

Partula survival in 2017, a survey of the Society islands

Justin Gerlach

August 2017



***Partula* survival in 2017, a survey of the Society islands**

Justin Gerlach

Summary

The majority of partulid snails (genera *Partula* and *Samoana*) of the Society islands (French Polynesia) were driven to extinction in the 1980s and 1990s. The extinction of all wild populations of 48 species and the threats to the surviving 14 (a further 10 species survive in captivity) are due to the introduced predatory snail *Euglandina rosea* and the flatworm *Platydemus manokwari*.

In August 2017 the surveys were made of all the Society islands with historical *Partula* populations. Surviving populations of three species were visited (*P. incrassa*, *P. otaheitana*, *P. taeniata*) and their abundance quantified. Searches were made for other species, of which one was recorded in its known range on Tahiti (*Samoana burchi*). On Huahine a population of *S. annectens* was suspected to exist, based on a photograph from 2005 attributed to this species. The identity and existence of the Huahine population was confirmed by the location of recent shells of *S. annectens*. On Maupiti island shells of an unidentified *Partula* had been found in 2010 despite the absence of any previous records from the island. In the absence of any specimens the identity of the species could not be determined with confidence. Two old shells were found enabling the species to be identified as *P. lutea* from nearby Bora Bora. This probably represents a 20th century introduction, which was apparently successful until the invasion of the island by predators.

In addition to searches for partulids the distribution of the predators was mapped. *Euglandina* remains present at low densities (with occasional population explosions) on Tahiti and Moorea. It still occurs at higher altitudes on Raiatea but appears to be extinct in lowland sites. There was no evidence of recent survival on Huahine, Tahaa, Bora Bora or Maupiti, with only very old shells located. *Platydemus manokwari* was found on all islands except Tahaa. It is only rarely encountered on Tahiti but is more frequently encountered on Moorea. These islands appear to have been the first to be colonised by the flatworm (before 2006). On Bora Bora and Maupiti it is present but at low densities. It is more common on Huahine and is extremely abundant in parts of Raiatea. It is in the process of spreading across the latter island and a pattern of expansion is apparent, with the highest densities being found in recently invaded areas. Based on the age structure of the flatworm populations it is probable that Huahine was recently invaded but populations are now declining to the lower, more stable levels found on Tahiti Moorea, Bora Bora and Maupiti.

In most areas of the islands snail diversity and abundance were extremely low. Extinction of most large species was probably driven by *Euglandina* but the absence of small leaf-litter inhabiting species may be due to an overlooked introduced predator, the ribbon worm *Geonemertes pelaensis*. The lack of sufficient food for the larger predator *Euglandina* may have caused the decline and extinction of most populations of this species. It persists on Tahiti and Moorea, and higher areas of Raiatea, due to the persistence of abundant prey at higher altitudes. These high-altitude reservoirs may enable the periodic population increases on Tahiti and Moorea. The impact of prey abundance on the dynamics of *Platydemus* is currently unknown. This is the current focus of research into this system.

Recommendations for the conservation of the remaining Society island *Partula* species can be found at the end of this report.



Human impacts on the natural environment have intensified greatly since the 17th century. These impacts have not been uniformly distributed and island ecosystems are under particular pressure. Their small size and isolation intensifies the threats they face. Principal among these are habitat loss, invasive species and climate change. Habitat loss has affected different systems in varying ways depending on topography, climate and diversity. As a result, some islands still retain significant areas of important habitat, mainly in upland areas. Most of these are not truly natural due to the impacts of invasive species. These affect all habitats to at least some extent and have been considered to be the most significant threats in the past. Climate change is now perceived as being increasingly important, threatening all island groups.

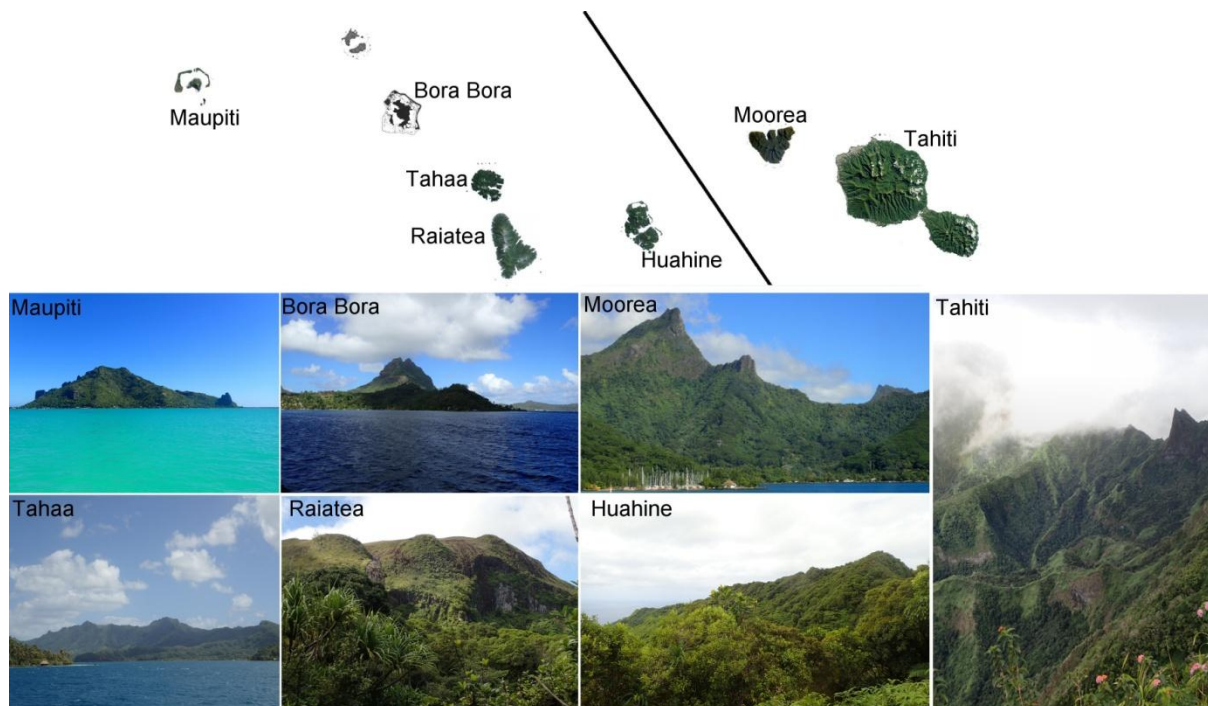
One of the most significantly impacted island species radiations is that of the Pacific Islands tree snails of the family Partulidae (*Samoana* and *Partula*). Due to invasive predators 80% of species were driven to extinction in the late 20th century. Today 14 species may survive in the wild and a further 10 survive only in captivity. Of the wild species, 4 species were found during visits to isolated sites in the 1997-2006. These have not been located since and it is not known how many survive.

Partulid tree snails survived habitat loss and plant invasions in the 18th and 19th centuries and were not considered to be at risk of extinction in Polynesia until the carnivorous snail *Euglandina rosea* was introduced in 1974. The species that survived are mostly at high altitudes where *Euglandina* has failed to establish permanent populations, due to the low temperatures at these altitudes. Only three species have survived in the presence of *Euglandina*, and even these survive only locally.

Another devastating snail predator has been introduced recently: the flatworm *Platydemus manokwari*. Elsewhere *Platydemus* has eliminated *Euglandina* and this alters the conservation prospects for the partulids. For some species this may be a positive change, but not for species living on the ground. Very little is known about *Platydemus*.

Determining what has enabled some partulids to survive in the presence of *Euglandina* and predicting the effects of *Platydemus* will make it possible to devise in situ conservation strategies to ensure the survival of the remaining populations and to refine reintroduction plans. The aim of which is to maximise the likelihood of survival and allow the possibility of adaptation to predator presence.

Fig. 1. Society islands



Methods

In order to determine the factors enabling some tree snails to survive in the presence of *Euglandina* and to evaluate the likely impacts of *Platydemus* invasion field surveys were carried out on all Society islands with historically recorded partulid populations (Tahiti 2-4th August 2017, Maupiti 4-8th August, Moorea 9-10th August, Huahine 10-12th August, Raiatea 12-19th August, Tahaa 16th August, Bora Bora 19-21st August). In all areas visited searches were made for the presence of partulids, *Lissachatina fulica*, *Euglandina* spp. and the flatworm *Platydemus manokwari*. In addition careful searches were made for all mollusc species in specific sites. In these searches trees (stems over 2m high) and arboreal molluscs were recorded in 5x5m quadrats. Plants were categorised as native on the basis of currently available information. For many wide species their origin is ambiguous and plants were considered to be native if they have formed part of partulid habitats for extended periods of time, for ample, *Inocarpus fragifer* is thought to have been a Polynesian introduction some 2,000 years ago and is here considered as 'native'. The vegetation surveys under-record small arboreal snails, and species over 3m above ground, but provides an indication of relative abundance. Litter snails were recorded by manually searching 10 quadrats of 1m² of leaf litter. Where time allowed 10 quadrats were examined. I have used these methods in many places over the past 30 years, including on Raiatea in 1992. They thus provide comparative data and some indication of how species composition and abundance have changed over the intervening period.

For all partulids found the height above ground was recorded (in 0.5m bands) and the snail categorised by age (adult – fully developed; subadult – nearly full size but lacking a developed shell lip, juvenile – less than ¾ adult size, neonate – newborn size; for most purposes juvenile and neonate categories were combined).

Results

Tahiti

Tahiti has been the focus of most partulid monitoring effort and the distribution of species is relatively well known. Accordingly survey effort in the present study was concentrated on other islands and only two sites were visited. Of these one is a relict lowland *Partula* population which has survived predator incursion. The other is a high altitude site which has never been permanently occupied by predators.

Tiapa valley

Tiapa is very degraded habitat, with areas of agriculture and invaded scrub and forest. This area is

Fig. 2. *Partula incrassa* in Tiapa valley and the site's habitat



probably a mosaic of historical clearances and any species persisting are adapted to disturbance. Snail life along the route included moderate numbers of *Lissachatina fulica*, many of which were large adults.

At the area occupied by *Partula incrassa* very little in the way of other snails were found; just single shells of *Ovochlamys fulgens*, *Subulina octona* and *Streptostele musaecola*. This scarcity of snails may explain why *Playdemus* has remained rare in the area, despite having been observed in the valley in 2006 (first record on Tahiti). Three *Partula incrassa* were observed (2 adults and a juvenile) at heights of 2.5-3m above ground. In an area of 25m² this gives a population density of 1,200 per hectare. This is an underestimate as it is probable that many more snails were present higher in the canopy.

Mt. Marau

The visit to Mt Marau comprised the surveying of two ravines selected by Trevor Coote as being known to be occupied by *Partula otaheitana* and the brief examination of other areas by the road.

Area 1 – this ravine was invaded by *Miconia calvescens* and *Spathodea campanulata*, but contains a mixture of native plants, especially tree and birds’ nest ferns. *Partula otaheitana* were moderately common on leaves various plants (at a density of 6,000 per hectare). Most were adults, all sinistral and mostly yellow. Shells were not uncommon, all fairly recent but not fresh. There were several shells of *Samoa burchii* but none was found alive. Two species of *Succinea* were present (*S. amoi*, *S. pudorina*).

	Plants over 2m tall in 25m ²	% native
<i>Miconia calvescens</i>	8	38
<i>Cyathea medullaris</i>	5	

		Snail number		Height of <i>Partula</i> off ground (m) [n=13]	
		Arboreal in 25m ²	Litter per m ²		
<i>P. otaheitana</i>	adult	12	0	adults	2.6±0.53
	subadult	3	0	subadult	2.1±0.85
	juvenile	0	0		
<i>Succinea amoi</i>		2	0		
<i>Succinea pudorina</i>		1	0		

Fig. 3. Areas surveyed on Mt. Marau, survey area 1 to left, survey area 2 to right. Inset: location of Mt. Marau

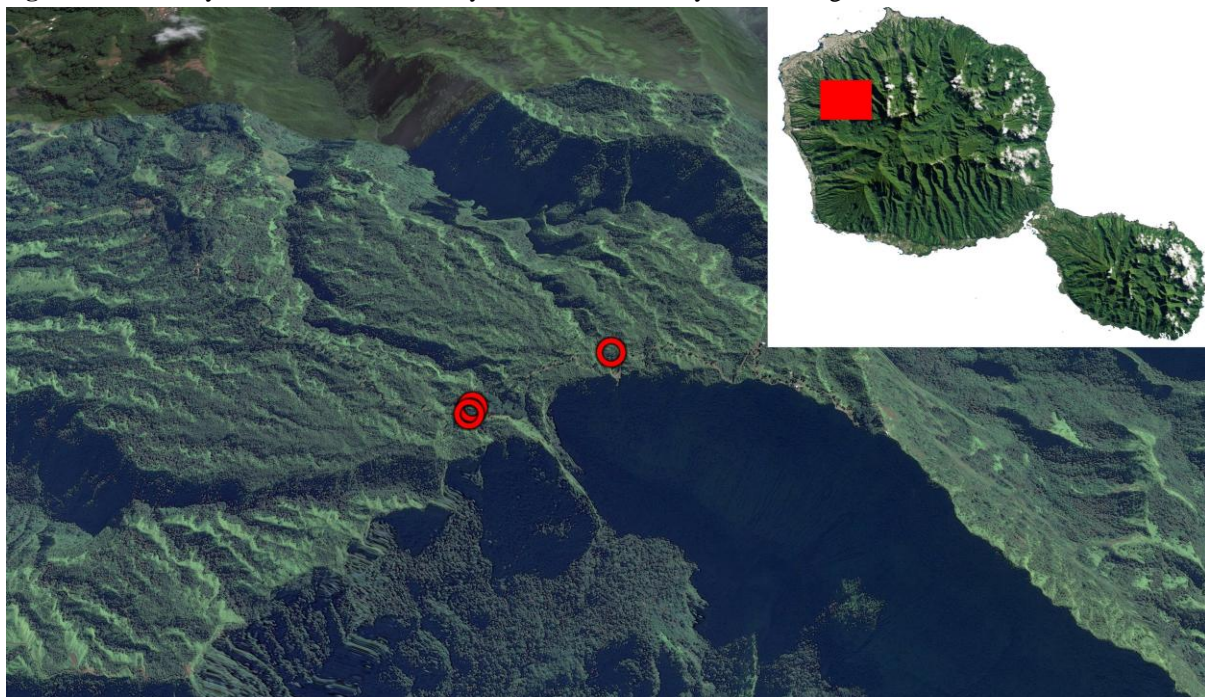
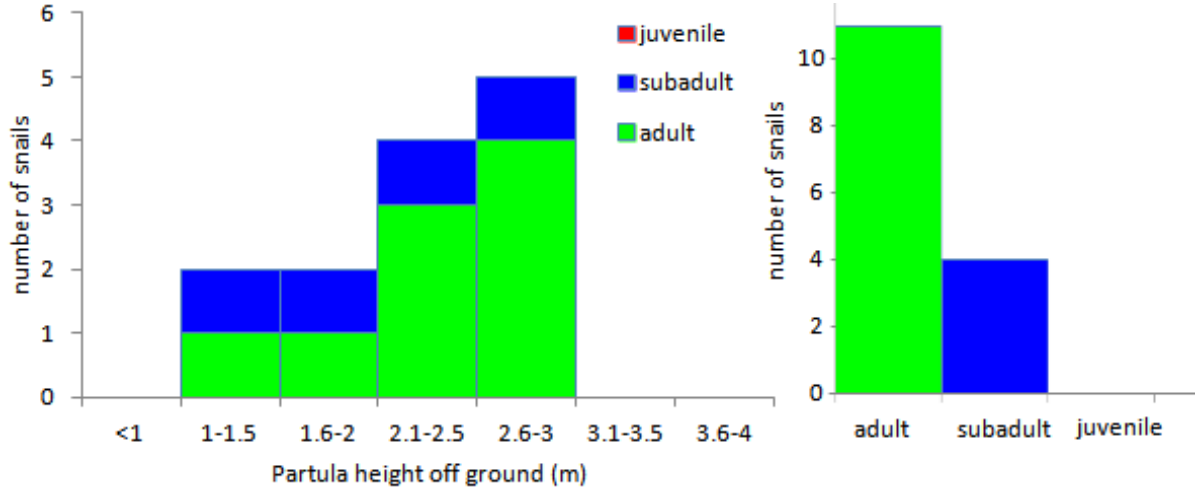


Fig. 4. *Partula otaheitana* in area 1

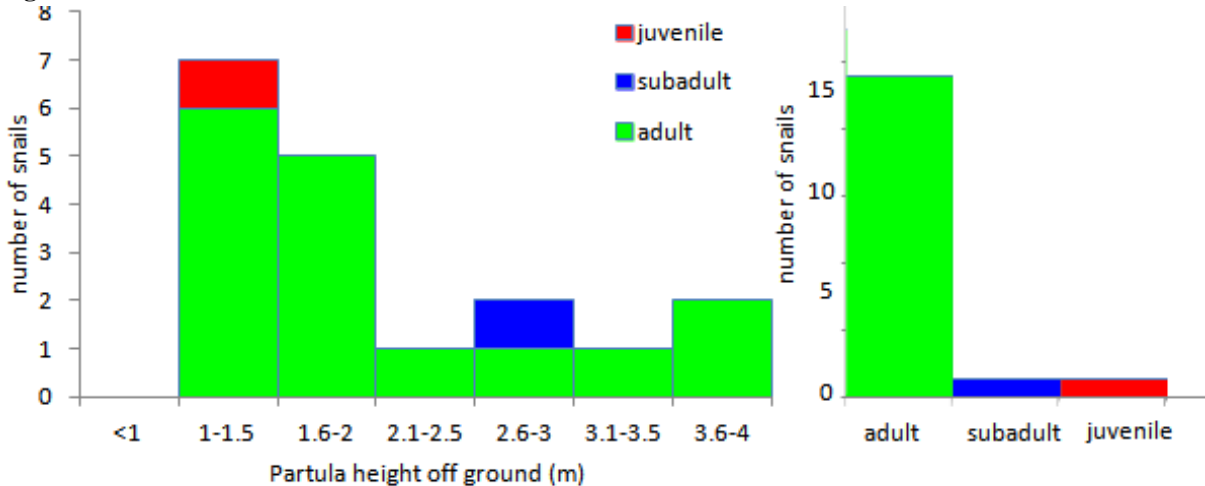


Area 2 – this ravine had been invaded by *Euglandina* previously, with three live seen by Trevor Coote in 2016. It has better vegetation, with very little invasion except where a stretch had been cleared in the past during the instalment of electricity cables. This has regenerated into forest, but is still relatively open and has a several invasives, including *Miconia* and *Rubus* sp.. *Partula otaheitana* were highly abundant (8,000 per hectare), with a range of sizes, including two neonates (85% adult, 10% subadult, 5% juvenile, n=20). As with the previous

	Plants over 2m tall in 25m ²	% native
<i>Cyathea medullaris</i>	15	86%
<i>Psidium littorale</i>	1	
<i>Angiopteris evecta</i>	1	
<i>Cyrtandra</i> sp.	2	
<i>Miconia calvescens</i>	2	

		Snail number		Height of <i>Partula</i> off ground (m) [n=13]	
		Arboreal in 25m ²	Litter per m ²		
<i>P. otaheitana</i>	adult	19	0	adult	2.2±0.96
	subadult	0	0	subadult	3
	juvenile	1	0	juvenile	1.5
<i>Nesiocina discoidea</i>		2	0		
<i>Deroceras laeve</i>		0	1		
<i>Leptinaria unilamellata</i>		0	1		

Fig. 5. *P. otaheitana* in area 2



site most were yellow sinistrals, but red was moderately common and a small number of dextral were found. Shells were highly abundant. Other snails were also more abundant and diverse; several species of *Succinea* (*S. amoi*, *S. humerosa*, *S. infundibuliformis*, *S. modesta*, *S. wallisi*) were found, *Diastole conula* and *Nesiocina discoidea*. In addition a shell of *Trochomorpha pallens* was found. Litter snails were scarce but some were present, including the invasive *Leptinaria unilamellata*, *Paropeas achatinaceum* and the slug *Deroceras laeve*. Three adult *Euglandina* shells were found (one recent) and two hatchling shells. This latter record indicates that *Euglandina* can breed at this site (altitude 1,239m), although it does not provide evidence of survival beyond hatching. Clearly they are not establishing significant populations at this altitude at present. In addition two flatworms were found (species not known currently – ‘Species A’), and a *Geonemertes pelaensis* ribbon worm. *Platydemus manokwari* has been seen at around this altitude (1,000m) on nearby Mt. Aorai (Justine et al. 2015).

Other sites – no *Lissachatina* or *Euglandina* shells were found in ditches up to 1400m. An exploration of one of the fern-covered outcrops on the ridge recorded no snails of any species. It appears that the areas of very poor vegetation: *Dicranopteris* fern and the open road surface itself may act as barriers to the movement many snails, especially *Partula*. It is likely that these ravines were mostly occupied by snails moving up from the valleys below them, only rarely would it have been possible for them to move over the ridge. The ravines on the south side are also probably less hospitable, being smaller and largely filled with *Dicranopteris*. This may hold true for *Euglandina* as well, although being more active over the ground than *Partula* the road would not act as a barrier. *Platydemus* may also spread up the valleys.

Fig. 6. *Partula otaheitana* on Mt. Marau and habitat of a ravine



Maupiti

The only evidence of partulids on Maupiti were reports of shells seen in 2006 by J.-F. Butaud and J.-Y. Meyer. No partulids had been recorded by earlier snail collectors (Garrett in the 1860s and the Mangareva expedition of 1934), so these records were enigmatic. A photograph of the shells suggested that they might have been *Partula lutea*, a species found on nearby Bora Bora, but in the absence of any specimens this was only speculative. Maupiti was visited in the hope of locating any remaining shells to identify which species had been present.

Road ditches on the east side of the island revealed no land snails. A survey of the forest recorded an exceptional scarcity of snails. No evidence of any snails at all was found below about 280m. At this altitude micro-snails were found in the cliff face, mostly pupillids and the introduced *Streptostele muscaeola*. The best quality forest occurs above this altitude and here areas with a cooler microclimate were occupied by arboreal

Fig. 7. Maupiti surveys (green) and survey points (red)



snails on *Pandanus* (*Elasmias apertum*, *Georissa insularis*, *Diastole conula* and *Ovochlamys fulgens*). In the litter shells of *Ovochlamys* were abundant and two old shells of juvenile *Euglandina* were found. At 350 and 370m two old *Partula* shells were collected. These were identifiable as *P. lutea*, supporting an earlier (Gerlach 2016) suggestion that this species may have been introduced to Maupiti in the 20th century. *Gastrocopta pediculus* was also located.

A large *Platydemus manokwari* was found at around 200m, along with *Geonemertes pelaensis*. Earthworms were also present under the same log, but no snails.

There was no evidence of *Lissachatina fulica* ever having been present on the island. Similarly, *Bradybaena similaris* was absent and the only subulinds found were on Motu Tiapaa (*Allopeas gracile*).

	point 1		point 2		point 3	
	>2m in 25m ²	% native	>2m in 25m ²	% native	>2m in 25m ²	% native
<i>Pandanus tectorius</i>	9	98%	10±1.0	98%	0	92%
<i>Hibiscus tiliaceus</i>	40		22.5±12.5		35	
<i>Serianthes falcataria</i>	0		0.5±0.5		3	
<i>Cordyline australis</i>	2		0		0	
<i>Mangifera indica</i>	1		0		0	
<i>Morinda citrifolia</i>	0		0		1	

At point 1 (no live snails found at points 2 and 3)

	Snails number	
	Arboreal in 25m ²	Litter per m ²
<i>Disastole conula</i>	20	0
<i>Elasmias apertum</i>	9	0
<i>Georissa insularis</i>	9	0

Fig. 8. *Partula lutea* from Maupiti and the habitat where the shells were found



Moorea

As with Tahiti, surviving partulid populations on Moorea are relatively well known. In the present study two main areas were focussed upon: an exceptional coastal population of *Partula taeniata* at Opuhohu bay and one of the current reintroduction sites near the Belvedere.

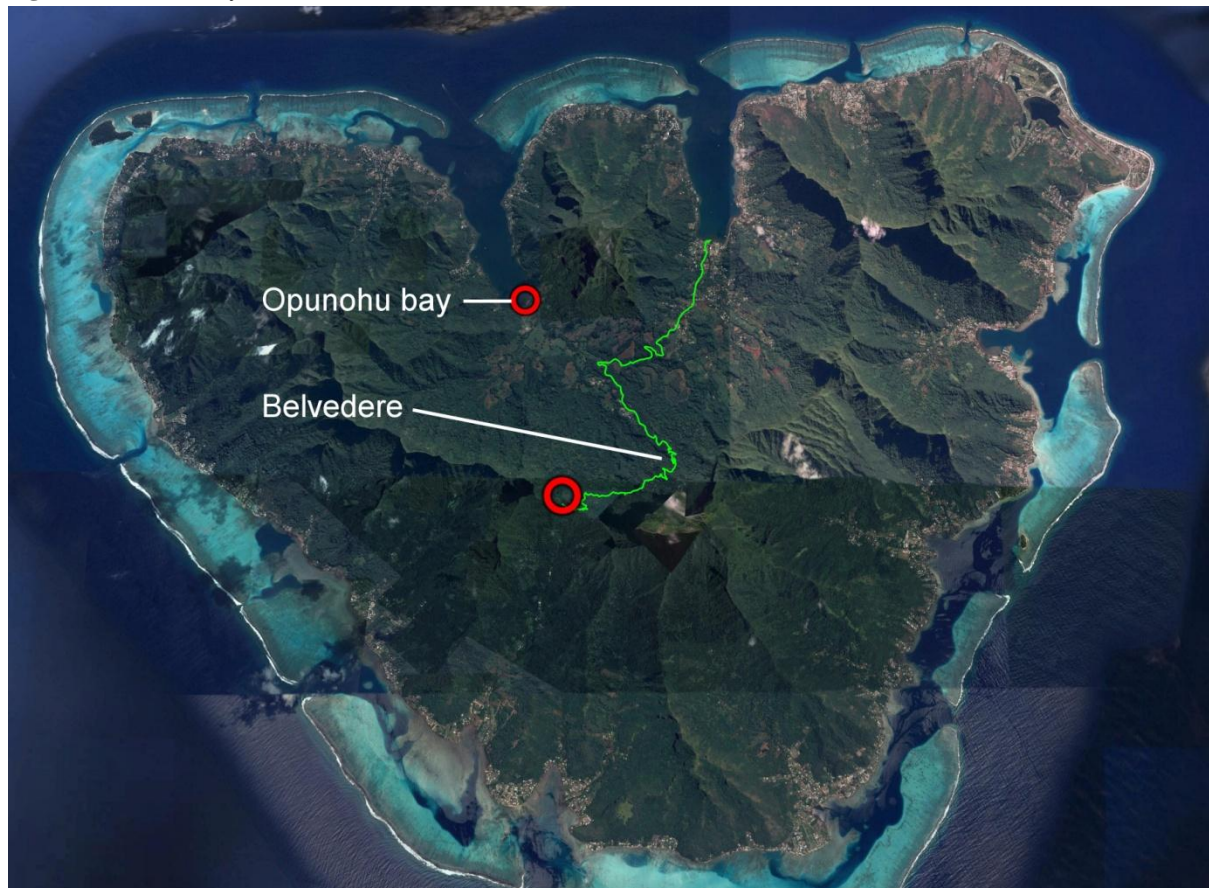
Opuhohu bay

The unique coastal population of *P. taeniata* was examined in the company of Trevor Coote and Cindy Bick. The snails are living on *Achrostichum aureum* mangrove ferns at the side of an inlet. The population is at higher density than any other surviving partulid population but occupies a very small area, bounded by a cleared area and the road on two sides, the inlet and a shrimp farm. Other arboreal snails were present (*Diastole conula* and *Elasmias peaseanum*). *P. taeniata* were only present in an area of the tallest ferns (3.5m high). This is a very healthy population at high density (19,200 per hectare) and with a high proportion of juveniles, including many new born.

The ground is open with a high density of crabs that remove any litter. It also appears to be inundated at extreme high tides. These conditions make it very unlikely that either *Euglandina* or *Platydemus* would pose a significant problem.

		Plants over 2m tall in 25m ²	% native
Partula area	<i>Achrostichum aureum</i>	7	100%
	<i>Hibiscus tiliaceus</i>	12	
unoccupied areas			
north	<i>Achrostichum aureum</i>	0 (plants <2 tall)	100%
by estuary	<i>Achrostichum aureum</i>	5 (=2m tall)	86%
	<i>Hibiscus tiliaceus</i>	8	
	<i>Cocos nucifera</i>	2	

Fig. 9. Moorea survey areas



		Snail number				Height of <i>Partula</i> off ground (m)
		Arboreal in 25m ²	Litter per m ²			
<i>P. taeniata</i>	adult	28	0	adult	1.6±0.22	
	subadult	3	0	subadult	1.75±0.35	
	juvenile	17	0	juvenile	1.5±0	
<i>Elasmias apertum</i>		31	0			
<i>Elasmias peaseanum</i>		17	0			
<i>Diastole conula</i>		31	0			

Fig. 10. *Partula taeniata* in Opunohu bay

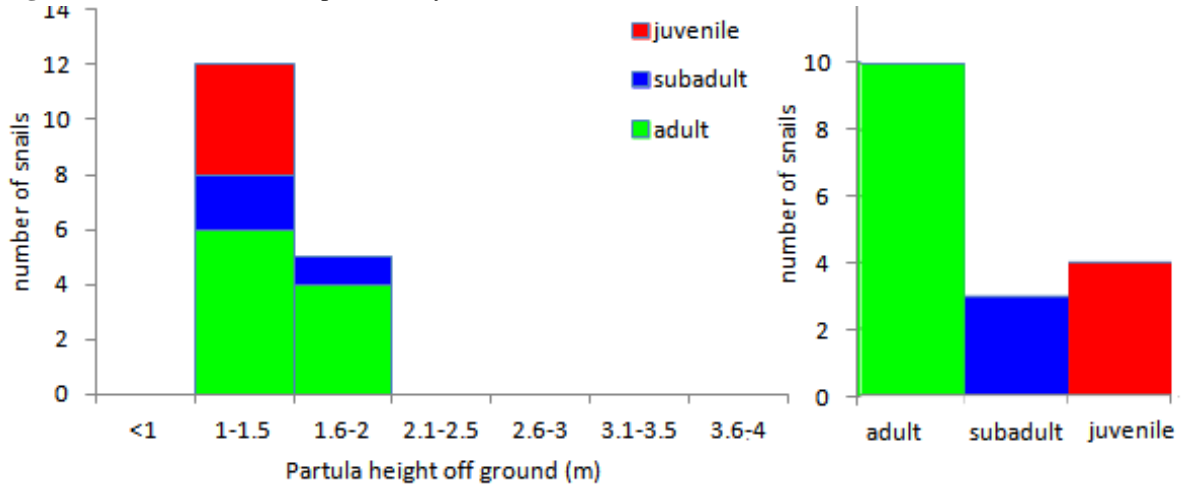


Fig. 11. *Partula taeniata* in Opunohu bay and habitat



Belvedere release sites

The sites of the 2016 *P. tohiviana* reintroductions were visited. Reintroductions were made on *Inocarpus fragifer* trees and *Freycinetia impavida*. All snails have disappeared from the *Inocarpus* sites but those on *Freycinetia* have been seen in the site of a reserve for *Partula* reintroductions, constructed in 1995. During the present study a live wild-born juvenile *P. tohiviana* and a shell of a juvenile *Samoana attenuata* were found in the old reserve. Other species included the arboreal *Elasmias apertum* and *Diastole conula*; and the terrestrial *Subulina octona*, *Paropeas achatinaceum*, *Leptinaria unilamellata* and *Sterptostele muscaeola*.

Old *Euglandina* shells were common and a *Platydemus manokwari* was found within the old reserve.

		Plants over 2m tall in 25m ²	% native
<i>Inocarpus</i> area (n=2)	<i>Inocarpus fragifer</i>	3.5	94%
	<i>Angiopteris evecta</i>	1	
	<i>Hibiscus tiliaceus</i>	0.5	
	<i>Miconia calvescens</i>	0.5	
	<i>Freyinetia</i>	2.5	
	<i>Neonorthea forseri</i>	0.5	
old reserve area	<i>Angiopteris evecta</i>	2	100%
	<i>Hibiscus tiliaceus</i>	12	
	<i>Freycinetia impavida</i>	1	

		Snail number			
		Arboreal in 25m ²	Litter per m ²		
<i>Inocarpus</i> area					
<i>Ovochlamys fulgens</i>		0	3		
<i>Leptinaria unilamellata</i>		0	+		
<i>Diastole conula</i>		+	0		
old reserve area					
<i>P. tohiviana</i>	juvenile	1	0	Height of <i>Partula</i> off ground (m)	juvenile 3
<i>Elasmias apertum</i>		5	0		
<i>Diastole conula</i>		3	0		
<i>Ovochlamys fulgens</i>		0	4		
<i>Paropeas achatinacea</i>		0	0.5		
Philomycidae sp.		0	0.5		

Fig. 12. *Partula tohiviana* wild born from reintroduced parents, and habitat



Flatworms in litter per m² (n=10)

area	<i>Inocarpus</i>	old reserve
<i>Platydemus manokwari</i>	0	0.5

Col des Trois Cocotiers

Several points were surveyed along the path from the Belvedere to the Col des Trois Cocotiers to characterise the habitat near the known *P. taeniata* population. A shell of a juvenile *P. taeniata* was found on the ridge. Many fresh empty shells of *Ovochlamys fulgens* were present on the south side of the ridge, suggestive of *Platydemus* predation. In addition to the widespread *Elasmias apertum* some *E. paeseanum* were also found. The lack of empty shells of the arboreal *Elasmias* and *Partula* species in this area indicates that *Platydemus* predation is most significant on ground-dwelling species such as *Ovochlamys*.

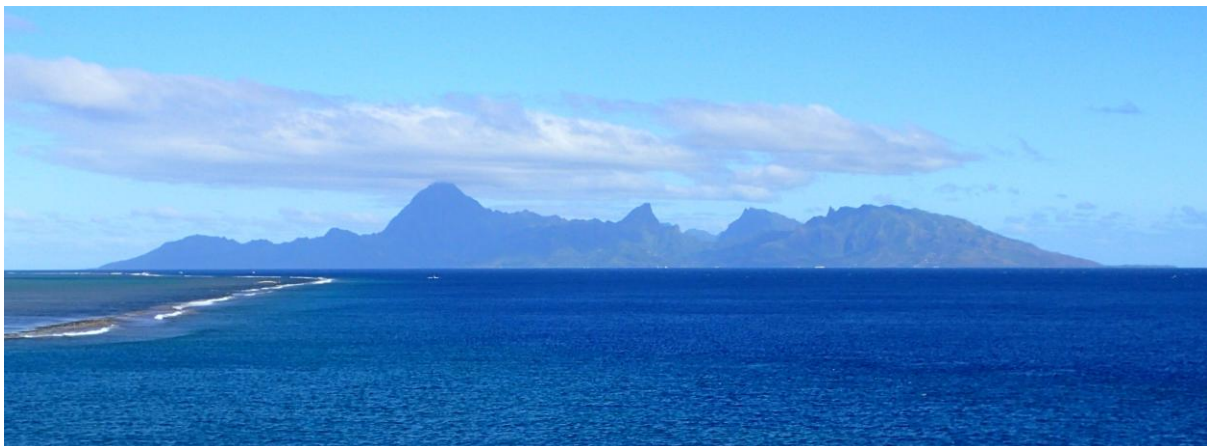
In *Inocarpus* forest a *Platydemus* was found, along with another species of flatworm, *Bipalium kewense*, and a *Geonemertes pelaensis* ribbon worm. At the same spot a baby *Euglandina* was found, the only live example of this species observed on any of the islands.

	Plants >2m (25m ²) (n=8)	% native
<i>Angiopteris evecta</i>	0.75	62-68%
<i>Freycinetia impavida</i>	3.16	
<i>Hibiscus tiliaceus</i>	2.00	
<i>Pandanus tectorius</i>	0.91	
<i>Barringtonia racemosa</i>	1.41	
<i>Inocarpus fragifer</i>	1.50	
<i>Cordyline</i>	0.16	
<i>Miconia calvescens</i>	4.75	
<i>Spathodea campanulata</i>	0.16	
<i>Serianthes falcata</i>	0.25	
unidentified	1.07	

	Snail number	
	Arboreal in 25m ²	Litter per m ²
<i>Diastole conula</i>	0.14±0.38	0
<i>Elasmias apertum</i>	0.71±1.50	0
<i>Georissa striata</i>	0	14.29±29.47
<i>Diastole conula</i>	0.14±0.38	0
<i>Paropea achatinaceum</i>	0	0.29±0.76
<i>Ovochlamys fulgens</i>	0.14±0.38	0.57±1.13
<i>Laevicaulis alte</i>	0	0.14±0.38

North-east lowlands

A survey of the lowland forests in the north-east recorded no species of note. *Lissachatina fulica* shells were abundant in agricultural areas, mostly very old, but including some fresh. No *Euglandina* were observed.



Huahine

Historically Huahine supported four partulid species, of which two (*Partula rosea* and *P. varia*) survive in captivity. Reintroduction of these species is planned for the near future. In addition, a partulid was photographed from the island's summit in 2005 by F. Jacq and J.-F. Butaud. This photograph has been attributed to *Samoana annectens*, with some uncertainty. A priority was to locate this population if it still survived and to confirm its identity.

Huahine-Nui lowlands

A survey of the lowlands of Huahine-Nui recorded old *Lissachatina fulica* shells at a number of points, mostly agricultural, but fresh shells only in the marshy agricultural area in the west. No *Euglandina* shells were located at any point. Other species recorded were *Subulina octona*, *Bradybaena similaris* (old shell) and the freshwater snail *Melanoides tuberculatus*.

Mt. Matouereere

The partulid photographed in 2005 was from the summit of Mt. Turi. In the present survey the ridge leading to Mt. Turi was climbed and the summit of Mt. Matouereere (the western most peak of the Mt. Turi ridge) was reached. Three *Samoana annectens* shells (two recent, one fresh) were found on the slopes and the ridge, at 309 and 360m. No recent *Euglandina* were found (two very old shells above point 3) but *Platydemus* was common (all small to medium adults). Other species present were the invasives *Subulina octona*, *Ovochlamys fulgens*, *Leptinaria unilamellata* and *Streptostele muscaeola*. More native species were present than in any other site other than Mt. Marau on Tahiti: *Georissa insularis*, *G. striata*, *Omphalotropis huaheinesis* and *O. viridescens*.

Fig. 13. Huahine survey areas



This confirms that a population of *Samoana annectens* exists. Even though no live individuals were observed the presence of very fresh shells indicates continued survival. The abundance of flatworms on the island, and the low canopy of the habitat may mean that the survival of the population is at serious risk from *Platydemus* predation.

Fig. 14. Survey areas on Mt. Matouereere



Plants over 2m tall in 25m ²	1	2	3
<i>Angiopteris evecta</i>	5	0	3
<i>Cyclophyllum barbatum</i>	0	0	1
<i>Hibiscus tiliaceus</i>	25	9	0
<i>Inocarpus fragifer</i>	5	0	2
<i>Freycinetia impavida</i>	0	0	4
<i>Merremia peltata</i>	0	20	0
<i>Serianthes falcata</i>	0	0	1
unidentified	0	0	1
% native	100%	31%	83-92%

Point		Snail number	
		Arboreal in 25m ²	Litter per m ²
1	<i>Diastole</i> spp.	25	0
	<i>Elasmias apertum</i>	18	0
	<i>Georissa insularis</i>	0	8
	<i>Georissa striata</i>	0	16
	<i>Omphalotropis huaheinensis</i>	0	42
2	<i>Georissa striata</i>	0	6
	<i>Omphalotropis huaheinensis</i>	0	5
	<i>Omphalotropis viridescens</i>	0	1
	<i>Paropeas achatinacea</i>	0	2
3	<i>Diastole conula</i>	2	0
	<i>Elasmias apertum</i>	2	1
	<i>Georissa striata</i>	0	48

Flatworms in litter per m² (n=10)

point	1	2	3
<i>Platydemus manokwari</i>	0	2	0

Fig. 15. *Samoana annectens* found on Mt. Matouereere in 2017 (left), collected in 1934 (right), and habitat



Raiatea

Historically Raiatea was the most important of all islands for partulids, with more species than any other island in the Pacific. The last survivors were thought to have been brought into captivity in 1992, but a new species (*Partula meyeri*) was discovered on the island's summit in 2006. *Samoana annectens* has also been observed on two occasions. In 2016 an attempt was made to reintroduce the three species that survive in captivity (*P. garrettii*, *P. hebe* and *P. navigatoria*), this was not successful due to very high levels of predation by *Platydemus* flatworms.

In the present study the status of *Platydemus* and *Euglandina* were to be evaluated and a search made for any surviving wild populations, especially of the high-altitude specialist *P. meyeri*. Due to logistic difficulties (the lack of a helicopter to provide transport) it proved impossible to reach Mt. Toomaru and another high-altitude site was used instead.

Temehani Ute Ute

As it was logistically impossible to climb the highest peak of Raiatea to look for *Partula meyeri* an ascent was made to Temehani Ute Ute, which has technically the third highest point (Mt. Tevaiuri 821m, compared to 825m at Mt. Tevaihue). The ascent was made through the Manuihi river valley. The only litter species present were very low numbers of *Ovochlamys fulgens*, *Subulina octona* and *Georissa striata*. Several old *Euglandina rosea* shells were found, mainly near the river, with a few as far as 200m above sea level. One recent *Lissachatina fulica* shell was found.

On the plateau of Temehani Ute Ute no snails were found; low heath habitat provided no pockets of litter as snail habitat and the very short *Pandanus temehaniensis* trees were too isolated for any arboreal species to form populations. Snails were found in ravines on the edge of the plateau. In the ravine at the summit these comprised a very low density of *Ovochlamys fulgens* and *Paropeas achatinaceum*, a single fragment of *Diastole conula* and recent but very eroded *Euglandina rosea* shells. In a lower ravine to the east the same species were found (three *Euglandina* shells) with the addition of a single *Subulina octona*. The *Euglandina* shells were all extremely fragile, resembling those of animals that had been unable to consume sufficient calcium for proper shell growth. All were juvenile or subadult.

This area had never been searched for snails previously. In 1992 the adjacent similar plateau of Temehani Rai was surveyed and in ravines of *Pandanus temehaniensis* arboreal snails were recorded (*Partula* spp., *Trochomorpha typus* and *Elasmias apertum*). Litter species were scarce (<0.1m⁻²) but did include subulinids, *Ovochlamys fulgens* and *Trochomorpha swainsoni*.

Fig. 16. Raiatea survey areas

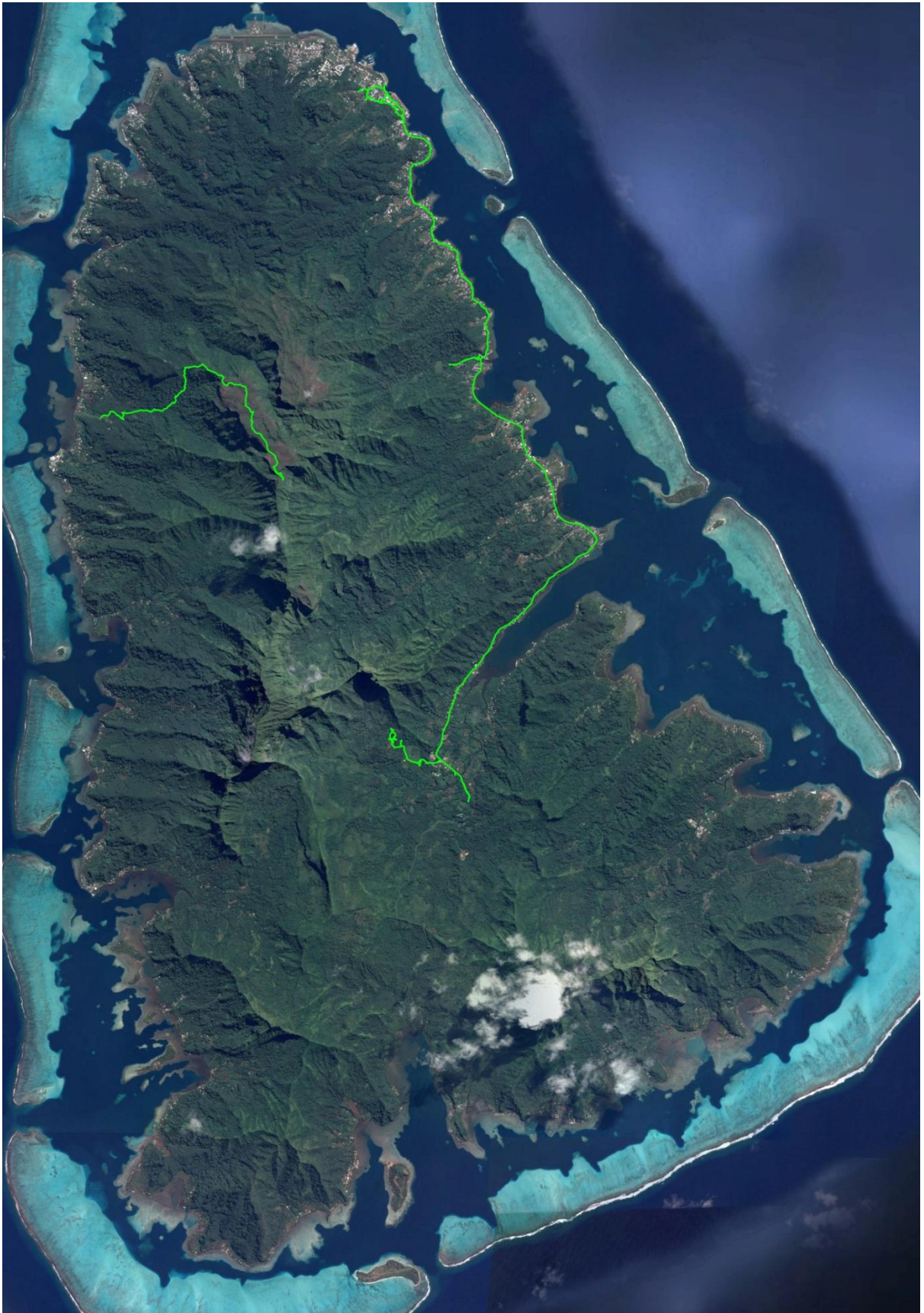
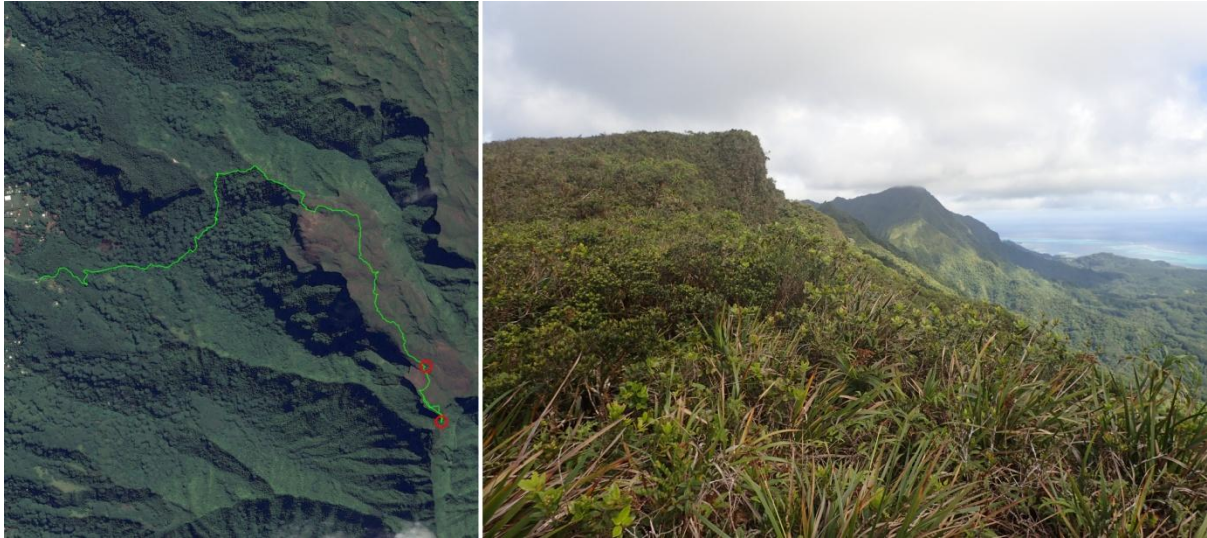


Fig. 17. Survey areas on Temehani Ute Ute and habitat



No flatworms were found in any site. All valley *Euglandina* were of the squat form. Plateau ones were of the more elongate form.

		Plants over 2m tall in 25m ²	% native
Summit ravine	<i>Pandanus temehaniensis</i>	7	100

		Snail number	
		Arboreal in 25m ²	Litter per m ²
valley	<i>Georissa striata</i>	0	35.0
	<i>Ovochlamys fulgens</i>	0	1.0
	<i>Paropeas achatinacea</i>	0	1.0
summit ravine	<i>Ovochlamys fulgens</i>	0	1.0±1.63

Uturoa

A survey of the area around Uturoa recorded *Paropeas achatinaceum*, *Subulina octona*, *Coneuplecta caluculosa* and old shells of *Lissachatina fulica*. Water-filled drains contained the freshwater snails *Melanoides tuberculatus* and *Physastra nasuta*. A small flatworm was found, apparently 'Species A', not *Platydemus*. There was no evidence of *Euglandina*.

Hamoia

This was the site of the last populations of *Partula faba* and *P. navigatoria*. These were in a vanilla plantation on the edge of degrade forest. Agricultural and housing areas have expanded in the intervening 25 years. The *Partula* site is now agricultural infrastructure. The existing habitat is a mix of native, agricultural and invasives. Snails are all invasives with the exception of *Georissa* spp. Invasive slugs were common: *Laeviculis alte*, *Veronicella cubensis* and *Deroceras levae* as on Tahiti. *Lissachatina fulica* shells are highly abundant, including fresh ones, a full range of sizes is present. No *Euglandina* were found. Flatworms were exceptionally common, with *Platydemus manowkari* at an average density of 3 per m² (locally 6m⁻²). In addition two individuals of cf. *Anisorhynchodemus* were found. The *Platydemus* population included adults significantly larger than those observed on other islands.

	Plants >2m in 25m ² (n=4)	% native
<i>Artocarpus utilis</i>	0.50	67-71%
<i>Inocarpus fragifer</i>	1.25	
<i>Musa</i> sp.	5.25	
unidentified	0.50	
<i>Cecropia peltata</i>	3.00	

	Snail number	
	Arboreal (25m ²)	Litter (1m ²)
<i>Georissa insularis</i>	6.00±12.00	10.50±21.00
<i>Georissa striata</i>	0	1.50±3.00
<i>Deroceras laeve</i>	0	0.50±0.58
<i>Leptinaria unilamellata</i>	0	0.25±0.50
<i>Opeas hannense</i>	0	0.25±0.50
<i>Ovochlamys fulgens</i>	0	0.25±0.50
<i>Paropeas achainaceum</i>	0	1.00±2.00
<i>Subulina octona</i>	0	0.75±1.50
<i>Veronicella cubensis</i>	0	0.50±0.58

Flatworms in litter per m² (n=10)

<i>Platydemus manokwari</i>	3.00±3.56
-----------------------------	-----------

In 1992 the leaf litter fauna was dominated by subulinids (5.4m⁻²), *Ovochlamys* (5.3), *Georissa* sp. (4.6), *Diastole* (1.3), *Lissachatina* (0.6) and *Bradybaena* (0.6). The great increase in *Georissa* abundance by 2017 (12.0) may be a result of changes in habitat. All other taxa have become much rarer, with subulinids reduced to 2.0 and *Ovochlamys* to 0.25. Given that the damp disturbed habitat would be expected to favour both of these taxa, their decline may be attributable to predation by *Euglandina*, and now *Platydemus*. This interpretation may be supported by a shift in subulinid species composition, from 87% *Subulina octona* in 1992 to 37% in 2017, and 13% *Paropeas achainaceum* to 50%. This latter species suffers much less predation by *Platydemus* than does *Subulina* as it produces a frothy mucus which has at least a partial deterrent effect.

Faaroa

Faaroa was the site of the reintroductions of three species in 2016. These were unsuccessful due to the predation by *Platydemus manokwari*. This species was not known to be present on the island previously, but was found to be common. The forest around the release site was surveyed to quantify the abundance of flatworms.

The habitat of Faaroa is very degraded due to a long history of agriculture and much of the area is low quality bamboo (*Schizostachyum glaucifolium*) forest. The releases were made in an area of *Inocarpus* and *Freycinetia impavida*. Snails recorded comprised the widespread species *Ovochlamys fulgens* (11% of individuals), subulinids (36%), *Elasmias apertum* (<1%), *Diastole conula* (<1%) and *Georissa* spp. (63%). In addition *Coneuplecta calculosa* was located.

In 1992 the leaf litter fauna was similarly dominated by *Georissa* sp. (48%), but subulinids were less abundant (9%) and *Ovochlamys* more so (20%). *Elasmias* were also more abundant (14%) and *Euglandina* was present (3%) (Gerlach 1994). This suggests that since 1992 there has been a decline in *Ovochlamys*, *Elasmias* and *Euglandina*, resulting in increased dominance of *Georissa* and subulinids. Of these, *Ovochlamys* at least

Fig. 18. Hamoa valley habitat and *Platydemus manokwari*



Fig. 19. Faaroa bay survey areas, inset detail of area near 2016 release sites (release sites marked in yellow)

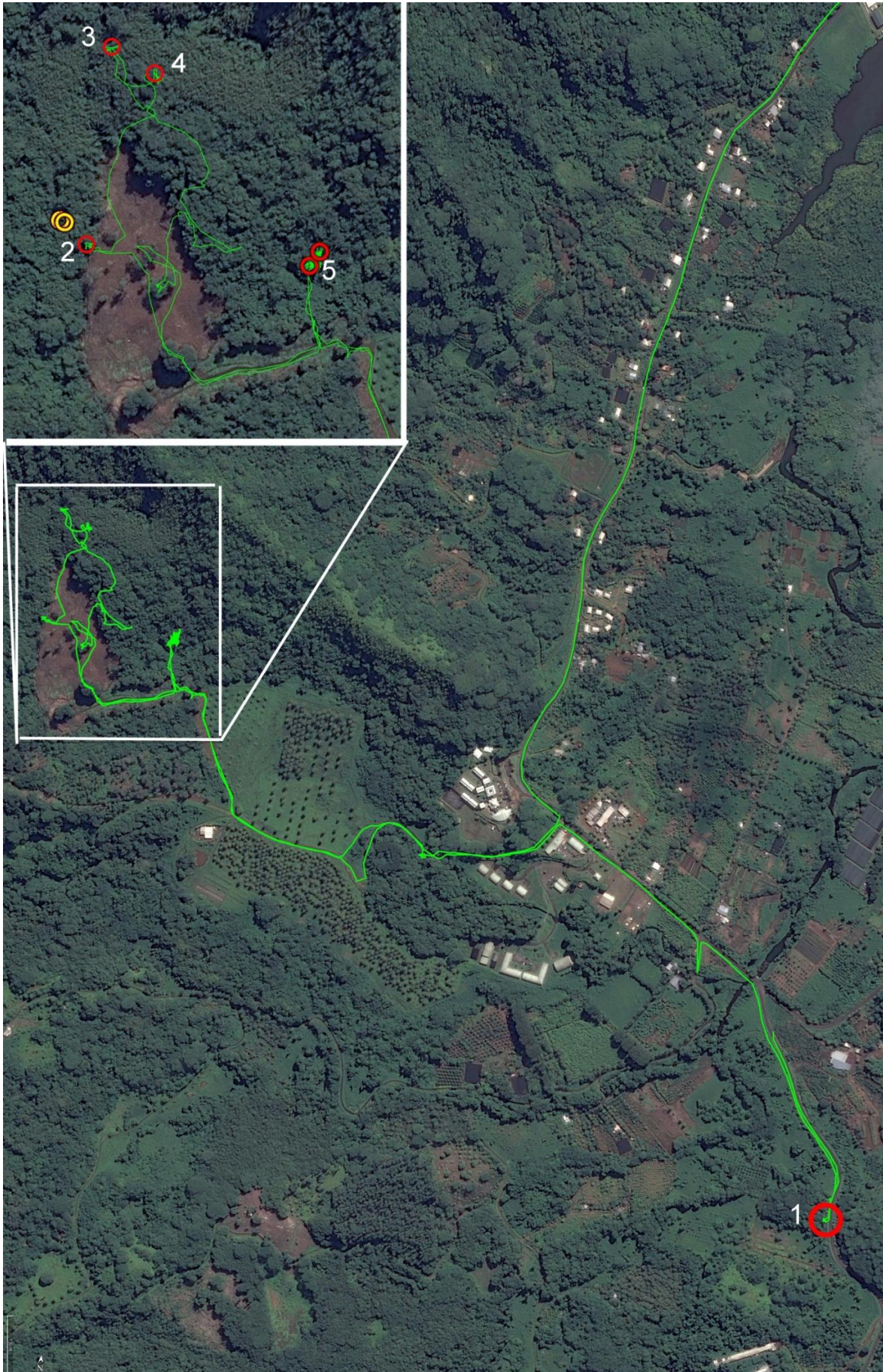


Fig. 20. Habitats in Faaroa bay: bamboo forest and *Inocarpus* forest



appears to be a favoured prey item of *Platydemus*; wherever the two species coincided large numbers of *Ovochlamys* shells could be found, whereas empty shells were scarce in *Platydemus*-free areas. As operculate species *Georissa* may be immune to *Platydemus* predation and, whilst at least some subulinids are vulnerable, *Paropeas achatinaceum* is largely immune. As in Hamoa there has been a change in subulinid species; in 1992 *Paropeas achatinaceum* was not located in the valley but made up 43% of subulinids in 2017. *Subulina octona* dropped from 75% to 29%. There was a general and unexplained increase in abundance in 2017: *Georissa* 8.7m⁻² compared to 3.0, subulinids 5.6 compared to 0.6. The exception was *Ovochlamys* which declined from 1.3 to 1.0.

point		Plants over 2m tall in 25m ²	% native
1	<i>Inocarpus fragifer</i>	3	27%
	<i>Ardisia elliptica</i>	2	
	<i>Cecropia peltata</i>	6	
2	<i>Inocarpus fragifer</i>	4	100%
	<i>Schizostachyum glaucifolium</i>	5	
3	<i>Schizostachyum glaucifolium</i>	78	100%
4	<i>Inocarpus fragifer</i>	5	72%
	<i>Schizostachyum glaucifolium</i>	3	
	<i>Ardisia crenata</i>	3	
5	<i>Freycinetia impavida</i>	0.67	42-49%
	<i>Hibiscus tiliaceus</i>	2.83	
	<i>Inocarpus fragifer</i>	1.67	
	<i>Ardisia crenata</i>	5.33	
	<i>Cecropia peltata</i>	0.17	
	<i>Miconia calvescens</i>	0.50	
	unidentified	0.83	

point		Snail number		point		Snail number	
		Arboreal in 25m ²	Litter per m ²			Arboreal in 25m ²	Litter per m ²
1	<i>Subulina octona</i>	0	4	4	<i>Ovochlamys fulgens</i>	0	2
	<i>Paropeas achatinaceum</i>	0	12		5	<i>Elasmias apertum</i>	37.50±30.62
2	<i>Georissa insularis</i>	0	16	<i>Georissa insularis</i>		75.83±103.22	18.50±32.83
	<i>Ovochlamys fulgens</i>	0	4	<i>Georissa striata</i>		8.33±12.91	1.83±2.04
3	<i>Subulina octona</i>	0	4	<i>Ovochlamys fulgens</i>		0	3.00±1.41
	<i>Opeas hannense</i>	0	8				
	<i>Georissa insularis</i>	0	4				

Flatworms in litter per m² (n=10)

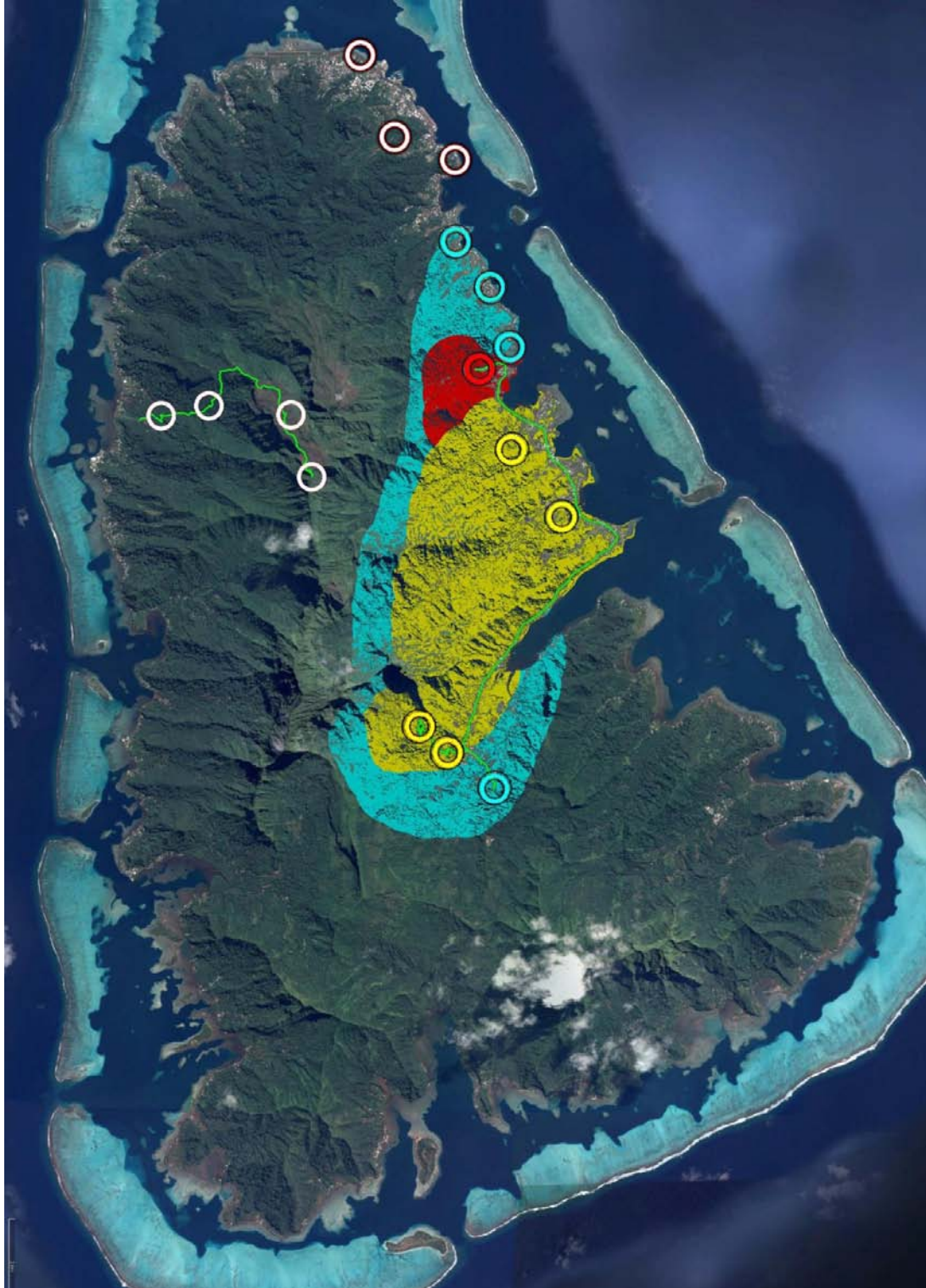
area	1	2	3	4	5
<i>Platydemus manokwari</i>	0	0	0	0	0.83±1.17

Distribution of *Platydemus manokwari* on Raiatea

Results of surveys for flatworm presence are shown in Fig. 13.

This pattern is suggestive of an ongoing invasion. The likely origin point is Faaroa bay; the extensive agriculture of that area involves the transportation of plant material and flatworms were probably accidentally imported with such material. The highest densities may represent newly invaded areas, with population decline behind this 'advancing front' due to food scarcity. Low density populations may occur ahead of the front.

Fig. 21. *Platydemus* on Raiatea. Survey points marked as circles. Levels of abundance are based on quantitative surveys in 1m² quadrats (white – absent, blue <0.1m⁻², yellow 0.1-1m⁻², red 4.>0.83m⁻²).



Tahaa

Tahaa's partulids are thought to have died out by 1995 when the island was searched for survivors. By this time *Euglandina* had become established in all areas of the island and only a small number of *Partula* shells could be found. The habitats are all highly modified due to a long agricultural history and extensive invasion by introduced plant species. No partulids have been observed by visiting botanists (unlike on neighbouring Raiatea and on Huahine) but no dedicated snail surveys had been made on the island since 1995 (for partulids) or 1934 (snails generally).

In the present study the slopes Mt. Paurauti were targeted. This was the only historical site for the most arboreal Tahaa partulid, *Partula saggita*. Of the island's partulids this was thought to be the most likely species to survive, as predation by *Euglandina* is most efficient at ground level.

No evidence of any partulid survival was found. *Platydemus* was not present. There was no evidence of the survival of *Euglandina* and *Lissachatina fulica* was extremely rare, although a recent shell was found. Other species included *Leptinaria unilamellata* and *Allopeas gracile*. This survey confirmed that Tahaa is biologically very impoverished, with a highly invaded flora and a depauperate snail fauna.

	Plants over 2m tall in 25m ²	% native
<i>Cecropia peltata</i>	4	0-14%
<i>Serianthes falcata</i>	1	
<i>Trema orientalis</i>	1	
unidentified	1	

	Snail number	
	Arboreal in 25m ²	Litter per m ²
<i>Georissa insularis</i>	0	2
<i>Ovochlamys fulgens</i>	0	2

Fig. 22. Survey areas of Tahaa and habitat



Bora Bora

Bora Bora's partulids are thought to have died out in the early 1990s. By the time the island was visited for *Partula* conservation surveys, in 1995, only old shells could be found. The present survey confirmed the extinction of *Partula* on the island. Unexpectedly, old *Partula lutea* shells are still present, more than 20 years after their presumed date of extinction. These were found in sampling point 1 (many shells), 3 (one shell) and 4 (two shells). In some cases shells were found under rock overhangs or in short lava tubes where they might be expected to persist for considerable periods of time. However, most shells were found lying on the ground, covered by leaves. In this situation they would only be expected to last for a few years before erosion was complete. The only sites where extinct partulid populations are still represented by empty shells are on Bora Bora and Maupiti. Shells were common on the other islands in 1995 but no longer exist. There is no obvious reason why shells would last longer on these islands than elsewhere, which suggests that *P. lutea* populations persisted for at least 10 years longer than was thought.

Flatworms are present but are mainly limited to damper areas of forest where they occur at moderate densities. Much of the forest is very dry at ground level and does not appear to support significant flatworm populations. At sampling point 1 the soil and litter were very dry and no flatworms were present. *Bipalium kewense* and the unidentified red-headed species were also recorded and the ribbon worm *Geonemertes pelaensis* is locally abundant. The only evidence of *Euglandina* was a small number of very old shells. Old *Lissachatina fulica* shells and eggs were highly abundant. Recent shells were found in the mangroves at Povaie bay.

In lower agricultural habitat snails are limited to subulinids (*Subulina octona*, *Allopeas kyotensis*, *Paropeas achatinaceum*) at very low density but forest habitats contain a greater diversity of snails than other islands, with tornatellids and *Liardetia normalis* occurring on trees from just below point 2, and *Lamellidea oblonga* and *Elasmias apertum* being highly abundant at point 3. No arboreal snails were found at point 4. A single old shell of *Orobophana pacifica* was found at sampling point 4. *Nesopupa tantilla* was also located.

Fig. 23. Survey areas of Bora Bora, with detail of sampling points on right



Fig. 24. Old *Euglandina* and *Partula lutea* shells found on Bora Bora



	Plants over 2m tall in 25m ²			
	area 1	area 2	area 3	area 4 (n=3)
<i>Angiopteris evecta</i>	0	0	0	0.67
<i>Cocos nucifera</i>	0	0	0	0.67
<i>Hibiscus tiliaceus</i>	12	20	8	8.33
<i>Inocarpus fragifer</i>	1	1	2	6.33
<i>Cananga odorata</i>	1	0	0	0
<i>Serianthes falcata</i>	0	0	1	0
% native	93	100	91	100

area		Snail number	
		Arboreal in 25m ²	Litter per m ²
1	<i>Diastole conula</i>	1	0
2	<i>Elasmias apertum</i>	2	0
3	<i>Ovochlamys fulgens</i>	0	0.4
	<i>Diastole conula</i>	0	0
	<i>Elasmias apertum</i>	38	0
	<i>Lamellidea oblonga</i>	7	0
4	<i>Ovochlamys fulgens</i>	0	0.5±0.71

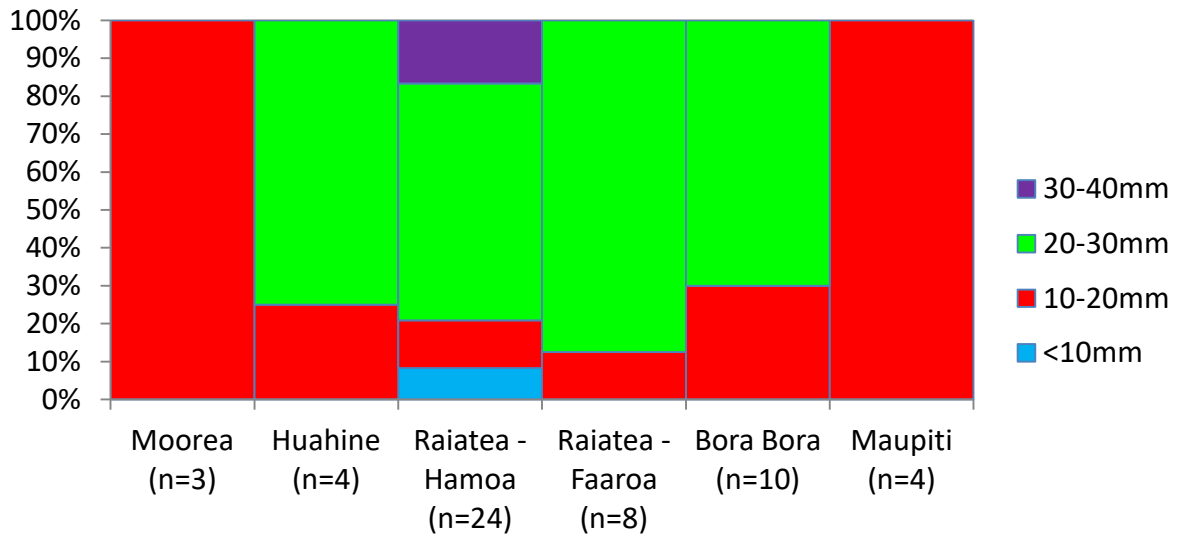
Flatworms in litter per m² (n=10)

area	1	2	3	4
<i>Platydemus manokwari</i>	0	0.1±0.32	0.1±0.32	0.2±0.42
<i>Bipalium kewense</i>	0	0.1±0.32	0	0
cf. <i>Anisorhynchodemus</i>	0	0	0	0.1±0.32
<i>Geonemertes pelaensis</i>	0	0	0	0.1±0.32

Platydemus age structure

Flatworms were assigned to four size classes. As the length of individual flatworms varies considerably as they move resting lengths were used. Although these measurements are approximate they do give an indication of the relative population structure in the different sites. From the data it is apparent that the high density populations have the greatest range of sizes, including both juveniles and large adults. Lower density sites are biased towards small adults. This may suggest a reduction in breeding in these areas (fewer juveniles) and food limitation (fewer large adults). These data may be suggestive of an expanding population in the north of Raiatea, with population growth having peaked at Faaroa bay, and on the islands of Huahine and Bora Bora, and with low, more stable populations on Moorea and Maupiti. The sporadic sightings reported from Tahiti (T. Coote pers. comm.) may also indicate similarly low populations. These interpretations are speculative at present and the ecology of this species needs further examination.

Fig. 25. *Platydemus* age structure on different islands



Platydemus densities (individuals per m²) recorded on different islands

Island	maximum	average	
Tahiti	0	0	known to be present
Moorea	0	0	observed
Huahine	2.0	0.67	
Raiatea	3.0	0.8-3.0	varies geographically
Tahaa	0	0	absent?
Bora Bora	0.2	0.1	
Maupiti	0	0	observed

Fig. 26. Flatworm species: *Platydemus manokwari* (Huahine); species A (Mt. Marau, Tahiti); cf. *Anisorhynchodemus* (Hamo, Raiatea); *Bipalium kewense* (Bora Bora)



***Euglandina* species distributions**

Two distinct forms of *Euglandina* were found, summarised as squat and elongate. The elongate form was recorded from Huahine (n=2), Raiatea (near Temehani Ute Ute, n=2) and Maupiti (n=1). The squat form was found on Tahiti (Mt. Marau, n=1), Moorea (n=1), Raiatea (Manuihi valley, n=1), Bora Bora (n=6) and Maupiti (n=4). These shell forms are known to correspond to distinct anatomical and genetic forms elsewhere and the differences between *Euglandina* species are currently being investigated (J. Slapcinsky pers. comm.).

Conclusion: status of surviving Society island partulids

The present study confirmed the survival of *Samoana annectens* and identified the extinct *Partula* on Maupiti island. Important data were gathered on the distribution and abundance of the invasive predators *Euglandina* and *Platydemus*. Research is now continuing into the ecology of the flatworm.

Euglandina is no longer the main threat as it is extremely rare in most areas. It may be extinct on Huahine, Tahaa, Bora Bora and Maupiti. There are periodic population resurgences in some valleys on Tahiti and Moorea and evidence of its continued survival was found at higher altitudes on Raiatea. Given the extremely eroded nature, and hence probable age of most of the shells, it seems that *Euglandina* populations collapsed before the arrival of *Platydemus* flatworms. Most *Lissachatina fulica* shells were of similar age, suggesting a similar timing in population collapse. As there are localised populations of *Lissachatina* surviving, the decline of this species cannot be attributed to *Euglandina* alone. The rise and collapse of both species can probably be explained by normal invasive population dynamics, where a ‘boom-and-bust’ pattern occurs. This was predicted for *Euglandina* (Gerlach 1994, 2001) but it was thought that the species would persist, sustained by abundant small leaf-litter snails. The disappearance of this fauna has removed the expected stabilising influence, resulting in complete collapse of most *Euglandina* populations. The cause of the loss of the small snails may be due to predation by the invasive ribbon worm *Geonemertes pleaensis*. This is known to be a snail predator (Gerlach 1998) but its impacts have largely been overlooked (C. Christensen pers. comm.). The surviving *Euglandina* populations are mainly at higher altitudes where relatively undisturbed native snail populations persist, providing a food source for the predators. However, these areas are climatically marginal for *Euglandina*, resulting in population instability.

Fig. 27. *Euglandina* forms: three recent shells (left) compared to two shells from Raiatea in 1992 (right). Recent shells: 2 x squat (Moorea, Raiatea), elongate (Huahine). 1992 shells: squat and elongate.



Platydemus is now the principal threat to partulids. At the high densities recorded on Raiatea it may have a major impact, but seems to be less of an issue on Tahiti and Moorea. It is mainly a terrestrial species but will pursue prey up trees, thus its impacts are likely to be most severe on terrestrial snails and species on low vegetation. Research is underway to determine how significant a threat it is to arboreal species and whether partulid populations could be established in areas where flatworm abundance has declined.

New records were made of other flatworm species (currently being identified), none of which appear to be significant snail predators (all were kept with a range of snail species for a week, with no predation recorded). Surveys of other snails species found that almost all Society island snails are now invasive species. The only non-partulid endemics found were *Nesiocina discoides*, *Omphalotropis huaniensis*, *O. viridis*, *Trochomorpha cressida*, *Succinea* spp., *Liardeia normalis* and *Elasmias peaesiana*. A large proportion of the other endemic species appear to be extinct. This is most certain in the large *Trochomorpha* species where three of the five species have been lost (*T. assimilis*, *T. swainsoni* and *T. typus*).

Of the 62 Society island partulid species, 24 are thought to survive at present. Monitored wild populations occur on Tahiti (*Partula clara*, *P. hyalina*, *P. incrassa*, *P. otaheitana*, *Samoana attenuata*, *S. burchi*, *S. diaphana*). In addition, in the late 1990s *P. affinis*, *P. compressa*, *P. cytherea* and *P. laevigata* survived in remote locations, outside of the range of permanently established *Euglandina* populations. Historically *P. jackieburchi* also occurred in some of these sites but continued survival has not been confirmed due to difficulties in distinguishing this species from *P. otaheitana*. Reintroduction of *P. nodosa* is currently being attempted. Thus there are probably 13 surviving Tahitian partulid species. It is probable that reintroductions will succeed with relatively small losses to *Euglandina* and *Platydemus*. Field surveys are still needed to confirm the survival of *P. compressa* (Viriviriterae plateau), *P. laevigata* (Teihomono plateau), *P. jackieburchi* (Mt. Aorai) and *P. cytherea* (highest parts of Mt. Marau).

Surviving wild Moorean species comprise *P. taeniata* and *S. attenuata*. With reintroductions currently being attempted for *P. mirabilis*, *P. mooreana*, *P. suturalis* and *P. tohiveana*. The impact of flatworms is a cause of concern but reintroduction seems to be achieving some success with *P. tohiveana* at least. Concentration of reintroductions near the *P. tohiveana* sites are likely to be successful with relatively small losses to predators. This would also facilitate monitoring.

On Huahine the present study has confirmed the survival of a population of *S. annectens*. These may be vulnerable to the large flatworm population on the island, especially as the occupied habitat has a low canopy. Reintroduction is planned for *P. rosea* and *P. varia*. The risk from *Platydemus* is higher on this island, but there are areas that may support a reintroduced *P. varia* populations. *P. rosea* is more difficult in that it was naturally associated with *Pandanus tectorius* and releases should use this same host plant, at least in the experimental phase.

Two species survived on Raiatea in the recent past: *P. meyeri* and *S. attenuata*. It was not possible to visit the only locality of *P. meyeri* and this still needs investigation. Given the scarcity of *Euglandina* at 800m on Raiatea it is probable that predation by this species is not significant at Mt. Toomaru (>1000m). This may also be the case for *Platydemus*, but both predators are a potential threat. *S. attenuata* was not located, the only evidence for its survival being two separate records, probably representing small relict populations. Reintroduction efforts for *P. hebe*, *P. garrettii* and *P. navigatoria* have been unsuccessful due to the very high numbers of flatworms in reintroduction sites. These should not continue until such time as *Platydemus* populations have declined, although experimental releases may provide valuable information prior to full reintroduction efforts.

There is no evidence of partulid survival on Tahaa since the 1990s, and from observations made in the present study any survival is unlikely. Similarly, all partulids appear to be extinct on Bora Bora and Maupiti. Of these Bora Bora appears to have habitat that could be used for conservation introduction of other partulids and from the number of shells still to be found it must have supported considerable partulid populations in the past. Experimental releases of Raiatean species should be considered, as these are more likely to succeed on Bora Bora than on Raiatea due to the lower abundance of predators on that island.

The Society islands snails (partulids in particular) probably represent the most rapid and extensive extinction event in history. Causes have ranged from habitat loss to predation, with *Euglandina*, *Platydemus*, and possibly *Geonemertes* being the main predators. The partulid extinction driven by *Euglandina* has now entered a new phase with the invasion by *Platydemus*. The present study has provided important data needed to

evaluate the likely future impacts of *Euglandina* and *Platydemus*. For some partulids this seems to offer some new hope for reintroduction and long-term survival. For others, there are new problems for which new solutions will need to be developed.

Acknowledgements

I am grateful to the support of everyone who provided financial assistance to this project. Equipment was provided by the Zoological Society of London and I am particularly grateful to Paul Pearce-Kelly for his continued enthusiasm and assistance. Trevor Coote provided a great deal of advice and information and help in the field on Tahiti and Moorea, excursions that were also facilitated by Eric Lenoble and Cindy Bick. Jean-Yves Meyer was also a great source of information and I am grateful for his efforts in trying to organise an expedition to climb Mt. Toomaru, and for his assistance and companionship on Temehani Ute Ute. On Raiatea Romy Tavaearii also provided valuable transport assistance and information.

References

- Gerlach, J. 1994. *The ecology of the carnivorous snail Euglandina rosea*. DPhil thesis, Oxford University
1998. The behaviour and captive maintenance of the terrestrial nemertine (*geonemertes pelaensis*). *J. Zool. Lond.* 246: 233-237
2001. Predator, prey and pathogen interactions in introduced snail populations. *Anim. Conserv.* 4: 203-209
2016. *Icons of Evolution: Pacific Island tree snails of the family Partulidae*. Phelsuma Press, Cambridge.
- Justine, J-L. et al. 2015. The invasive land planarian *Platydemus manokwari* (Platyhelminthes, Geoplanidae): records from six new localities, including the first in the USA. *PeerJ*

