SPECIAL ISSUE

CSIRO PUBLISHING

Pacific Conservation Biology
http://dx.doi.org/10.1071/PC14931

Disappearing jewels: an urgent need for conservation of Fiji's partulid tree snail fauna

Gilianne Brodie[A,E], *Gary M. Barker*[B], *Helen Pippard*[C], *Cindy S. Bick*[D] *and Diarmaid Ó Foighil*[D]

[A]School of Biological and Chemical Sciences, University of the South Pacific, Suva, Fiji Islands.
[B]Landcare Research, Private Bag 3127, Hamilton, New Zealand.
[C]Species Program, IUCN Oceania Office, Suva, Fiji Islands.
[D]Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA.
[E]Corresponding author. Email: gilianne.brodie@usp.ac.fj

Abstract. Where conservation status of island non-marine molluscs is known, snails tend to be one of the most threatened faunal groups. However, published information regarding island gastropod conservation status, diversity and endemism is frequently unavailable despite the importance of this information for the formulation of biodiversity action plans and conservation strategy. Fiji, for example, has a diverse native land snail fauna (>240 species) with an endemism level of ~80%, but only within the last few years has any information about any of these species been available to the national biodiversity reporting repository. For one lineage in particular, members of the tree snail family Partulidae, with four endemic Fiji Island species, the conservation status of the group has never been assessed. However, based on the alarming extinction rates documented in partulid snail species on other Pacific Islands, information about the occurrence and status of these taxa is urgently needed for Fiji's biodiversity action plan. To redress this information void, we formulated the Fijian Partulid Tree Snail Project, consisting of five components: (1) raising awareness; (2) locating populations and monitoring population trends; (3) elucidating patterns of genetic diversity; (4) creating action partnerships; and (5) conducting disturbance gradient analyses. The overall goal was to characterise mechanisms leading to persistence of partulids in the face of increasing anthropogenic disturbance. In the initial stages of this project, existing information on Fiji's partulids was collated and two small, remote islands in the Fiji archipelago were surveyed to investigate whether tree snails persisted there. Living populations of *Partula lanceolata* and empty shells of *Partula leefei* were found on Cicia Island in Lau, and on Rotuma Island in the Rotuma Group, respectively. DNA analyses confirm a sister relationship between the two *Partula* species in north-eastern Lau, *P. lirata* and *P. lanceolata*, with both sharing a sister relationship with a member of the same genus in Vanuatu – *P. auraniana* Hartman, 1888. Prioritisation and further sampling of additional islands, and residual native habitat on less accessible islands and islets, is needed to fully assess the conservation status of all four Fijian species via the IUCN Red List process. Moreover, the basic descriptive information and associated studies reported here will serve to raise awareness of Fiji's endemic tree snails particularly in communities that had no prior knowledge of their special conservation status; and also at a wider national, regional and global level. Community awareness is particularly vital as the willing support of land owners in the relevant small island communities is critical to implementing any future conservation action plans.

Additional keywords: endemic, island, invasive, invertebrate, threatened species.

Received 21 October 2015, accepted 22 March 2016, published online 17 June 2016

Introduction

Land snails, and their freshwater gastropod and bivalve counterparts, have the highest recorded modern extinctions of all animal groups, and many remaining species are in serious decline (Lydeard *et al.* 2004). Decline in land snails has been particularly pronounced in species endemic to oceanic islands, not least in the islands of the Pacific (e.g. Solem 1976; Hadfield 1986; Cowie 1992; Hopper and Smith 1992; Coppois 1995; Bouchet 1998; Preece 1998; Abdou and Bouchet 2000; Neuweger *et al.* 2001; Bouchet and Abdou 2001, 2003; Boyko and Cordeiro 2001; Coote and Loève 2003; Murray and Clarke 1984; Coote 2007; Murray *et al.* 1988; Chiba *et al.* 2009; Kirch *et al.* 2009; Brook 2010; Brook *et al.* 2010; Chiba and Roy 2011; Richling and Bouchet 2013; Sartori *et al.* 2013, 2014). The causes of decline are anthropogenic, but often poorly understood as there have been few attempts to evaluate either the

range of plausible anthropogenic drivers, or the interactions and synergies among these drivers in oceanic island systems. The demise of the Polynesian Partulidae has received considerable attention in the scientific literature, with the critical role of introduced biological control agents such as rosy wolf snail [*Euglandina rosea* (Férrusac, 1821)] implicated in the precipitous extinction of island faunas in near entirety (Coote and Loève 2003; Clarke *et al.* 1984; Coote 2007; Lee *et al.* 2007a; Murray *et al.* 1988). It is unclear if the decline in Polynesian Partulidae, considered to result from the rosy wolf snail, was also codependent on additional anthropogenic factors. Introduced predators rarely act alone in causing decline in native species, and there are often interactions between habitat loss and modification with invasive species (e.g. Chiba and Roy 2011; Norbury *et al.* 2013). These interactions complicate the distinction between the proximate versus ultimate causes of population decline (Didham *et al.* 2007). Elsewhere in the Pacific, decline in Partulidae has also been of concern, but the loss rate has been less dramatic than that in Polynesia where decline was associated with the introduction of the rosy wolf snail and other predatory snails (e.g. Cowie and Cook 2001; Lee *et al.* 2008). In at least some regions, partulid extinction was initiated in the Holocene (Bauman and Kerr 2013), as has been the case in several other land snail families. A significant component of extinction in island faunas can be attributed to habitat loss and degradation associated with human land-use (Hadfield 1986; Coppois 1995; Preece 1998; Lydeard *et al.* 2004; Chiba *et al.* 2009), often spanning several centuries. Furthermore, it is not unreasonable to expect pressures on native species to vary spatially depending on evolutionary history, and past and present ecological contexts (Balmford 1996; Chiba *et al.* 2009; Chiba and Roy 2011; Lee *et al.* 2014). Therefore it is likely that both the extent of decline in partulid land snails and the drivers of decline will vary among and within Pacific island archipelagos, a hypothesis that needs to be tested in the future.

Of greatest concern is that extinctions in Pacific island land snails are ongoing in residual indigenous forests (e.g. Brook 2010; Brook *et al.* 2010), and thus diminish the value of montane areas, which are considered important biodiversity refugia in island systems otherwise heavily impacted by human activities (Olson and Dinerstein 1998; Allison and Eldredge 1999; Olson *et al.* 2010; Schmitt *et al.* 2009; Woinarski 2010).

Partulids collectively range over 10 000 km^2 in the Pacific, from Palau and the Marianas in the north-west to the Marquesas, Austral and Society Islands in the south-east (Lee *et al.* 2014). Apart from a single Papua New Guinean record of anthropogenic origin (Ó Foighil *et al.* 2011), partulids do not extend into continental habitats, and lack a fossil record. Most species are endemic to single islands and the only known partulids with multiarchipelago distributions represent prehistoric anthropogenic introductions (Lee *et al.* 2007*a*, 2007*b*; Ó Foighil *et al.* 2011).

Assessment of the conservation status of partulid species across the region, based on IUCN Red List criteria, is available for 107 (82%) of the estimated 130 species in the family (Table 1), and from 10 (77%) of the 13 partulid-occupied island archipelagos, indicating an incomplete understanding of vulnerability and spatial structure of extinction risk in the family. Furthermore, several assessments are outdated. Nonetheless, the highly threatened status of partulids is clear, with almost 50% of the assessed species (52 of 107) considered 'Extinct' and an additional 35% (37 of 107) either 'Extinct in the Wild' or 'Critically Endangered' (Table 1). Species documented as extinct are represented across much of the geographic range of the family, but with a predominance in French Polynesian Society Islands which is the hotspot of partulid diversity. Several of the eleven species assessed as 'Extinct in the Wild' are held in captive breeding programs or reintroduction sites, where they are protected from the threats that caused their demise in the first place (Coote *et al.* 2004).

Table 1. Comparison of the conservation status of members of the land snail family Partulidae across different Pacific regions
Data are from the IUCN Red List (IUCN 2014)

Island archipelagos	No. of species assessed in IUCN Red List categories							Total no. of species assessed
	Extinct	Extinct in the wild	Critically endangered	Endangered	Vulnerable	Least concern	Data deficient	
Samoa	–	–	2	3	–	–	–	5
Society Islands, Morea and Austral Islands	51	11	12	1	2	–	3	80
Federated States of Micronesia	–	–	3	–	–	–	–	3
Guam and Northern Mariana Islands	1	–	4	–	–	–	–	5
Palau	–	–	2	1	–	–	–	3
Admirality and Bismarck Islands	–	–	–	–	–	–	3	3
Solomon Islands	–	–	–	–	–	1[A]	2	3
Tonga	–	–	2	–	–	–	–	2
Vanuatu	–	–	1	1	–	–	–	2
Wallis and Futuna	–	–	1	–	–	–	–	1
Total	52	11	27	6	2	1	8	107

[A]Species also occurs in eastern PNG as an anthropogenic adventive.

Four endemic members of the land snail family Partulidae occur in the Fijian archipelago – three species of *Partula* Férussac, 1821 and a single species of *Samoana* Pilsbry, 1909 (Table 2). The conservation status of these four species has never been assessed using the IUCN Red List criteria nor included in Fiji's national conservation policy statements. They have, however, been included in 2014 in at least one official national document for protection.

Until the current study, available evidence indicated that *Partula lanceolata* Cooke & Crampton, 1930 was a single-island endemic, having been recorded only from the island of Mago in Lau. *P. lanceolata* was recorded as plentiful at the type locality surveyed by E. H. Bryan during a visit by the Whitney Expedition in 1924 (Evenhuis 2007). *Partula leefei* E. A. Smith, 1897 is restricted to the isolated far northern Rotuma Group (Fig. 1*a*), with records from the main island of Rotuma and the small offshore islet of Uea. The species was plentiful during a survey by H. St John and colleagues in 1938, on behalf of the Bernice P. Bishop Museum, Hawaii (see Brodie *et al.* 2012). The third Fijian *Partula* species, *Partula lirata* Mousson, 1865 has previously been found to be widely distributed in Lau, with records from 12 islands (Table 2) and extending to the coastal eastern areas of Taveuni (Fig. 1*b*). The species was found to be abundant on various islands during the Whitney Expedition in 1924 and in Bishop Museum surveys in 1934. More recently, L. Price collecting in 1970 for the Field Museum, Chicago (pers. comm.) and P. Bouchet in 1999 for the Museum National d'Historie Naturelle, Paris (pers. comm.) found the species persisting in numbers on Vanua Balavu and Cikobia-i-Lau, respectively. The population in Taveuni has not been recorded as sighted for over a century.

The fourth Fijian partulid species, *Samoana alabastrina* (Pfeiffer, 1856) has been reported from three islands of the Moala Group (Moala, Matuku and Totoya) in south-western Lau (Fig. 1*a* and *b*). The species was found to be abundant at various sites visited by the Whitney Expedition in 1924 and the Bishop Museum survey in 1938. The most recent record of the species is by L. Price collecting for the Field Museum, Chicago, in 1970, with modest numbers of live snails found at a site on the island of Moala.

These data indicate that partulids had persisted at least well into the 20th century in Fiji despite a long history of human occupation in the archipelago and thus the pattern of partulid extinction so prevalent elsewhere in the Pacific may not hold for Fiji. To date, Fiji has been free of the giant African snail [*Lissachatina fulica* (Bowdich, 1822)] and the associated risks of introduction of the rosy wolf snail and other predatory snails. However, Fiji has not been without ongoing pressures from a growing human population, increasing interisland trade and tourism, changes in land-use, and the establishment of various invasive species including the snail predator *Platydemus manokwari* (Brodie *et al.* 2014; Justine *et al.* 2014). Furthermore, for the most part the Fijian partulids have not been adequately documented or surveyed in recent years and thus there is no collated reliable information on their appearance, characteristics or current status that might inform national conservation policy and action plans.

In this paper, we describe our recently initiated project focusing on the Partulidae of Fiji, with the primary objective of creating awareness and advocating conservation policy development and species management strategies. We present data on partulid field surveys in Rotuma and Cicia islands,

Table 2. The four endemic members of the land snail family Partulidae recorded from Fiji, their current IUCN Red List conservation status, known occurrence locations plus the numbers of individual living specimens found in the past

Names in square brackets represent island names as spelt in the relevant report or publication

Species	Current IUCN Red List Status	Recorded islands (no. of locations; no. of specimens collected) before current study	Year last recorded alive before current study	Information sources
Partula lanceolata Cooke & Crampton, 1930	Not assessed	Mago [Mango] (1; ~120)	1924 (Mago)	Cooke and Crampton (1930); Kondo (1955); Barker and Bouchet (2010)
Partula leefei E. A. Smith, 1897	Assessment in progress	Rotuma (11; 545) Uea (1; 6)	1938 (Rotuma, Uea)	Smith (1897); Barker and Bouchet (2010); Brodie *et al.* (2014)
Partula lirata Mousson, 1865	Not assessed	Avea (1; 10) Cicia [Thithia] (1; 11) Cikobia-i-Lau [Thikombia-i-Lau] (1; ~10) Kanacea [Kanathea](1; ~2) Laucala [Lauthala] (1; 1) Mago [Mango] (~4; 85) Munia (2; 22) Nayau [Naiau] (4; 73) Oneata (3; 11) Tavenui (1; 5) Tuvutha [Tuvuca] (2; 2) Vanua Balavu (~15; 675)	1999 (Cikobia-i-Lau)	Mousson (1865); Cooke and Crampton (1930); Pilsbry and Cooke (1934); Kondo (1955); Barker and Bouchet (2010); Lee *et al.* (2014); P. Bouchet (pers. comm., 2006)
Samoana alabastrina (Pfeiffer, 1856)	Not assessed	Matuku (8, 172) Moala (~15, 585) Totoya (3, 202)	1970 (Moala)	Pfeiffer (1856); Barker and Bouchet (2010)

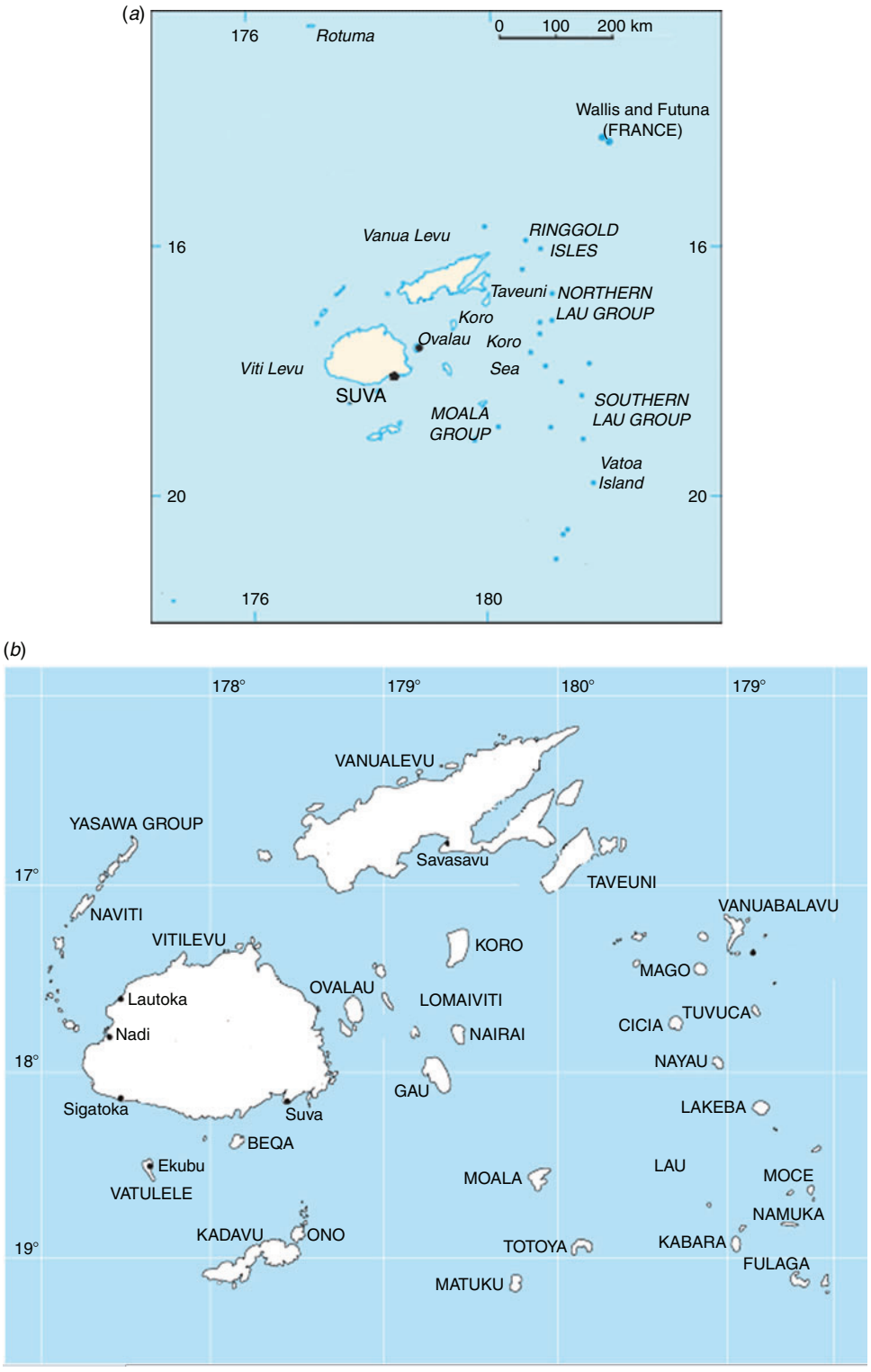

Fig. 1. Maps of the Fiji Islands showing (*a*) the location of Rotuma in the far north of Fiji Group and (*b*) the location of Cicia Island and Moala Island in Fiji's relatively dispersed Lau Island Archipelago.

where we initially focused on the expectation that, because of comparative isolation and freedom from invasive species, partulid land snails may have the greatest opportunities for persistence in the presence of human occupation.

Background of the Fijian Partulid Tree Snail Project

There have been some efforts to establish conservation priorities among Fijian land snail taxa (e.g. Barker *et al.* 2005; Brodie *et al.* 2010) and many Fijian land snail species have recently

been assessed for the first time using the IUCN Red List criteria through support from the Critical Ecosystem Partnership Fund (Pippard 2012; Brodie *et al.* 2013). The flagship family Partulidae, however, was not included because of a lack of contemporary information – and the four Fijian endemic partulid species have therefore received little recent attention due to lack of local capacity. Nonetheless, as recommended in regional initiatives and national frameworks (i.e. DoE 2007; Pippard 2013) species that were not included in previous IUCN Red List assessments should be included in future research efforts and be of highest priority when threatened status is indicated as likely from experiences in neighbouring regions and when the taxa in question are of unique faunal importance. As outlined in the Introduction, Partulidae are of high conservation priority because species throughout their range in the Pacific are highly endangered by anthropogenic disturbances. In at least some areas within the Fijian archipelago the nature and extent of anthropogenic disturbances has strong parallels with other Pacific regions where partulids are recognised as threatened with extinction. The situation with respect to invasive species and the potential imperilment of the Fijian land snail fauna is considered dynamic (Brodie 2009, 2010; Brodie and Copeland 2010; Brodie and Barker 2011; Brodie *et al.* 2012, 2013), indicating that the four Fijian members of the family may well be in need of conservation management. Nonetheless, the biogeographic setting, cultural history and thus anthropogenic environment are uniquely Fijian, and the need for active conservation intervention, and the urgency for this, cannot be properly determined without field studies specifically directed to Partulidae.

Besides their endemic status, the Fijian partulids are of ecological and evolutionary importance. Within the context of biodiversity patterns within the Fijian archipelago, islands with known partulid members have faunal relationships not primarily with the topographically dominant Viti Levu and Vanua Levu of the Fijian Western Provinces, but with other Pacific regions (Barker *et al.* 2005; G. M. Barker, unpubl. data). Rotuma, with its unique and highly threatened land snail fauna (Brodie *et al.* 2012, 2014), cannot simply be seen as a Melanesian outlier, a point well acknowledged in Fiji's National Biodiversity Strategy Action Plan (DoE 2007). Additionally, the Lau Group, culturally as well as biogeographically, is a meeting point between Polynesia and Melanesia (Nakoro 2013). Such infraregional relationships are critical to conservation plans that seek to ensure adequate representation of biological diversity both in protected natural area networks and across sites being actively managed.

In the context of the entire partulid radiation in the Pacific, Lee *et al.* (2014) point to Fiji as critical to advancing understanding of the evolutionary history of *Partula* and *Samoana* alike, as geographically Fiji lies at the margin of pronounced east–west disjunctions exhibited by these genera. As yet the Fijian members are poorly represented – just one of the four species (i.e. *P. lirata*) having been included in phylogenetic analyses of partulid evolution to date (Lee *et al.* 2014).

As indicated already, earlier faunal inventory surveys of Fiji found that, when present, *Partula* and *Samoana* species were often abundant at sites and certainly dominant in the arboreal community. Nonetheless, their indigenous associations with specific plants or vegetation types, and responses to ingress of invasive understorey plants and predatory animals, remains poorly known.

Materials and methods

Our Fijian Partulid Tree Snail Project has five components as follows:

1. Awareness. Our project targets island communities where the presence of partulid snails are recorded (e.g. Rotuma, Lau Islands) and the Fiji government departments that support them (e.g. Department of Environment; Department of Fisheries and Forests). Until the start of the current project there was poor awareness of the unique nature of Fiji's tree snails, their heritage and scientific value. This, of course, reduces the effectiveness of island natural resource management and that situation needed to be addressed before any future conservation action was considered or undertaken. Optimally, to begin discussions with land owners, communities need to be able to visualise the target species being discussed. However, before the current project no comparative photograph of the appearance of Fiji's partulids was readily available.

Awareness raising also needs to include scientific data in peer-reviewed journals that can be used for decision making (e.g. IUCN Red-list assessment) and then distilled and adapted into more appropriate resource documents for communities and government. Thus multistakeholder awareness via different types of outputs is a vital baseline component of the current project as without it further collaborative conservation research, in partnership with landowners and government, will be ineffective and unsustainable.

2. Locating populations and monitoring population trends. Sampling was conducted at nine locations on Rotuma Island in May 2012, and at 12 locations on Cicia Island in December 2012. In both instances surveys were undertaken to obtain information on the current overall species composition of the land snail faunas (Brodie *et al.* 2012, 2013; 2014). The surveys primarily focussed on documenting the non-native fauna and thus most of the sampling effort was in relatively disturbed sites close to settlements and associated gardens and agricultural areas. Nonetheless, sampling at several locations in Rotuma also extended into residual 'forested' sites to document both the level of persistence in the native land snail fauna and the extent of spread of non-native land snails. On Cicia, several sites were also specifically targeted for Partulidae.

Rotuma Island is the main land mass in the Rotuma Group (12°S, 177°E) that otherwise comprises eight small islets (Uea, Hafliua, Hatana, 'Afgaha, Haf haveiaglolo, Solnoho, Haua ti'u and Solkope). These remnants of a late Quaternary age basaltic volcano total ~43 km^2, located over 600 km north of Fiji's capital city Suva and ~550 km west of its closest neighbour, Futuna Island in the French overseas collectivity of Wallis and Futuna (Fig. 1*a*). Rotuma has been inhabited since Lapitan times (2500–3500 years). The current human population of a little over 1900 people reside primarily along the coast but in former times much of the island was under some form of cultivation. Much of the island vegetation comprises gardens and human-disturbed 'bushland', with coconut trees in abundance. Undisturbed indigenous forest does not remain on Rotuma, but forests and shrub lands of largely indigenous character persist as remnants in less accessible areas, notably on coastal cliffs and

on upland volcanic rubbles (Zimmerman 1943; Stattersfield *et al.* 1998). Previous land snail faunal studies in the Rotuma Group have primarily been limited to that of Smith (1897) (12 native species), H. St John for the Bishop Museum in 1938 (unpublished) (11 native species) and Brodie *et al.* (2014) (13 native species).

Cicia Island lies in the north of Fiji's relatively dispersed Lau Island archipelago (Fig. 1*b*). The island has a land area of less than 35 km^2. The indigenous forest has undergone major decline in area and quality, and is now confined to small relatively hard-to-access coastal headlands, limestone ridges and ravines occupying less than 10% of the island (Barker 2012; G. Brodie, pers. obs.). Previous land snail surveys on Cicia have been limited, with records for four species that include *P. lirata* by L. Price in 1970.

Sampling at all sites was qualitative, but with a similar overall time of ~2 h at each location. Searching was conducted during 'cooler' daylight hours when the normally nocturnal snails were located in their daytime refuges. Since the objective was to locate as many species as possible in the limited time available, sampling effort and method varied slightly depending on the physical complexity of the habitat in the location being searched. Thus samples were primarily obtained by targeted visual searching by hand beneath the leaves of vegetation below eye level, beneath stones, logs and rotting organic debris. However, in the locations where a relatively dense tree canopy and/or understorey vegetation occurred, two line transects 10 m long were used to provide focus to visual searches of the tree trunks and understorey vegetation below eye level. Two directed 1 m × 1 m leaf litter areas were also searched at sites where leaf litter occurred and two directed small rock crevice soil surface samples were taken by trowel on rocky slopes. Partulid species identifications were based on our prior extensive experience with the Fijian land snail fauna and comparison with authoratively identified material (including type specimens) in various collections. All collected vouchers were assigned to species. Voucher specimens are deposited in the reference collections of the University of the South Pacific.

While some inferences about the trends and thus longer-term fate of surviving partulid populations may be made from local density estimates and demographic structure, trends are best established by repeated quantitative censuses. Such data would serve to not only refine initial assessments of conservation status (e.g. under IUCN (2001) Red List criteria A and E), but would also be useful in assessing the impacts of particular threats, and measuring whether conservation actions are succeeding. We therefore propose to establish a network of permanent plots across the Fijian archipelago at which partulids would be periodically censused using the mark–recapture methodology. Mark–recapture provides not only estimates of local densities, but estimates of total population size and demographic data important to understanding population processes that may ultimately be critical to effective conservation management. Individual snails will be marked using nail varnish – this marking method has been shown to be enduring (i.e. limited loss of marks within the time frame of the study) and does not affect the life history of the marked snails (Henry and Jarne 2007; Janks and Barker 2013).

3. Geographic Patterns of Genetic Diversity. Our primary focus is phylogenetic and phylogeographic analyses based on DNA samples from across the range of genus- and species-group taxa to delineate evolutionarily significant units (ESUs), see Holland and Hadfield 2002) and inform conservation plans that seek to ensure adequate representation of Fijian partulid genetic diversity both in protected natural area networks and across sites being actively managed. We are also interested in gaining the ability to detect changes in population genetic structure both along an anthropogenic disturbance gradient and over time at selected monitoring sites.

Our preference for genetic sampling was the use of non-lethal methods of DNA sampling, with pedal mucus fixed on Whatman FTA cards as described by Régnier *et al.* (2011) and biopsies of posterior foot tissue (Thacker and Hadfield 2000). In the field and in the laboratory, mucus samples were obtained. DNA was isolated from a ~5-mm segment of each FTA card using the E.Z.N.A.® Mollusc DNA Kit (Omega Biotech, Norcross, GA) according to the manufacturer's instructions. A 655 nucleotide fragment of Cytochrome Oxidase I (COI) mitochondrial gene was amplified with GoTaq DNA Polymerase (Promega, Madison, WI) using the 'universal' primer pairs LCO1490/HCO2198 (Folmer *et al.* 1994).

The amplification conditions consisted of an initial denaturation temperature of 95°C for 4 min, 40 cycles of denaturation (95°C, 30 s), annealing (45°C for COI, 40 s), extension (72°C, 1 min), and a final extension at 72°C for 10 min. Amplification products were prepared for cycle sequencing by diluting 1 : 5 in sterile water. Sequencing was performed in both directions, using the PCR primers, at the University of Michigan DNA Sequencing Core Facility. The resulting chromatograms were edited by comparing both strands using Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA) and the edited sequences were aligned by eye in CodonCode Aligner 5.1. (CodonCode Corporation, Centerville, MA, USA).

The haplotypes obtained were added to a pre-existing database of homologous mitochondrial COI sequences from 37 congeners sampled across the entire range of the genus (Lee *et al.* 2014). This combined dataset was then subjected to a Bayesian phylogenetic analysis (MrBayes 3.2.1) (Ronquist and Huelsenbeck 2003) with the two Palauan species, *P. thetis* Semper, 1865 and *P. calypso* Semper, 1865, designated as outgroups (Lee *et al.* 2014). The Corrected Akaike information criteria from jModelTest 2 (Darriba *et al.* 2012) selected the HKY+I+G model, including invariant sites (P-inv = 0.5590) and the gamma distribution (1.0960). The Bayesian searches were then run for 5 000 000 generations and trees were sampled every 1000 cycles. A consensus tree was calculated and the posterior probability values were estimated after omitting the first 25% of trees as burn-in using FigTree 1.4.2.

4. Action Partnerships. Ultimately, our project team is open to collaborative partnerships between scientific researchers and relevant stakeholders, with particular focus on potential donors, island communities, local government and non-government organisations and development and implementation of conservation action plans for preservation of remaining populations of endemic Fijian partulid tree snails.

5. Disturbance Gradient Analysis. It is recognised that to determine the current status of partulid populations, ideally all islands within the Fijian archipelago for which there are historical records of partulids should be resurveyed. However,

logistically this is very hard in the short term because of the relative isolation of the islands involved and the need for relationship building in order to obtain multiple land owner permissions. We therefore needed to adopt a stratified sampling and predictive approach. Specifically we sought to rank islands with known partulid records along a gradient of anthropogenic disturbance, and select a maximally representative subsample of these islands for field survey. We then proposed to analyse data gathered on the status of partulid populations in relation to our *a priori* assessment of anthropogenic disturbance to (1) test the relationship between persistence of partulids and level of disturbance, predict status on unsampled islands, and thus estimate status across all partulid species and the entire Fijian archipelago, and (2) examine any residual variation in persistence of partulids that could not be related to our index of anthropogenic disturbance to identify conditions existing on individual islands that were incorrectly coded in our *a priori* identification of the anthropogenic disturbance gradient, or to identify other factors influencing partulids. We acknowledge that such a pilot gradient of anthropogenic disturbance will be an imprecise starting point and a working hypothesis due to spatially variable quality of data, especially for the prehistoric period of human occupation.

Our proposed anthropogenic disturbance gradient will be based on a principal component analysis of six factors that we consider might drive decline in the Partulidae: (1) best estimate of the intensity of prehistoric occupation and land-use, extending three millennia from the Lapita period to European contact in 1774, based on a review of the published literature on extensive but nonetheless spatially incomplete archaeological studies; (2) extent of post-European contact deforestation for exploitative land-uses, especially plantation and other broad-acre forms of agriculture; (3) current human population per square kilometre; (4) current proportion of land area devoted to agricultural and forestry activity; (5) current botanical composition of residual forests, both native and non-native, with extent of replacement by non-indigenous species as an indicator of disturbance; and (6) species richness of invasive animals, such as predatory and herbivorous vertebrates, predatory ants or predatory flatworms. The probable level of local partulid extinction on the *y*-axis would therefore be the best-estimate cumulative impacts in the rather specialist snail arboreal habitat, namely the leafy branches of understorey broadleaf shrubs and low trees, and is based on experience with partulids elsewhere in the Pacific while taking into account the likely persistence of both the host plants and the snails themselves. Placements of islands in respect to both axes will be hypotheses to be tested through further literature review, consultation with archaeologists, geographers, historians and ecologists, and new field studies. Initial results of field surveys for partulids are presented in this paper for the islands of Cicia and Rotuma.

Results

Awareness

We provide for the first time comparative high-resolution pictures of adult shell morphology for the four endemic partulid species endemic to Fiji (Fig. 2). The species are clearly distinguishable on the basis of their shell morphologies; *P. lirata* is very different because of its distinctly elevated spiral lirae (ridges) and *P. leefei* has an oval aperture and blunt rounded apex that contrasts with the other three species (Table 3). The species are further distinguishable when their recorded geographical occurrences are taken into account; for example, the Rotuman endemic *P. leefei* is found over 600 km away from the Lau Island Group, i.e. where the other three species are recorded (Fig. 1*a*; Table 2).

During the initial partulid land snail surveys that have been undertaken in Fiji by the authors it was observed that most members of relevant local communities did not realise their partulid species resources were unique in the world and did not see them as having value. Awareness of the presence of these endemic land snails on surveyed islands was, however, variable (some community members on Cicia knew exactly where to find the snails) and this may relate to snail appearance, history, distribution and abundance. Communities had a comparatively

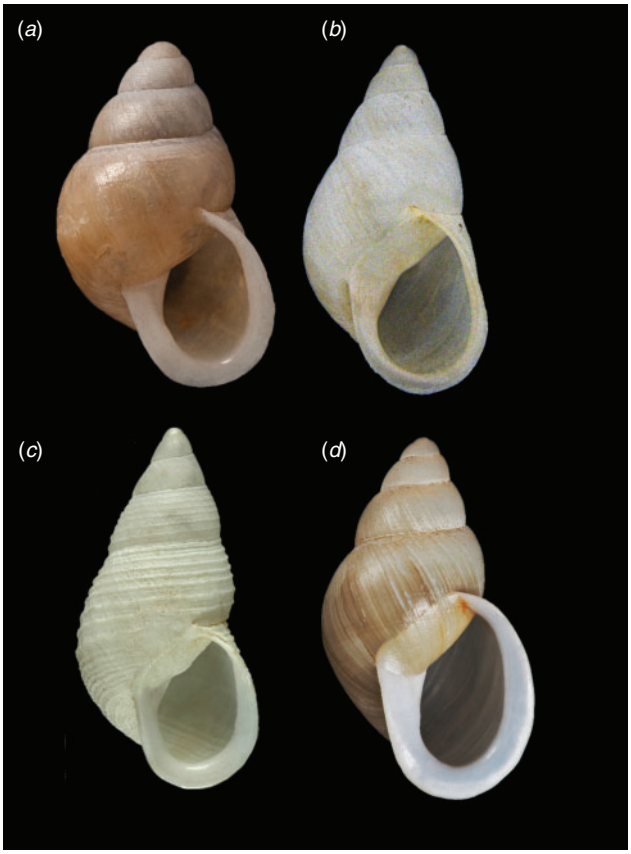

Fig. 2. Comparative photograph of Fijian partulid shells. (*a*) *Partula leefei* E. A. Smith, 1897 (Rotuma: Syntype NHMUK18971896.4.2.35–44 (a)). (*b*) *Partula lanceolata* Cooke & Crampton, 1930 (Mago: Paratype MCZ63766). (*c*) *Partula lirata* Mousson, 1865 (Vanua Mbalavu: Syntype MNHN26716). (*d*) *Samoana alabastrina* (Pfeiffer, 1856) (Moala: Topotype: BPBM77160). The shell dimensions of each species can be found in Table 3. NHMUK = Natural History Museum, London, UK; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNHN = Museum National d'Histoire Naturelle, Paris, France; BPBM = Bernice P. Bishop Museum, Honolulu, HI, USA. Photographs by G.M. Barker (*a*, *b*, *d*) and P. Maestrati (*c*).

Table 3. A comparative table of the adult shell conchological features of the four species of Fijian Partulidae

Feature	*Partula leefei*	*Partula lanceolata*	*Partula lirata*	*Samoana alabastrina*
Apex	Rounded, blunt	Narrowly conic, pointed	Narrowly conic, pointed	Conic, moderately pointed
Number of whorls	5	5.5	5.5	5.5
Whorl periphery	Strongly convex (rounded)	Weakly convex (nearly flat)	Weakly convex (nearly flat)	Distinctly convex (rounded)
Suture	Deep	Shallow, vaguely marginated	Shallow, vaguely marginated	Deep
Teleconch sculpture	Fine spiral striae and fine radial growth striae	Fine spiral and radial growth striae	Elevated, distinct spiral lirae and prominent radial growth striae	Fine spiral striae and fine to prominent radial growth striae
Aperture shape	Oval	Subovate	Subovate	Subovate
Peristome	White, reflected, expanded, forming broad flange	White, reflected, expanded but not broad	White, reflected, expanded but not broad; margin crenulated due to lirae terminating at edge	White, reflected, expanded, forming broad flange
Apertural callus	Distinct to indistinct, transparent, shining	Distinct, shining white	Distinct, shining white	Distinct, shining white to weakly brown
Aperture parietal barrier	Absent	Weak, when present	Prominent to weak when present	Absent
Height (mm)	14	21	21	23
Width {mm)	9	12	11	13
Aperture height : shell height	0.43–0.51	0.50–0.53	0.47–0.53	0.52–0.58
Colour	Periostracum present, brown to greenish yellow, glossy	Periostracum often eroded; brownish to white	Periostracum often eroded, horn brownish or purplish-brown to white	Periostracum present, corneous brown, glossy

stronger interest in the introduced land snail species present in their gardens, as they saw that these may have crop quality, therefore economic, impacts. However, considering the possible historical use of partulid shells in traditional costume, a questionnaire on community knowledge of land snails, with an emphasis on partulids, is now in progress.

The current project also revealed that there is very low awareness of the presence of Fiji's four endemic partulid snail species, and other native or endemic land snail species, in the relatively large and active local conservation sector, including research organisations, government departments, non-government organisations and relevant management agencies.

Locating populations and monitoring population trends

Information on the overall land snail faunas of Rotuma and Cicia has been published elsewhere (Brodie *et al.* 2012, 2013, 2014) and here we focus only on the Partulidae. Only one species of partulid land snail was found on each of the two islands surveyed.

On Rotuma, five shells of *Partula leefei* were found at a single location on the north-western end of the island (district of Itumuta) at an elevation of ~120 m. These empty shells were found on the ground within rock crevices and among tree roots. All shells were of similar length and width (Table 4) and all but the smallest were intact. The largest shell retained some periostracum, indicating animal death within the preceding few years, and thus suggests the possibility of an extant population. A colour photograph of this latter specimen can be found in Brodie *et al.* (2013).

On Cicia, the presence of *P. lirata*, previously recorded from the island, could not be confirmed. However, a partulid identified as *P. lanceolata* was found at three different locations, representing a new and first record of the species beyond Mago Island. Our voucher samples comprised living specimens taken from low vegetative foliage at two sites, and empty shells gathered on the ground at a third site (Table 5). A colour photograph of one of these living specimens *in situ* can be found in Brodie *et al.* (2013). At all three sites both juvenile and adult snails were represented, as determined by the size of the shells and relative thickness of the apertural lip, an adult characteristic in partulids.

Table 4. Comparative dimensions and condition of the five empty shells of *Partula leefei* (Brodie Reference Code Number B122) found on Rotuma at Mount Solrorea on 11 May 2012

Shell length (mm)	Shell width (mm)	Condition
14	9	Intact, retained some periostracum
13	8	Intact, no periostracum present
13	8	Intact, no periostracum present
10	7	Intact, no periostracum present
9	7	Broken shell, no periostracum present

Patterns of genetic diversity

Two pedal mucous samples from two different *Partula lanceolata* specimens from Cicia were obtained from living snails via FTA card. We were able to successfully genotype these two samples of *P. lanceolata* for COI. The two resulting haplotypes were phylogenetically analysed together with the pre-existing basin-wide database of *Partula* species COI sequences as per Lee *et al.* (2014). The topological placement of the *P. lanceolata* mitochondrial genotypes (Fig. 3) revealed they were robustly

Table 5. Details of the specimens of *Partula lanceolata* found at three different locations on Cicia Island between 6 and 10 December 2012

Date	Location	No. of specimens seen	DNA card samples	Elevation	Code no.	Additional comment
6 Dec. 2012	Babaji, Tarukuo	5 (4 adults, 1 juvenile)	Not applicable	59 ft	B162	Empty shells only, one intact (19 mm high × 10 mm wide), rest damaged (22 × 10, 21 × 10, 20 × 10, 14 × 7)
7 Dec. 2012	Rasea above Natokalou village	5 (at least 2 adults)	1 card sample obtained on Cicia	178 ft	B171	All alive, two adults collected, three left in habitat. One adult 20 mm high, other slightly smaller with less pronounced aperture lip
10 Dec. 2012	Votu-ko-Cicia, Mabula village	11 (7 adults, 4 juveniles)	Several card samples obtained back in Suva	216 ft	B179	One adult and one juvenile collected

sister to the GenBank sample of *P. lirata* that was previously analysed by Lee *et al.* (2014) from the Fijian island of Cikobia-i-Lau. This sister relationship is not unexpected as Cooke and Crampton (1930), in their original description of *P. lanceolata*, remarked that it 'is obviously a close relative of *Partula lirata* from which it differs most markedly in the absence of the spiral ridges that render *P. lirata* unique within its genus'. The two Fijian *Partula* species now examined form a clade with *P. auraniana* Hartman, 1888 from the Torres Archipelago in Vanuatu (Fig. 3).

Action partnerships

Action partnerships have been initiated with Läje Rotuma Initiative and the community of Cicia Island, both of whom wish to strengthen their sustainable development. A connection between substantial changes in habitat, which clearly hinder ecosystem function, and the survival of their unique, microclimate-dependent endemic species, such as native partulid snails, is clear. Despite this, it has been relatively hard to generate interest in native land snails at a local level and limited human resource capacity makes developing the relationships needed to survey multiple, often remote, islands challenging. As discovered during this study, however, land snail surveys can be successfully 'piggybacked' onto other projects related to agricultural pest management, vegetative cover, food security or climate change mitigation or faunal surveys of more recognised iconic or totem species such as trees, birds or iguanas.

Disturbance Gradient Analysis

As stated earlier, we selected six factors that we consider most likely to drive decline in Partulidae on the 22 Fijian islands considered likely to have partulid species (Table 6). Included are 17 islands on which partulid snails are previously recorded and five islands in Lau without prior partulid records but which appear to have suitable microclimate and habitat. Our data collection on each of the six factors for all 22 islands is still incomplete and is therefore not presented here but when finalised is expected to give us a working hypothesis that can be tested and refined. Most importantly, this hypothesis will also help us to prioritise further sampling strategy and our preliminary results show a high likelihood of partulid extinction probability on the two relatively disturbed islands already surveyed to date, Rotuma and Cicia, and the importance of surveying the islet of Uea off the main island of Rotuma.

Discussion

Partulid land snails were found on Rotuma and Cicia islands, as predicted, in that there have been previous reports from these islands by Mousson (1865), Smith (1897), Cooke and Crampton (1930), and Pilsbry and Cooke (1934). However, no living specimens were found on Rotuma, only empty shells of *Partula leefei*, the endemic previously found in large numbers by the Bishop Museum in 1938 (Brodie *et al.* 2014). On Cicia, our surveys failed to locate any population of *P. lirata*, but did confirm at least two relict populations of *P. lanceolata*, representing a new island record.

The persistence of at least one species of Partulidae on Cicia Island, despite the extensive modification of the island's vegetation, may relate to the presence of remnant native vegetation on land areas not suitable for cultivation and thus acting as refugia. Further survey work on Cicia is needed to establish the fate of *P. lirata* on that island, and to more definitively define the distribution of *P. lanceolata*. On Rotuma, there has been more comprehensive reforestation, even though land-use changes in recent decades have allowed establishment of secondary, non-indigenous vegetation, and might account for the apparent local demise of *P. leefei*. However, much of the land cover change occurred on Rotuma over several centuries, yet *P. leefei* was abundant in 1938. Thus, a more comprehensive search for partulids on Rotuma is urgently needed to confirm our initial observations, which suggest either recent local extinction or possible persistence of a relictual population. Urgency is paramount here as the recently documented establishment on the island by the invasive predatory flatworm *Platydemus manokwari* de Beauchamp, 1963 (Brodie *et al.* 2012, 2014) could compromise any surviving population of *P. leefei* in the absence of active management.

COI sequences are now available for two Fijian *Partula* collected from north-eastern Lau, *P. lirata* (to GenBank by Lee *et al.* 2014) and *P. lanceolata* (via current study), and phylogenetic analyses confirm a sister relationship among these two distinct species, with an ancestral relationship with a member of the same genus in Vanuatu. Sequence data are needed for *P. leefei* and *Samoana alabastrina* to advance our understanding of the evolutionary affinities of the Fijian Partulidae and provide

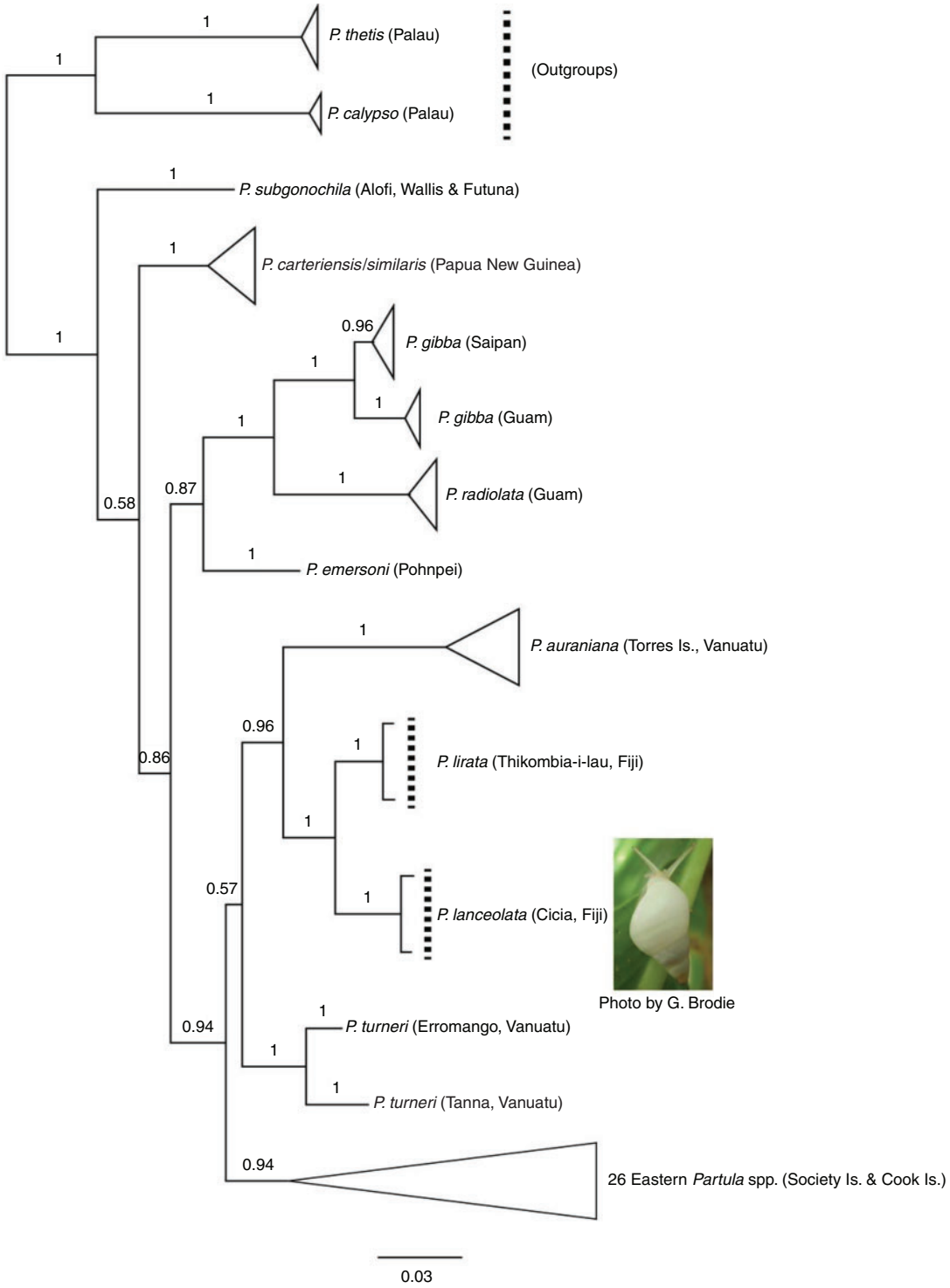

Fig. 3. Bayesian phylogenetic tree of the COI dataset sequences of *Partula* species from GenBank (Lee *et al.* 2014), which includes a sequence of *Partula lirata* from Fiji, combined with our two new sequences of *Partula lanceolata*. The two Palauan species (*P. thetis* and *P. calypso*) were employed as outgroups (Lee *et al.* 2014). For clarity, terminal clades containing large numbers of mitochondrial lineages are collapsed (see Lee *et al.* (2014) for details). Posterior probability values ≥50 are given on their respective nodes.

Table 6. The 22 islands in Fiji on which partulid snails have (1) been recorded and (2) not been surveyed but islands are considered to have suitable microclimate and habitat to support possible partulid presence

(1) Surveyed Islands in Fiji with known partulid records
Avea, Cicia, Cikobia-i-Lau, Kanacea, Laucala, Nayou, Mago, Matuku, Moala, Munia, Oneata, Taveuni, Totoya, Tuvuca, Uea (islet off Rotuma), Vanua Balavu
(2) Unsurveyed Islands in Fiji considered to have suitable microclimate and habitat
Kabara, Lakeba, Moce, Naitauba, Yacata

a higher-level framework for conservation policy and planning. Looking to the future, infraspecific phylogeographic information is also needed to guide conservation action plans to ensure that sites targeted for management collectively encompass the full breadth of genetic diversity in Fijian Partulidae.

There are several islands in Lau that likely support partulids and the absence of partulid records on at least some of these islands may reflect the very extensive ecosystem transformations that have occurred due to human activities. Wherever possible these islands will be represented in our future field surveys to document partulid fate at the most extreme poles of a hypothesised disturbance gradient. Prior occupation with extinction will need to be confirmed by searches for subfossil shell deposits. Despite considerable effort and interest by expatriate scientists, including those in-country, progress towards the successful conservation of Fiji's unique partulid tree snail fauna remains relatively poor. Unless capacity and interest can be found in local citizens or communities, with support from government or conservation agencies it is unlikely that these four endemic species will survive in the future. This follows a situation already predicted by Solem (1964) when he stated 'The famed endemic land snails of the Pacific islands are restricted to the rapidly shrinking patches of native forest. In all too short a time the land snail fauna of the Pacific islands will consist solely of a homogeneous blend of the introduced forms … It is with a real sense of sadness that I have attempted to chronicle for the terrestrial malacologist of 2020 the places where the living land snails of Polynesia and Micronesia originated'.

The way forward is to strengthen awareness and inclusion of land-owning communities in conservation efforts particularly via production of island-focussed identification guides. This will also help to promote understanding that loss of these unique species resources is a clear and visible indicator of deterioration in overall island ecosystem health and function.

Acknowledgements

We sincerely thank Monifa Fiu (LRI), Dr Jimaima Lako (USP) and their respective communities for facilitating and supporting partulid surveys on Rotuma and Cicia respectively. We also thank the Rotuman Island Council and the Fiji Government (Rotuma Affairs) for their approvals. We are grateful to Froseann Stevens and Jale Naivalurua plus several community volunteers for assistance with field surveys. We thank Jon Ablett (NHMUK), Adam Baldinger (MCZ), Philippe Maestrati (MNHN) and Regie Kawamoto (BPBM) for loan of specimen material in their care. Funding for field surveys in Rotuma and Cicia came from the Critical Ecosystem Partnership Fund (CEPF) and the University of the South Pacific Faculty of Science, Technology and Environment. Molecular work was supported by National Geographic Grant 9180-12 to D. Ó Foighil.

References

Abdou, A., and Bouchet, P. (2000). Nouveaux gastéropodes Endodontidae et Punctidae (Mollusca: Pulmonata) récemment éteints de l'archipel des Gambier (Polynésie). *Zoosystema* **22**, 689–707.

Allison, A., and Eldredge, L. (1999). Polynesia and Micronesia. In 'Hotspots. Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions'. (Eds R. A. Mittermier, N. Myers, C. G. Mittermeier and P. Robles Gil.) pp. 390–401. (Cemex and Conservation International.)

Balmford, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution* **11**, 193–196. doi:10.1016/0169-5347(96)10026-4

Barker, G. M. (2012). *Thaumatodon spirrhymatum*. In 'IUCN Red List of Threatened Species. Version 2012.2'. Available at: www.iucnredlist.org [accessed 18 February 2016].

Barker, G. M., and Bouchet, P. (2010). A catalogue and identification guide to the land snail fauna of Fiji, and associated database. Unpublished report.

Barker, G. M., Price, R., and Briggs, C. (2005). Priorities for additions to the Fijian protected natural areas network: an assessment based on complementarity in land snail assemblages. New Zealand Landcare Research contract report prepared for Wildlife Conservation Society, Suva.

Bauman, S., and Kerr, A. M. (2013). *Partula desolata* sp. nov. (Pulmonata: Partulidae), an extinct land snail from Rota, Mariana Islands, Micronesia. *Micronesica* **5**, 1–12.

Bouchet, P. (1998). Mangareva: splendour and decline of a Pacific island land snail fauna. In 'Abstracts of the World Congress of Malacology, Washington D.C.'. (Eds R. Bieler and P. M. Mikkelsen.) pp. 39. (Unitas Malacologica.)

Bouchet, P., and Abdou, A. (2001). Recent extinct land snails (Euconulidae) from the Gambier Islands with remarkable apertural barriers. *Pacific Science* **55**, 121–127. doi:10.1353/PSC.2001.0011

Bouchet, P., and Abdou, A. (2003). Endemic land snails from the Pacific islands and the museum record: documenting and dating the extinction of the terrestrial Assimineidae of the Gambier Islands. *The Journal of Molluscan Studies* **69**, 165–170. doi:10.1093/MOLLUS/69.3.165

Boyko, C. B., and Cordeiro, J. R. (2001). The terrestrial Mollusca of Easter Island. *Basteria* **65**, 17–25.

Brodie, G. (2009). Preliminary observations of terrestrial gastropods of the Nakauvadra Range, Ra Province, Fiji. In 'A Rapid Biodiversity Assessment of the Nakauvadra Range, Ra Province, Fiji'. (Eds C. Morrison, S. Nawadra, and M. Tuiwawa.) RAP Bulletin of Biological Assessment 57, Chapter 6. (Conservation International: Arlington, USA.)

Brodie, G. (2010). Conservation of Fiji's unique land snail fauna: is it an achievable goal? Tropical Natural History, Supplement 3, 213. Published Abstracts of World Congress of Malacology, Phuket, Thailand, 2010.

Brodie, G., and Barker, G. M. (2011). Introduced land snails and slugs in the Fiji Islands: are there risks involved? In 'Island Invasives: Eradication and Management'. (Eds C. R. Veitch, M. N. Clout and D. R. Towns.) pp. 32–36. (International Union for Conservation of Nature: Gland, Switzerland.)

Brodie, G., and Copeland, C. (2010). An investigation of the land snails and slugs of Nakorotubu Range, Viti Levu, Fiji Islands. In 'A Rapid Biodiversity Assessment of the Nakorotubu Range, Ra Province, Fiji.

(Eds C. Morrison, S. Nawadra and M. Tuiwawa.) RAP Bulletin of Biological Assessment 59, Chapter 5. (Conservation International: Arlington, USA.)

Brodie, G., Barker, G. M., Haynes, A., and Singh, R. (2010). Land snails of the Fiji Islands: a summary of their biodiversity, quarantine and agricultural status and human health relationships. Summary report to the Fiji Government Departments of Environment, Forestry and Agriculture.

Brodie, G., Stevens, F., and Barker, G. M. (2012). Report on a preliminary survey of the land snail fauna of Rotuma. School of Biological and Chemical Sciences, University of the South Pacific.

Brodie, G., Barker, G. M., Haynes, A., Singh, R., Stevens, F., Fiu, M., Bogitini, L., Matewai, M., and Naivalurua, J. (2013). Documentation of Fiji's endemic and introduced land snail fauna. Biodiversity Conservation Lessons Learned Technical Series 23. Conservation International – Pacific Islands.

Brodie, G., Barker, G. M., Stevens, F., and Fiu, M. (2014). Preliminary re-survey of the land snail fauna of Rotuma: conservation and biosecurity implications. *Pacific Conservation Biology* **20**, 94–107.

Brook, F. J. (2010). Coastal land snail fauna of Rarotonga, Cook Islands: systematic, diversity, biogeography, faunal history, and environmental influences. *Tuhinga: Records of the Museum of New Zealand Te Papa Tongarewa* **21**, 161–252.

Brook, F. J., Walter, R. K., and Craig, J. A. (2010). Changes in the terrestrial molluscan fauna of Mitiāro, southern Cook Islands. *Tuhinga: Records of the Museum of New Zealand Te Papa Tongarewa.* **21**, 75–98.

Chiba, S., and Roy, K. (2011). Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 9496–9501. doi:10.1073/PNAS.1100085108

Chiba, S., Okochi, I., Ohbayashi, T., Miura, D., Mori, H., Kimura, K., and Wada, S. (2009). Effects of habitat history and extinction selectivity on species-richness patterns of an island land snail fauna. *Journal of Biogeography* **36**, 1913–1922. doi:10.1111/J.1365-2699.2009.02115.X

Clarke, B., Murray, J., and Johnson, M. J. (1984). The extinction of endemic species by a programme of biological control. *Pacific Science* **38**, 97–104.

Cooke, C. M., and Crampton, H. E. (1930). New species of *Partula*. *Bernice P. Bishop Museum Occasional Papers* **9**, 3–9.

Coote, T. (2007). Partulids on Tahiti: differential persistence of a minority of endemic taxa among relict populations. *American Malacological Bulletin* **22**, 83–87. doi:10.4003/0740-2783-22.1.83

Coote, T., and Loève, E. (2003). From 61 species to five: endemic tree snails of the Society Islands, French Polynesia fall prey to an ill-judged biological control programme. *Oryx* **37**, 91–96. doi:10.1017/S0030605303000176

Coote, T., Clarke, D., Hickman, C. S., Murray, J., and Pearce-Kelly, P. (2004). Experimental release of endemic *Partula* species, extinct in the wild, into a protected area of natural habitat on Moorea. *Pacific Science* **58**, 429–434. doi:10.1353/PSC.2004.0028

Coppois, G. (1995). The vulnerability of "island" species. Threatened Galapagos bulimulid land snails: an update. In 'The Conservation Biology of Molluscs'. (Ed. E. A. Kay.) pp. 8–11. Occasional Paper of the IUCN Species Survival Commission, No. 9.

Cowie, R. H. (1992). Evolution and extinction of Partulidae, endemic Pacific island land snails. *Philosophical Transactions of the Royal Society of London. B* **335**, 167–191. doi:10.1098/RSTB.1992.0017

Cowie, R. H., and Cook, R. P. (2001). Extinction or survival: partulid tree snails in American Samoa. *Biodiversity Conservation* **10**, 143–159.

Darriba, D., Taboada, G. L., Doallo, R., and Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**, 772. doi:10.1038/NMETH.2109

Didham, R. K., Tylianakis, J. M., Gemmell, N .J., Rand, T. A., and Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* **22**, 489–496. doi:10.1016/J.TREE.2007.07.001

DoE (2007). Fiji's National Biodiversity Strategy Action Plan. Fiji Department of Environment.

Evenhuis, N. L. (editor) (2007). Field notes of E. H. Bryan, Jr. on the Whitney South Seas Expedition (February–November 1924). Bishop Museum Technical Report No. 37.

Folmer, O., Black, M., Hoeh, R., Lutz, R. A., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Hadfield, M. G. (1986). Extinction in Hawaiian achatinelline snails. *Malacologia* **27**, 67–81.

Henry, P.-Y., and Jarne, P. (2007). Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. *Invertebrate Biology* **126**, 138–153. doi:10.1111/J.1744-7410.2007.00084.X

Holland, B. S., and Hadfield, M. G. (2002). Islands within an island: phylogeography and conservation genetics of the endangered Hawaiian tree snail *Achatinella mustelina*. *Molecular Ecology* **11**, 365–375. doi:10.1046/J.1365-294X.2002.01464.X

Hopper, D. R., and Smith, B. D. (1992). Status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H. E. Crampton in 1920. *Pacific Science* **46**, 77–85.

IUCN (2001). 'IUCN Red List Categories and Criteria: Version 2.1.' (IUCN Species Survival Commission, IUCN: Gland and Cambridge.)

IUCN (2014). 'IUCN Red List of Threatened Species. Version 3.1.'

Janks, M. R., and Barker, N. P. (2013). Using mark–recapture to provide population census data for use in Red Listing of invertebrates: the rare terrestrial snail *Prestonella bowkeri* as a case study. *Biodiversity and Conservation* **22**, 1609–1621. doi:10.1007/S10531-013-0495-3

Justine, J.-L., Winsor, L., Gey, D., Gros, P., and Th'evenot, J. (2014). The invasive New Guinea flatworm *Platydemus manokwari* in France, the first record for Europe: time for action is now. *PeerJ* **2**, e297. doi:10.7717/PEERJ.297

Kirch, P. V., Christensen, C. C., and Steadman, D. W. (2009). Subfossil land snails from Easter Island, including *Hotumatua anakenana*, new genus and species (Pulmonata: Achatinellidae). *Pacific Science* **63**, 105–122. doi:10.2984/1534-6188(2009)63[105:SLSFEI]2.0.CO;2

Kondo, Y. (1955). A revision of the family Partulidae (Gastropoda, Pulmonata). Ph.D. Thesis, Harvard University, Cambridge, MA.

Lee, T., Burch, J.B., Coote, T., Fontaine, B., Gargominy, O., Pearce-Kelly, P., and Ó Foighil, D. (2007*a*). Prehistoric inter-archipelago trading of Polynesian tree snails leaves a conservation legacy. *Proceedings. Biological Sciences* **274**, 2907–2914. doi:10.1098/RSPB.2007.1009

Lee, T., Burch, J.B., Jung, Y., Coote, T., Pearce-Kelly, P., and Ó Foighil, D. (2007*b*). Tahitian tree snail mitochondrial clades survived recent mass extirpation. *Current Biology* **17**, R502–R503. doi:10.1016/J.CUB.2007.05.006

Lee, T., Meyer, J-Y., Burch, J.B., Pearce-Kelly, P., and Ó Foighil, D. (2008). Not completely lost: two partulid tree snail species persist on the highest peak of Raiatea, French Polynesia. *Oryx* **42**, 615–619. doi:10.1017/S0030605308001427

Lee, T., Li, L., Churchill, C., and Ó Foighil, D. (2014). Evolutionary history of a vanishing radiation: isolation-dependent persistence and diversification in Pacific Island partulid tree snails. *BMC Evolutionary Biology* **14**, 202. doi:10.1186/S12862-014-0202-3

Lydeard, C., Cowie, R. H., Ponder, W. F., Bogan, A. E., Bouchet, P., Clark, S. A., Cummings, K. S., Frest, T. J., Gargominy, O., Herbert, D. G., Hershler, R., Perez, K. E., Roth, B., Seddon, M., Strong, E. E., and Thompson, F. G. (2004). The global decline of nonmarine molluscs. *BioScience* **54**, 321–330. doi:10.1641/0006-3568(2004)054[0321:TGDONM]2.0.CO;2

Mousson, A. (1865). Coquilles terrestres et fluviatiles de quelques iles de l'ocean Pacifique, recueillies par M. le Dr E Graeffe. *Journal de Conchyliologie* **13**, 164–209.

Murray, J., and Clarke, B. (1984). Movement and gene flow in *Partula taeniata*. *Malacologia* **25**, 343–348.

Murray, J, Murray, E., Johnson, M.J., and Clarke, B. (1988). The extinction of *Partula* on Moorea. *Pacific Science* **42**, 150–153.

Nakoro, E. (2013). Archeological surveys: summary report. In 'Rapid Biological Assessment Survey of Southern Lau, Fiji'. (Eds M. Tuiwawa and W. Aalbersberg.) pp. 9–14. Biodiversity Conservation Lessons Learned Technical Series 22. Conservation International Pacific Islands Program.

Neuweger, D., White, P., and Ponder, W. F. (2001). Land snails from Norfolk Island sites. In 'The Prehistoric Archaeology of Norfolk Island, Southwest Pacific'. (Eds A. Anderson and P. White.) *Records of the Australian Mus*eum, Supplement 27, pp. 115–122. (Australian Museum: Sydney.)

Norbury, G., Byrom, A., Pech, R., Smith, J., Clarke, D., Anderson, D., and Forrester, G. (2013). Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. *Ecological Applications* **23**(7), 1707–1721. doi:10.1890/12-1958.1

Ó Foighil, D., Lee, T., and Slapcinsky, J. (2011). Prehistoric anthropogenic introduction of partulid tree snails in Papua New Guinean archipelagoes. *Journal of Biogeography* **38**, 1625–1632. doi:10.1111/J.1365-2699.2011.02489.X

Olson, D. M., and Dinerstein, E. (1998). The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology* **12**, 502–515. doi:10.1046/J.1523-1739.1998.012003502.X

Olson, D. M., Farley, L., Patrick, A., Watling, D., Tuiwawa, M., Masibalavu, V., Lenoa, L., Bogiva, A., Qauqau, I., Atherton, J., Caginitobas, A., Tokor'a, M., Prasad, S., Naisilisili, W., Raikabula, A., Mailautoka, K., Morely, C., and Allnutt, T. (2010). Priority forests for conservation in Fiji: landscapes, hotspots and ecological processes. *Oryx* **44**, 57–70. doi:10.1017/S0030605309990688

Pilsbry, H. A., and Cooke, C. M. (1934). Partulidae of Tonga and related forms. *Bernice P Bishop Museum Occasional Papers* **10**, 3–22.

Pippard, H. (2012). The current status and distribution of land snails in the Pacific Islands of Oceania. IUCN Oceania report.

Pippard, H. (2013). Strengthening information for regional assessments of the conservation status and distribution of biodiversity in the Pacific Islands. Biodiversity Conservation Lessons Learned Technical Series 21. Conservation International Pacific Islands Program.

Pfeiffer, L. (1856). Descriptions of twenty-five new species of land-shells, from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London* **24**, 32–36.

Preece, R. C. (1998). Impact of early Polynesian occupation on the land snail fauna of Henderson Island, Pitcairn group (South Pacific). *Philosophical Transactions of the Royal Society of London. B* **353**, 347–368. doi:10.1098/RSTB.1998.0214

Régnier, C., Gargominy, O., Falkner, G., and Puillandre, N. (2011). Foot mucus stored on FTA® cards is a reliable and non-invasive source of DNA for genetics studies in molluscs. *Conservation Genetics Resources* **3**, 377–382. doi:10.1007/S12686-010-9345-8

Richling, I., and Bouchet, P. (2013). Extinct even before scientific recognition: a remarkable radiation of helicinid snails (Helicinidae) on the Gambier Islands, French Polynesia. *Biodiversity and Conservation* **22**, 2433–2468. doi:10.1007/S10531-013-0496-2

Ronquist, F., and Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574. doi:10.1093/BIOINFORMATICS/BTG180

Sartori, A. F., Gargominy, O., and Fontaine, B. (2013). Anthropogenic extinction of Pacific land snails: a case study of Rurutu, French Polynesia, with description of eight new species of endodontids (Pulmonata). *Zootaxa* **3640**, 343–372. doi:10.11646/ZOOTAXA.3640.3.2

Sartori, A. F., Gargominy, O., and Fontaine, B. (2014). Radiation and decline of endodontid land snails in Makatea, French Polynesia. *Zootaxa* **3772**, 1–68. doi:10.11646/ZOOTAXA.3772.1.1

Schmitt, C. B., Burgess, N. D., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D., Humphries, K., Kapos, V., Loucks, C., Lysenko, I., Miles, L., Mills, C., Minnemeyer, S., Pistorius, T., Ravilious, C., Steininger, M., and Winkel, G. (2009). Global analysis of the protection status of the world's forests. *Biological Conservation* **142**, 2122–2130. doi:10.1016/J.BIOCON.2009.04.012

Smith, E. A. (1897). On a collection of land and freshwater shells from Rotuma Island. *Annals and Magazine of Natural History* **20**, 519–523. doi:10.1080/00222939709487394

Solem, A. (1964). New records of New Caledonian nonmarine mollusks and an analysis of the introduced mollusks. *Pacific Science* **18**, 130–137.

Solem, A. (1976). 'Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part I: Family Endodontidae.' (Field Museum of Natural History: Chicago.)

Stattersfield, A. J., Crosby, M. J., Long, A. J., and Wege, D. C. (1998). 'Endemic Bird Areas of the World: Priorities for Biodiversity Conservation.' BirdLife Conservation Series No. 7. (BirdLife International: Cambridge, UK.)

Thacker, R. W., and Hadfield, M. G. (2000). Mitochondrial phylogeny of extant Hawaiian tree snails (Achatinellinae). *Molecular Phylogenetics and Evolution* **16**, 263–270. doi:10.1006/MPEV.2000.0793

Woinarski, J. C. Z. (2010). Biodiversity conservation in tropical forest landscapes of Oceania. *Biological Conservation* **143**, 2385–2394. doi:10.1016/J.BIOCON.2009.12.009

Zimmerman, E. C. (1943). Some Curculionidae from Rotuma Island (Coleoptera). *Bernice P. Bishop Museum Occasional Papers* **17**, 183–189.