conservation of Wildlife: Bangkok.)

Martin, L. B., Weil, Z. M., and Nelson, R. J. (2008). Seasonal changes in vertebrate immune activity: mediation by physiological trade-offs. *Philosophical Transactions of the Royal Society, London. Series B. Biological Science* **51**, 933–938.

Martyn, T. (2015). The Impact of Customary Inter-Household Transfers on Labour-led Cash Crop Intensification among the Smallholder Farmers of Malekula Island, Vanuatu. PhD thesis, University of Adelaide.

Matisoo-Smith, E., and Robins, J. H. (2004). Origins and dispersals of Pacific peoples: evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences, USA* **101**, 9167–9172. doi:10.1073/pnas.0403120101

Matisoo-Smith, E., and Robins, J. (2009). Mitochondrial DNA evidence for the spread of Pacific rats through Oceania. *Biological Invasions* **11**, 1521–1527. doi:10.1007/s10530-008-9404-1

McFarlane, R., Sleigh, A., and McMichael, T. (2012). Synanthropy of wild mammas as a determinant of emerging infectious diseases in the Asia–Australasian region. *EcoHealth* **9**, 24–35. doi:10.1007/s10393-012-0763-9

Medway, L., and Marshall, A. G. (1975). Terrestrial vertebrates of the New Hebrides: origin and distribution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **272**, 423–465. doi:10.1098/rstb.1975.0096

Meerburg, B. G., Singleton, G. R., and Kijlstra, A. (2009). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology* **35**, 221–270. doi:10.1080/10408410902989837

Mulungu, L. S. (2017). Control of rodent pests in maize cultivation: the case of Africa. In 'Achieving Sustainable Maize Cultivation. Vol. 2'. (Ed. D. Watson.) pp. 317–337. (Burleigh Dodds Scientific Publishing: Cambridge, UK)

Musser, G. G., and Carleton, M. (2005). Superfamily Muroidea. In 'Mammal Species of the World. A Taxonomic and Geographic Reference. Vol. 2'. 3rd edn. (Ed. D. E. Wilson, and D. M. Reeder.) pp. 894–1531. (Johns Hopkins University: Baltimore, MD.)

Nunome, M., Ishimori, C., Aplin, K. P., Tsuchiya, K., Yonekawa, H., Moriwaki, K., and Suzuki, H. (2010). Detection of recombinant haplotypes in wild mice (*Mus musculus*) provides new insights into the origin of Japanese mice. *Molecular Ecology* **19**, 2474–2489.

Ostfeld, R. S., Levi, T., Jolles, A. E., Martin, L. B., Hosseini, P. R., and Keesing, F. (2014). Life history and demographic drivers of reservoir competence for three tick-borne zoonotic pathogens. *PLoS One* **9**, e107387. doi:10.1371/journal.pone.0107387

Park, S. E., Howden, S. M., and Crimp, S. (2012). Informing regional level policy development and actions for increased adaptive capacity in rural livelihoods. *Environmental Science & Policy* **15**, 23–37. doi:10.1016/j.envsci.2011.09.004

Parkes, J., and Murphy, E. (2003). Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology* **30**, 335–359. doi:10.1080/03014223.2003.9518346

Parkes, J. P., Nugent, G., Forsyth, D. M., Byrom, A. E., Pech, R. P., Warburton, B., and Choquenot, D. (2017). Past, present and two potential futures for managing New Zealand's mammalian pests. *New Zealand Journal of Ecology* **41**, 151–161. doi:10.20417/nzjecol.41.1

PCCAPHH (2015). 'Fiji Climate Change and Health Adaptation. Proceedings of the Symposium', 9 February 2015, Suva, Fiji. Piloting Climate Change Adaptation to Protect Human Health Project in Fiji. Available at http://www.health.gov.fj/wp-content/uploads/2017/03/CCHAF-Symposium-Booklet-for-submission_21Aug2015_FINAL.pdf [Accessed 26 January 2018]

Perez, J., and Goarant, C. (2010). Rapid *Leptospira* identification by direct sequencing of the diagnostic PCR products in New Caledonia. *BMC Microbiology* **10**. doi:10.1186/1471-2180-10-325

Robins, J. H., Hingston, M., Matisoo-Smith, E., and Ross, H. (2007). Identifying *Rattus* species using small fragments of mitochondrial DNA: a barcoding approach. *Molecular Ecology Notes* **7**, 717–729. doi:10.1111/j.1471-8286.2007.01752.x

Rowe, K. C., Reno, M. L., Richmond, D. M., Adkins, R. M., and Steppan, S. J. (2008). Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the old endemic rodents (Muroidea: Murinae). *Molecular Phylogenetics and Evolution* **47**, 84–101. doi:10.1016/j.ympev.2008.01.001

Rowe, K. C., Aplin, K. P., Baverstock, P. R., and Moritz, C. (2011). Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Systematic Biology* **60**, 188–203. doi:10.1093/sysbio/syq092

Ruffino, L., Zarzoso-Lacoste, D., and Vidal, E. (2015). Assessment of invasive rodent impacts on island avifauna: methods, limitations and the way forward. *Wildlife Research* **42**, 185–195. doi:10.1071/WR15047

Russell, J. C., and Broome, K. G. (2016). Fifty years of rodent eradications in New Zealand: another decade of advances. *New Zealand Journal of Ecology* **40**, 197–204. doi:10.20417/nzjecol.40.22

Searle, J. B., Jamieson, P. M., Gündüz, I., Stevens, M. I., Jones, E. P., Gemmill, C. E. C., and King, C. M. (2009). The diverse origins of New Zealand house mice. *Proceedings. Biological Sciences* **276**, 209–217. doi:10.1098/rspb.2008.0959

Singleton, G. R. (1997). Integrated management of rodents: a Southeast Asian and Australian perspective. *Belgian Journal of Zoology* **127**, 157–169.

Singleton, G. R., and Brown, P. R. (1999). Management of mouse plagues in Australia: integration of population ecology, bio-control and best farm practice. In 'Advances in Vertebrate Pest Management'. (Eds D. P. Cowan and C. J. Feare.) pp. 189–203. (Filander-Verlag: Berlin.)

Singleton, G. R., Leirs, H., Hinds, L. A., and Zhang, Z. (1999). Ecologically-based management of rodent pests: re-evaluating our approach to an old problem. In 'Ecologically-based Management of Rodent Pests'. ACIAR Monograph No. 59. (Eds G. R. Singleton, L. A. Hinds, H, Leirs, and Z. Zhang.) pp. 17–29. (Australian Centre for International Agricultural Research: Canberra.)

Singleton, G. R., Brown, P. R., and Jacob, J. (2004). Ecologically-based rodent management; its effectiveness in cropping systems in South-east Asia. *Netherlands Journal of Agricultural Science* **52**, 163–171.

Singleton, G. R., Belmain, S. R., Brown, P. R., Aplin, K. P., and Htwe, N. M. (2010). Impacts of rodent outbreaks on food security in Asia. *Wildlife Research* **37**, 355–359. doi:10.1071/WR10084

Spriggs, M. (1997). 'The Island Melanesians.' (Blackwell Publishers: Cambridge, MA.)

Stinson, D. W. (1994). Birds and mammals recorded from the Mariana Islands. *Natural History Research Special Issue* **1**, 333–344.

Sudarmaji, S. G. R., Brown, P. R., Jacob, J., and Herawati, N. A. (2010). Rodent impacts in lowland irrigated intensive rice systems in West Java, Indonesia. In 'Rodent Outbreaks: Ecology and Impacts'. (Eds G. R. Singleton, S. R. Belmain, P. R. Brown, and B. Hardy.) pp. 115–127. (International Rice Research Institute: Los Baños, Philippines.)

Summerhayes, G. R., Leavesley, M., and Fairbairn, A. (2009). Impact of human colonization on the landscape: a view from the western Pacific. *Pacific Science* **63**, 725–745. doi:10.2984/049.063.0412

Suzuki, H., Nunome, M., Kinoshita, G., Aplin, K. P., Vogel, P., Kryukov, A. P., Jin, M.-L., Han, S.-H., Maryanto, I., Tsuchiya, K., Ikeda, H., Shiroishi, T., Yonekawa, H., and Moriwaki, K. (2013). Evolutionary and dispersal history of Eurasian house mice *Mus musculus* clarified by more extensive geographic sampling of mitochondrial DNA. *Heredity* **111**, 375–390. doi:10.1038/hdy.2013.60

Swanepoel, L. H., Swanepoel, C. M., Brown, P. R., Eiseb, S. J., Goodman, S. M., Keith, M., Kirsten, F., Leirs, H., Mahlaba, T. A. M., Makundi, R. H, Melabane, P., von Maltitz, E. F., Massawe, A. W., Monadjem, A., Mulungu, L. S., Singleton, G. R., Taylor, P. J., Soarimalala, V., and Belmain, S. R. (2017). A systematic review of rodent pest research in Afro-Malagasy small-holder farming systems: are we asking the right questions? *PLoS One* **12**, e0174554. doi:10.1371/journal.pone.0174554

Tahana, Y. (2010). Rare rats off the hook as DoC gives them island sanctuary. New Zealand Herald 3 June 2010. Available at http://www.nzherald.co.nz/environment/news/article.cfm?c_id=39&objectid=10649358. [Accessed 5 June 2017]

Tamarin, R. H., and Malecha, S. R. (1971). The population biology of Hawaiian rodents: demographic parameters. *Ecology* **52**, 383–394. doi:10.2307/1937622

Tamarin, R. H., and Malecha, S. R. (1972). Reproductive parameters in *Rattus rattus* and *Rattus exulans* of Hawaii, 1968 to 1970. *Journal of Mammalogy* **53**, 513–528. doi:10.2307/1379041

Tate, G. H. H. (1935). Rodents of the genera *Rattus* and *Mus* from the Pacific Islands, collected by the Whitney South Sea Expedition, with a discussion of the origin and races of the Pacific Island Rat. *Bulletin of the American Museum of Natural History* **68**, 145–178.

Taylor, J. M., Calaby, J. H., and van Deusen, H. M. (1982). A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinean region. *Bulletin of the American Museum of Natural History* **173**, 177–336.

Theuerkauf, J., Perez, J., Taugamoa, A., Niutoua, I., Labrousse, D., Gula, R., Bogdanowicz, W., Jourdan, H., and Goarant, C. (2013). Leptospirosis risk increases with changes in species composition of rat populations. *Naturwissenschaften* **100**, 385–388. doi:10.1007/s00114-013-1033-6

Thomson, V., Aplin, K. P., Cooper, A., Hisheh, S., Suzuki, H., Maryanto, I., Yap, G., and Donnellan, S. C. (2014). Molecular genetic evidence for the place of origin of the Pacific rat, *Rattus exulans*. *PLoS One* **9**, e91356. doi:10.1371/journal.pone.0091356

Timm, R. M., Weijola, V., Aplin, K. P., Donnellan, S. C., Flannery, T. F., Thomson, V., and Pine, R. H. (2016). A new species of *Rattus* (Rodentia: Muridae) from Manus Island, Papua New Guinea. *Journal of Mammalogy* **97**, 861–878. doi:10.1093/jmammal/gyw034

Tomich, P. Q. (1986). 'Mammals in Hawaii: a Synopsis and Notational Bibliography. 2nd edn. Volume 76 of Bernice P. Bishop Museum Bulletin.' (Bernice P. Bishop Museum Bulletin: Honolulu, Hawaii.)

Towns, D. R., West, C. J., and Broome, K. G. (2013). Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: an historical perspective. *Wildlife Research* **40**, 94–107. doi:10.1071/WR12064

Tristiani, H., Priyono, J., and Murakami, O. (1998). Seasonal changes in the population density and reproduction of the ricefield rat, *Rattus argentiventer* (Rodentia: Muridae), in West Java. *Mammalia* **62**, 227–239. doi:10.1515/mamm.1998.62.2.227

Tubiana, S., Mikulski, M., Becam, J., Lacassin, F., Lefèvre, P., Gourinat, A., Goarant, C., and D'Ortenzio, E. (2013). Risk factors and predictors of severe Leptospirosis in New Caledonia. *PLoS Neglected Tropical Diseases* **7**, e1991. doi:10.1371/journal.pntd.0001991

White, J. P., Clark, G., and Bedford, S. (2000). Distribution, present and past, of *Rattus praetor* in the Pacific and its implications. *Pacific Science* **54**, 105–117.

Wickler, S. (2004). Modelling colonisation and migration from a zooarchaeological perspective. In 'Colonisation, Migration, and Marginal Areas: a Zooarchaeological Approach'. (Eds M. Mondini, S. Munoz, and S. Wickler.) pp. 28–41. (Oxbow Books: Oxford, UK.)

Wilkinson, I. S., and Priddel, D. (2011). Rodent eradication on Lord Howe Island: challenges posed by people, livestock, and threatened endemics. In 'Island Invasives: Eradication and Management. Vol. 42'. (Eds C. R. Veitch, M. N. Clout, and D. R. Towns.) pp. 508–514. (IUCN: Gland, Switzerland.)

Wirtz, W. O. (1973). Growth and development of *Rattus exulans*. *Journal of Mammalogy* **54**, 189–202. doi:10.2307/1378879

Yosida, T. H. (1980). 'Cytogenetics of the Black Rat.' (University of Tokyo Press: Tokyo.)