Can Oceanic Island Endemic Partulid Tree Snails Survive the Anthropocene?

by

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DEDICATION

E momoli atu la’u fa’afetai i o’u matua matutua mo lo laua alofa ma le lagolagoina o mea oute fiafia iai. Fa’afetai tele lava mo le fa‘atupuina i totonu ia te au o le naunautaiga ma le malosi o le amio galue. Ou te tuuto fa’apitoa lenei su’esu’ega i lo‘u tamamatua ona o ana fautuaga atamai ma upu o le poto na aumaia ai a’u i le taimi tonu lenei ma fa’ataunu’u manuia ai lenei sini. Na e maliu ae le‘i mafai ona ou fa’auma ina lenei mea ae ou te mana‘o ia e iloa ou te alofa ia te oe mai le ta‘ele o lo‘u fatu ma lo’u agaga.

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ABSTRACT

Partulid tree snails are endemic to Pacific high oceanic islands and have experienced extraordinary rates of extinction in recent decades involving approximately half of the 120 described species. The main extinction agents are continental predators introduced as part of misguided biological control programs across Oceania. My research focused on surviving populations at either end of the familial range (eastern populations in the Society Islands and western populations in Near Oceania and the Marianas) that may hold clues as to how members of this clade may be able to survive in the Anthropocene. The first part of my dissertation concerned the island of Tahiti, where two endemic taxa, *Partula clara* and *Partula hyalina*, have differentially survived 40 years of predation by *Euglandina rosea*. Using historical databases, I found that higher clutch size was correlated with partulid survival on Tahiti. I further corroborated this association of survival with fecundity using birth rate data from captive populations and with parallel historical and captive demographic analyses of additional island populations: Moorea (Society Islands) and Guam and Saipan (Marianas Islands).

I also tested the role of a putative ecological "solar refuge" on one of the two valley survivors on Tahiti, *Partula hyalina*, with a white high albedo shell. This species regularly occurs in forest edges being exposed to prolonged direct sunlight, and in interior forests. I hypothesized that these edge habitats create "solar refuges" for surviving *P. hyalina* in which ambient solar irradiation conditions are significantly higher than those tolerated by foraging *E. rosea*. My results corroborate the hypothesis, although any protective effect gained from being in a "solar refuge" is absent on overcast days.

The second part concerns the enigmatic systematics, ecology and biogeography of Partulidae in the least-studied part of their familial range: the Near Oceania archipelagos of Papua New Guinea (PNG) and the Solomon Islands (SIs). A recent study on this regional fauna has uncovered highly atypical synanthropic distributions and cryptic multi-archipelago ranges, indicating a role for prehistoric humans in their distribution.

From 2012-2016, I have collected partulid tree snails targeting known type locality sites in both Papua New Guinea (PNG) and the Solomon Islands (SIs) as well Remote Oceania (Santa Cruz archipelago). Many of these species are very poorly studied but their taxonomy has been recently revised. Specimens were genotyped using Next Generation Sequencing (NGS) ddRADseq and a mitochondrial COI gene approach. The results indicated that only 5 corroborated species are represented in the region. In particular, I recovered a discrete Near Oceania clade composed of two species in PNG and the main SIs archipelago instead of the 4 nominal species currently recognized. One, *Partula grisea*, is restricted to littoral forest edges in PNG and the other, *Partula micans,* is spread throughout both PNG and the SIs. *Partula micans* is the oldest available name and therefore has taxonomic priority. A notable feature of *Partula micans* is its strikingly aberrant synanthropic ecology, a characteristic that is unprecedented for *Partula* and strongly implicating prehistoric human introduction as the dispersal mechanism. Currently, I lack evidence of a source population for *P. micans*' multi-archipelagic distribution raising compelling questions regarding its ecology and evolutionary life history. Finally, I summarized the main attributes enabling partulids to survive under anthropogenic impacts and highlighted prerequisites to developing a rational conservation strategy for the entire family.

CHAPTER 1

Introduction to the Study System

The loss of global biodiversity is among the most pressing ecological concerns of the 21st century (Cardinale *et al*., 2012; Hooper *et al*., 2012). A major driver of this loss has been the explosive growth in human populations since the beginning of the Industrial Revolution and the knock-on impacts of anthropogenic activities on natural ecosystems (Smith & Zeder, 2013; Waters *et al.*, 2016). Present day rates of extinction are 3 orders of magnitude above the background extinction rate (Pimm *et al.*, 2014; De Vos *et al.*, 2015) and >50% of terrestrial plants and animals are in danger of disappearing by the end of the 21st century (Braje & Erlandson, 2013; IUCN Red List). Conservation efforts are devoted mostly to vertebrates (Hoffman *et al.*, 2010) and to a small number of charismatic megafauna (Mace *et al.*, 2007). However, the highest number of recorded extinctions by any major taxonomic group of animals belongs to molluscs and not vertebrates: 42% of all 693 metazoan extinctions recorded since 1500 are molluscs (Lydeard *et al.*, 2004; Figure 1-1) and it has been recently estimated that up to 7% of land snails, in particular, may have already become extinct (Régnier *et al.*, 2015).

Biodiversity hotspots are of particular conservation interest because they are significant reservoirs of endemic biodiversity restricted to relatively small areas, such as the many small Pacific islands spread across Oceania containing endemic taxa. Regarding molluscan extinctions, the overwhelming number of known cases involves Pacific Island land snails (Régnier *et al.*, 2015; Régnier *et al.*, 2009; Figure 1-2). This pattern of extinction applies not just to land snails but it is also a common theme in other Pacific oceanic island terrestrial taxa such as birds [*i.e.* the Hawaii avifauna (Steadman, 1995), reptiles [(*i.e.* mekosuchine crocodiles in Vanuatu (Mead *et al*., 2002) and Fiji (Molnar *et al*., 2002)], and bats (Helgen *et al*., 2009; Koopman & Steadman, 1995).

The Pacific Ocean contains thousands of oceanic islands that have never been connected to continental landmasses and they represent some of the most isolated environments on earth (Neall & Trewick, 2008; Nunn, 1994; Kaplin, 1981). They receive their terrestrial biotas solely through dispersal from geographically distant source populations and from subsequent *in situ* diversification (Paulay, 1994). In general, classical oceanic island biotas start out with a depauperate and disharmonic composition, *i.e.*, large suites of taxa prevalent in continental ecosystems are missing (Carlquist, 1974). Such a composition acts to facilitate the survival of relict taxa, which may have been driven to extinction in continental settings, and the emergence of endemic adaptive radiations (Paulay, 1994).

These islands therefore represent highly distinctive evolutionary settings and they have attracted considerable biological interest for two very different reasons. Classically, they have been viewed as influential examples of evolutionarily rapid endemic species radiations (Baldwin & Sanderson, 1998; Givnish *et al*. 1995, Wagner & Funk, 1995). Studies on island biotas have generated a huge body of both empirical and theoretical literature, providing the clearest illustrations for species radiation and speciation (Baldwin, 1997; Bengtson & Enckell, 1983; MacArthur & Wilson, 1967; Mayr, 1963). Some notable examples of endemic speciation and radiation on islands include Darwin's finches on the Galapagos Islands (McKay & Zink, 2014; Cain, 1984), as well as drosophilids and honeycreepers on Hawaii (Freed *et al*., 1987; Carson & Kaneshiro, 1976).

However, oceanic island species are exceedingly vulnerable to human-introduced continental predators (Woinarski, 2010) and the rate of such introductions is accelerating as a result of modern societies becoming increasingly globalized with trans-oceanic trade now taking up a large and growing fraction of the world economic activity (Ehrenfeld, 2005). This has had a huge impact on species distributions even in the most remote oceanic islands inhabited by humans. Because they have evolved in isolation, oceanic island endemics often lack highly developed defensive or competitive capabilities (Vermeij, 1999; Solem, 1979; Carlquist, 1974) and, unfortunately, are now best known as the victims of mass extinction events (Vermeij, 1999; Paulay, 1994). Opportunistic continental predators such as cats, rats, dogs, and mongooses have been responsible for a number of island extinctions and extirpations not only worldwide, but also across multiple taxa (Watari *et al*., 2008; Nogales *et al*. 2004; Iverson, 1978). For instance, on the island of Guam, the accidental introduction of the brown tree snake (*Boiga irregularis*) in the 1950s has resulted in a cascade of extirpation impacting the island's endemic forest fauna (Clark & Savarie, 2012).

Partulidae as a conservation study system

One of the most infamous recent cases of mass extinctions involves Partulidae, a family of land snails endemic to tropical Pacific high oceanic islands: approximately half of its species have gone extinct or been extirpated (extinct in the wild) over the past 40 years (Coote & Loéve, 2003; Cowie, 1992). Partulidae is an ancient family of land snails derived from late Paleozoic pulmonate ancestors (Slapcinsky & Kraus, 2016; Cowie, 1992; Kondo & Burch, 1972). There are ~120 described species comprising 5 genera – *Partula* (89 species), *Samoana* (23 species), *Eua* (4 species), *Palaopartula* (3 species), and *Sphendone* (1 species) (Slapcinsky & Kraus, 2016; Figure 1-3). This land snail family has an extraordinary collective distribution, extending across 10,000 km of Oceania from the Marianas and Palau in the northwest to the Marquesas and Australs in the southeast (Figure 1-3), although most species are endemic to single islands (Cowie, 1992). Approximately half of the 120 partulid species are endemic to a single hot-spot archipelago: the Society Islands of French Polynesia. This hyperdiverse regional fauna attracted a lot of interest from evolutionary biologists for over a century, starting with the classic work of H.E. Crampton (Crampton, 1932; Crampton, 1916), due to their high levels of shell phenotypic (color, pattern, shape, size, and chirality) polymorphisms (Cowie, 1992).

Partulid species are predominantly arboreal, occurring on a wide variety of tree species (Murray *et al.*, 1982). They are nocturnal forest detritivores that aestivate during the daylight on trees and shrubs (Murray *et al.*, 1982). Individuals rarely disperse more than a few meters during their lives (Murray & Clarke, 1984) and, in favorable habitats; they achieved densities of 1-10 m^2 (Murray, 1972). Partulids are ovoviviparous hermaphrodites that typically reproduce by non-reciprocal copulation (Lipton & Murray, 1979), although some species are also capable of self-fertilization (Murray and Clarke, 1966; 1976a; 1976b). Sexual maturity is typically attained within a year and mature individuals can reproduce steadily throughout their adult lives, *e.g.*, lab-raised *Partula taeniata* gave birth to single juveniles at approximately 20 day intervals (Murray & Clarke, 1966) and this Moorean species can live for >5 years in the wild (Murray & Clarke, 1984).

Over the past 60 years, a two-step sequence of continental snail introductions has been repeated across much of Oceania, with devastating consequences for endemic Pacific Island land snails, including Partulidae (Cowie, 1992; Civeyrel & Simberloff, 1996). The initial step involved importation (primarily for food) of the Giant African land snail *Lissachatina fulica* (Bowdich, 1822), a broad-spectrum herbivore. Escaped individuals were viewed as a serious agricultural pest, leading to importation of a wide spectrum of putative *L. fulica* continental predators. These included a suite of carnivorous snail species, most notably the North American rosy wolf snail, *Euglandina rosea* (Férrusac, 1821). This predator proved much more effective at eradicating endemic land snail species than its intended target species, *L. fulica* (Civeyrel & Simberloff, 1996) and it has been implicated in the extinction of at least 134 terrestrial snail species (Régnier *et al.*, 2009). A significant fraction of that total involves the endemic Pacific Island land snail family Partulidae: an estimated 32-39% of 104 species in the genus *Partula* are now considered extinct, another 9% are extinct in the wild and 50% are classified as threatened (Gerlach, 2016).

Strategic goal of my thesis

The fundamental question regarding partulid conservation biology is whether they can survive modernity outside of captivity? To address this question, my thesis focus is on the parts of their range where at least some species show evidence of being able to survive anthropogenic impacts. Knowing what factors have enabled the persistence of these surviving taxa may help develop a rational conservation plan not only for the remnant partulid species but also for other threatened Pacific Island endemics. Chapters 2-4 of my thesis concern the endemic species of the Marianas and Society islands two archipelagos at opposites ends of the familial range for which robust historical demographic data are present that predate predator introductions. Chapter 5 concerns the partulids of Near Oceania, where preliminary data indicate that a number of nominal species may be synanthrophic. My results collectively show that with proactive, targeted conservation steps, it may still be possible to protect the surviving lineages in Near Oceania, the Marianas and the Society Islands.

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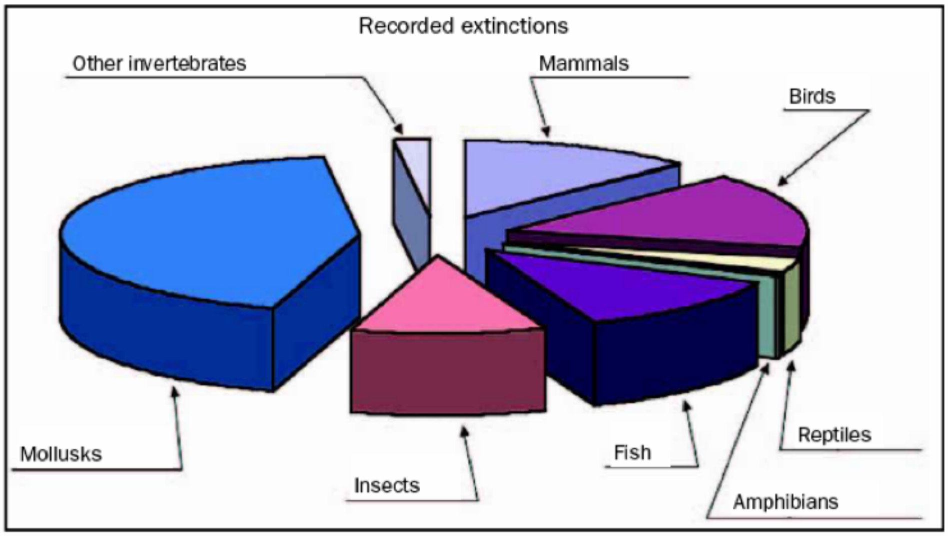

Figure 1–1. Proportion of recorded extinctions by major taxonomic groups of animals. Data are from the 2002 IUCN Red List of Threatened Species (www.redlist.org) (Lydeard *et al*., 2004).

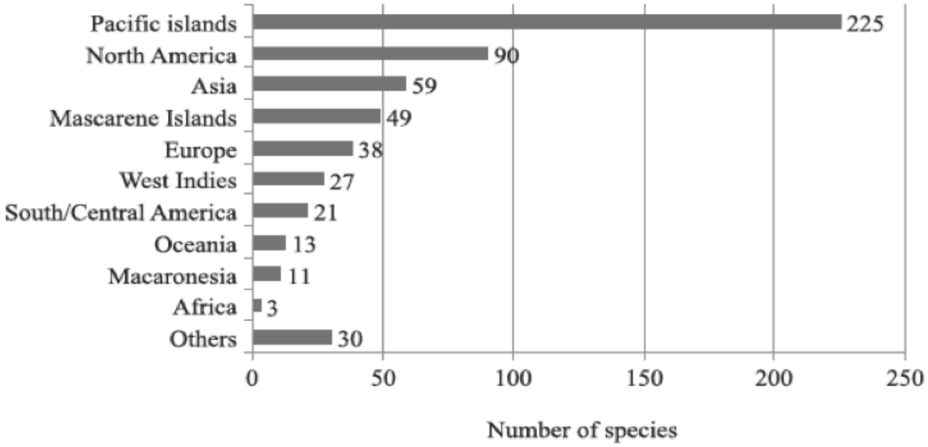

Figure 1–2. Geographical distribution of extinct molluscs with the most recorded from Pacific Island land snails (Regnier *et al*., 2009).

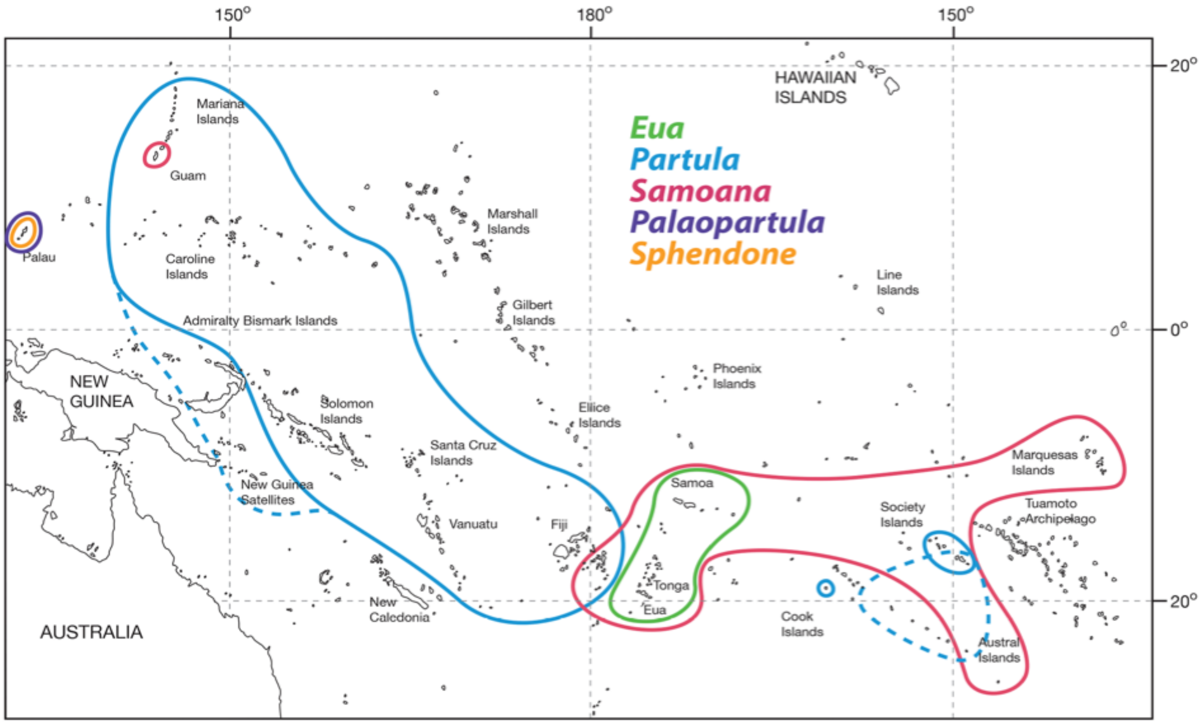

Figure 1–3. Partulidae distribution range map showing the complex distribution patterns of the 5 genera and inferred anthropogenic introductions in Papua New Guinea and Cook/Austral Islands (dashed lines) modified from Lee *et al*., (2014) and Slapcinsky & Kraus (2016).

CHAPTER 2

Differential Survival Among Tahitian Tree Snails During a Mass Extinction Event: Persistence of the Rare and Fecund

Abstract

The deliberate introduction of the rosy wolf snail *Euglandina rosea* to the Society Islands in the 1970s led to the mass extirpation of its rich Partulidae (Pilsbry, 1900) fauna, comprising approximately half of all species in this Pacific island tree snail family. On Tahiti ongoing field surveys have documented the survival of two of seven endemic species of *Partula* (*P. hyalina* and/or *P. clara*) in 38 valleys. *E. rosea* is now a potent extinction agent across Oceania and determining the factors enabling these two taxa to endure may have wide conservation import. I hypothesized that *P. hyalina* and *P. clara* have survived because they were the most abundant and/or widespread species and that they will eventually become extinct. I lack demographic data contemporaneous with predator introduction, but an early 20th century study by H.E. Crampton provides historical demographic data for intact Tahitian partulid populations. Crampton found that *P. clara* and *P. hyalina*, although widespread, were consistently rarer than their now-extirpated congeners, including in the 23 valleys he surveyed that retain surviving populations. Given this result, and the recent finding that *P. clara* and *P. hyalina* comprise a discrete founding lineage in Tahiti, it is plausible that some shared biological attribute(s) may have contributed to their survival. Crampton recorded the clutch sizes of thousands of gravid Tahitian partulids and found that these two taxa had higher instantaneous mean clutch sizes than did co-occurring

congeners. Higher fecundities may have contributed to the survival of *P. hyalina* and *P. clara* in the valleys of Tahiti.

Introduction

Oceanic islands represent some of the most isolated habitats on earth and their endemic biotas are characterized by small ranges and the absence of highly co-evolved defensive capabilities, such as anti-predator behaviors and morphologies (Paulay, 1994; Vermeij, 1999; Roff & Roff, 2003; Fullard *et al*., 2007). Consequently, island biotas are exceptionally vulnerable to introduced continental predators (Paulay, 1994; D'Antonio & Dudley, 1998). This is perhaps best exemplified by Guam's 'empty forest' (Redford, 1992) phenomenon, where a single introduced predator, the brown tree snake (*Boiga irregularis*), has severely impacted the endemic forest fauna (Savidge, 1987; Wiles *et al*., 2003; Mortensen *et al*., 2008), prompting extraordinary conservation interventions (Clark & Savarie, 2012).

Another alien predator, the carnivorous rosy wolf snail *Euglandina rosea*, has also had an outsized impact on oceanic island endemic faunas, being implicated in the extinction of at least 134 terrestrial snail species (Régnier *et al*., 2009). A North American native, *E. rosea* stalks its gastropod prey by following their mucous trails, consuming small prey whole and larger individuals piecemeal (Gerlach, 2001; Shaheen *et al*., 2005; Davis-Berg, 2012). It is highly mobile and can climb trees, a detrimental characteristic for many arboreal Pacific island terrestrial snails (Kinzie, 1992; Meyer & Cowie, 2011). *E. rosea* was introduced to multiple Pacific island archipelagos in a misguided strategy to control outbreaks of the introduced giant African snail *Lissachatina fulica*, most notably to the Hawaiian Islands in 1955 (Cowie, 1998) and to the Society Islands in 1974 (Coote, 2007). It rapidly extirpated large numbers of endemic land snail species on both archipelagos including members of the Achatinellidae in Hawaii (Hadfield *et al*., 1993) and Partulidae in the Society Islands (Clarke *et al*., 1984).

The loss of Society Islands Partulidae has been of particular concern because this hot spot archipelago is home to c. 50% of partulid species diversity (Cowie, 1992). It has also been the main setting for 20th century partulid studies, starting with the classic work of H. E. Crampton (1916, 1932) and continuing with decades of research by B. Clarke, J. Murray, M. Johnson and associates (Clarke & Murray, 1969; Murray & Clarke, 1980; Johnson *et al*., 1993). The collapse of Society Island partulid populations following the introduction of *E. rosea* prompted the emergency establishment of off-archipelago captive populations for 15 Society Island species (Murray *et al*., 1988; Tonge & Bloxam, 1991; Pearce-Kelly *et al*., 1997). Until recently, only 5 of 61 endemic Society Islands Partulidae species were thought to persist in the wild (Coote & Loève, 2003) but subsequent field surveys have found scattered extant populations on Raiatea, Moorea and Tahiti representing four additional species (Lee *et al*., 2008, 2009). Seven of these surviving taxa (*Partula otaheitana, Partula hyalina, Partula clara, Partula affinis, Samoana attenuata, Samoana burchi, Samoana diaphana*) occur on Tahiti, the largest and highest island in the archipelago (Coote, 2007; Lee *et al*., 2007a, 2009). The predominant Tahitian pattern is one of low elevation extirpation and montane persistence: partulid survivors are most common in cloud forest refuges of >1000 m altitude (Coote, 2007; Lee *et al*., 2007a, 2009), where the predator's activity is probably impaired by cooler temperatures (Gerlach, 1994, 2001). However, extensive field surveys beginning in 2004 have located small clusters of low elevation survivors in a number of Tahitian valleys (Coote, 2007), currently totalling 38 (Figure 2-1, Table 2-1). Of Tahiti's eight species of *Partula*, two now dominate low elevation extant populations; i.e. 37 of

38 of the valleys with known survivors were exclusively populated by *P. clara* and/or *P. hyalina* (Figure 2-1, Table 2-1).

Partula hyalina and *P. clara* are closely-related species, distinguished by shell coloration, that together represent a discrete Tahitian founder lineage of Moorean origin (Lee *et al.* , 2009). Their ability to endure almost 40 years of *Euglandina rosea* predation pressure in the valleys of Tahiti is surprising because predation models predict partulid extirpation within 3 years of initial predator contact (Gerlach, 2001). I was interested in understanding what aspect(s) of their biology underlies this survival, not just for their individual conservation, but also for the possible implications regarding the survival of many endemic land snails across Oceania now threatened by *E. rosea* (Régnier *et al*., 2009).

The inverse relationships of population size (Pimm *et al*., 1988; Schoener & Spiller, 1992) and geographical range (Payne & Finnegan, 2007; Cardillo *et al*., 2008) to extinction risk have been well documented. The initial hypothesis is therefore that *P. hyalina* and *P. clara* have survived because they were the most abundant and/or widespread species in Tahitian valleys and that they too will eventually be driven to extinction by the predator. To test this, I ideally need a detailed census of Tahitian partulid populations contemporaneous with the 1974 introduction of *Euglandina rosea*. Although such a resource is not available, I do have access to a century-old dataset of Tahiti's intact partulid populations. During 1906–1909 Crampton (1916) surveyed and collected Tahitian valley tree snail populations, publishing a detailed account that has been lauded as 'among the finest work ever done on the evolution of land snails' (Gould, 1994). I therefore have an extensive demographic profile of intact Tahitian partulid populations with individual valley-level resolution. This allows us to calibrate present day extant populations with their pre-*Euglandina rosea*-introduction equivalents across the island as a whole, as well as for the 23 valleys Crampton surveyed that retain surviving populations (Table 2-1).

Methods

Crampton (1916) systematically surveyed the partulid populations of Tahiti. He divided the island of Tahiti into five subunits: Tahiti-Nui, comprising 4 quadrants (north, south, east and west) and the peninsula Tahiti-Iti (Taiarapu). Over four annual surveys during 1906–1909 he surveyed a large fraction of the coastal valleys present in each geographical subunit: 10 western, 20 southern, 10 northern, 10 eastern and 12 in Tahiti-Iti. Crampton (1916) did not detail his sampling methodology except to state that he walked into each valley along the primary trails during daylight hours, collecting snails from the adjacent trees and vegetation. He was particularly interested in population-level variation and typically obtained large sample sizes (hundreds) from each valley.

Modern day surveys of Tahitian valleys for surviving partulids largely follow Crampton's (1916) methodology, except that the snails are much rarer and that more valleys have been surveyed (Coote, 2007). Each survey of a valley is restricted to a single day and involves walking along existing forest trails as deep as possible into the valley, stopping at regular intervals for intense searches of adjacent 5 m^2 patches of habitat. Where snails are encountered, all individuals within the immediate patch are enumerated within a 20-minute search period (Coote, 2007).

At the end of each day's sampling Crampton (1916) preserved the snails for later analyses (identification, measurement, dissection) in his Columbia University laboratory. In total, Crampton (1916) collected 24,085 individuals of seven Tahitian species: *P. affinis* [as *P. otaheitana affinis*; reclassified by Kondo (1980)], *P. clara, Partula filosa, P. hyalina, Partula* *nodosa, P. otaheitana* and *Partula producta*. I extracted his frequency data for each valley surveyed, combining data for subspecies categories into totals for each species. Although the scale of Crampton's (1916) collecting was extraordinary by today's standards, it is unlikely to have been the main driver in their subsequent extirpation. His sampling was restricted to snails adjacent to the main valley paths and, as late as 1970, the valleys of Tahiti continued to support very significant populations of partulids (John B. Burch, pers. comm.).

Partulids are ovoviviparous hermaphrodites and adults typically contain a small number of progeny at different stages of development, giving birth to single young at multi-week intervals (Murray & Clarke, 1966). Crampton (1916) dissected the adults he collected, recording the number of eggs, embryos and shelled young present in individual gravid female reproductive tracts when collected (i.e. instantaneous clutch size). He presented these data as means per valley population for five species: *P. affinis, P. filosa, P. nodosa, P. otaheitana* and *P. producta*. As a result of the relatively low abundance of *P. clara* and *P. hyalina*, he calculated their mean instantaneous clutch sizes over multiple valleys, grouped into his five geographical subunits.

I compiled Crampton's (1916) mean instantaneous clutch size data, combining his subspecies data into single species values for each valley/quadrant. I then calculated estimates of mean clutch sizes across the entire island for each species.

Results

Crampton (1916) calculated the relative frequency of each species he collected across Tahiti from 1906 to 1909 (Figure 2-2). Of the seven species of *Partula* he collected on Tahiti, *P. otaheitana* was the most abundant (a total of 18,955 individuals were collected) and the most widespread, being found in 51 of the 62 valleys surveyed. It was the most numerous partulid species in 48 of the 51 valleys in which it was recorded, usually comprising >90%, of all individuals collected in each valley (Appendix I).

Partula nodosa was the second most abundant Tahitian partulid species collected by Crampton (1916). The 1,922 specimens he collected (Figure 2-2) had a regional distribution within the island, being restricted to seven western valleys and predominating in three of them (Appendix I). *P. affinis* was almost as numerous: 1,560 individuals (Figure 2-2) were collected from 10 valleys distributed in the northern, eastern and southern quadrants, as well as in Tahiti-Iti (Crampton, 1916). In eight of these valleys *P. affinis* predominated, comprising >80% of all tree snails collected (Appendix I). The two rarest species collected, *P. filosa* and *P. producta* (Figure 2-2), were both single-valley endemics. They formed minor components of their respective valley partulid totals (*P. filosa* 17% and *P. producta* 6%; Appendix I) and both species are now extinct.

A century ago *P. clara* and *P. hyalina* were both widespread in Tahiti, recorded from 43 and 51 valleys, respectively (Crampton, 1916). Although they approached *P. otaheitana*'s extensive range across the island of Tahiti, *P. clara* and *P. hyalina* were much rarer; the island-wide survey yielded 819 and 589 individuals respectively (Figure 2-2). Each of these two species typically composed <5% of the tree snails collected in individual valleys, with their highest incidence being 28% for *P. clara* and 21% for *P. hyalina* (Appendix I).

Ongoing field surveys of Tahitian valleys since 2004 have encountered remnant populations of *P. clara* and/or *P. hyalina* in 38 valleys (Coote, 2007, unpubl. data; Figure 2-1, Table 2-1). I cross-referenced these with the 64 valleys that Crampton surveyed in 1906–1909 and identified 23 valleys containing present day survivors that were also collected by Crampton (Table 2-1). Figure 2-3 shows that, a century ago, the relative frequencies of *P. clara* and *P.*

hyalina among the 23 Tahitian valleys they survive in today were not exceptional, but closely matched their relative frequencies across the island as a whole (Figure 2-2). *Partula otaheitana* was the most common species and *P. clara* and/or *P. hyalina* were minor constituents. This general pattern was maintained at the level of individual valleys with the exception that *P. otaheitana* was replaced as the locally dominant species by either *P. affinis* or *P. nodosa* in a few valleys (Appendix I). *Partula clara* survives today in three valleys (Fautaua, Ahonu and Faarapa; Table 2-1) where it was sufficiently rare a century ago undetected by Crampton, despite his intensive collecting (*e.g.* his Fautaua Valley sample size was 1,084 snails). Given the very low migration rates of partulid tree snails (*e.g.* 1-10 m per year; Murray & Clarke, 1984) I consider it likely that these three valley populations of *P. clara* represent local survivors rather than de novo colonists from other valleys. The formerly locally dominant species in these three valleys, *P. otaheitana*, has been extirpated, despite having being at least 2 to 3 orders of magnitude more common than the surviving *P. clara*.

Figure 2-3 is a summary of Crampton's (1916) mean instantaneous clutch sizes for Tahitian valley partulids. The surviving taxa, *P. clara* and *P. hyalina*, had markedly higher clutch sizes than their now-extirpated congeners.

Discussion

The introduction of *Euglandina rosea* to Tahiti in 1974 exposed naïve endemic tree snails to an uncontrolled predator–prey experiment in which each valley population represented a discrete iteration. Outcomes in 37/38 valleys with known survivors have been strikingly uniform: persistence of two of seven endemic Tahitian species of *Partula: P. clara* and/or *P. hyalina* (Figure 2-1; Table 2-1). Our initial hypothesis, that the surviving taxa endured because they were the most abundant and/or widespread species, is clearly refuted by Crampton's (1916) data. A century ago these two species were relatively rare, typically representing <5% of the original species diversity in most valleys, including those valleys where they still persist (Figure 2-3; Table 2-1). Although *P. hyalina* and *P. clara* were widely distributed, this cannot explain their survival relative to the widespread, co-occurring and much more abundant *P. otaheitana*, now completely extirpated from the valleys of Tahiti (Coote, 2007; Figure 2-1).

Molecular phylogenies have shown that *P. clara* and *P. hyalina* are two color morphs of a founding lineage that is distinct from other Tahitian congeners (Lee *et al.*, 2007b, 2009). It is therefore plausible that some shared phylogenetic trait has contributed to their differential survival. One such potential trait is evident in Crampton's (1916) dataset: *P. clara* and *P. hyalina* exhibited similar instantaneous clutch sizes that were markedly higher than those of their extinct congeners (Figure 2-4). These data raise an obvious paradox regarding the population structure of tree snails in Tahitian valleys in 1906–1909. If mean clutch sizes in *P. clara* and *P. hyalina* were so much higher, why were they so rare relative to three of their congeners, especially *P. otaheitana*? This discrepancy implies that, a century ago, *P. clara* and *P. hyalina* were inferior competitors to their now-extirpated Tahitian valley congeners.

Species with a low intrinsic rate of increase, as a result of factors such as low fecundity, are at increased risk of extinction from stochastic events (Beissinger, 2000). Island endemics with greater reproductive effort are therefore predicted to have a higher likelihood of surviving the introduction of non-native predators. In the Guam avifauna, for example, species with larger clutch sizes have exhibited better survival (Wiles *et al.*, 2003). Introduction of the alien predator *E. rosea* to the Society Islands affected the population dynamics of local partulids by increasing their mortality rates (Clarke *et al.*, 1984). The significantly higher instantaneous clutch sizes of

P. clara and *P. hyalina* relative to their extirpated congeners (Figure 2-4) may be a major factor contributing to their continued survival in Tahitian valleys.

However, there are inherent shortcomings in Crampton's (1916) data that complicate the inference of meaningful reproductive rate comparisons among Tahitian partulids. Instantaneous clutch size estimates were compiled from diverse valleys and individual valley-level clutch size estimates are not available for the two surviving taxa, making within-valley comparisons of survivors and non-survivors impossible. In addition, the exact gestation period is unknown for individual Tahitian species. I cannot at present rule out the possibility of longer gestation periods in *P. clara* and *P. hyalina* than in the extirpated species, a developmental pattern that could yield higher instantaneous clutch sizes (Figure 2-4) but not necessarily higher birth rates.

The impact of introduced predators may vary across island microhabitats; e.g. in addition to larger clutch sizes, survival in the Guam avifauna is associated with the ability to nest in locations inaccessible to the brown tree snake (Wiles *et al*., 2003). On Tahiti more low elevation sites with known survivors (Figure 2-1; Table 2-1) contain *P. hyalina* (31 of 38) than *P. clara* (20 of 38) and this outcome may reflect microhabitat differences among the two taxa. Crampton (1916) noted a discrete distributional trait of *P. hyalina* that distinguished it from its Tahitian congeners. In addition to occurring in dense forest (the typical partulid habitat) he regularly observed *P. hyalina* at forest edges and clearings where it was exposed to prolonged direct sunlight. *P. hyalina* has a distinctively white shell and a correlation between light shell coloration and an enhanced ability to withstand exposure to direct sunlight is well known among land snail species (Jones, 1973, 1982; Hazel & Johnson, 1990; Ozgo, 2011). If *E. rosea* has a lower tolerance of direct sunlight, it is possible that this microhabitat distinction plays an additive role in the survival of *P. hyalina*.

The persistence of two of seven species of endemic Tahitian *Partula* under selection pressure from an introduced continental predator has some parallels with the fate of Guam's avifauna (Wiles *et al.*, 2003). In both cases endemic species with larger clutch sizes exhibited better survival, being able to persist in the presence of the predator for multiple decades (40 years on Tahiti, 60–70 years on Guam). I suspect that this general pattern may also apply to diverse clades of endemic taxa across Oceania. If so, this would provide important guidelines for prioritizing limited conservation resources for the preservation of Pacific island species that are threatened with extinction. For instance, when a novel introduced predator appears on an island, it may be appropriate to give endemic prey species with lower reproductive potential the highest immediate conservation priority.

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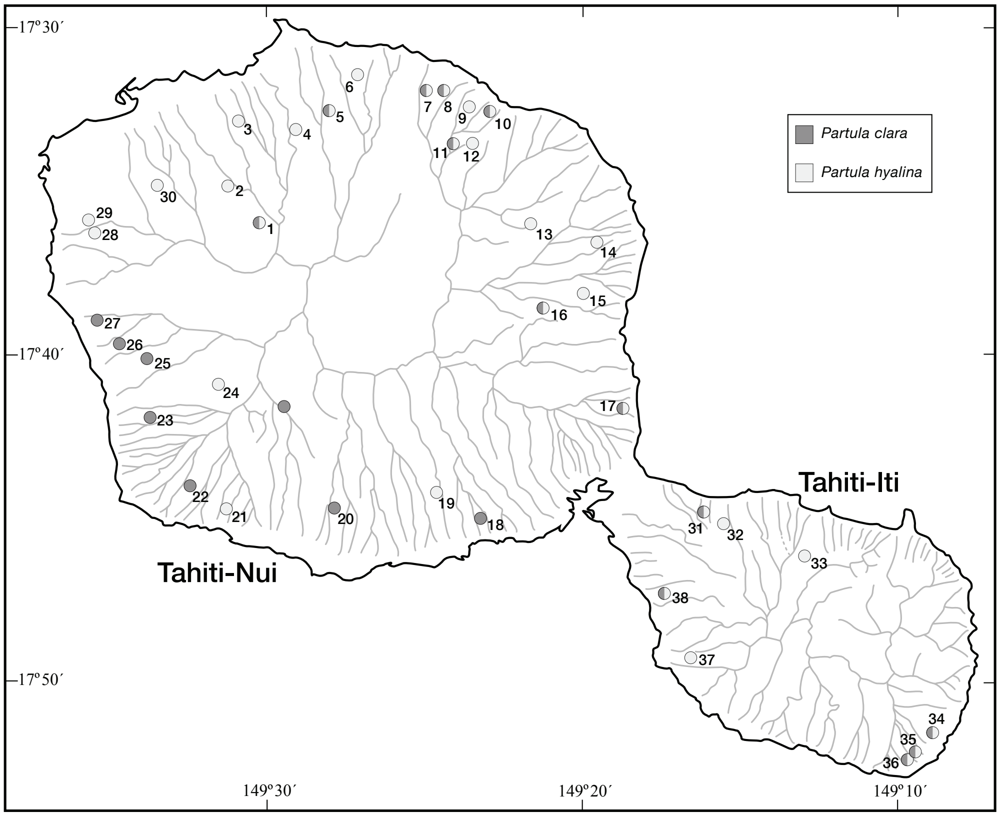

Figure 2–1. Map of Tahiti showing the distribution of surviving low elevation partulid populations detected by Trevor Coote (2007; pers. observ.) during field surveys he performed from 2005-2010. The survivors in 37/38 valleys were exclusively composed of *P. clara* and/or *P. hyalina*. A third species, *P. affinis* was found in one valley (Faaroa (36)), together with *P. clara* and *P. hyalina*. See Table 2-1 for the names of specific valleys and for frequency data of survivors.

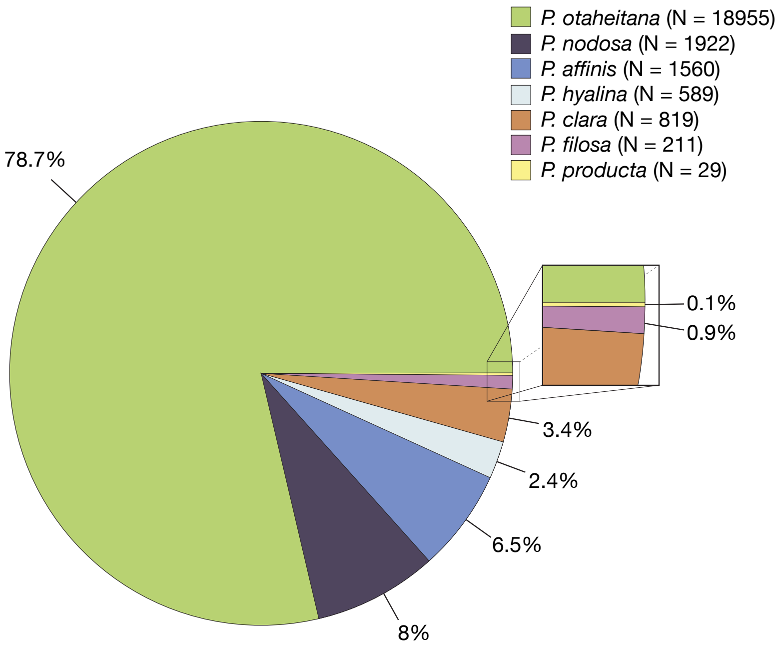

Figure 2–2. Pie chart showing the relative frequencies of 7 endemic species of Tahitian *Partula* sampled by Crampton (1916) among all 62 valleys he surveyed from 1906-1909.

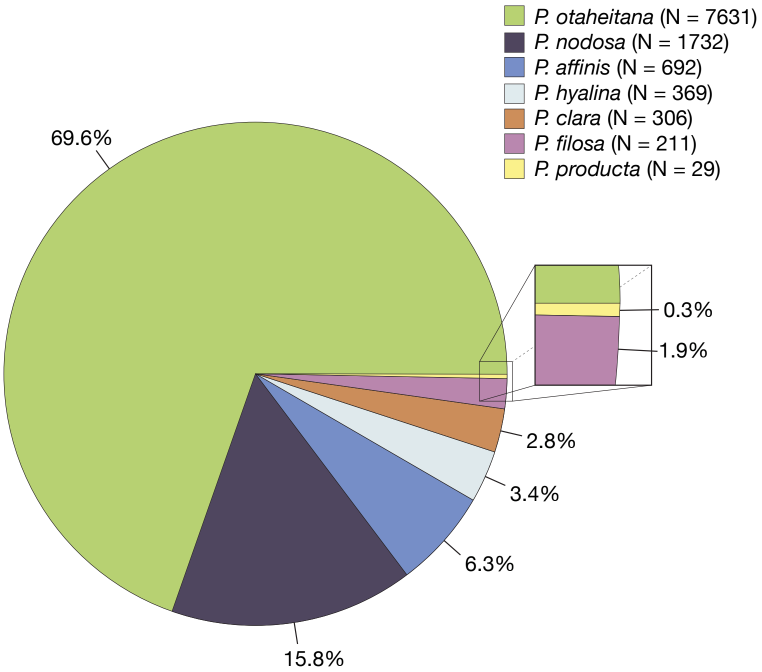

Figure 2–3. Pie chart showing the relative frequencies of 7 endemic species of Tahitian *Partula* sampled by Crampton (1916) from 1906-1909 among 23 Tahitian valleys that retain recent survivors (Table 2-1).

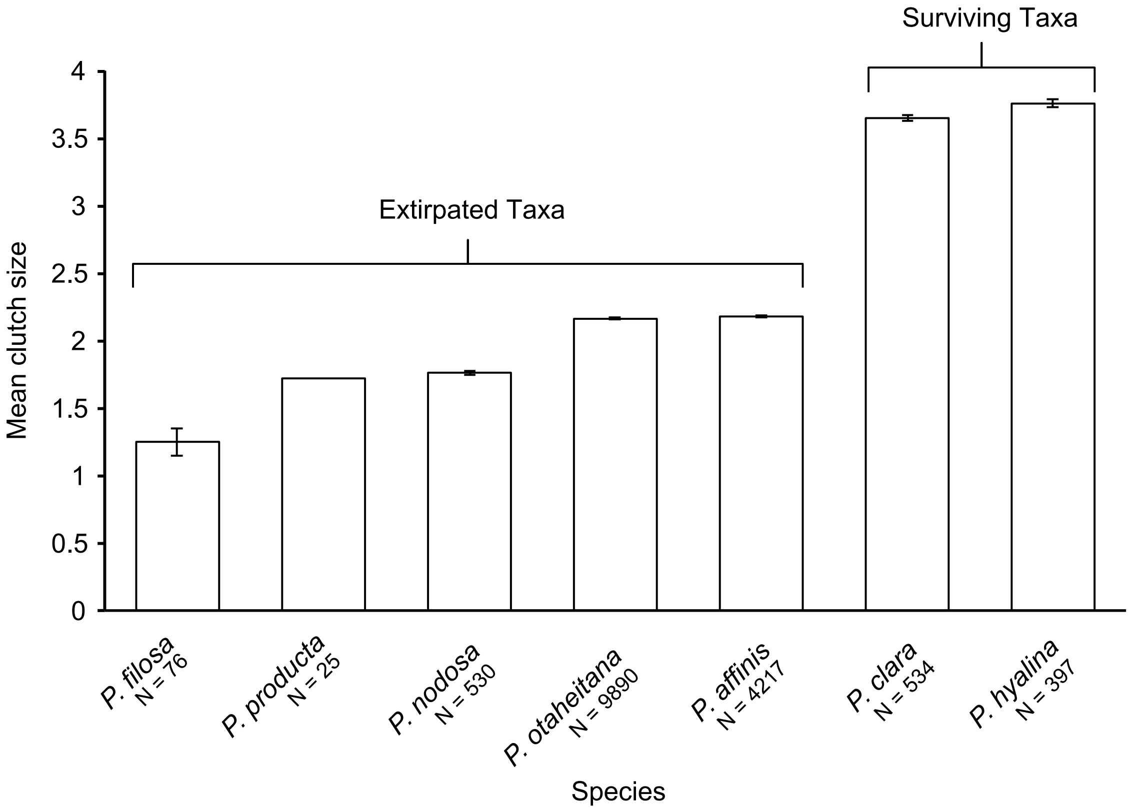

Figure 2–4. Mean instantaneous clutch sizes for 15,669 gravid individuals of 7 partulid species sampled by Crampton (1916) across 64 Tahitian valleys during 1906-1909. Standard error bars are included for all taxa except for *P. producta* (one sampling event). *P. clara* and *P. hyalina* are labeled as surviving taxa, because they dominate extant low elevation partulid populations on Tahiti (Figure 2-1). The remaining 5 species, labeled as extirpated taxa, are absent from Tahitian valleys; with the exception of one valley population of *P. affinis* (Figure 2-1)

Table 2-1. The 38 Tahitian valleys with surviving low elevation populations of *Partula clara*, *Partula hyalina* and *Partula affinis* detected by T. Coote (2007, unpubl. data) during 2004-2010 (given as number of snail populations and/or number of snails located per 20-minute search), and the species and number of snails in 23 of these 38 valleys where Crampton (1916) collected partulids during 1906-1909. The valley names used by Crampton (1916) are indicated in parentheses if they differ from the current names. See Figure 2-1 for numbered locations of the valleys.

	Coote		
Valley	No. of snail populations[1,2]	Snails per 20-minute search[2]	Crampton's counts of adult snails per valley[2]
Tahiti-Nui			
1, Fautaua	Several (*hy, cl*)		129 (*hy*), 955 (*otah*)
2, Fautaua-Faaiti	1	10 (*hy*)	
3, Nahoata (Pirai)	Several (*hy*)		55 (*hy*), 211 (*filo*), 988 (*otah*)
4, Tuauru	1 (*hy*)		14 (*hy*), 374 (*aff*)
5, Ahonu	2 (*hy, cl*)	5 (*hy*)	5 (*hy*), 295 (*otah*)
6, Orofara	1 (*hy*)		
7, Puhi	2 (*hy, cl*)	2 (*cl*)	
8, Faarapa (Farapa)	Several	8 (*hy*), 4 (*cl*)	9 (*hy*), 591 (*otah*)
9, Farromai (Faarumai)	1	2 (*hy*)	12 (*hy*), 1 (*cl*), 353 (*otah*)
10, Haapoponi	Several	27 (*hy*), 7(*cl*)	
11, Onohea-Faaiti	2	12 (*hy*), 17 (*cl*)	
12, Onohea-Faarahi (Tiarei)	1	3 (*hy*)	1(*hy*), 166 (*otah*)
13, Tahaute (Mahaena)	1	2 (*hy*)	2 (*hy*), 3 (*cl*), 147 (*otah*)
14, Faaiti	1	2 (*hy*)	
15, Faatautia	1	2 (*hy*)	12 (*aff*)
16, Vaiiha (Papeiha)	2	11 (*hy*), 2 (*cl*)	6 (*hy*), 3 (*cl*), 273 (*otah*)
17, Vaitoare	Several	24 (*hy*), 3(*cl*)	
18, Vaioo	2	8 (*cl*)	
19, Faurahi (Faarahi)	1 (*hy*)		2 (*hy*), 10 (*cl*), 467 (*otah*), 29 (*prod*)
20, Taapua (Taharua)	1	1 (*cl*)	2 (*hy*), 2 (*cl*), 325 (*otah*)
21, Afererii	1	1 (*hy*)	
22, Tereia (Tereehia)	2	4 (*cl*)	33 (*cl*), 130 (*otah*)
23, Vaipoe (Atitara)	2	10 (*cl*)	36 (*cl*), 154 (*otah*)
24, Orofero (Orofere)	Several (*hy*)		2 (*hy*), 49 (*cl*), 18 (*nod*), 197 (*otah*)
25, Tiapa (Aoua)	2	14 (*hy*)	19 (*hy*), 67 (*cl*), 396 (*nod*), 650 (*otah*)
26, Papehue	1	1 (*cl*)	4 (*hy*), 35 (*cl*), 210 (*nod*), 143 (*otah*)
27, Maruapo (Maruapoo)	1	4 (*cl*)	11 (*hy*), 4 (*cl*), 795 (*nod*), 135 (*otah*)
28, Matatia (Taapuna)	Several	3 (*hy*)	13 (*hy*), 313 (*nod*), 225 (*otah*)
29, Tihiute	1 (*hy*)		
30, Tipaerui-Faaiti	1 (*hy*)		22 (*hy*), 937 (*otah*)
Tahiti-Iti (Taiarapu)			
31, Rarouri	Several (*hy, cl*)		
32, Tehoro	Several (*hy*)	1	11 (*hy*), 1 (*cl*), 306 (*aff*)
33, Ahaavini (Haavini)	1	1 (*hy*)	20 (*hy*), 40 (*cl*), 273 (*otah*)
34, Vaita	Several (*hy, cl*)		
35, Taapeha	Several (*hy, cl*)		
36, Faaroa	Several (*hy, cl, aff*)		
37, Vavi (Vavii)	1 (*hy*)		26 (*hy*), 22 (*cl*), 225 (*otah*)
38, Faaana	1 (*hy, cl*)		

[1]Several = > 2 scattered remnant populations, [2] *hy* = *Partula hyalina*, *otah* = *Partula otaheitana*, *filo* = *Partula filosa*, *aff* = *Partula affinis*, *cl* = *Partula clara*, & *nod* = *Partula nodosa*

CHAPTER 3

Survival Among Critically Endangered Partulids Is Correlated with Higher Clutch Sizes in The Wild and Higher Reproductive Rates in Captivity

Abstract

Endemic Pacific Island land snails are the planet's most endangered taxa and many have fallen victim to misguided biological control programs involving the rosy wolf snail, *Euglandina rosea*. The family Partulidae has been heavily impacted but a recent study of Tahitian species found that survivors had differentially higher clutch sizes. Here, I further tested the inference that higher fecundities may promote survival of *Partula* species by incorporating historical field demographic data from additional island populations (Guam, Saipan and Moorea) that collectively span the range of the family, as well as complementary demographic data from captive populations sourced from these islands and from Tahiti. Our primary result broadly corroborated the earlier study: species with higher reproductive output, whether measured by historic field clutch sizes or by reproductive rates in captivity, are more likely to have survived. However, this generality does not apply to all island populations and it is unlikely to be the sole determining factor in any of these cases. Detailed ecological and behavioral studies of extant wild *P. radiolata* (Guam), *P. gibba* (Guam and Saipan), *P. taeniata* (Moorea), *P. hyalina* and *P.clara* (Tahiti) populations, and of their co-occurring introduced predators, are urgently required.

Introduction

Although most estimates of Anthropocene biodiversity loss are heavily skewed toward vertebrates (Ceballos *et al.* 2015; Régnier *et al.* 2015), mollusks are the most heavily impacted taxon by recent and ongoing extinction. Lydeard *et al*. (2004) estimated that non-marine mollusks comprised 40% of known extinctions since 1500 and the large majority (>70%) of these have involved oceanic island land snail endemics (Régnier, Fontaine & Bouchet, 2009; Régnier *et al.*, 2015).

Oceanic islands typically have never been connected to continental landmasses and isolation is their primary biological characteristic (Gillespie & Roderick, 2002). Their terrestrial biotas are depauperate and disharmonic, *i.e.*, they lack suites of continental taxa that are incapable of trans-oceanic dispersal (Paulay, 1994). Oceanic island endemics typically have small ranges (many are single-island endemics) and lack co-evolved defensive capabilities (Paulay, 1994; Vermeij, 1999, 2004); both factors contribute to their heightened extinction risk. Human agency has been the primary driver of oceanic island land snail extinction, either through habitat destruction or by introduction of continental predators (Chiba & Cowie, 2016).

Over the past 60 years, a two-step sequence of continental snail introductions has been repeated across much of Oceania, with devastating consequences for endemic Pacific Island land snails (Cowie, 1992; Civeyrel & Simberloff, 1996). The initial step involved importation (primarily for food) of the Giant African land snail *Lissachatina fulica* (Bowdich, 1822), a broad-spectrum herbivore. On Hawaii, escaped individuals were viewed as a serious agricultural pest, leading to the formation of a multi-decadal biological control program (Davis & Butler, 1964). This involved importation and experimental release of a wide spectrum of putative *L. fulica* continental predators. These included a suite of carnivorous snail species, most notably the North American rosy wolf snail, *Euglandina rosea* (Férrusac, 1821), although this introduction may have contained a cryptic species complex (Meyer *et al.* 2017).

Euglandina rosea is a highly mobile predator (by land snail standards) that stalks its snail prey by following their mucus trails, consuming small individuals whole and larger ones piecemeal (Gerlach, 2001; Davis-Berg, 2012). It is capable of climbing trees (Meyer & Cowie, 2011) and on Hawaii it proved much more effective at eradicating endemic land snail species, including arboreal taxa (Hadfield, Miller & Carwile, 1993), than its intended target species, *L. fulica* (Civeyrel & Simberloff, 1996). Subsequent ill-advised introductions of *E. rosea* to additional oceanic island archipelagos as an *L. fulica* biocontrol agent have led to similar outcomes (Civeyrel & Simberloff, 1996) and this predator has been implicated in the extinction of at least 134 terrestrial snail species (Régnier *et al.*, 2009).

A significant fraction of that total involves the endemic Pacific Island land snail family Partulidae: an estimated 32-39% of 104 species are now considered extinct, another 9% are extinct in the wild and 50% are classified as threatened (Gerlach, 2016). Much of that loss occurred in the Society Islands following the deliberate release of *Euglandina rosea* on Tahiti in 1974, on Moorea in 1977, and on other Society Islands in the 1980s and 1990s (Murray *et al.* 1988; Coote & Loève, 2003). Although most Society Islands partulids are now extinct, a subset collectively persists in captivity (Gerlach, 2016), in montane refuges where the predator may be less effective (Gerlach, 2001; Lee *et al.*, 2007, 2008), and as surviving valley populations on Tahiti and Moorea (Coote, 2007; Lee *et al.*, 2009).

On Tahiti, field surveys have documented the collective survival of two closely related (Lee *et al.*, 2009) endemic species of *Partula* - *P. hyalina* and *P. clara* - in 38 valleys (Coote, 2007). Their ability to endure 40 years of predation by *Euglandina rosea* in the valleys of Tahiti was surprising because predation models predicted partulid extirpation within 3 years of initial predator contact (Gerlach, 2001). Bick, Coote & Ó Foighil (2016) initially hypothesized that these two species have survived because they were the most widespread and/or common. They tested this hypothesis using a century-old dataset, predating predator introduction, of intact Tahitian partulid valley populations compiled by early evolutionary biologist H.E. Crampton (1916). They found that *P. clara* and *P. hyalina* had not been the most widespread, and were the least abundant species of *Partula* in most Tahitian valleys, usually representing less than 10 % (combined) of the original valley populations. Despite their relative rarity, Crampton's (1916) data revealed that *P. hyalina* and *P. clara* adults had higher mean instantaneous clutch sizes [(ICS) (developmentally-staggered embryos in the female reproductive tracts)] than did their (now extirpated) co-occurring congeners. Bick *et al.* (2016) proposed that higher fecundities, rather than relative abundance or larger ranges, may have been a critical factor in enabling *P. hyalina* and *P. clara* to differentially survive four decades of *Euglandina rosea* predation in Tahitian valleys.

However, the generality of Bick *et al.*'s (2016) results remain to be established. They are based on a single island and, given that Partulidae ranges across 10,000 km of Oceania (Cowie, 1992), it is not clear how applicable they are to other threatened populations. Other shortcomings include potential biases associated with Crampton's (1916) Tahitian field fecundity data. This island experiences a significant rain shadow effect (Hildenbrand *et al*., 2008) and Crampton (1916) collected from both "wet" and "dry" valleys, complicating comparative inferences of fecundity (higher in wet valleys). Individual valley-level clutch size estimates are not available for *Partula clara* and *P. hyalina*, making within-valley comparisons of survivors and non-survivors impossible. In addition, I cannot rule out the possibility of longer gestation periods among the survivors, a developmental pattern that could yield higher ICS but not necessarily higher birth rates (Bick *et al.* 2016).

In this study, I aimed to test the generality of Bick *et al.*'s (2016) inference that higher fecundities may promote survival of partulid species impacted by *Euglandina rosea* predation. I do so by incorporating historical field demographic data from additional island populations as well as complementary demographic data from captive populations. The detailed study of partulid demographics prior to the introduction of *E. rosea* by Crampton was not restricted to Tahiti (Figure 1): he engaged in parallel field work on Guam and Saipan, two Western Pacific Marianas archipelago islands (Crampton, 1925), as well as on another Society Island: Moorea (Crampton, 1932). As in Tahiti, Moorea (Lee *et al.*, 2009) and the Marianas (Sischo & Hadfield, 2017) retain surviving populations of some endemic *Partula* species, despite the long-term presence of *Euglandina rosea* (Mead, 1979; Murray *et al.*, 1988). These populations have also survived the subsequent introduction of another introduced snail predator, the New Guinea flatworm *Platydemus manokwari* (Hopper & Smith, 1992; Justine *et al.*, 2015; Gerlach, 2016), that has significantly replaced *E. rosea* as a major threat in the Marianas (Hopper & Smith, 1992), but whose impact on surviving Tahitian and Moorean endemics remains to be established.

Apart from Crampton's studies, I also had access to an independent source of demographic data: a subset of partulids from Guam, Moorea and Tahiti have been maintained as long-term captive populations by the Partulid Global Species Management Programme coordinated by the Zoological Society of London (ZSL). These captive populations allow estimation of reproductive rates and approximate a "common garden experiment" because keeping conditions, though highly artificial, are substantially standardized across all of the captive populations. Accessing these additional historical field and captive datasets gives us the opportunity to further test the linkage of ICS to reproductive rate and to survival among 4 island populations that span the range of the Family Partulidae (Figure 3-1).

Methods

Historical field data

The historical field fecundity data for Marianas and Moorean species were obtained directly from Crampton's published observations for the islands of Guam and Saipan (Crampton, 1925) and for Moorea (Crampton, 1932). He visited the Marianas archipelago in 1920 and systematically surveyed the partulid populations on two islands: Guam and Saipan (Crampton, 1925). On Guam, Crampton collected from a total of 38 localities spanning all 8 administrative regions and on Saipan, he sampled 8 representative localities. He did not detail his sampling methodology except to state that he walked along the primary trails during daylight hours, collecting snails from adjacent trees and vegetation. Crampton was particularly interested in population-level variation and often obtained large sample sizes (hundreds) from a locality. Partulids are ovoviviparous hermaphrodites and adults typically contain a small number of progeny at different stages of development in the female reproductive tract, giving birth to single young at multi-week intervals (Murray & Clarke, 1966). Crampton's sampling methodology involved promptly dissecting all of the adults he field-collected each day to record the number of eggs, embryos and shelled young present in the reproductive tracts of individual gravid snails (*i.e.*, ICS).

In total, Crampton (1925) collected 3,990 individuals on Guam in 1920, comprising four species: *Partula gibba* (N=2,400), *Partula radiolata* (N=1535), *Partula salifana* (N=19), *Partula fragilis* [N=36; reclassified as *Samoana fragilis* by Kondo (1968)]. On the island of Saipan, he collected a total of 2,666 *Partula gibba*, the only *Partula* species that exists on the island, over a period of 6 days (Crampton, 1925).

Crampton engaged in multiple partulid sampling trips on the island of Moorea extending over 17 years (1907, 1909, 1919, 1923 and 1924), with the most comprehensive sampling occurring during the latter two years (Crampton, 1932). In total, he collected an astonishing 116,166 individuals of 10 Moorean species: *Partula taeniata* (N=32,440), *P. suturalis* (N=14,640), *P. mooreana* (N=5,959), *P. mirabilis* (N=4,632), *P. aurantia* (N=1,624), *P. dendroica* (N=128), *P. olympia* (N=51), *P. tohiveana (*N=680), *P. exigua* (N=161), and a newly described species, *P. solitaria* (N=1), later reassigned to the genus *Samoana* (Kondo, 1973). Although the scale of Crampton's collection of Moorean *Partula* species was extraordinary by modern standards, it is unlikely to have been the main driver in their subsequent extirpation. His sampling was restricted to snails adjacent to the main valley paths on the island and, as late as the 1977 introduction of *Euglandina rosea*, the valleys of Moorea continued to support very significant populations (Clarke *et al*., 1984). In his 1932 publication, Crampton calculated the mean instantaneous clutch sizes for each species from each discrete Moorean sampling locality and sampling year.

I compiled Crampton's mean instantaneous clutch size data for Guam and Saipan (Crampton, 1925) and Moorea (Crampton, 1932) sampling localities then calculated estimates of mean clutch sizes across each island for each species. In doing so, I updated Crampton's (1932) taxonomy to comply with Gerlach's (2016) taxonomic revisions (*Partula diminuta* for *P. filosa*; collapsing all *P. taeniata* subspecies, but retaining two *P. suturalis* subspecies), with one exception: *Partula incrassa*. I was compelled to retain its original name, *P. exigua*, due to the recent clarification of *P. clara incrassa's* complex inter-island cytonuclear phylogenetic ties (Haponski *et al*., 2017).

Captive data

The rapid extinction of partulid species in the Society Islands, following the introduction of the predator *Euglandina rosea*, prompted the establishment of captive populations, initially in university laboratories, then in zoos (Murray *et al.*, 1988). Emergency interventions in the 1980s and 1990s led to the establishment of the Partulid Global Species Management Programme for 15 Society Island species, including 5 Tahitian and 5 Moorean species, coordinated by ZSL (Tonge & Bloxam, 1991; Pearce-Kelly *et al.*, 1997). The conservation program included rescue efforts to other parts of the familial range, including the Marianas archipelago, and established captive populations of *Partula gibba* (sourced from Saipan) and *P. radiolata*, (sourced from Guam). Over the years, culture attempts have been attempted for a total of 33 species of *Partula*, with mixed success (Gerlach, 2016). A total of 15 taxa still survive in captivity, maintained in 15 European and North American zoos.

Captive breeding protocols have been developed for partulids (Mace, Pearce-Kelly & Clarke, 1998). As part of that process, large amounts of demographic data have been recorded regarding growth rate, longevity and reproductive rate per holding tank of captive snails. Upon reaching adulthood, partulids form a reflected shell lip, indicating the enlargement of reproductive organs and the cessation of shell growth (Cowie, 1992). Weekly censuses of the different developmental stages *e.g.* newborn, juvenile, sub-adult, and adult have been recorded for each captive population (all snails in a particular glass tank) and entered into a dedicated database (Burlingham-Johnson *et al.*, 1994) which developed into the Partulid Species Management System (PSMS). Access to this database can be obtained by contacting Paul Pearce-Kelly (ppk@zsl.org) at the ZSL.

In 2011, I accessed and extracted all of the captive demographic data collected by the ZSL, at that point in time, for Moorean (6 species, including two subspecies), Tahitian (5 species) and Marianas (2 species) taxa (Table 3-1). Because the number of partulid taxa in captivity at the ZSL has varied significantly through time (Gerlach, 2016), as have details of captive culture, a 7-year focal time window – 1999-2005 – was chosen to maximize the number of species of interest within a contemporaneous demographic dataset. Our final comparative dataset comprised 29,751 total weekly tank census records (Table 1). The number of adults and births per census were used to calculate weekly per capita adult snail reproductive rates for each tank population. I then aggregated these values to calculate the mean reproductive rates in captivity for each of the Marianas, Moorean and Tahitian *Partula* taxa over the study period.

Statistical analyses

The association between Crampton's (1916) historical mean ICS data and the aggregated mean captive birth rate per adult per week for Moorean (6 species, including two subspecies), Tahitian (4 species) and Marianas (2 species) taxa was initially tested using a simple linear regression analysis. This recovered a positive relationship between the two variables and the strength of this relationship was further evaluated using a Pearson Correlations test. I then used independent T-tests to determine if surviving and extirpated taxa had significant differences in their historical wild population ICS values and in their mean captive birth rates.

Results

Historical field data

Figure 3-2 summarizes Crampton's (1925) ICS data for the three Marianas species he sampled and their current survival status. *Partula radiolata* had the highest clutch size: mean=4.121. It is a single island endemic and remains locally common on Guam, "persisting in numerous locations and in very high local densities" (Sischo & Hadfield, 2017). *P. gibba*'s distribution spans the archipelago, occurring on 8 islands (Sischo & Hadfield, 2017), but Crampton (1925) only sampled it from Guam and Saipan. It exhibited significantly different instantaneous clutch sizes on these two islands: Guam populations had a mean clutch size of 2.958, the lowest among Crampton's (1925) Marianas dataset, whereas Saipan populations had 3.723, the second highest (Figure 3-2). Once the most common partulid on Guam (Crampton, 1925), *P. gibba* has experienced precipitous population declines there and on Saipan, persisting in only a few isolated locations (Smith *et al.*, 2008; Kerr, 2013; Hadfield, 2015; Sischo & Hadfield, 2017). *P. salifana* was the least sampled by Crampton (N=17) and had the second lowest clutch size: mean=3.176 (Figure 3-2). A single island endemic, it had a very limited distributional range on Guam, restricted to the summit of Mt. Alifan and to two adjacent peaks (Crampton, 1925; Kerr, 2013). *Partula salifana* was deemed extinct by Hopper & Smith (1992) and that remains its official IUCN Red List status.

Crampton's (1932) ICS data for Moorean taxa, and their current survival status, are summarized in Figure 3-3. All 7 Moorean species of *Partula* were presumed extirpated in the wild by 1987 (Murray *et al.*, 1988; Coote & Loève, 2003). However, 6 small, scattered clusters of *Partula taeniata* survivors were subsequently discovered (Lee *et al.*, 2009) and at least 3 of these persisted as of September 2017 (T. Coote, unpublished observations). Mean ICS values for the Moorean species were lower than that of Marianas congeners (Figure 3-2) and ranged in ascending order from 1.995 (*P. mooreana*), 2.150 (*P. suturalis strigosa*), 2.249 (*P. tohiveana*), 2.336, (*P. exigua*), 2.344 *P. mirabilis*, 2.403 (*P. taeniata*), 2.933 (*P. suturalis vexillum*) to 2.957 (*P. aurantia*). Two details of these comparative data stand out. One concerns the significant difference in clutch size of the two *P. suturalis* subspecies, although it is worth noting that they had allopatric distributions on the island (Clarke *et al*., 1984). The other is the intermediate mean clutch size exhibited by *P. taeniata*, the only Moorean *Partula* species that has withstood (if only barely) 4 decades of predation by *Euglandina rosea* (Lee *et al*., 2009) and at least 8 years of predation by the invasive New Guinea flatworm *Platydemus manokwari* (Justine *et al*., 2015). Although *P. suturalis vexillium* and *P. aurantia* had overlapping distributions with, and higher ICS than, *P. taeniata*, both of them have been extirpated (Coote & Loève, 2003).

I also combined my new assessment of Crampton's data with Bick *et al.*'s (2016) study to provide a collective overview of the association of ICS in wild, intact populations of Tahitian (Crampton, 1916), Saipan and/or Guam (Crampton, 1925), and Moorean (Crampton, 1932) *Partula* species and their fates. Mean clutch sizes among the 17 species ranged from a low of 1.250 in the now extinct Tahitian single valley endemic *P. diminuta* to a high of 4.121 in the surviving Guam endemic *P. radiolata* (Figure 3-4). It is notable that the 4 highest clutch sizes involved surviving Marianas, *P. radiolata* and *P. gibba* (Saipan), and Tahitian, *P. hyalina* and *P. clara*, taxa and populations and that the 10 lowest clutch sizes corresponded to extirpated Moorean and Tahitian taxa or populations. An independent T-test analysis of the collective field clutch size data for Guam, Saipan, Tahitian and Moorea *Partula* taxa found that survivors in the wild (M=3.530, SD=0.655) had significantly higher field instantaneous clutch sizes than their extirpated congeners (M=2.222, SD=0.337); t(5)=4.132, p = 0.009.

Captive data

Mean birth rates among the 12 captive *Partula* taxa from the four islands (Guam, Saipan, Moorea, and Tahiti) sampled by Crampton ranged over an order of magnitude from 0.012 – 0.267 per adult per week (Figure 3-5). The lowest birth rate (by far) was recorded for the Tahitian species *P. otaheitana*. This captive population was the only one sourced from a cool montane cloud forest population, at an altitude of 1,000m on Mount Marau. Here, environmental temperatures range from 11-20˚C, typically ~8˚C lower than that of valley population habitats from which the other captive Society Island taxa were sourced (Appendix II). It is also lower than the temperature range (21-24˚C) typically maintained for captive taxa from 1999-2005 and that may have been a factor in the much lower reproductive rate of *P. otaheitana* in captivity.

Despite the numerous caveats entailed by the artificiality of the captive environment, the ZSL data yield valuable additional insights into the association of captive reproductive rates and survival (Figure 3-5). The top four captive mean reproductive rates were recorded by species that remain extant in the wild: *P. hyalina* (Tahiti, 0.267 births/adult/week), *P. gibba* (Saipan, 0.200 births/adult/week), *P. radiolata* (Guam, 0.172 births/adult/week) and *P. clara* (Tahiti, 0.144 births/adult/week). Of the six Moorean taxa (5 species and two subspecies) represented in the dataset (Figure 3-5), the sole survivor in the wild, *P. taeniata*, had the highest mean birth rate in captivity, 0.094 births/adult/week, whereas the extirpated Moorean taxa ranged from 0.053–0.075 births/adult/week. Apart from the exceptionally poorly performing montane population of *P. otaheitana*, the 6 lowest captive mean reproductive rates were recorded by extirpated Moorean and Tahitian taxa (Figure 3-5). An independent T-test analysis of the collective captive data for Guam, Saipan, Tahitian and Moorea *Partula* taxa (Figure 3-5), found that survivors excluding the montane population of *P. otaheitana*, in the wild (M=0.175, SD=0.064) had significantly higher captive birth rates than their extirpated congeners (M=0.068, SD=0.018); t(4)=3.617, p = 0.022.

Correlation of historical and captive data

A direct comparison of the historical field clutch size dataset (Figure 3-4) with the captive birth rate dataset (Figure 3-5) is complicated by missing data. The former has a total of

19 taxa and populations whereas the latter has only 13, the balance being absent from the captive dataset through extinction prior to the possibility of captive rescue (*Partula diminuta*, *P. producta*, *P. salifana*), use of another island as a source captive population (Guam *P. gibba*), or loss of captive populations prior to our 1999-2005 time window (*P. aurantia*, *P. exigua*). An additional incompatibility issue concerns the Tahitian species *P. otaheitana* for which the historical field clutch size data is exclusively from low altitude valley populations and the captive data, characterized by abnormally low birth rates, is exclusively from high altitude cloud forests.

On assessing the relationship between historical field mean clutch sizes and captive mean birth rates per week for the remaining 12 taxa and populations, the two variables indicated a positive linear relationship (R^2=0.6292, Figure 3-6). I then further confirmed this with a Pearson correlation test and found that these two very distinct measures of reproductive activity are significantly correlated ($p = 0.002$). Four of the five surviving species - *P. hyalina* and *P. clara* (Tahiti), *P. gibba* (Saipan) and *P. radiolata* (Guam) - had distinctly higher reproductive production metrics, both in the wild and in captivity, than their extirpated congeners; the 5th survivor, *P. taeniata* (Moorea), did not (Figure 3-6).

Discussion

My main goal in this study was to test the generality of Bick *et al.*'s (2016) inference that for Tahitian *Partula* species, higher clutch sizes are positively correlated with survival in this highly endangered genus. Incorporating complementary field and captive datasets for Marianas and Society Islands congeners enabled us to do so for the endemic faunas of 4 islands that collectively span 8,000 km of the generic range (Figure 3-1). My primary result broadly corroborates the earlier study: species with higher reproductive output, whether measured by field instantaneous clutch sizes or by reproductive rate in captivity, are more likely to have survived in the wild, but this generality does not apply for all island populations.

Marianas

I recovered the clearest linkage of partulid reproductive output and survival on Guam where *Partula radiolata* has maintained high population densities in many locations (Sischo and Hadfield, 2017) despite being exposed to predation by a diverse series of introduced predators over the past 6 decades. During the 1950's three alien carnivorous snails were introduced to control the giant African land snail, *Lissachatina fulica*: initially *Gonaxis kibweziensis* (Civeyrel & Simberloff, 1996), followed by *Gonaxis quadrilateralis* (Davis & Butler, 1964) and *Euglandina rosea* (Mead, 1979). A fourth snail predator, the flatworm *Platydemus manokwari,* appeared in 1977 (Muniappan, 1983) and this has apparently extirpated at least some populations of both *Gonaxis* species and *Euglandina rosea* (Hopper & Smith, 1992). The continued survival of robust *P. radiolata* populations in the face of these waves of novel predation pressure is quite remarkable and Sischo & Hadfield (2017) proposed that an unknown aspect of its life history or behavior, possibly including higher fecundity, has facilitated its persistence. My results indicate that fecundity may be an important factor: *P. radiolata* had the largest mean ICS (4.121) of the 19 species studied by Crampton (Figure 3-4) and also had the third highest captive reproductive rate (0.172 births/adult/week) of the 13 taxa in captivity (Figure 3-5). In contrast, *P. gibba*, originally the most common partulid on Guam (Crampton, 1926), had a smaller (2.958) mean clutch size (Figure 3-2) and is reduced to a few vestigial surviving populations in a small fraction of its former range (Sischo & Hadfield, 2017). The other Marianas island of Saipan is considerably smaller than Guam (115 vs 540 km^2) and received the same suite of predators (Mead, 1979; Muniappan, 1983). Its population of *P. gibba*, characterized by the third highest

(3.723) mean field clutch size (Figure 3-4) and the second highest (0.200 births/adult/week) captive reproductive rate (Figure 3-5) also survives in small numbers, but is critically threatened (Sischo & Hadfield, 2017).

Tahiti

Bick *et al*. (2016) documented a clear linkage of historical field clutch size (Crampton, 1916) with survival in Tahitan valley populations: *Partula hyalina* and *P. clara* had much higher clutch sizes than their extirpated congeners (Figure 3-4) and have differentially survived >40 years of exposure to *Euglandina rosea* in 38 valleys. Our novel captive reproductive rate data (Figure 3-5) broadly corroborate this inference: these two species had significantly higher per capita weekly rates, 0.267 for *P. hyalina* and 0.144 for *P. clara,* than had their now-extirpated Tahitian valley congeners: *P. nodosa* (0.104) and *P. affinis* (0.060); the 5th Tahitian species *P. otaheitana*'s rate (0.012) is not directly comparable due to its montane cloud forest source population.

Nevertheless, the almost two-fold difference in captive reproductive rates for the two surviving Tahitian valley species was unexpected because they had very similar ICS values in the wild: respective means of 3.755 for *Partula hyalina* and 3.648 for *P. clara* (Figure 3-4). In addition, both species are closely related: they stem from a discrete founding Tahitian lineage, are polyphyletic in mitochondrial gene (Lee *et al*. 2007, 2009) and phylogenomic (Haponski *et al*, 2017) trees and are distinguishable primarily by *P. hyalina*'s white shell coloration (Crampton, 1916; Gerlach, 2016). Although I cannot rule out variation in gestation times as a contributing factor, it seems unlikely: field clutch sizes and captive reproductive rates are significantly correlated (Figure 3-6), implying that gestation rates do not vary dramatically among these taxa. This points to an environmental effect of captivity that differentially impacted

P. clara's reproductive output relative to *P. hyalina*'s. It is well established that shell coloration/albedo can profoundly affect land snail thermal regulation and ecology (Heath, 1975; Chiba, 1999; Ozgo, 2011) and according to Crampton (1916), the white-shelled *P. hyalina* was relatively more abundant in wider and drier valleys and at forest edges and clearings. Although it is not possible to directly compare Crampton's (1916) field observations with captive rearing conditions, our reproductive rate data suggest that, during our 1999-2005 time window, *P. hyalina* may have been less stressed by captive holding tank micro-climates than were congeners with similar field clutch sizes: *P. clara*, *P. gibba* and *P. radiolata* (Figures 3.4 & 3.6).

Moorea

The survival pattern on the island of Moorea differs from that of its near neighbor Tahiti. The two Moorean taxa with the highest mean instantaneous clutch sizes, *Partula aurantia* and *Partula suturalis vexillum* (Figure 3-3), were extirpated by *Euglandina rosea* within a decade (Murray *et al.*, 1988). In contrast, the sole surviving Moorean species, *Partula taeniata*, had an intermediate clutch size, ranked 3rd highest (Figure 3-3). However, it exhibited a higher birth rate in captivity than it's extirpated Moorean congeners, including *P. s. vexillum*, although I do not have equivalent captive data for *P. aurantia* (Figure 3-4). It is interesting to note that *P. taeniata* is sister to the Tahitian valley survivors, *P. hyalina and P. clara* (Lee *et al*., 2009) and that all three species have endured 40 years of predation by *E. rosea*. However, the surviving Tahitan species have much higher reproductive rates in the wild and in captivity (Figure 3-6), implying that some other aspect of *P. taeniata*'s biology may have facilitated its survival.

The surviving *Partula taeniata* populations have been carefully monitored in recent years and the most stable population, in Oponuhu Bay (Appendix III), may be relatively inaccessible to *Euglandina rosea* and to the invasive New Guinea flatworm *Platydemus manokwari*.

Discovered in 2002 by C. Hickman, the Oponuhu Bay population occurs in a highly unusual partulid habitat: a patch of mangrove forest that is regularly flooded by brackish water (Lee *et al.*, 2009). The five other monitored populations have been directly exposed to *E. rosea* and three of them may have been extirpated in recent years: the respective last live sightings in Haumi, Morioahu and Maatea occurred in October 2009, October 2012 and August 2013 (Appendix IV to VI). The species is barely hanging on in the remaining two localities, Moruu and Maramu (Appendix VII and VIII). Invasive *E. rosea* population densities can vary markedly over small spatial scales and that heterogeneity might enable survival of endemic prey in low predator density niches (Meyer & Cowie, 2011). It is notable that in the Moruu population, all color morphs apart from white-shelled individuals have disappeared during the monitoring period. A correlation between light shell coloration and an enhanced ability to withstand exposure to direct sunlight is well known among land snail species (Jones, 1973; Heath, 1975; Chiba, 1999; Ozgo, 2011) and Bick *et al*. (2016) speculated that the white-shelled Tahitian species *P. hyalina* may have a partial solar refuge from *E. rosea* predation.

Captive populations

Although our captive birth rates are germane to this study, I do not know how well they match (or matched in the case of extirpated taxa and populations) actual birth rates in the wild. One initial surprise was that they are much lower than available birth rates from the limited number of previously published studies on captive populations. Murray & Clark (1966) recorded birth intervals in two lab-raised Moorean species of approximately 22 days for *Partula suturalis* and of 19 days for *P. taeniata*. This corresponds to respective weekly rates of 0.318/week/adult and 0.368/week/adult, much higher that our respective captive data for these two species: 0.075 for *P. suturalis strigosa*; 0.054 for *P. suturalis vexillum* and 0.094 for *P. taeniata*, or even for our highest rate of 0.267 for *P. hyalina* (Figure 3-5). Murray and Clark (1966) recorded those rates for individual adults that were actively producing young and they noted that in these two species there was a prolonged temporal gap between formation of a reflected shell aperture (adult shell morphology) and birth of first young: *P. suturalis*: 121-373 days (median 192); *P. taeniata*: 110-232 days (median 145). In the ZSL captive populations, individuals were deemed adult upon formation of reflected shell apertures and birth rates were calculated for each tank population, not for individual snails. Temporal gaps until first births, likely equivalent to 7-8 birth intervals (Murray & Clark, 1966), were therefore not taken into account in our calculations of weekly adult birth rates and this methodological difference may account for much if not all of the discrepancy. Irrespective of these details, prolonged captive culture of *Partula* species has proven to be highly challenging with a success rate of 15 taxa out of 33 attempts. Of the 13 taxa in our 1999-2005 time-window (Figure 3-5) 4 have subsequently failed in culture: *P. otaheitana* in 2007, *P. radiolata* in 2009, *P. clara* in 2012 and *P. gibba* in 2015.

Summary

Euglandina rosea's disproportionate role as an agent of oceanic island land snail extinction (Régnier, Fontaine & Bouchet, 2009) has elicited interest in "resistant" endemic species that have differentially endured its predation pressure (Coote, 2007; Meyer & Cowie, 2011; Bick *et al*., 2016). What common attributes might they possess and how could such knowledge help design optimal conservation measures for the hundreds of Pacific Island endemics currently at risk from this and other introduced snail predators across Oceania? Our results corroborate and extend Bick *et al*'s (2016) inference that heightened reproductive output is linked with survival in low-altitude *Partula* species exposed to *E. rosea* and *Platydemus manokwari*. But this attribute does not explain all cases of differential survival, e.g., *P. taeniata*, and it is unlikely to be the sole determining factor in any of these cases. This general result is intuitive because species with lower intrinsic rates of population growth are at increased risk of extinction from stochastic events (Beissinger, 2000). It follows that oceanic island endemics with greater reproductive effort should have a higher likelihood of surviving the biogeographic equivalent of a stochastic event: anthropogenic introduction of a continental predator (Gerlach, 2001). There are clear parallels here with Guam's infamous "empty forest" phenomenon, where a single introduced predator, the brown tree snake *Boiga irregularis*, has led to the extinction of much of the endemic forest vertebrate fauna (Redford, 1992). In the case of Guam's endemic avifauna, the ability to nest in locations where snakes were uncommon and to produce large clutch sizes has enabled some species to endure (Beissinger, 2000; Wiles *et al.*, 2003). Detailed ecological and behavioral studies of extant wild *Partula radiolata* (Guam), *P. gibba* (Guam and Saipan), *P. taeniata* (Moorea), *P. hyalina* and *P. clara* (Tahiti) populations and of their co-occurring introduced predators, *e.g.*, Meyer & Cowie (2011), are urgently required to attain a more informed understanding of their ostensibly unlikely survival.

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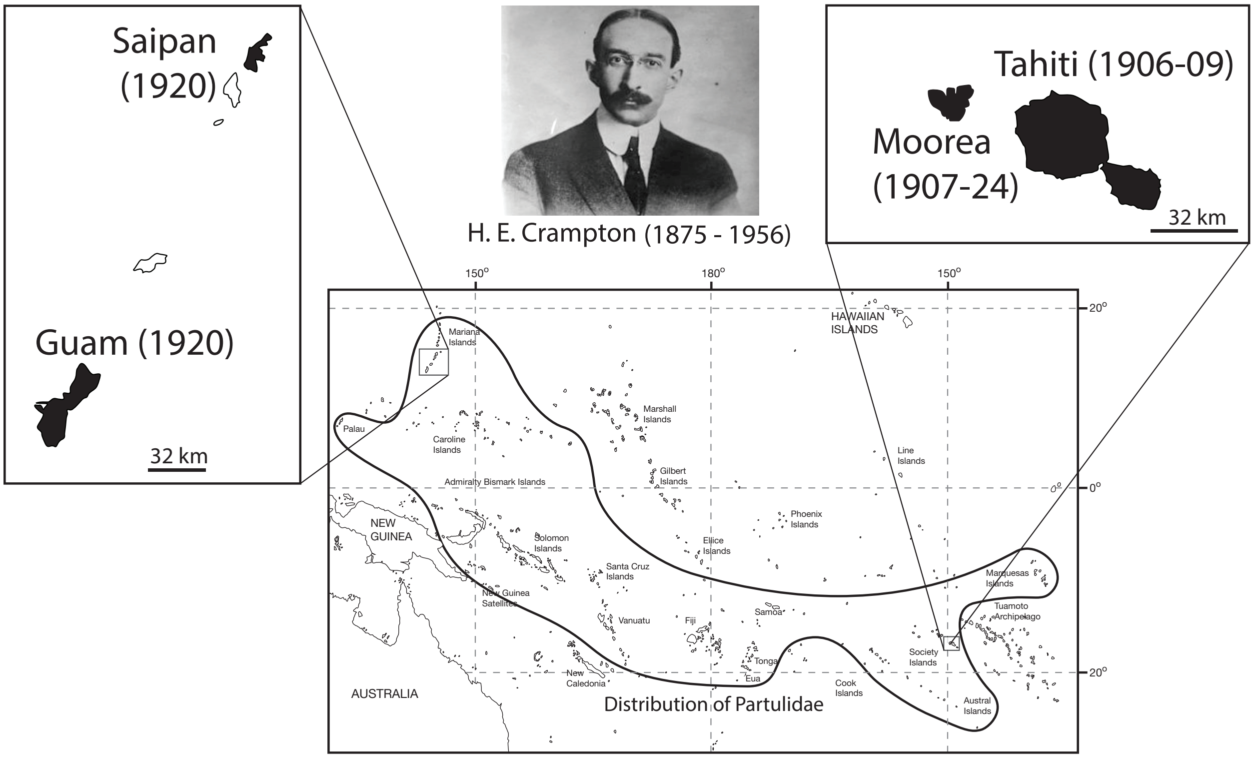

Figure 3–1. Map of Oceania showing the distributional range of Partulidae (modified from Cowie, 1992) together with H.E. Crampton's main study sites and their respective sampling timeframes: Guam and Saipan in the Marianas (Crampton, 1925) and 8,000 km to the southeast, Tahiti (Crampton, 1916) and Moorea (Crampton, 1932) in the Society Islands. Photograph of H.E. Crampton is from the Library of Congress (www.loc.gov/item/ggb2004004638).

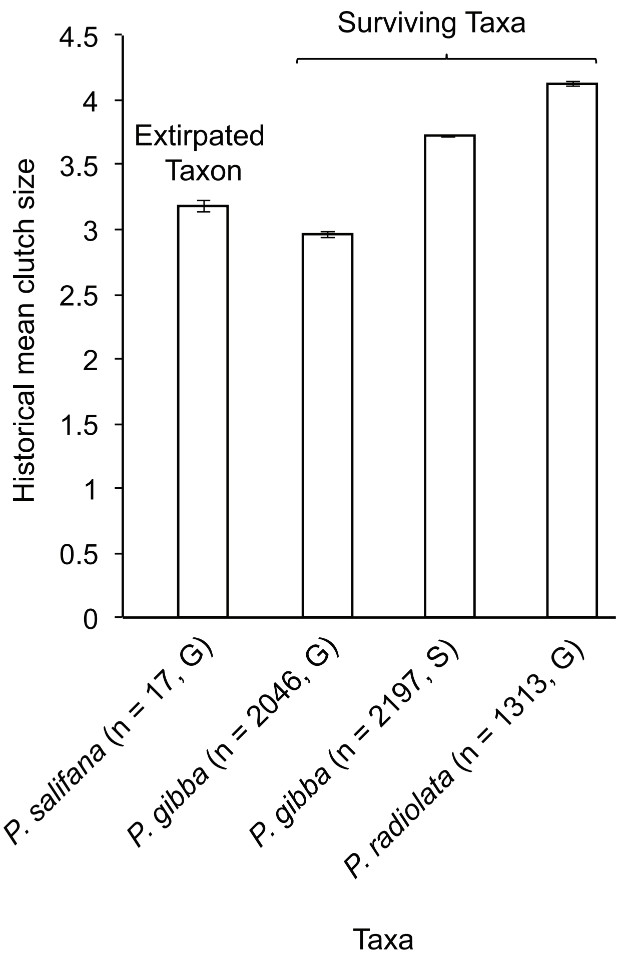

Figure 3–2. Mean instantaneous clutch sizes (± Standard Error) for the 5,573 gravid individuals of three endemic partulid species collected by Crampton (1925) on Guam and/or Saipan in 1920. Sample sizes as well as source islands (G, Guam; S, Saipan) are given for each taxon. *Partula gibba* (both Guam and Saipan) and *P. radiolata* have maintained extant wild populations but *P. salifana* has not (it is deemed extinct by the IUCN Red List).

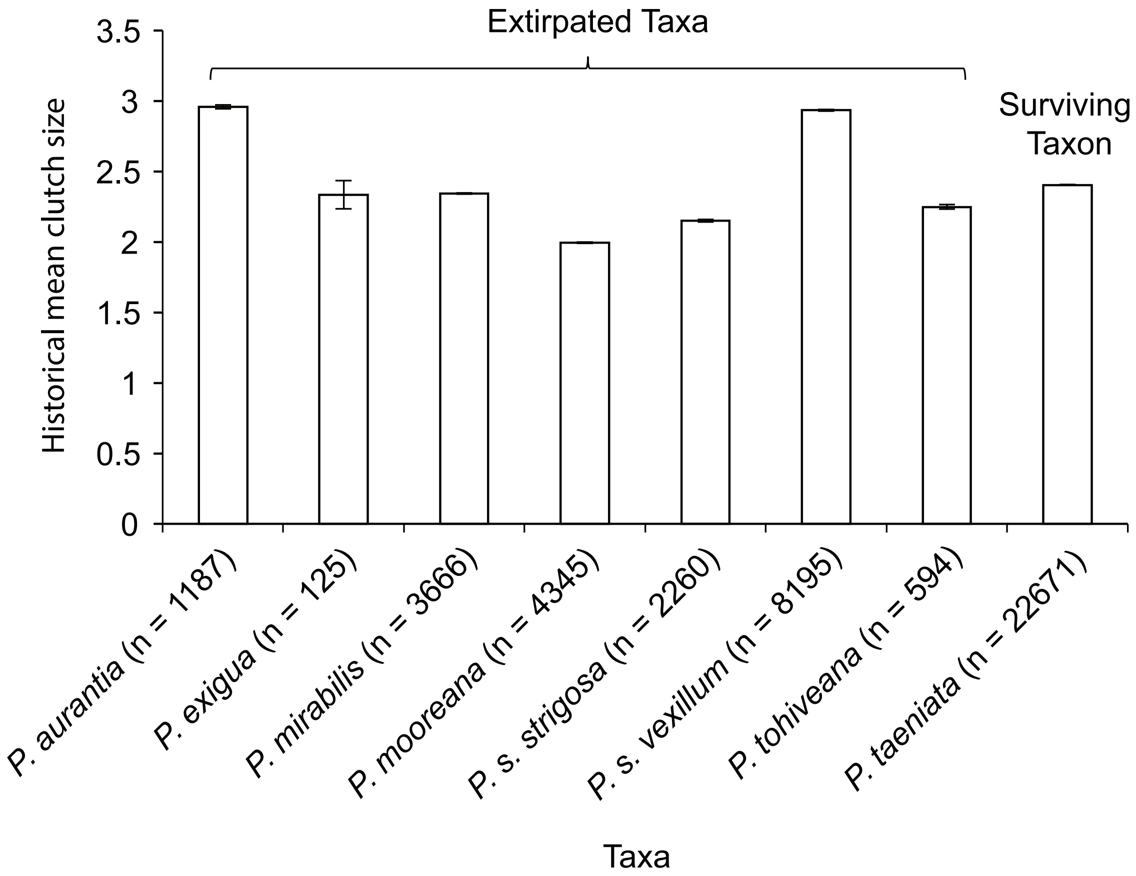

Figure 3–3. Mean instantaneous clutch sizes (± Standard Error) of the 43,360 gravid individuals representing seven endemic Moorean partulid species collected between 1907 and 1924 by Crampton (1932). Sample sizes are given for each species and *Partula taeniata*, the only Moorean species to have maintained extant wild populations, is labeled as a surviving taxon; the remaining six species (included two subspecies) are labeled as extirpated.

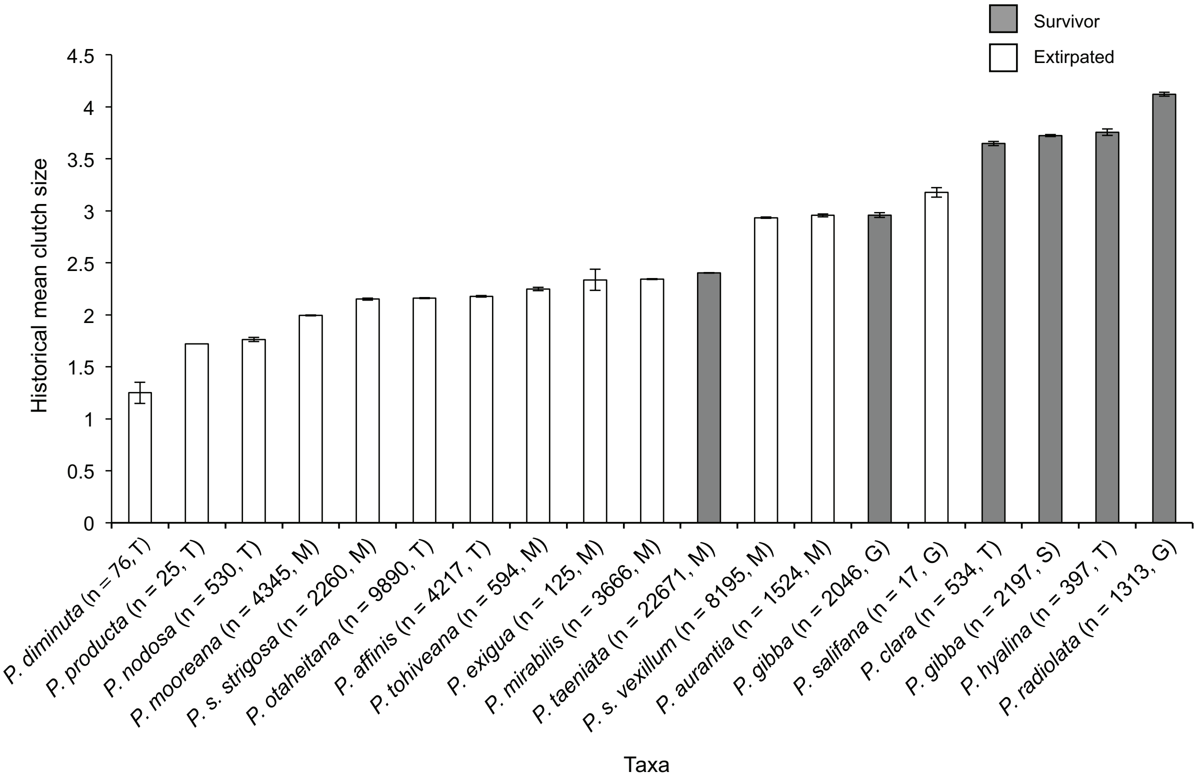

Figure 3–4. Mean instantaneous clutch sizes (± Standard Error) of the 64,602 gravid individuals collectively estimated by H. E. Crampton on Tahiti (Crampton, 1916), Guam and Saipan (Crampton, 1925) and Moorea (Crampton, 1932), representing a total of 17 *Partula* species. Sample sizes and respective survival status in the wild are given for each taxon. Note that the numerically dominant (Bick *et al*., 2016) Tahitian valley populations of *P. otaheitana* that Crampton (1916) sampled have been extirpated. Although this species still survives in Tahitian cloud forests >1000m in elevation (Lee *et al*., 2005), clutch size data for these enduring montane populations are not presently available. The surviving population of Tahitian endemic *P. affinis* detected by Coote & Loève (2003) is now extirpated and this species' last sighting in the wild was a single specimen in 2013 (Coote, pers. observ.). Note that I comply with Gerlach's (2016) nomencular taxonomic revisions, except for *Partula crassa*. I was compelled to retain its original name, *P. exigua*, due to the recent clarification of *P. clara incrassa's* complex inter-island cytonuclear phylogenetic ties (Haponski *et al*., 2017).

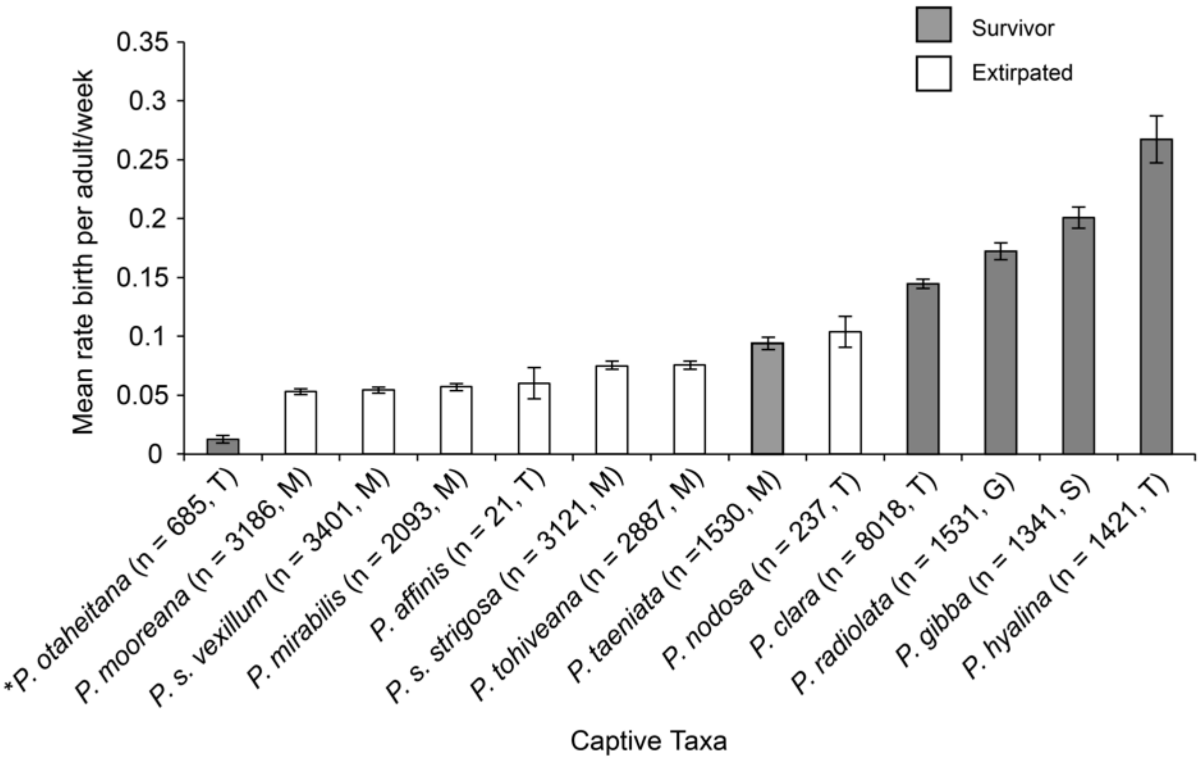

Figure 3–5. Mean per capita birth rates (± Standard Error) for the Partulid Global Species Management Programme captive populations, held at the Zoological Society of London, of Tahitian, Moorean and Marianas *Partula* taxa. Birth rates were estimated from a total of 68,437 weekly tank population surveys. Taxa are arranged by increasing captive birth rate and the respective number of weekly population surveys, source islands (T, Tahiti; M, Moorea, G, Guam; S, Saipan) and survival status in the wild are indicated. Note that the **P. otaheitana* captive population is the only one sourced from a montane cloud forest habitat. See Table 3-1 for the census timeframe for each taxon.

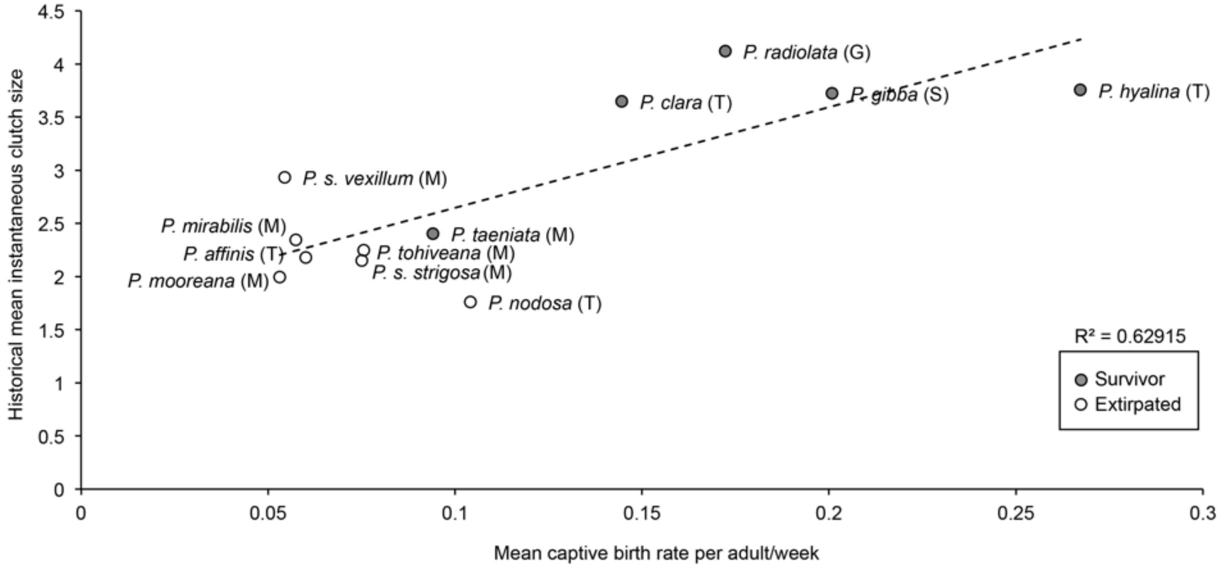

Figure 3–6. Correlation of H. E. Crampton's historical mean field clutch sizes of 12 *Partula* taxa and populations from 4 Pacific islands (T, Tahiti; M, Moorea, G, Guam; S, Saipan) with their mean reproductive rates in captivity.

Table 3-1. The 12 species maintained simultaneously in captivity by the Partulid Global Species Management Programme at London Zoo over the 6-year time window (1999 – 2005) analyzed in this study. For each captive taxon, the total number of individual tank populations counted are given together with the total number of weekly censuses performed.

Species	Year in captivity	Total Number of Weekly Censuses (N)	Number of Individual Tanks
P. affinis	1999 (1 year only)	21	1
P. clara	1999-2005	8018	118
P. gibba (Saipan)	1999-2005	1340	21
P. hyalina	1999-2005	1412	22
P. mirabilis	1999-2005	2093	23
P. mooreana	1999-2005	3186	41
P. nodosa	2001-2005	346	4
P. otaheitana (montane)	1999-2005	685	12
P. radiolata	1999-2005	1531	22
P. suturalis strigosa	1999-2005	3121	26
P. suturalis vexillum	1999-2005	3401	29
P. taeniata	1999-2005	1445	18
P. tohiveana	1999-2005	2887	45

CHAPTER 4

Surviving a Mass Extinction: The Tahitian Tree Snail *Partula hyalina* has a Solar Refuge from the Alien Predator *Euglandina rosea*

Abstract

Endemic Pacific Island land snails are the planet's most endangered taxa and form a disproportionate share of known and ongoing extinctions. A large fraction of that loss stems from misguided biological control programs that involved the deliberate introduction of snail predators, most notably the North American rosy wolf snail, *Euglandina rosea*. The family Partulidae has been heavily impacted, especially the Society Island endemic radiation that contained approximately half of partulid species and is now largely extinct. A small number of Society Island *Partula* species have endured 40 years of predation by *E. rosea*, most notably the white-shelled *P. hyalina*, which persists in a total of 31 Tahitian valleys. Land snails are mostly restricted to shaded habitats, but those with high albedo light shell coloration have an enhanced ability to colonize open, sunlit environments. *P. hyalina* has been recorded from forest edges and I hypothesized that these edge habitats may form "solar refuges" for surviving *P. hyalina* in which ambient solar irradiation conditions are significantly higher than those tolerated by foraging *E. rosea*. Our goal in this study was to test the solar refuge hypothesis in the field. I used custom-designed and manufactured smart, millimeter size solar sensors to characterize the solar ecologies of predator populations and of surviving *P. hyalina* populations. My results indicate that their solar ecologies are significantly different, as predicted by the hypothesis, but that any protective effect is intermittent, being attenuated or absent on overcast days. Long-term

survival of this species in Tahitian valleys may require proactive conservation of its forest edge solar refuges.

Introduction

Although most estimates of Anthropocene biodiversity loss are heavily skewed toward vertebrates (Ceballos *et al*. 2015; Régnier *et al*. 2015) molluscs are the most heavily impacted taxon by recent and ongoing extinction (Lydeard *et al*. 2004) and the large majority of molluscan extinctions have involved oceanic island land snail endemics (Régnier *et al*. 2009, 2016). Human agency has been the primary driver of oceanic island land snail extinction, either through habitat destruction or by introduction of continental predators (Chiba & Cowie 2016). A large fraction of that loss stems from misguided biological control programs initiated in the mid-20th century that involved the deliberate introduction of snail predators, most notably the North American rosy wolf snail, *Euglandina rosea* (Cowie 1992; Civeyrel & Simberloff 1996).

Euglandina rosea is a highly mobile predator, capable of climbing trees, that stalks its snail and slug prey by following their mucus trails, consuming small individuals whole and larger ones piecemeal (Gerlach 2001; Davis-Berg 2012; Meyer & Cowie, 2011). It was introduced to multiple oceanic island archipelagos in an ill-advised attempt to control populations of a perceived agricultural pest, the Giant African snail *Lissachatina fulica*, a broad-spectrum alien herbivore (Davis & Butler, 1964; Civeyrel & Simberloff 1996). Unfortunately, *E. rosea* proved much more adept at extirpating endemic species than its intended target (Civeyrel & Simberloff 1996; Hadfield *et al*. 1993) and this predator has been implicated in the extinction of at least 134 terrestrial snail species (Régnier *et al*. 2009).

A significant fraction of that total has involved the endemic Pacific Island land snail family Partulidae: an estimated 32-39% of 104 species are now considered extinct, another 9%

are extinct in the wild and 50% are classified as threatened (Gerlach, 2016). Most partulid extinction has occurred on the Society Islands following the deliberate release of *Euglandina rosea* on Tahiti in 1974, on Moorea in 1977, and on other Society Islands in the 1980s and 1990s (Coote & Loève 2003). Their loss was compounded by the scientific prominence of Society Islands partulids as the subject of classic studies in zoology, population biology and evolutionary genetics (Crampton 1916, 1932; Murray & Clarke 1980; Johnson *et al*. 1993). Although a large majority is now extinct (Coote & Loève 2003), a subset collectively persists in captivity (Pearce-Kelly *et al*., 1997; Gerlach, 2016), in cool, cloud forest montane refuges where the predator may be less effective (Gerlach, 2001; Lee *et al*. 2007, 2008), and as surviving valley populations on Tahiti and Moorea (Coote 2007; Lee *et al*. 2009).

Tahitian field surveys have documented small, scattered remnant populations, generally less than 50 individuals, of two closely related (Lee *et al*. 2009) endemic species of *Partula* - *P. hyalina* and *P. clara* - in a combined total of 38 valleys (Coote 2007). Their ability to endure 40 years of predation by *Euglandina rosea* was surprising because predation models predicted partulid extirpation within 3 years of initial predator contact (Gerlach, 2001). A recent revaluation of a century-old Tahitian demographic dataset (Crampton 1916) found that *P. hyalina* and *P. clara* had higher clutch sizes than did their (now extirpated) Tahitian valley congeners (Bick *et al*. 2016). This general result is intuitive because species with lower intrinsic rates of population growth are at increased risk of extinction from stochastic events (Bessinger 2000), but it is unlikely to be the sole reason for their survival (Bick *et al*. 2016). Although *Partula hyalina* and *P. clara* stem from a single Tahitian founding lineage (Haponski *et al*. 2017) and share similarly high clutch sizes in the wild (Bick *et al*. 2016), they have not fared equally well in the presence of *Euglandina rosea*. Field surveys have detected more and larger surviving populations of *P. hyalina*, in 31 valleys, than of *P. clara*, in 20 valleys (Coote 2007; Bick *et al.* 2016).

Partulid tree snails aestivate during the day while attached to the undersides of leaves of trees and other vegetation, and descend to the forest floor at night to forage (Crampton, 1916). Crampton (1916) noted a discrete distributional trait of *Partula hyalina*: in addition to occurring in dense forest (the typical partulid habitat) he observed most individuals of this distinctly white-shelled species aestivating at forest edges and stream borders where "larger forest trees are fewer and there is more sunlight". Land snails are physiologically limited by moisture availability and are mostly found in shaded areas such as valleys and deep forests (Prior, 1985). However, it is well established that land snails with light shell coloration, and therefore high albedo, have an enhanced ability to colonize open, sunlit environments (Jones, 1973, Heath, 1975; Chiba, 1999; Ozgo, 2011).

Bick *et al*. (2016) hypothesized that forest edge habitats may form in effect "solar refuges" for *Partula hyalina* in Tahitian valleys. The solar refuge hypothesis predicts that surviving populations of *P. hyalina* will be restricted to forest edges where the ambient solar irradiation conditions are, during periods of maximum sunlight, significantly higher that those tolerated by foraging *Euglandina rosea*. This is consistent with Hawaiian field studies showing that *Euglandina rosea* exhibits higher activity levels and population densities in shaded, moist habitats (Meyer & Cowie 2011). If the predator is unable to engage in continuous hunting behavior in forest edge environments tolerated by *P. hyalina*, this environmental effect may play an additive role, along with larger clutch sizes, in the latter's differential survival.

My goal in this study was to test the solar refuge hypothesis in the field by characterizing the ambient light ecology of predator populations and of surviving *Partula hyalina* populations.

Behavioral biologists have deployed a variety of sophisticated light sensors in recent years to address diverse research questions including the solar geolocation of migrating birds (Bridge *et al.*, 2011), the effect of artificial light pollution on perceived day length in European blackbirds (Dominoni & Partecke, 2017) and the foraging activity of ground squirrels (Williams *et al.*, 2017). To my knowledge, light sensors have not previously been developed for land snails and my colleagues (Lee & Blaauw) and I, therefore custom-designed and manufactured smart, millimeter size solar sensors for this specific purpose. The results were consistent with the solar refuge hypothesis' predictions but any protective effect was intermittent, being attenuated or absent on overcast days.

Methods

Solar sensors

Custom sensors were developed to measure the snail solar ecologies. The sensor design incorporated three key functionalities: measuring light dose (measured in lux hour) at 10-minute time intervals and storing this data over several days, wirelessly retrieving the data at the end of deployment, and recharging the sensors so that they could be reused. Sensors needed to be small enough (≤4mm) to minimize interfere with the movement of the highly mobile *Euglandina rosea* predators. This ruled out using readily available "off the shelf components" and required us to develop a custom sensor specifically for this study at the University of Michigan. The sensor leveraged a general mm-scale sensor platform (Lee *et al.*, 2013) called the *Michigan Micro-Mote* (M^3) that was enhanced for the required light dose recording.

Each sensor contained a small microprocessor (ARM Cortex M0, 2009) with 8kB of memory that controlled its operation. In addition, each sensor had a battery for power, energy harvesting for replenishing the battery during operation (Jung *et al.*, 2014), a built in radio for wireless communication with a 5cm range used for data retrieval (Ghaed *et al*., 2013), sensors for measuring temperature and battery voltage, power management to convert the Lithium battery voltage of 4.2V to the voltages used by the electronics (1.2V and 0.6V) (Jung *et al*., 2016) and an optical communication link for programming and configuring the sensor (Kim *et al*., 2012). The sensor was constructed from 8 custom design chips each measuring 1.05mm by 1.5 - 2.5mm which were stacked in a staircase manner to minimize overall sensor size (Figure 4-1a). Each chip performed a particular function (radio, sensing, processor, etc.) and the chips were connected through a bus called Mbus (Pannuto *et al*., 2016) using wirebonding.

The final chip stack was encased in epoxy to create a robust, fully sealed enclosure (Figure 4-1b) and was tested to withstand immersion in water at pressures up to 600 atm. The top portion of the sensor was encased with clear epoxy to allow light penetration, thereby enabling energy harvesting and optical communication. The bottom portion was encapsulated with black epoxy to protect the sensitive electronics from light. Due to the very low power design used, small parasitic diodes in the silicon could generate enough current when exposed to light to affect the circuit operation. After encapsulation, the sensors were wirelessly charged and programmed using light.

Techniques for Reducing Sensor Size

One of the key challenges in constructing a small, autonomous sensor is battery size. In the M^3 sensor platform, two custom designed $1.7 \times 3.0 \text{mm}^2$ batteries provided a capacity of 16µAh restricting the power consumption from the electronics to < 100nA on average, yielding a one-week lifetime. Although the light harvester can extend this lifetime, the capacity to do so depends on ambient illumination levels. To achieve a < 100nA current draw, the sensor node was heavily duty-cycled meaning it made periodic measurements and spent the vast majority of its life in sleep mode where all non-essential electronic functions were powered off. In sleep mode, only a timer, the memory, the optical link and the power management remained powered on. These components were designed with special circuit structures to achieve ultra-low sleep mode current (Jung *et al*., 2016; Kim *et al*., 2012; Lee *et al*., 2016; Chen *et al*., 2010) and were implemented in 180nm CMOS because it supports transistors with very high threshold voltage, resulting in low leakage currents. Jointly, the components that remained on in sleep mode drew 40nA in sleep mode.

Periodically, the timer switched the sensor to active mode, enabling the processor to execute instructions to acquire and store measurement data, perform radio communication, etc. The optical link could also activate the sensor to allow configuration, programming or the instigation of data retrieval. In active mode, the sensor drew 10µA due to the use of so-called "near threshold operation" where the circuit operated at much reduced supply voltage (600mV). While current draw in active mode was 250× higher than sleep mode, the active mode time period was minimized (< 1sec) resulting in an acceptable average current draw of 57nA with a wake-up period of 10 minutes. Note that this average power consumption of M^3 was up to two orders of magnitude lower than that of typical sensor systems. This allowed operation on extremely small batteries and enabled a small system size of $3.0\times1.7\times1.6\text{mm}^3$ before encasing with epoxy and $4.2\times2.0\times2.0\ \text{mm}^3$ final packaged form (Figure 4-1).

Continuous Light Intensity Monitoring

Although duty cycling lowers average current draw from the battery, it means that measurements can only be taken intermittently, when the sensor is awake. This raised a particular difficulty for measuring the solar ecology of snails where continuous light monitoring is desirable. Keeping the sensor in active mode continuously would deplete the batteries in only a few hours and hence, the light intensity had to be monitored during sleep mode. To achieve this without significantly increasing the sleep mode current draw, my colleagues observed that the power harvester inherently integrated and quantized the harvested energy from the photovoltaic (PV) cell. To up-convert the output voltage of the PV cell (250 – 450mV) to that of the battery (3.9 – 4.2V) the harvester placed charge from the PV cell on its internal capacitors and then connected these charged capacitors in series to sum their voltages and charge the battery. Each time the capacitors were charged by the PV cell and reconfigured in series, a finite amount of charge was transferred from the PV cell to the battery. Hence, the frequency of reconfiguration indicated the power produced by the PV cell. Because the power of the PV cell was approximately linear with incident light intensity, it could be used as a measure of the ambient light level. Therefore, to measure the light dose over the 10min sleep mode interval, my colleagues simply had to count the number of reconfigurations during that time. This counting of reconfigurations was performed with a small modification of the harvester chip and entailed a negligible increase in sleep mode power (< 1nW). The resulting sensors continuously monitored light level and recorded the integrated light dose for every 10min interval without the need for additional hardware or an increase in sensor size.

Sensor Testing and Calibration

For the project, my colleagues manufactured 201 sensor systems augmented to include the light monitoring capability. Most were used for bench top testing and green house testing at the University of Michigan, the latter using locally caught specimens of *Cepaea nemoralis* land snails, to ensure proper operation and to develop the sensor software prior to field deployment in Tahiti. A total of 55 tested units were taken to Tahiti and were re-used a number of times while there. A total of 40 functioning units were returned after 2 weeks of measurements – 7 units were lost during field measurements and 8 units failed.

Because the reconfiguration frequency of the harvester had dependency on temperature and battery voltage, a temperature and battery voltage reading were stored along with the light intensity code at every 10-minute interval. After data retrieval, this code was then converted to light intensity using a model which accounted for the temperature and battery voltage dependency. To construct the model, four sensor nodes were measured at 6 light levels (500, 1k, 5k, 10k, 50k, and 100klux) and 4 temperatures (25, 35, 45, and 55°C) and 4 battery voltages (3.9, 4.0, 4.1, and 4.2V), a total of 96 measurements per sensor. After averaging their light sensor codes across the 4 sensors, a multidimensional, piecewise linear model was extracted to establish the relationship between the recorded digital code and the real light intensity at a particular temperature and battery voltage (Figure 4-2a). To adjust this model for each sensor, light intensity, temperature, and battery voltage in controlled conditions of completed sensors for different temperature (25, 45, and 55°C) in a fixed light intensity (5klux) and battery voltage (4.1V) were measured. These conditions were selected based on the expected temperature and battery operating range in the field and on what the discriminating light intensity was expected to be. This was balanced with the time required to measure 55 systems in a controlled environment.

In addition, 3 systems were tested to verify the accuracy of the calibration method. Figure 4-2b, right graph, shows the resulting measurement error after calibration for 5 light levels (500, 1k, 5k, 10k, and 50klux) and 2 temperatures (25 and 35°C) and 3 battery voltages (3.9, 4.0, and 4.1V). These testing conditions were selected to match the conditions that sensors were found to have experienced during the field testing and hence are representative of the error in light readings for the collected data. The ratio between the sensor light reading and the actual controlled light intensity ranged from 0.6 to 2.2.

Study Populations and Field Work

Two field populations of *Euglandina rosea* and three of *Partula hyalina* were investigated in August 2017, located in five northern valleys of Tahiti-Nui, the main Tahitian peninsula (Figure 4-3). These locations were selected by T. Coote, who has conducted extensive field surveys on Tahiti since 2004, as being the most accessible populations of both species currently available.

Although *Euglandina rosea* remains widely distributed throughout Tahiti, it has become less numerous in many valleys in recent years, possibly due to the introduction of another snail predator, the New Guinea flatworm *Platydemus manokwari* (Justine *et al*., 2015; Gerlach, 2016). Dead *E. rosea* shells were more common at our three *Partula hyalina* study populations than live specimens and I focused instead on the robust populations present in the nearby main Fautaua Valley and in its side-valley Fautaua-Iti (Figure 4-3) where I succeeded in recording the solar ecology of a total of 39 individuals. In both locations, I picked sites where foraging *E. rosea* had ready access to shaded and to open habitats. The Fautaua-Iti Valley location consisted of an open sunlit trail through the rainforest (Figure 4-4a) and the solar ecology of 10 predators was monitored here on two days: 5 on August 8th and another 5 on August 11th. The Fautaua Valley location consisted of a forest edge adjoining an open grassy area (Figure 4-4b) and 29 predators was monitored here over two days: 12 on August 12th and 17 on August 14th.

All three of our *Partula hyalina* study sites (Figure 4-3) consisted of discrete patches of vegetation between the edge of the forest and the primary stream, or *captage*, within each valley. The Tahitian valley of Tipaerui encompasses a small side valley - Tipaerui-Iti (Figure 4-3) – that contains the most robust known surviving population of *P. hyalina* on Tahiti, consisting of hundreds of individuals. They were restricted to a linear stand of *Etlingera cevuga* extending for 60-70 meters (Figure 4-4c) and the solar ecology of 28 aestivating Tipaerui-Iti *P. hyalina* was recorded over two days: 10 on August 10th and 18 on August 15th. *P. hyalina* population sizes were much smaller in the other two valleys, Faarapa and Matatia (Figure 4-3), requiring us to monitor all the individuals I encountered. The Faarapa Valley site consisted of a mixed stand of *Barringtonia asiatica*, *Alocasia macrorrhiza* and *Pisona umbellifera* (Figure 4-4d). I detected 6 individuals at this site and their solar environment was monitored on August 8th. Our remaining *P. hyalina* study site was in Matatia Valley (Figure 4-3) where a small, low-density population occurred in scrubby habitat attached to foliage of *Z. officinale*, *P. umbellifera* and *Inocarpus fagifer* (Figure 4-4e). A total of 8 individuals were detected and assayed on August 7th.

Deployment of smart solar sensors

Each working day, I along with two other colleagues (Coote & Lee) entered the study valley in the early morning between 8-9am, prior to the appearance of the sun above the valley walls, and searched systematically for our respective target species. *Euglandina rosea* individuals were found foraging actively, either on the ground or climbing on vegetation, and they typically maintained this searching activity throughout the day. In contrast, *Partula hyalina* individuals were aestivating attached to the underside of leaves and specimens typically remained *in situ* on the same leaf during the observation period.

To track the solar ecology of each predator, a smart solar sensor was reversibly attached to the dorsal surface of its shell using a nut and screw method (Figure 4-5). The nut (McMaster-Carr, Brass Hex Nut, narrow, 0-80 thread size) was glued (Loctite, Super Glue) directly on the predator's shell and, after allowing 10 mins for bonding, a sensor, pre-glued to a compatible screw (McMaster-Carr, 18-8 Stainless Steel Socket Head Screw 0-80 thread size, 1/16" long) was attached mechanically. Each predator was numerically labeled using nail polish and released at the exact spot it had been discovered. For the rest of the study period, each predator was visually tracked as it continued its foraging until the mid-afternoon when the sun descended below the valley walls and the snails and sensors were recovered. These invasive predators were then euthanized.

Aestivating *Partula hyalina* attach to the underside of leaves and, because our permit did not allow the direct attachment of light sensors to this endangered species, I deployed two under leaf sensors bracketing each individual (Figure 4-6) using a nut/screw/magnets combination. This involved gluing, in advance, the screw to the sensor base and the nut to a round magnet (Radial Magnet Inc., Magnet Neodymium Iron Boron (NdFeB) N35, 4.78mm diameter, 1.60mm thickness). In the field, these components were assembled and held in place using another magnet positioned on the upper leaf surface. In addition to recording the under leaf light intensities experienced by the aestivating *P. hyalina* specimens, I also recorded the ambient light intensity: the solar irradiation environment that foraging *Euglandina rosea* would need to traverse to prey on them. In order to obtain this information, I attached a third sensor to the upper surface of the leaves harboring the aestivating specimens (Figure 4-6).

Data programming and recovery

Each working day, the data recording function of the smart sensors was activated before going to the field and was terminated after returning from the field, when the data were egressed via the sensors' wireless communication link. For each sensor, the recording start time, meaningful time of the measurement start time, meaningful measurement end time, and sensor recording end time were recorded to properly calibrate the time of the recorded samples. The received raw data in digital format was then translated to time and light intensity information using a MATLAB program and the calibration data specific for that sensor.

Results

Released *Euglandina rosea* specimens with attached light sensors promptly resumed active foraging behavior (see video in Appendix IX) and crawled linear distances of ≤5 meters prior to data recovery in the late afternoon. A large majority of this time was spent in undergrowth, especially during dry, sunny conditions, and one initial concern was whether the process of handling the predators changed their subsequent behavior. I inadvertently got an opportunity to test this for a Fautaua-Iti specimen equipped with a light sensor on August 8th that eluded recapture until August 11th. Its sensor yielded similar light intensity profiles for 2 consecutive days (Figure 4-7a), the sensor's recording time limit, suggesting that the process of sensor attachment did not significantly affect its immediate foraging behavior. The August 9th profile (Figure 4-7b) is of particular interest because it represents the light ecology of an unimpeded free-ranging predator throughout a full solar day. August 9th was sunny and clear on Tahiti and the sensor recordings show that, once the sun cleared the valley walls ~9:20 am, the predator experienced a rapid initial increase in light intensity to 675 lux, followed by an equally rapid decrease to 117 lux. As Tahitian solar irradiation levels, measured by satellite, rose on August 9th to a peak of at 786-790 watts/m^2 by 12:00-1:00pm (Figure 4-7b), the light sensor attached to the predator recorded two further sharp cycles of increase and decrease: 117-858-090-864-001lux. Afternoon readings remained relatively low, not exceeding 140 lux. I infer from these data (Figure 4-7b) that the predator sought progressively greater cover as its ambient light intensity increased during the morning and that it remained primarily under cover into the mid afternoon.

Figures 4-8 and 4-9 respectively summarize the mean light intensity profiles (± standard errors) recorded for 29 Fautaua *Euglandina rosea* specimens over two days (August 12th: dry, mixed sun and cloud, and 14th: sunny am, rain in pm) and 10 Fautaua-Iti specimens over two days (August 8th: rainy and overcast, and 11th: dry, mixed sun and cloud). With one exception, mean readings taken at the two locations over four days of monitoring did not exceed 1500 lux and the summary profiles broadly parallel the singleton data (Figure 4-9). Fautaua snails collectively showed a rapid increase in light readings, peaking at 10:40-10:50am, followed by an equally rapid drop by 11:20am, and a gradual further decline after 1:50pm (Figure 4-8). Fautaua-Iti specimens maintained slightly higher light intensities until 1pm, before declining gradually (Figure 4-9). The most anomalous data point was the Fautaua-Iti 12:50pm value, showing a mean of 2,109 lux and a greatly increased standard error. This was due to a single specimen recorded on August 11. While it was crossing the open trail that bisected this study site (Figure 4-4a), a break in the cloud cover briefly exposed it to 13,449 lux of sunlight (Figure 4-10). This was by far the highest light intensity recording I obtained for *E. rosea* during the study; the next highest being a Fautaua Valley individual on August 12th that recorded a single peak 4,774 lux reading followed by a rapid drop to 847 lux.

Partula hyalina specimens spent the daylight hours aestivating while attached on the undersides of leaves of a variety of host plant species. The sensors were placed adjacent to the aestivating snails to record their immediate light environments and sensors on the upper surfaces of the supporting leaves to record their ambient light environments. The highest immediate and ambient light intensity readings were recorded at the Tipeaerui-Iti site on August 10th, both on *Zingiber officinale* leaves: an aestivating *P. hyalina* was exposed to 45,192 lux at 12:40pm and a nearby leaf top sensor logged a peak reading of 71,165 lux at 12:10pm.

Figures 4-11, 4-12 and 4-13 respectively show the *Partul*a *hyalina* mean light intensity profiles (± standard errors) recorded for our three study populations. The Tipaerui-Iti Valley data (Figure 4-11) are summarized for two day's recordings: August 10th and August 15th (both dry, mixed sun and cloud). Mean leaf top readings initially increased rapidly in light intensity from the 9:50 am recording of 2,139 lux to 7,441 lux by 10:30. They dipped to 2,807 lux by 10:50am, before peaking at 10,865 at 12:00pm, then falling steadily after 12:50pm to 551 lux by 3:30pm. Tipaerui-Iti Valley under leaf mean recordings tracked the leaf top fluctuations, but at lower levels of intensity, building to a peak of 5,622 lux at 12:40 pm. The Faarapa Valley *P. hyalina* light intensity data (Figure 4-12), representing a single day's recording (August 8th; dry, mixed sun and cloud), broadly resembled the resultant Tipaerui-Iti profile (Figure 4-7a) with peak light intensities of 13,956 lux (leaf top) and 6,054 lux (under leaf) at 12:30 pm. In contrast, the single-day Matatia Valley recording (August 7th, a wet, overcast day) yielded much lower light readings: respectively dropping to a mere 224 lux (leaf top) and 60 lux (lower leaf) at 12:00 pm and 12:10pm, before peaking at 2,117 lux (leaf top) and 1194 lux (lower leaf) at 12:40 pm (Figure 4-13).

The low light intensities recorded for Matatia Valley *Partula hyalina* specimens (Figure 4-13) were not unique to this site. This was evident when the Tipaerui-Iti Valley leaf top sensor data (Figure 4-11) were parsed into their two constituent days of recording: August 10th and 15th. Both days were dry with mixed sun and cloud, but the 10th was predominantly sunny (once the cloud cover lifted after 11am), whereas the 15th was predominantly overcast with two brief exceptions (before 10:30 am and again from 1:30-1:50 pm). Consequently, the Tipaerui-Iti study population produced two very distinctive daily mean leaf top light intensity profiles that differed by 5,000-15,000 lux for much of the solar day, with the August 15th mean converging on the Matatia Valley mean during overcast periods (Figure 4-14).

Figure 4-15 summarizes the light intensity data recorded for our Tahitian study populations of *Euglandina rosea* (2 sites and 39 specimens over 4 days) and *Partula hyalina* (3 sites and 42 specimens over 4 days). The data indicate that the two species have highly distinctive daily solar irradiation profiles. This is especially apparent for the leaf top sensor data. Leaves supporting aestivating *P. hyalina* experienced significantly higher mean ambient irradiation levels than did the predators throughout the solar day (10:00 am to 3:30pm; Figure 4-15). That difference was maximal around noon (12:10-12:50 pm) with ≥10-fold higher mean readings for leaf top sensors (7,674-9,072 lux) relative to those attached to *E. rosea* individuals (540-762 lux). The *P. hyalina* under leaf sensors also recorded significantly higher light intensities than the predator-attached sensors for much of the solar day (11 am to 3 pm), with a maximum 7-fold mean difference (4,415 lux versus 606 lux) recorded at 12:40 pm (Figure 4-15).

Discussion

My results corroborate the main predictions made by the solar refuge hypothesis (Bick *et al*, 2016) regarding the distribution pattern and solar ecology of extant populations of *Partula hyalina* in Tahititan valleys. I did not encounter this species in interior forest habitats and neither has one of the authors, T. Coote, during his 13 years of surveying Tahitian valleys for surviving partulids. It appears that the interior forest populations of *P. hyalina* detected by Crampton (1916) have been extirpated and that survivors endure only in edge habitats.

Of particular note is the importance of a single host plant, the wild red ginger *Etlingera cevuga*, in the ecology of surviving *Partula hyalina.* By far the largest known surviving Tahitian population of the snail occurs in the extensive linear stand of *E. cevuga* in our Tipaerui-Iti Valley study site (Figure 4-4c). In a 2004 survey of 70 Tahiti-Nui valleys, 75% of remnant *P. hyalina* populations occurred on this host species alone, growing within 10 meters of valley streams (Coote, 2007). *Etlingera cevuga*, known locally as *opuhi* or *avapuhi*, is considered to be endemic, or else a prehistoric Polynesian introduction, to the Society Islands, grows to 2-4 meters in height and its foliage was traditionally used for thatch and bedding (Brown, 1931). It is currently not cultivated and is commonly found near rivers in semi-open habitats but not in closed canopy forests, *e.g.*, *Inocarpus fagifer* or *mape* forest (J-Y. Meyer, *pers. comm.*).

My solar sensor data demonstrate that surviving *Partula hyalina* populations are exposed to significantly higher ambient solar irradiation levels than those endured by the alien predator *Euglandina rosea* foraging in forest edge and clearing habitats (Figure 4-15). This result corroborates the main prediction of the solar refuge hypothesis, implying that small solar refuges actually exist for this species in Tahitian valley forest edge habitats and that they may have played an important role in its differential survival.

My data also yielded additional insights into the abiotic ecological factors limiting *Euglandina rosea*'s effectiveness as a predator. Meyer and Cowie (2011) focused on the role of environmental temperature and humidity in shaping the distribution of the predator. Our results indicated that environmental light intensity may be a potent additional abiotic factor. Although one of the sensor-equipped predators briefly endured 13,449 lux of sunlight (Figure 4-10), the data show that foraging predators rarely exposed themselves to >2,000 lux in the mornings and >1,000 lux in the afternoons. In contrast, forest edge host plant harboring aestivating *Partula hyalina* were exposed to mean solar irradiation intensities >3,000 lux throughout much of the solar day (10:10am – 2:00pm), reaching a peak mean of ~9000 lux at midday (Figure 4-15), with individual host plant leaf top sensors recording up to 71,165 lux.

The solar refuge effect is intermittent, being necessarily limited to daylight hours and being further restrained by overcast daytime weather conditions. My predator field data (Figures 4-8 and 4-9) imply that an ambient light intensity >2,000 lux may be required to effectively deter foraging *Euglandina rosea*. Consequently, the protective solar effect experienced by endemic tree snails at the Matatia Valley site on August 7th, an overcast day, appears to have been marginal at best (Figure 4-13) and, in Tipaerui-Iti Valley, it fluctuated in intensity and duration over the two days of observation (Figure 4-14). The intermittent nature of the protective solar effect in these forest edge habitats may dilute their effectiveness as solar refuges for *Partula hyalina*, allowing predators to gain access to the surviving tree snails overnight and/or during overcast days.

Gerlach (1994) estimated an average movement for adult *Euglandina rosea* of 0.3 meters per hour, implying that a sequence of two overcast days and three nights (~60 hours) could allow predators from adjacent shaded forest habitats to migrate up to 18 meters towards/into a solar refuge. However, our field data imply that the *Partula hyalina* solar refuge protective effect may operate on very small spatial scales (<1-5 meters), *e.g.*, a substantial population (hundreds) survive on a stand of *Etlingera cevuga* in Tipaerui-Iti Valley but they were absent from the immediately adjacent forest (Figure 4-4c). Meyer and Cowie (2011) considered Gerlach's (1994) 0.3 meters per hour rate to be an overestimate, because much of the movement of adult *E. rosea* in Hawaii is non-linear and their study individuals exhibited a mean resultant movement of <2.5 meters per week. This latter estimate seems more consistent with the persistence of small, scattered remnant populations of *P. hyalina* in forest edge habitats, primarily on *E. cevuga* host plants, in total of 31 Tahitian valleys (Coote 2007).

The results, together with the available Tahitian valley survey data (Coote, 2007), highlight the importance of stream edge *Etlingera cevuga* stands in the continued survival of *Partula hyalina* on the island. The Tipaerui-Iti Valley site, in particular, deserves follow up detailed ecological study and characterization in an effort to identify what factor(s) have enabled it to support an exceptional population of *P. hyalina*. One potential factor may be the presence of leaf litter. Meyer and Cowie (2011) emphasized the importance of leaf litter habitat to adult *E. rosea* as their preferred microhabitat and it is possible that presence of a well-developed leaf litter within solar refuges could undermine their protective effect by allowing predators to shelter *in situ* during daylight hours.

The results also indicate that long-term proactive conservation planning for *Partula hyalina* should involve mapping, protection and maintenance of wild red ginger stands in as many Tahitian valleys as possible. Active maintenance of solar refuges could involve removal of leaf litter within the stands and selective removal of encroaching tree canopies. Stands currently lacking *Partula hyalina* populations could be repopulated with transplanted individuals, ideally from the same valley. Research is also required on the solar ecology of the other surviving Tahitian valley endemic, *Partula clara*, which has a variety of different shell color morphs and is frequently also found on *Etlingera cevuga* stands (Coote, 2007), and on the more recently introduced snail predator, the New Guinea flatworm *Platydemus manokwari*. With assiduous maintenance of forest edge solar refuge habitats, it may be possible to ensure the long-term survival of these two partulid taxa in Tahitian valleys.

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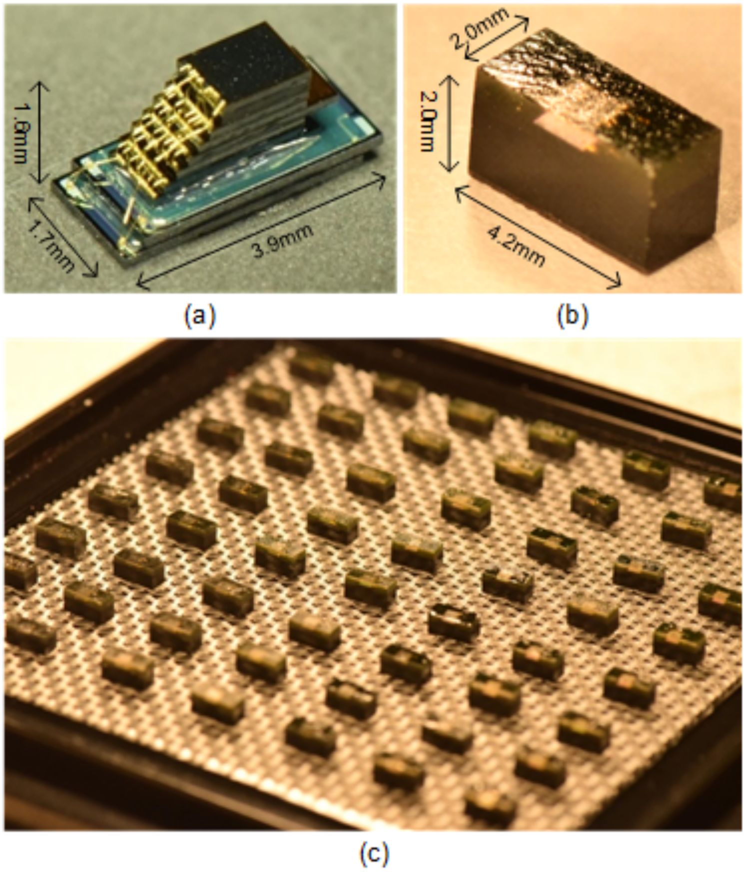

Figure 4–1. a) View of pre-encapsulation light sensor showing the stack of custom designed M3 chips arranged in staircase fashion and interconnected with Mbus. b) A light sensor after encapsulation with epoxy. c) Encapsulated light sensors ready for field deployment in Tahiti.

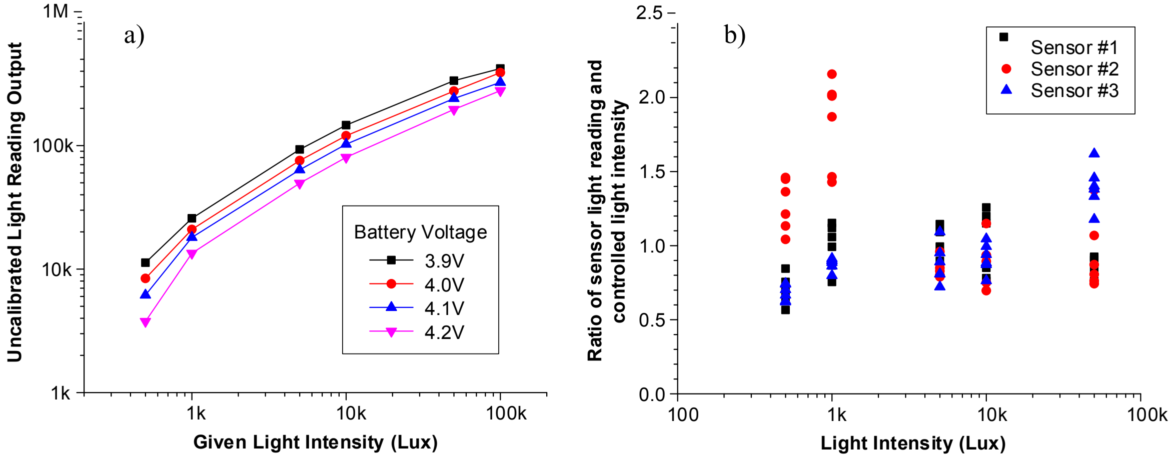

Figure 4–2. Sensor testing and calibration data. a) Measured data for four sensor systems showing the uncalibrated output code across a range of applied light and battery conditions from which the piecewise linear model translating output code to light intensity was constructed. b) Verification data for 3 sensors showing the ratio between the controlled light intensity applied to the sensors and the light value reported by the sensors across 2 temperatures (25 and 35°C) and 3 battery voltages (3.9, 4.0, 4.1V).

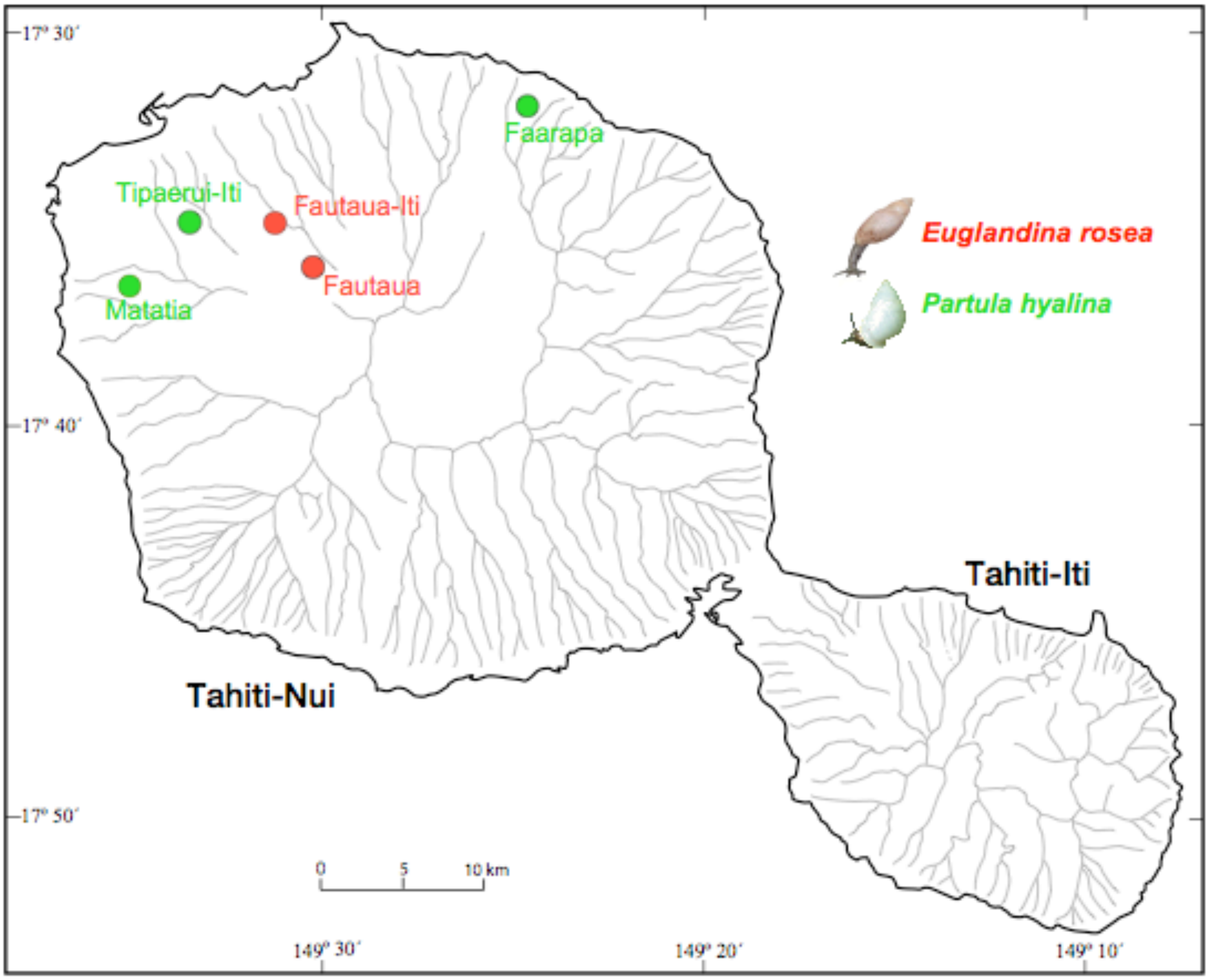

Figure 4–3. Map of Tahiti showing the valley sampling locations for the endemic Tahitian tree snail Partula hyalina (green circles) and the invasive alien predator *Euglandina rosea* (red circles) study populations.

Figure 4–4. Representative views of the 5 Tahitian field locations used in this study. a) shows the Fautaua-Iti Valley site consisting of an open trail through the rainforest. Arrows point to the vegetation on either side of the trail where the predator (*Euglandina rosea*) specimens were located and released after sensor attachment. b) shows a representative portion of the Fautaua Valley study site, consisting of a forest edge adjoining an open grassy area. Arrows indicate the undergrowth just inside the forest where *E. rosea* specimens were caught and released. c) is a view of the Tipaerui-Iti Valley study site showing a portion of the linear *Etlingera cevuga* stand (arrows) where the aestivating *Partula hyalina* specimens had their solar ecologies characterized. Finally, d) and e) are respectively views of the Faarapa Valley and Matatia Valley sites with arrows again pointing out the location of the aestivating specimens of *P. hyalina* specimens I investigated.

Figure 4–5. A foraging *Euglandina rosea* specimen bearing an attached solar sensor, Fautaua Valley study site.

Figure 4–6. An aestivating specimen of *Partula hyalina* attached to the underside of an *Alocasia macrorrhiza* leaf, Faarapa Valley study site. The tree snail is flanked by two light sensors measuring its immediate (under leaf) environment and by a magnet anchoring an upper leaf light sensor measuring the leaf's ambient (leaf top) environment.

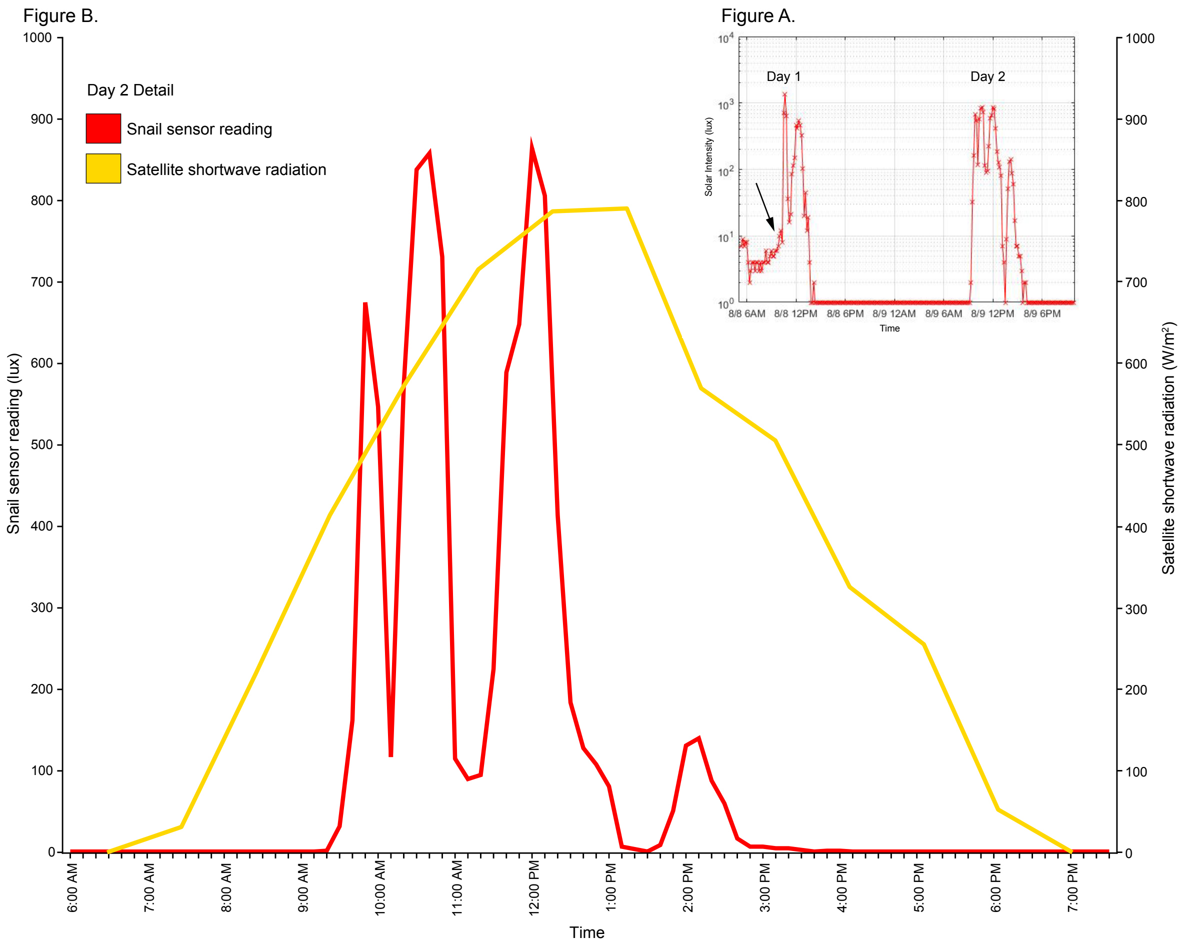

Figure 4–7. Solar ecology readings for a single Fautaua-Iti specimen of *Euglandina rosea* over two days. A) The predator's light intensity profiles for August 8th (Day 1) and, after it eluded recapture, on August 9th (Day 2). The black arrow indicates when *E. rosea* was released after the sensor was attached to the shell. B) A detailed view of the predator's August 9th light intensity profile superimposed with that day's record of Tahitian solar irradiation levels, measured by satellite and obtained from www.meteoblue.com.

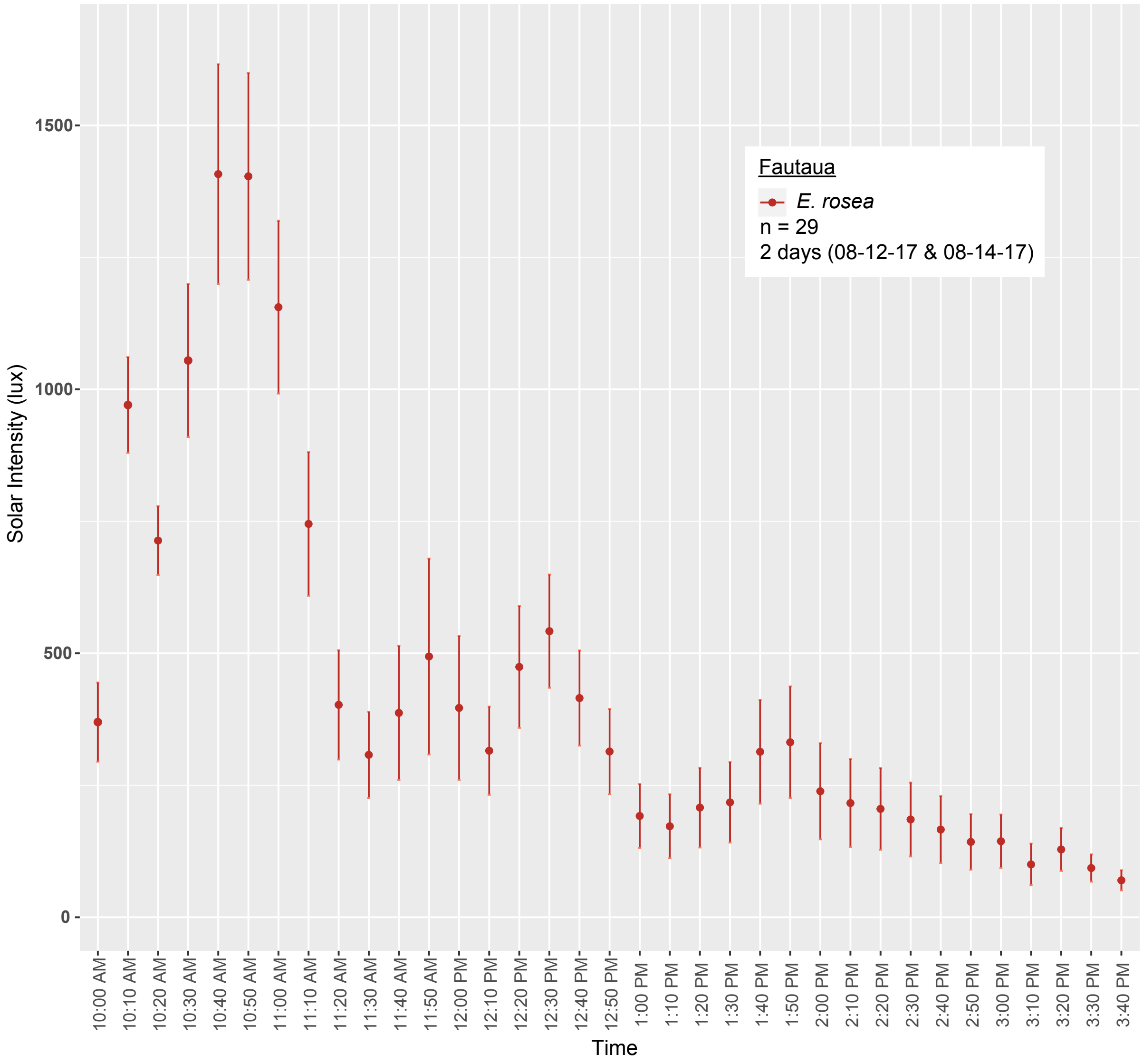

Figure 4–8. Recorded daily solar ecology profiles, integrated over 10-minute intervals, for field specimens of *Euglandina rosea*. Fautaua Valley study site mean and standard errors of light sensor readings obtained from a total of 29 *E. rosea* specimens over two days (August 12th and 14th).

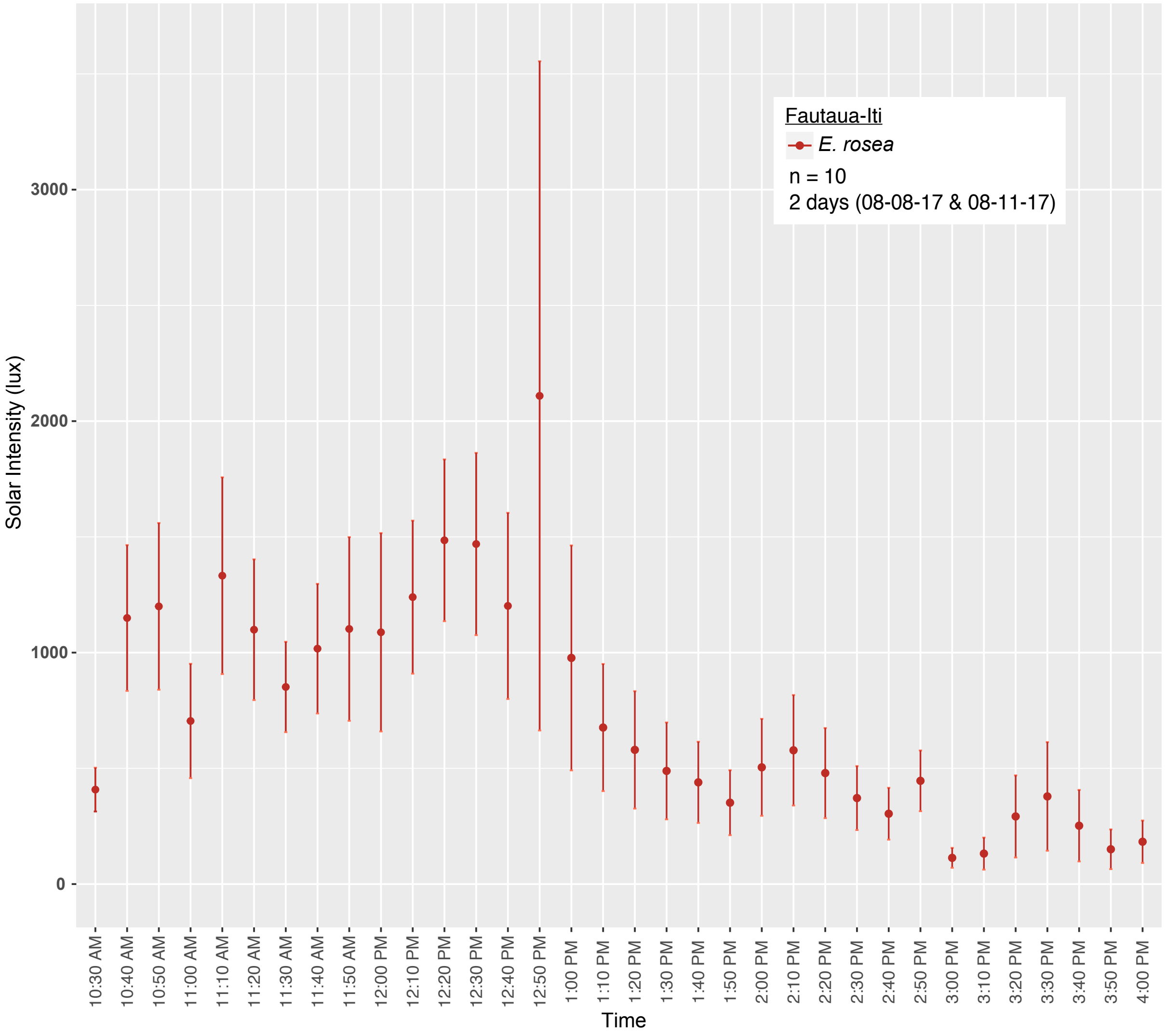

Figure 4–9. Fautaua-Iti Valley study site mean and standard errors of light sensor readings obtained from a total of 10 *E. rosea* specimens over two days (August 8th and 11th).

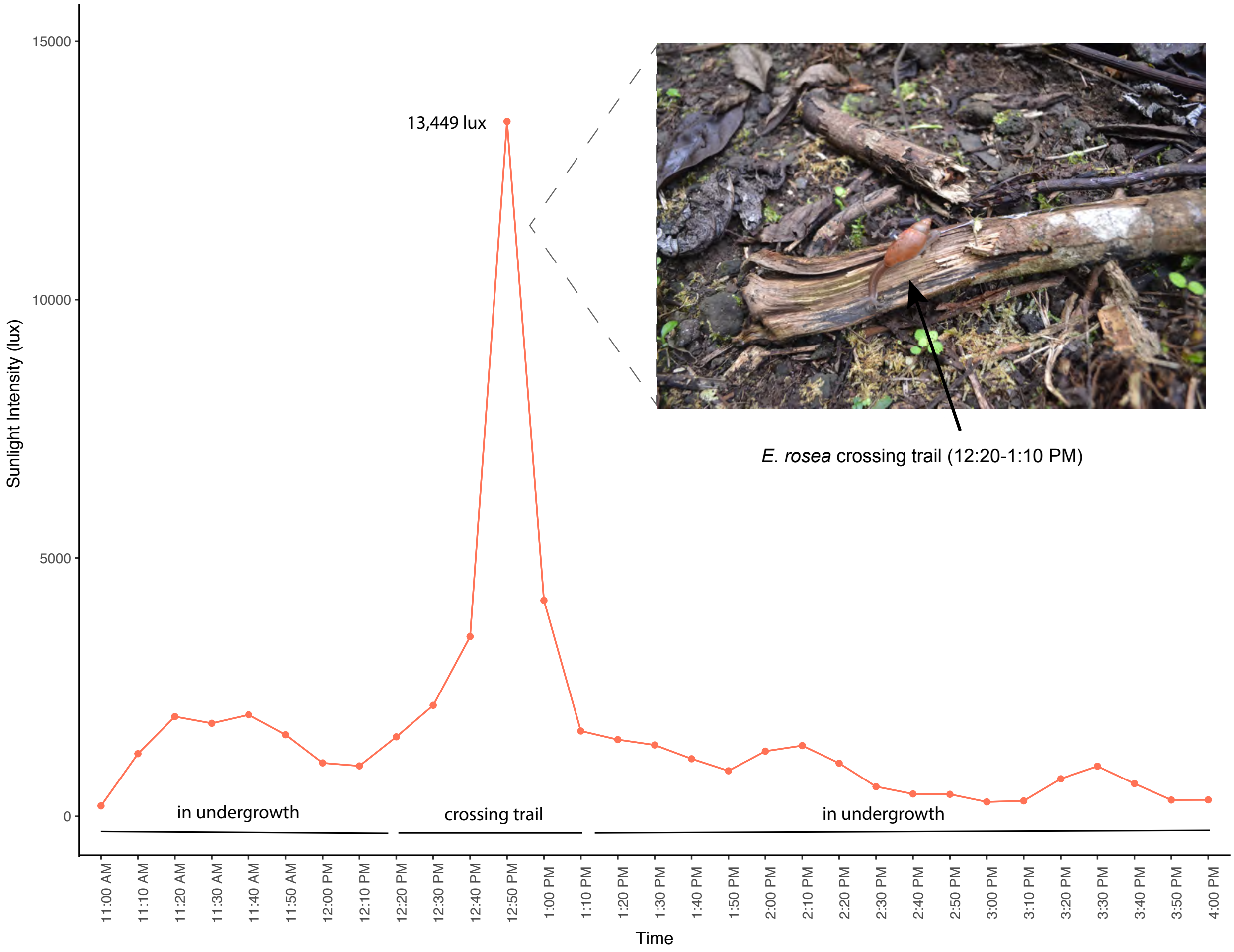

Figure 4–10. August 11th solar ecology profile of a Fautaua-Iti Valley *E. rosea* specimen that briefly recorded the highest predator light intensity reading recovered in this study while crossing the open trail that bisected the study site (Figure 4-4a).

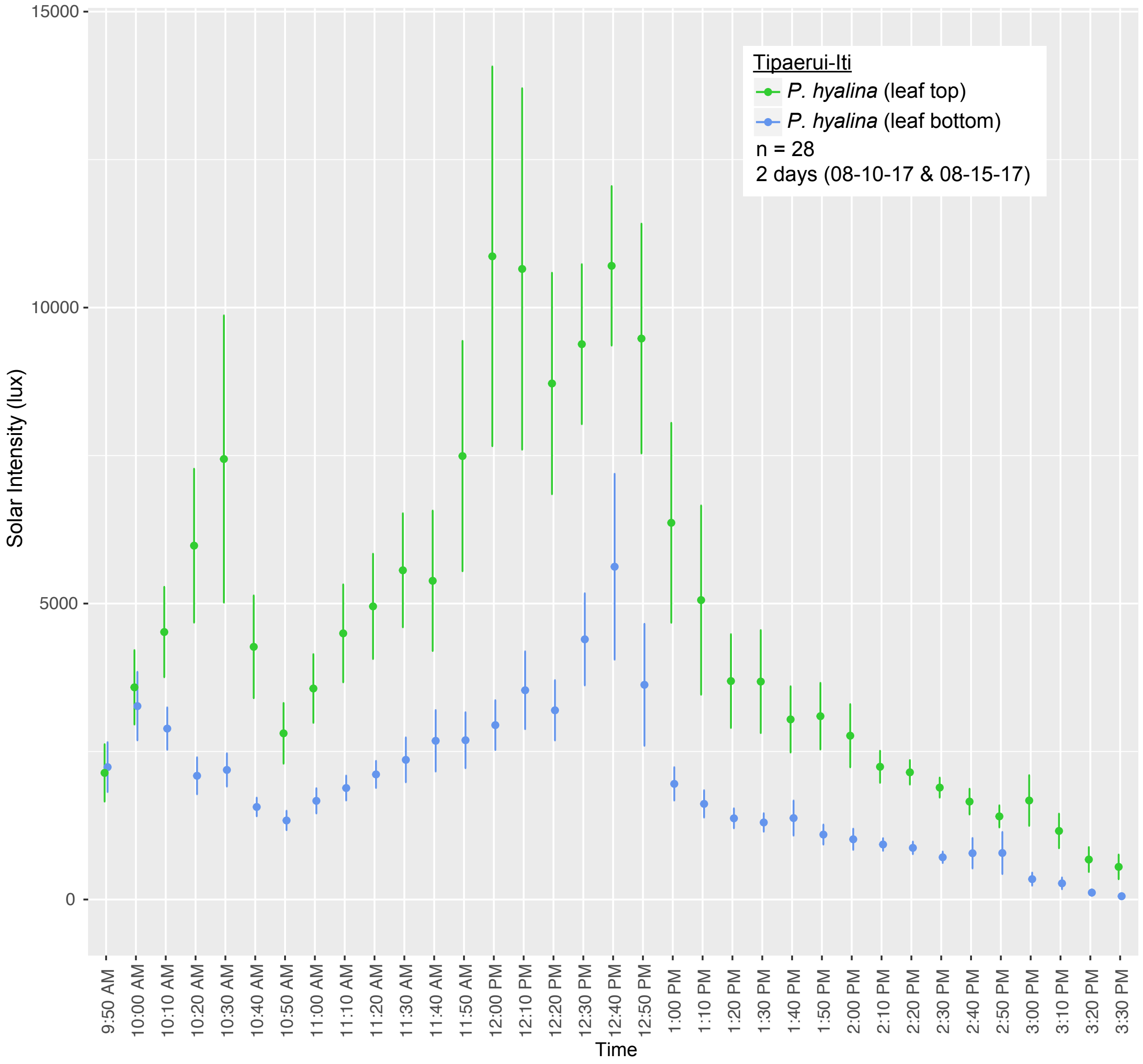

Figure 4–11. Solar ecology profiles obtained for aestivating field specimens of *P. hyalina*. Sensor readings were integrated over 10-minute time intervals and are presented as mean values with standard errors. Under leaf sensors (Figure 4-6) recorded the tree snails' immediate light environment whereas leaf top sensors recorded the ambient light environment of the supporting leaves. a) Tipaerui-Iti Valley study site records for a total of 28 aestivating tree snail specimens over two days (August 10th and 15th).

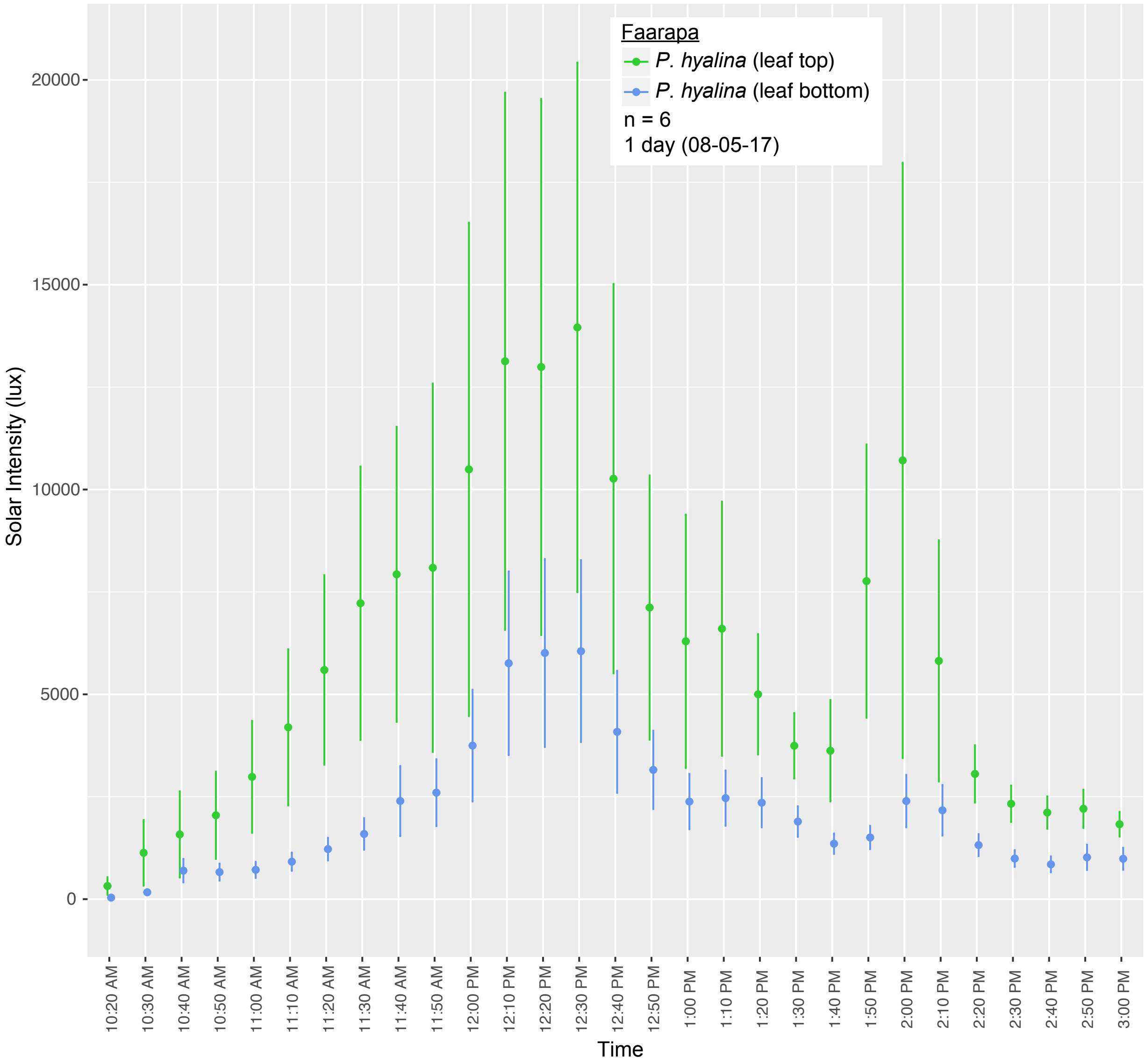

Figure 4–12. August 5th data obtained for 6 Faarapa Valley *P. hyalina.*

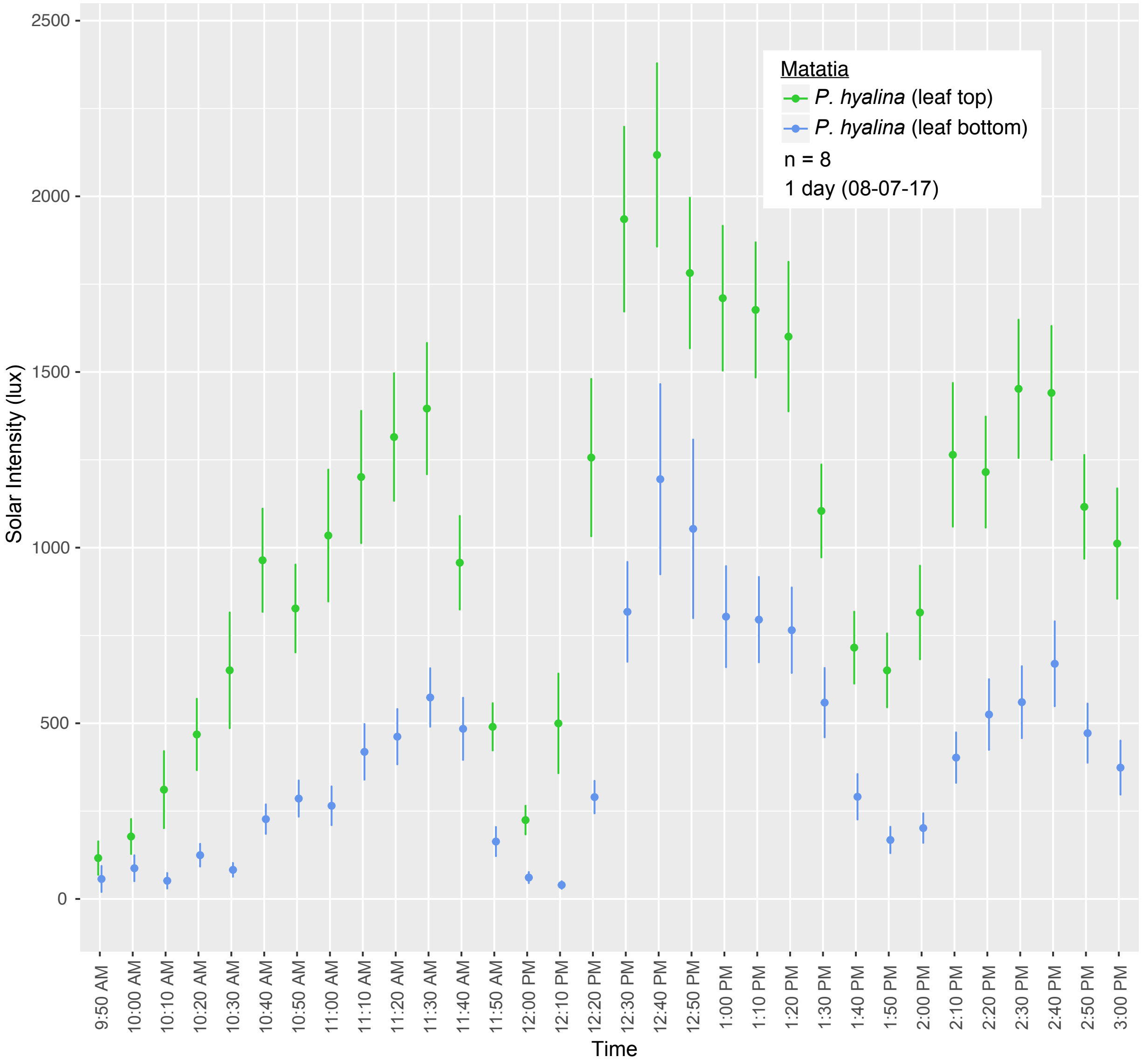

Figure 4–13. August 7th readings for 8 Matatia Valley specimens.

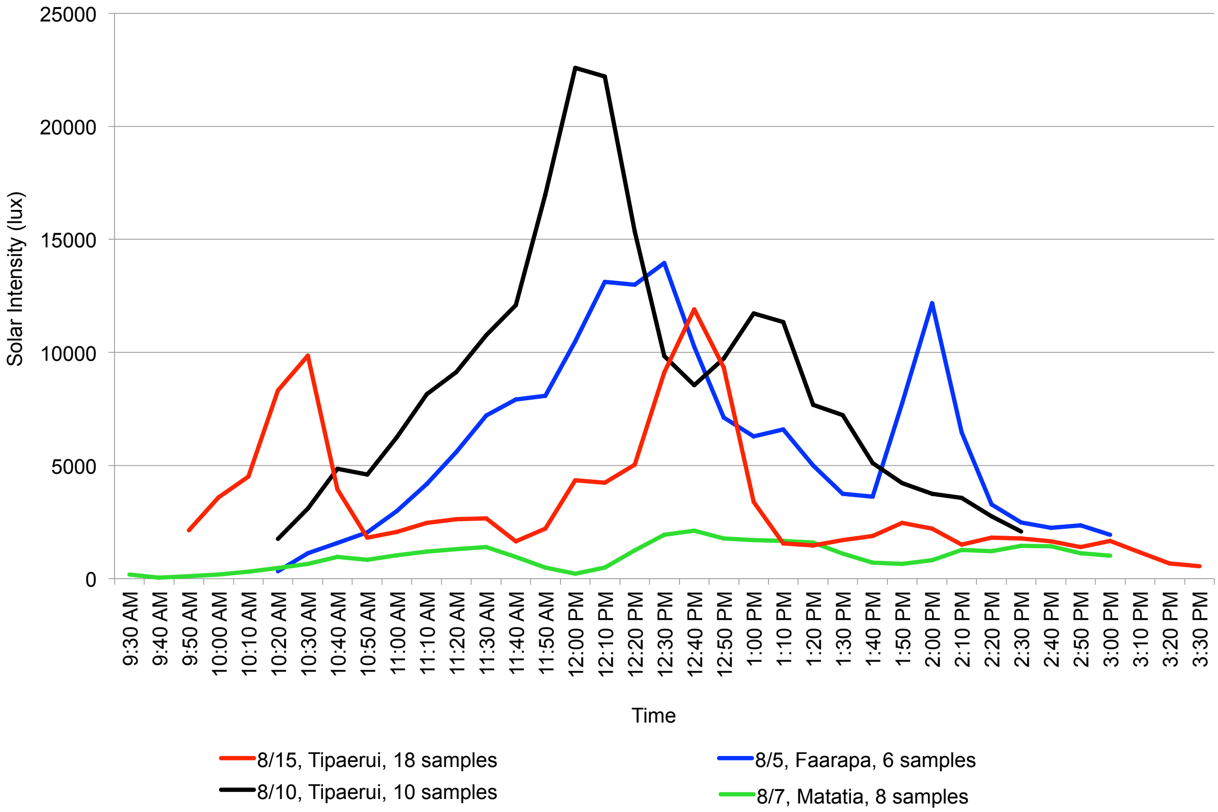

Figure 4–14. Daily mean leaf top sensor light intensities recorded for aestivating field specimens of *Partula hyalina*. Sensor readings were integrated over 10-minute time intervals. Note the divergent August 10th and 15th solar irradiation profiles of leaves supporting Tipaerui-Iti Valley tree snails.

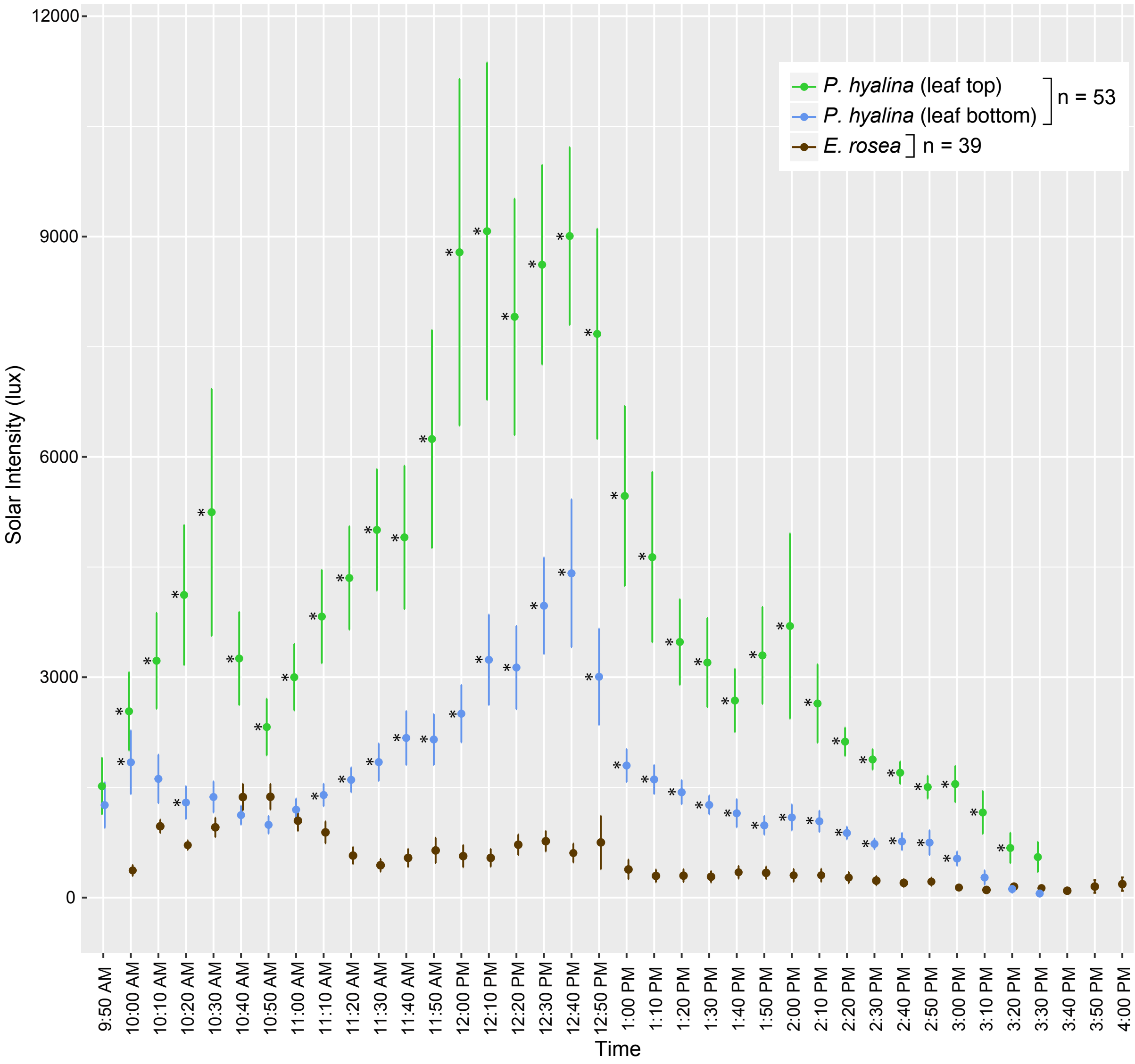

Figure 4–15. Field solar irradiation intensities recorded for the endemic tree snail *Partula hyalina* and the alien predator *Euglandina rosea* in August 2017. Daily light intensity data (means and standard errors) were integrated over 10-minute time intervals for 39 *E. rosea* in two localities over four days and for 53 *P. hyalina* specimens (both leaf top and under leaf sensor readings) in three localities over four days. Each mean *P. hyalina* reading that differed significantly (P<0.05) from the chronologically-equivalent mean *E. rosea* reading is indicated by an *.

CHAPTER 5

Systematic Relationships Among Partulid Tree Snails of Near Oceania Clarify Their Taxonomic Status and the Role of Regional Prehistoric Exchange Networks in Their Distributions

Abstract

This portion of the thesis aimed to produce the first systematic study of the partulid tree snails of Near Oceania, revise the taxonomy of these poorly-studied snails and establish the extent of anthropogenic introductions in their multi-archipelagic distribution and survival. It involved extensive field sampling throughout the island archipelagoes of Papua New Guinea (PNG) and the Solomon Islands (SI), including the adjacent Remote Oceania Santa Cruz archipelago, from 2012-2016. Specimens were genotyped using two very distinct approaches: Next Generation Sequencing (NGS) double digested Restriction Associated DNA sequencing (ddRADseq) encompassing 4819 loci, as well as a traditional targeted gene approach using a single mitochondrial "barcoding" gene (Cytochrome Oxidase I). Phylogenetic results support the presence of only 3 species of *Partula* in Near Oceania and 2 more in the Santa Cruz archipelago; in contrast to the respective 5 and 1 species recognized in a recent taxonomic revision. Three of the currently recognized Near Oceania species are instead cryptic populations of a single human-associated (restricted to coastal villages, absent from native forest) partulid, *Partula micans*. It occurs in small scattered synanthropic populations throughout the main SIs archipelago and in multiple PNG archipelagoes, including one record from a coastal village on the PNG mainland as well as a single island record from Vanuatu. It is not possible to identify at present convincing source non-synanthropic populations for *P. micans*, but the phylogenomic

data outline three among-island potential regional prehistoric trading exchange networks linking Woodlark with Boiaboiawaga and New Britain; New Britain with Buka and Shortlands; and New Georgia with Sanata Isabel and Guadalcanal. A revised taxonomy is presented for the 5 regional species: *P. grisea*, *P. micans*, *P. cramptoni*, *P. auraniana* and *P. vanikorensis*.

Introduction

The Near Oceania archipelagos of Papua New Guinea (PNG) and the Solomon Islands (SIs) represent the least-studied part of Partulidae's range. Near Oceania is distinguished from Remote Oceania by its proximity to a continental landmass (Sahul PNG), by its short inter-island distances and by its much earlier (≥36 kyrs BP) settlement by humans (Green, 1991; Kirch, 2010). It represents a biotic transition zone characterized by a decreasing prevalence of continental taxa with increasing distance from Sahul PNG (Keast & Miller, 1996).

The boundary between Near and Remote Oceania is represented by the 441km stretch of open ocean separating the easternmost island, San Cristobal (Makira), of the main SIs archipelago from Nendo, the westernmost island in the Santa Cruz archipelago (Figure 5-1). Although the Santa Cruz group is politically part of the Solomon Islands, it is biogeographically linked to Vanuatu (Mueller-Dombois & Fosberg, 1998) and was the first Remote Oceania archipelago settled by humans with the arrival of Lapita Culture Complex ~3200 BP (Kirch, 2010).

Prior to the recent taxonomic revision by Gerlach (2016), the Near Oceania literature listed 14 endemic species of *Partula*; 13 described by 19th century conchologists, most of whom assumed that snails from distinct island groups were necessarily separate species. During the 20th century, these snails received scant scientific attention, apart from brief comment on their phenotypic similarity and questionable taxonomic validity (Solem, 1959). The most intensive sampling was performed by the now deceased partulid expert Yoshio Kondo in 1966. Kondo identified all of the partulids he encountered throughout the main SIs archipelago as *Partula micans*, a species that he found on small low islands and around coastal villages of larger islands but not in native forest. In an unpublished 1971 manuscript kept in his Bishop Museum files, Kondo had proposed a radical taxonomic rationalization: synonymizing under *P. micans* all but two (*P. cramptoni* and *P. vanikorensis*) of the 8 nominal Solomons partulid species, in addition to the PNG *P. similaris*. He viewed this species as invasive but thought that variation in shell size among archipelagoes (smaller on small islands, larger on large islands) and its unusually extensive range ruled out anthropogenic introductions. Kondo's unpublished observations were based primarily on qualitative assessment of shell phenotypes. This was also the case with Gerlach's (2016) taxonomic revision, who reduced the number of recognized Near Oceania species from 14 to 5: *Partula grisea*, *P. similaris*, *P. flexuosa*, *P. micans*, *P. cramptioni*, and *P. vanicorenisis* (Figure 5-2). Notably, Gerlach (2016) split Kondo's unpublished concept of *P. micans* into three difficult to distinguish (no diagnostic key was provided) species - *P. similaris*, *P. flexuosa* and *P. micans* – on the basis of minor qualitative shell phenotype differences. He described largely-discrete multi-island distributions for each of these three taxa, apart from Guadalcanal where he recorded the co-presence of both *P. flexuosa* and *P. micans*.

My thesis concerns the survival of partulid tree snails in the Anthropocene and my interest in the partulids of Near Oceania stems from a study by Ó Foighil *et al*. (2011) on *P. similaris* in PNG archipelagos (Massim Region and New Britain). Populations had highly atypical ecologies, occurring on tiny low-elevation islets (no other such partulid record) and also on larger high islands (including the PNG mainland; the only continental partulid record) but restricted to coastal villages and being absent from native forest. This synanthrophic pattern of distribution appears to be unique among partulids and makes this species of particular interest in conservation biology terms, given its ability to survive. In addition, populations that inhabited geologically distinct archipelagos (on separate tectonic plates) surprisingly exhibited within-population levels of genetic differentiation (Ó Foighil *et al.* 2011). Most partulid tree snails are single island endemics and interisland/archipelago dispersal events are likely very rare (Cowie, 1992 & Kondo, 1968) and may involve aerial transport (via birds and/or typhoons) rather than rafting (Vagvolgyi, 1975; Wada, 2012). The only other known species with a multi-archipelago distribution, *Partula hyalina*, stems from prehistoric anthropogenic introduction events (Lee *et al.*, 2007). Ó Foighil *et al.* (2011) hypothesized that *P. similaris* may have been similarly translocated among PNG archipelagos but insights into the timeframe (apart from regional prehistory), directionality and cultural context of these inferred introductions were unavailable.

By far the most likely source populations for human-introduced PNG partulid populations appeared to be the SIs (Ó Foighil *et al.*, 2011). SIs species of *Partula* have been grouped conchologically (Solem, 1959; Pilsbry, 1909-1910) and anatomically (Rensch, 1937) with their PNG congeners; indeed Kondo (unpublished) considered that the PNG *P. similaris* (Massim Region) was conspecific with the SIs *P. micans*. In addition, molecular phylogenetic analyses of partulids from more distant Western Pacific archipelagos [Palau, Carolines, Marianas, Vanuatu (including the northern Torres Group, closest to the SIs), Fiji, Futuna] have failed to identify convincing sister lineages of the PNG taxa, l*et al*one putative source populations (Lee *et al.*, 2014). Kondo's unpublished observations were based on shell phenotypes only but they raise the possibility that a large fraction of partulid populations throughout Near Oceania may be products of prehistoric human introductions.

The goal of this thesis chapter was to perform the first phylogenomic study of PNG and SIs partulids in order to corroborate their conchologically-based taxonomy and to establish the extent of anthropogenic introductions in their multi-archipelagic distribution and survival.

Materials & Methods

Field Sampling

See Table 5-1 for the targeted sampling locations in PNG and the SIs. These were chosen to represent either nominal partulid species type localities sites or else 1960's era recorded areas of occurrence by deceased partulid expert Yoshio Kondo, obtained from his unpublished Bishop Museum (Honolulu) records. In addition to these new collections, previously sampled museum specimens from three PNG islands (New Britain, Woodlark and Boiaboiawaga) used by Ó Foighil *et al*. (2011) were available for genotyping.

Molecular and phylogenetic methods - ddRADseq data collection and bioinformatics

The quality and quantity of DNA extractions was assessed using a Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA) housed at University of Michigan's Genomic Diversity Laboratory (GDL; http://www.lsa.umich.edu/gdl/samplequality/default.asp). I targeted 200 ng of DNA for library preparation, any individuals with DNA quantities less than this were re-extracted using an E.Z.N.A. Mollusk DNA kit (Omega Bio-Tek, Norcross, GA) following manufacturer's instructions. ddRADseq libraries then were prepared and followed the protocols of Peterson *et al*. (2012).

Genomic DNA was digested using the restriction enzymes Eco-RI-HF and MspI (New England Biolabs, Ipswich, MA) and a 294–394 bp fragment (excluding adapters) was targeted for sequencing using a Pippen Prep (Sage Science, Beverly, MA) following the manufacturer's instructions. Prepared ddRADseq libraries then were submitted to the University of Michigan's

DNA sequencing core (http://medicine.umich.edu/medschool/ research/office-research/biomedical-research-core-facilities /dna-sequencing) and run in two different lanes using 100 or 150 bp paired-end sequencing on an Illumina HiSeq 2500. The raw data for each of the *Partula* individuals were deposited in NCBI's Sequence Read Archive (SRA; Accession #XXXX).

Sequence quality first was assessed using Fastqc v.0.11.5 (Andrews, 2016) and showed the presence of Illumina adapters in 1/2 sequencing lanes and and average Phred quality scores ranged from 14-38. Raw sequences then were transferred to the Flux high computing cluster at the University of Michigan's Center for Advanced Computing for further processing and analyses. The alignment-clustering algorithm in ipyrad v.0.6.17 (Eaton & Overcast, 2018) was used to process and identify homologous ddRADseq tags with parameters modified to reflect the Fastqc results. In comparison to other methods, ipyrad allowed aligned tags to include insertions and deletions, which can be especially beneficial for studies with broad taxonomic coverage (Eaton, 2014). Illumina sequences first were de-multi-plexed by sorting reads by barcode, allowing no barcode mis-matches (parameter 15 setting 0), a maximum of five low quality bases (parameter 9) and merged reads then detected in ipyrad. Restriction sites, barcodes, and Illumina adapters (based on Fastqc results; parameter 16 setting 2) then were trimmed from raw sequence reads and bases with low quality scores (Phred-score <20, parameter 10 setting 33) replaced with *N.* Sequences with >5 *N*s (parameter 19) were discarded. Reads then were clustered and aligned within each individual sample at three different similarity thresholds, 85, 90, and 95%. Clusters of aligned loci with a depth of coverage <6 (parameters 11 and 12) were discarded. Remaining reads then were clustered and aligned across individuals, filtered for paralogs, and finally concatenated into consensus loci at 85, 90, and 95% similarity *de novo* in ipyrad. I also varied the minimum number of individuals required for a consensus locus to be retained in the final dataset with a final filtering step that removed any consensus loci not recovered across (1) 75% (N=41), (2) 50% (N=27), or (3) 25% (N=13) of individuals. Output files for these final nine concatenated datasets were exported for further downstream analysis and file conversion where needed. The parameter files used to generate the 85, 90, and 95% threshold datasets for 25, 50, and 75% of taxa were deposited in the Dryad Digital Repository (doi:10.5061/dryad.gs0gv).

Phylogenomic analyses of *Partula* lineages

To determine phylogenomic relationships I analyzed the nine concatenated ddRADseq alignment files using maximum likelihood in RAxML v8.2.8 (Stamatakis, 2014) (see Appendix XA). Analyses utilized the general time reversible model (Lanave *et al*., 1984) and included invariable sites and a gamma distribution. Support for nodes were determined from 100 fast parametric bootstrap replications. Since these nine datasets showed congruent relationships and similar support values among major clades, I then selected the 90% similarity threshold with 75% of individuals included (90-75 hereafter) for all remaining analyses. This is the ideal threshold for acquiring the highest number of similar loci and also getting the highest coverage of all individuals in the genomic dataset.

In addition to the RAxML analyses, I also conducted a Bayesian analysis on the concatenated 90-75 alignment in the parallel version of MrBayes v3.2.6 (Ronquist *et al*., 2012). Bayesian analyses also included the general time reversible model with invariable sites and a gamma distribution and used a Metropolis-coupled Markov chain Monte Carlo (MC^3) approach and ran for 5,000,000 generations, with sampling every 100. Two analyses were performed each with four separate chains run simultaneously. Stationarity and burn-in period for the MC^3 were determined by plotting log likelihood values for each generation. The first 25% of the generations, trees, and parameter values sampled were discarded as burn-in. The runs were considered to have reached convergence when the average split standard deviation was <0.01 and the potential scale reduction factor was between 1.00-1.02 (Ronquist *et al.*, 2012). A 50% majority rule consensus tree was based on the remaining generations, whose branch support was determined from the posterior probability distribution (Holder & Lewis, 2003) in MrBayes. All data matrices used to construct the maximum likelihood and Bayesian trees were deposited in the Dryad Digital Repository (doi:10.5061/dryad.gs0gv).

Molecular and phylogenetic methods – Mitochondrial Marker

Total genomic DNA was isolated using the E.Z.N.A.® Mollusc DNA Kit (Omega Bio-tek, Norcross, GA, USA) or the DNeasy Kit (Qiagen Inc., Valencia, CA, USA) following the manufacturers' instructions. A 655-nucleotide (nt) mitochondrial (mt) cytochrome *c* oxidase subunit I (COI) target fragment was amplified with GoTaq DNA Polymerase (Promega, Madison, WI, USA) using the 'universal' (Folmer *et al.*, 1994) primer pair LCO1490/HCO2198 and a negative control (no template) was included in each amplification run. After 2 min denaturation at 95ºC, an initial annealing temperature of 53°C was decreased by 1°C/cycle (30 s denaturing at 95ºC, 40 s annealing and 1 min extension at 72ºC) until the final annealing temperature (45°C) was reached and subsequently maintained for an additional 30 cycles. Polymerase chain reaction (PCR) products were prepared for cycle sequencing by diluting them 1:5 in sterile water. Both strands of the amplified fragments were directly sequenced, using the PCR primers, at the University of Michigan's Sequencing Core Facility. The resulting chromatograms were edited using Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Two types of phylogenetic analyses were performed. A parsimony network was constructed using the statistical parsimony (Templeton *et al.*, 1992) method in TCS 1.21 (Clement *et al*., 2000) employed with a 90% connection limit. In addition, phylogenetic analyses of the Mt COI haplotypes were performed by incorporating additional partulid haplotypes from the Lee *et al*. (2014) study accessed through the National Institute of Health's GenBank database (http://www.ncbi.nlm.nih.gov/genbank). To determine the phylogenetic relationships, the initial step was to find the best nucleotide substitution model using the jModelTest v2.1.10 nucleotide substitution program (Posada, 2008). A maximum likelihood analysis was then generated using RAxML v8.2.8 as well as a Bayesian analysis in the parallel version of MrBayes v3.2.6. (Ronquist *et al*., 2012). Both analyses utilized the HKY+I+G model determined in the jModelTest v2.1.10 and included invariable sites and a gamma distribution and ran for 5,000,000 generations, with sampling every 100.

Results and Discussion

The regional taxa of interest were genotyped using two very different methods. A relatively small number (N=54) of representative individuals were characterized using ddRADseq methodology, yielding high-resolution genomic information across thousands of loci. These data provide definitive phylogenomic insights into among- and within-species evolutionary relationships. A considerably larger number (N=256) of regional snails were genotyped for the single mt COI "barcoding" marker. Although these mt data represented a much narrower phylogenetic perspective, the larger number of individuals genotyped provide valuable additional characterization of within-population variation.

Summary ddRADseq and mt COI data

Illumina sequencing returned raw read numbers ranging from 165,507–6,393,291across the 54 samples, with 11 individuals having fewer than 1,000,000 reads (Table 5-2). Clustering at 85, 90, and 95% similarity thresholds also resulted in similar numbers of loci across the 54 individuals that passed quality filtering. The overall number of loci increased across the three similarity thresholds likely a result of homologous reads being split into multiple loci due to the high stringency of the 90 and 95% thresholds. The mean coverage depth of loci ranged from 9.0–143.5 for the 85% threshold, 9.0–141.4 for 90%, and 8.8–135.1 for 95%, with *P. turneri* (PTUR7) having the lowest coverage and *P. micans* (SU3218) having the highest coverage (Table 5-2). The number of loci in the final datasets greatly increased as the minimum number of individuals (75%, 50%, 25%) required for retaining a locus decreased. For the 85% threshold across all 75% of the 54 samples (N=41 individuals), 3,689 loci were recovered in the final ddRADseq dataset whereas the number of loci for the 90 and 95% levels increased to 4,819 and 4,971, respectively. When the minimum taxon coverage was decreased from 75% to 50% (N=27), the number of loci increased by ~2–3x the original dataset, with the 85% threshold dataset having 9,497 loci, 10,735 for 90%, and 15,396 for 95%. The number of loci also increased greatly when only 25% (N=14) of individuals were required to retain a locus (85% - 23,977, 90% - 27,026, 95% - 39,946).

An exemplary phylogenomic analysis, obtained for a 4,819 locus dataset (with 90% similarity threshold clustering across 75% of individuals), is presented in Figure 5-3. See Appendix X for the 8 very similar phylogenomic topologies obtained for the other combinations of similarity thresholds and minimum number of individuals/per locus. Figure 5-3 shows the inferred phylogenomic relationships of the 6 regional species of *Partula* recognized by Gerlach (2016) with each other and with a representative sampling of congeneric taxa sampled across the generic range. This is the first such range-wide phylogenomic analysis of the genus – the only other range-spanning studies involved single gene trees (Goodacre & Wade, 2001; Lee *et al.*, 2014) – and it contains a number of important new insights. Apart from the poorly supported basal placement of *P. lirata* (Fiji), all other ingroup stem nodes were robustly supported and formed three discrete clades, each containing one or more of Gerlach's (2016) regional species.

The basal clade was restricted to Vanuatu and the Santa Cruz archipelago and contained three taxa: *P. turneri*, *P. auraniana* and *P. vanikorensis*. Gerlach (2016) had concluded that *P. vanikorensis* occurred on both main Santa Cruz islands, Nendo and Vanikoro, and that pronounced differences in shell morphology among the two islands reflected exceptional intraspecific variability. However, our phylogenomic data (Figure 5-3) clearly showed that these two islands had two very distinct species: *P. vanikorensis* on Vanikoro (its type locality) and *P. auraniana* on Nendo (and also on the Torres Islands, Vanuatu). This result was corroborated in the mt COI phylogenetic analyses (Figure 5-4) that included a significantly larger number of genotyped individuals (4 from Vanikoro, 4 from Nendo; and 25 from Torres Islands) and revealed a paraphyletic relationship among *P. auraniana* Nendo and Torres Island haplotypes.

Moving up the phylogenomic tree topology (Figure 5-3), the next clade contained the Rennell and Bellona endemic *Partula cramptoni*. It had a highly divergent placement, relative to its Near Oceania congeners, in that it was sister to two Western Pacific Marianas species, *P. gibba* and *P. radiolata*. This sister relationship was corroborated in the mt gene tree (Figure 5-4), with one additional detail: the mt clade contained another Western Pacific species, the Pohnpei (Micronesia) endemic *P. emersoni* that placed sister to *P. cramptoni*, as previously reported (Lee *et al.*, 2014). Unfortunately, no tissue samples of *P. emersoni* were available for ddRADseq genotyping. In Figure 5-3, *P. cramptoni*, *P. gibba* and *P. radiolata* were collectively sister to *P. subgonochila* (Wallis & Futuna) and to Society Islands congeners (Figure 5-3). This latter result is notable because it represents the first identification of a convincing sister species (*P. subgonochila*) for the well-studied Society Island radiation. It is also notable that this clade collectively spans the entire range of the genus (8000 km from the Marianas to the Society Islands).

The remaining clade contained all of Gerlach's (2016) 4 remaining Near Oceania species of *Partula* (Figure 5-3). One of them *P. grisea*, behaved as expected in the phylogenomic (Figure 5-3) and mtCOI (Figure 5-4) analyses: individuals from both Manus and New Ireland formed a discrete clade. This was not the case for the other 3 species: *P. similaris*, *P. flexuosa* and *P. micans*. In the phylogenomic analyses (Figure 5-3), they collectively formed a sister lineage to *P. grisea*, composed of three tip clades, but each taxon was polyphyletic: *P. similaris* clustered with *P. micans* as well as with nominal conspecifics; *P. flexuosa* clustered with *P. micans* (Figure 5-3). Notably, the Guadalcanal specimens (from three different locations) formed a clade, sister to nominal *P. micans* from Santa Isabel and nominal *P. flexuosa* from New Georgia. According to Gerlach (2016), both *P. micans* or *P. flexuosa* occur on Guadalcanal. However, his conchological descriptions of these two taxa were non-exclusive with overlapping phenotypes (see range of shell phenotypes in his Figures 9.1.4 and 9.1.5) and, in the absence of a definitive key, I was unable to unambiguously identify many of the Guadalcanal specimens as either *P. micans* or *P. flexuosa*. These specimens were therefore labeled as *P. flexuosa*? In the mt COI phylogeny (Figure 5-4), these three nominal taxa were also robustly sister to *P. grisea* and polyphyletic: two clades, one solely composed of *P. similaris* (New Britain and the Massim Region), the other containing *P. similaris* (New Britain), *P. flexuosa* (New Georgia), *P. micans* (Buka, Shortland Islands, Santa Isabel) and *P. flexuosa* (Guadalcanal)?

The phylogenomic and mt COI data indicate that a single species of *Partula* has attained an extraordinarily wide distribution in Near Oceania, extending from Guadalcanal in the SIs, westwards through the central and western provinces of the SIs, into PNG to include New Britain in the north and the Massim Islands in the south. This overlaps the type localities of 18 nominal species of *Partula*, although Gerlach (2016) recently synonymized them to 3: *P. micans* Pfeiffer, 1854 (type locality: Shortland Islands), *P. flexuosa* Hartman 1885 (two potential type localities mentioned in the original description: San Jorge and Eddystone (Simbo) islands), and *P. similaris* Hartman 1886 (type locality: Woodlark (Muyua) Island). Our molecular dataset includes specimens of *P. similaris* and *P. micans* from their respective type localities and *P. flexuosa* specimens from Munda, New Georgia, within ~80km of it one of its type localities, Simbo Island. Our molecular data are inconsistent with retention of a specific status for each of these three taxa; their respective topotype populations are members of the same well-supported and phylogenetically-shallow clade. *P. micans* Pfeiffer, 1854 is the earliest available name and therefore has taxonomic priority. This proposed taxonomic rationalization is largely in agreement with an unpublished Kondo (1971) manuscript, kept in his files at the Bishop Museum in Honolulu, in which he inferred the same collective geographic range for *P. micans* (Massim Islands and Bougainville-to-Guadalcanal) apart from New Britain.

Summary comments on the 5 Regional *Partula* species

Partula grisea (Lesson, 1830)

Genotyped *P. grisea* specimens, obtained from 2 PNG island provinces, Manus and New Ireland, corroborated Gerlach's (2016) taxonomy in that they formed a phylogenomically discrete species (Figure 5-3). On these two islands, the tree snails were found on nearshore trees and shrubs (Figure 5-5), as was also recorded in Kondo's unpublished manuscript, but they were absent from interior forest (more typical partulid habitat) and were not associated with human settlements. The snails were quite abundant on Manus where they were readily found in multiple locations, but less so in New Ireland where they were recovered from 2/7 sampling locations along 100 km of coastline, both in the north of the island (Figure 5-6). The species shows relatively little conchological or mitochondrial gene differentiation among the Manus and New Ireland populations (Figure 5-6). Note that Gerlach (2016) lists this species from multiple other nearby islands in the Bismarck Archipelago, including Mussau, New Hanover (Lavongai) and a number of smaller islands off New Ireland, but not on neighboring New Britain.

***Partula micans* (Pfeiffer, 1853)**

Partula micans Pfeiffer, 1853: 451
Partula cinerea Albers, 1857: 98
Partula coxi 'Angas', Cox 1868: 46
Partula pellucida Pease, 1871: 457
Partula flexuosa Hartman, 1885: 204
Partula coxi Hartman, 1885: 217
Partula similaris Hartman, 1886: 30
Partula incurvum Hartman, 1886: 31
Partula perlucens Hartman, 1886: 31
Partula regularis Hartman, 1886: 31
Partula minor Hartman, 1886: 31
Partula minima Hartman, Hartman, 1892: 99 (misspelling)
Partula hastula Hartman, 1886: 33
Partula woodlarkiana Hartman, 1886: 33
Partula kubaryi Hartman, 1888: 284
Partula occidentalis Hedley, 1892: 98
Partula hollandia Pilsbry, 1909: 293
Partula milleri Solem, 1959: 72

Dextral. Oblong-conic to ovate-conic, corneous to light brown shells with 4.5-5.5 convex whorls bearing close spiral striae, apex broadly pointed to obtuse, weakly to faintly violet or brown, aperture ovate, lip moderately to well expanded, shell 11x7 to 21x11mm, with smaller sizes often on smaller islands.

Type specimen:

Partula micans Pfeiffer, 1853 – Syntypes ANSP 151448
Partula cinerea Albers, 1857 – Lectotype ZMB Moll-101545a
Partula pellucida Pease, 1871 – Syntypes MCZ94837; NHMUK 96.1130.5
Partula flexuosa Hartman, 1885 – Holotype CMNH 62.4238
Partula coxi Hartman, 1885 – Holotype CMNH 62.4245
Partula similaris Hartman, 1886 – Holotype NHMUK 96.11.30.1
Partula incurvum Hartman, 1886 – Holotype CMNH 62.4240
Partula perlucens Hartman, 1886 – Holotype NHMUK96.11.30.1
Partula regularis Hartman, 1886 – Holotype CMNH 62.4241
Partula minor Hartman, 1886 – Syntypes CMNH 62.4243
Partula hastula Hartman, 1886 – Syntypes CMNH 62.4239
Partula woodlarkiana Hartman, 1886 – Holotype NHMUK 96.11.30.10
Partula kubaryi Hartman, 1888 – CMNH 62.4247
Partula occidentalis Hedley, 1892 – Syntypes QM M02811
Partula hollandia Pilsbry, 1909 – Holotype CMNH 62.4237
Partula milleri Solem, 1959 – Holotype USNHM 619738

The novel molecular data indicate that a single species of *Partula* has attained an extraordinarily wide distribution in Near Oceania, extending from Guadalcanal in the SIs, westwards through the central and western provinces of the SIs, into PNG to include New Britain in the north and the Massim Islands in the south (Figure 5-7a). This overlaps the type localities of 16 nominal species of *Partula*, although Gerlach (2016) recently synonymized them to 3: *P. micans* Pfeiffer, 1854 (type locality: Shortland Islands), *P. flexuosa* Hartman 1885 (two potential type localities mentioned in the original description: San Jorge and Eddystone (Simbo) islands), and *P. similaris* Hartman 1886 (type locality: Woodlark (Muyua) Island). Ó Foighil *et al.* (2011) had previously genotyped *P. similaris* specimens from its type locality and my new results added *P. micans* specimens from its type locality and *P. flexuosa* specimens from within ~80km of its type locality. Our molecular data were inconsistent with retention of a specific status for each of these three taxa; their respective topotype populations were members of the same well-supported and phylogenetically-shallow clade. *Partula micans* Pfeiffer, 1854 is the earliest available name and therefore has taxonomic priority. This proposed taxonomic rationalization is largely in agreement with an unpublished Kondo (1971) manuscript, kept in his files at the Bishop Museum in Honolulu, in which he inferred the same collective geographic range for *P. micans* (Massim Islands and Bougainville-to-Guadalcanal) apart from New Britain.

A notable feature of *Partula micans*' multi-archipelago distribution is its synanthropic (human-affiliated) association with coastal villages and settlements, often within meters of houses (Figure 5-8), but absence from native forest. This strongly indicates prehistoric human dispersal within a Massim-New Britain- Bougainville-Solomon Islands regional exchange network but the identity of source populations remains unclear. In none of my field sites did I encounter *P. micans* in native forest habitat and nearby island groups are inhabited by phylogenetically-distinct taxa (Figure 5-9): its sister species, *P. grisea* in the Northern Bismarck Archipelago (to the northwest), *P. emersoni* in Pohnpei (Micronesia, to the north), *P. cramptoni* in the Rennell Archipelago (to the south) and *P. vanikorensis* and *P. auraniana* in the Santa Cruz archipelago (Temotu, to the east).

Although extraordinarily widespread, *Partula micans* was not abundant in many of the Solomon Islands locations: it often took many hours of searching to find specimens. This experience corroborates Bishop Museum malacologist Yoshio Kondo's unpublished 1966 SIs field notes where he makes similar observations. In addition, I was successful in recovering snails only in approximately 50% of Kondo's SIs locations that I revisited, including some very small islands that were searched comprehensively (Table 5-1). The remarkable multi-archipelago and multi-national distribution of this species may lead to a false sense of confidence in its conservation status. A simple change in gardening practices, *e.g.*, no longer cultivating hibiscus bushes next to houses, could have an outsized impact on its ability to endure.

Partula micans **and Near-Oceania Prehistoric Exchange Networks**

One of the goals of this research was to identify convincing source island populations for the human-introduced PNG New Britain/Massim Region partulid lineage (Ó Foighil *et al.*, 2011) using genetic markers and to use these data to reconstruct regional prehistoric exchange networks. Based on Partulidae norms, I predicted that source populations would be located in high island native forest habitat and that they will be genetically inclusive of the founder PNG populations. In addition, the source island group was also predicted to contain sister species of the translocated partulid taxon either on the same island or on nearby islands. The proposed methodology has been successfully used to reconstruct the prehistoric exchange network underlying *Partula hyalina*'s multi-archipelagic range in Eastern Polynesia (Lee *et al.*, 2007).

Although my molecular data (Figures 5-3 & 5-4) comprehensively support Kondo's unpublished interpretation of *P. micans*' extraordinary biogeography, they failed to identify a source population for this far-flung species. Throughout its extraordinary range (Massim Region, New Britain, Bougainville in PNG and the SIs apart the remote Santa Cruz group/Temotu Province), it was resolutely synanthropic, being absent from interior forest. Nevertheless, the *P. micans* data contain evidence of genetic structuring within this inferred regional prehistoric exchange network. The ddRADseq topological data are consistent with three regional subsets of interaction, one for each tip clade, linking Woodlark Island to Boiaboiawaga and New Britain; New Britain to Buka and Shortlands and New Georgia to Santa Isabel and Guadalcanal (Figures 5-3 & 5-9). The mitochondrial data are broadly consistent with this, especially the Woodlark-Boiaboiawaga-New Britain linkage. New Britain snails exhibited the most diversity and had disjunct placements in both ddRADseq and mt topologies (Figures 5-3, 5-4 & 5-9), consistent with both East-West and North-South regional exchange networks for that island.

There remains one intriguing loose end to this species' enigmatic biogeography. It concerns a very poorly studied population on the distant, Remote Oceania island of Espiritu Santo (Vanuatu), known only from a single museum lot that was described as an endemic species, *Partula milleri*, by Solem (1959). Solem (1959) noted its similarity to Near Oceania congeners, stating that is was most closely related to Guadalcanal populations. Indeed, Gerlach (2016) has formally synonymized *Partula milleri* with *P. micans* on conchological grounds, a conclusion I agree with, and speculated that this population was inadvertently transferred to Espiritu Santo from Guadalcanal by U.S. army shipments during the Second World War. Another, perhaps more remote, possibility of course is that the transfer was prehistoric and in the opposite direction, with Espiritu Santo as a source. I unfortunately know nothing about *P. micans*' ecology on Espiritu Santo and it is not clear if this population is extant. There has been no subsequent record after the initial description and no living partulid was sampled on Espiritu Santo during a French-led 2006 biotic survey of the island, which unfortunately documented the presence of the invasive snail predator *Euglandina rosea* (Bouchet *et al*. 2007; P. Bouchet, pers. comm.). Nevertheless, a targeted sampling effort directed at this species in its Palikula Bay habitat might still uncover survivors and yield new insights into its ecology and its genetic relations to Near Oceania populations.

Partula cramptoni **(Clench, 1941)**

In 2015, I sampled in Rennell and Bellona Province, home to the endemic species *Partula cramptoni*, the only recorded partulid in that archipelago. The main island, Rennell, is being heavily logged and, despite much effort, no living specimens were recovered. However, a small number of dead *P. cramptoni* shells were discovered at Lake Tegano Village, Rennell (see Figure 5-10 for exemplar of dead shell; middle photo). It is not clear if this species survives on Rennell. I had better success on the neighboring island of Bellona, where I encountered living specimens of *P. cramptoni* at Nggonggona Village, in a garden behind the local church and at Pauta Village, again near the local church. The phylogenetic data indicate that this highly distinctive species' closest relatives are not in Near Oceania, but rather in Micronesia and in the Marianas (Figures 5-3 & 5-4). It is critically endangered and needs proactive conservation protection to survive.

Partula vanikorensis **(Quoy & Gaimard, 1832)**

One of the major achievements of this thesis was the successful sampling of *Partula vanikorensis*. This species has been practically unstudied, apart from the 1832 type specimens in the *Muséum national d'histoire naturelle* in Paris. I encountered abundant populations in the interior of Vanikoro Island (Figure 5-11a) and the ddRADseq and mt phylogenies (Figures 5-3 & 5-4) show it to be a highly distinctive single-island endemic, in contrast with Gerlach's (2016) conclusion of a multi-island distribution in the Santa Cruz archipelago – see below. Although *P. vanikorensis* appears to have maintained significant populations on Vanikoro (Figure 5-12), one of the main topics of conversation among the islanders during my 2016 visit was the ongoing threat of illegal logging operations becoming established there. Such a development could very quickly threaten the survival of this highly distinctive species.

Partula auraniana (Hartman, 1888)

Previously, this species was only known from Vanuatu. It is apparently now extinct in its type locality, the island of Aroe, just south of Espiritu Santo, but endures on 5 islands in the Torres Group (Lee *et al*., 2014). Kondo's unpublished notes tentatively identified specimens from Nendo, the main island in the Santa Cruz archipelago, as *P. auraniana*. Gerlach (2016) came to different conclusion, identifying Nendo snails as *P. vanikorensis* and describing the species as "very variable" and occurring on both Nendo and Vanikoro.

My initial sampling efforts on Nendo Island in 2015 were unsuccessful. Conditions on the ground were less than ideal: I lacked local contacts and found it difficult to obtain permission from landowners to search for snails. I subsequently identified, through the IUCN, local contacts and guides in Temotu Province. This paid major dividends in 2016 and, after much effort, I was successful in sampling a species of *Partula* from multiple locations in the remote interior forest of Nendo Island (Figure 5-14). My ddRADseq and mt phylogenies (Figures 5-3 & 5-4) indicate that the sampled Nendo specimens were *P. auraniana*, not *P. vanikorensis*, and that the conchological distinctions among the two taxa [see Figures 5-11 to 5-14 and also Figure 9.1.7 in Gerlach (2016)] reflect among species variation rather than intraspecific variation.

These results confirm that *P. vanikorensis* is a Vanicoro Island endemic but reveal an unexpected multi-archipelagic range extension (~250km) for *P. auraniana* that includes Nendo Island as well as the Torres Group (Figure 5-13). Interestingly, the two island populations were paraphyletic in the mt tree (Figure 5-13) and the available topology is consistent with a Nendo Island origin for at least some of the Torres Islands snails.

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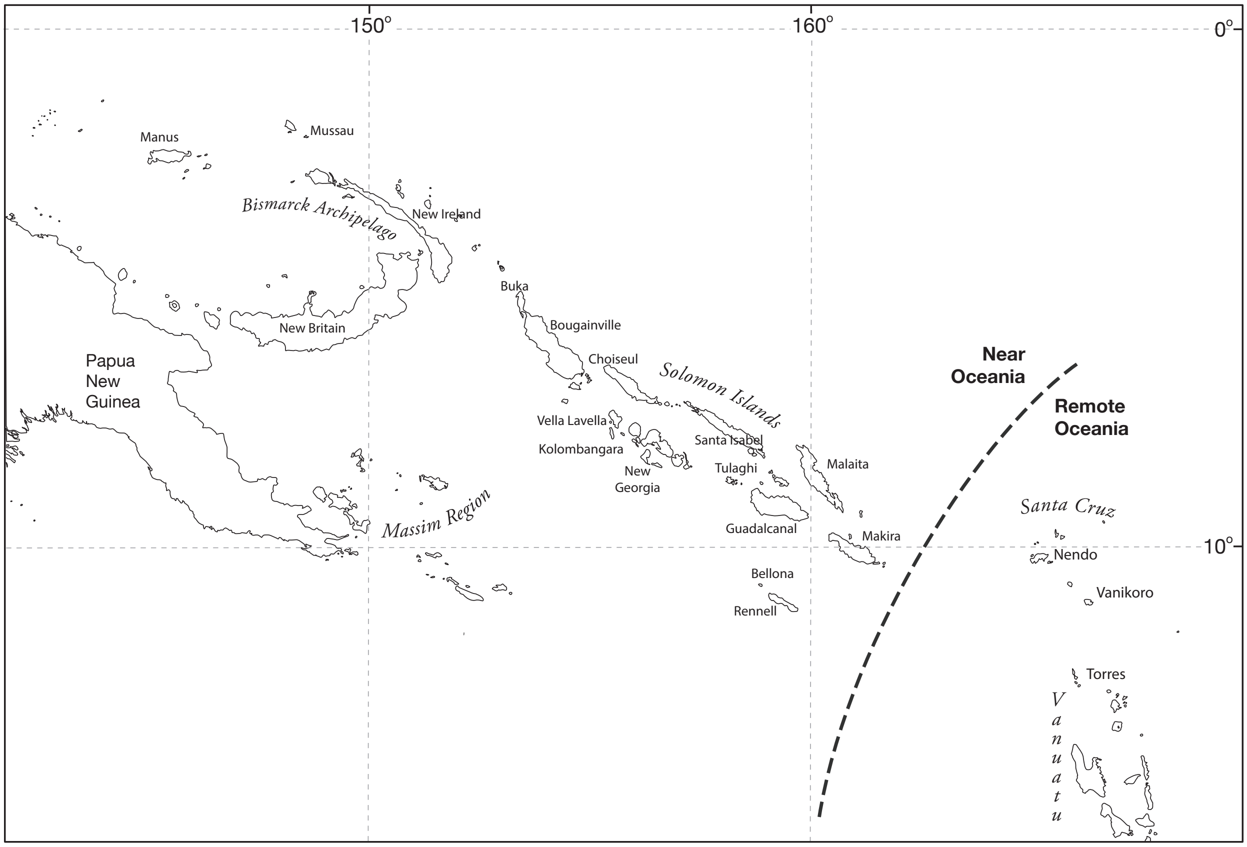


Figure 5–1. Map of the Western Pacific study area showing the archipelagoes sampled. Dashed line shows the boundary between Near and Remote Oceania. Note that politically, Bougainville is part of Papua New Guinea and that the Santa Cruz archipelago us part of the Solomon Islands.

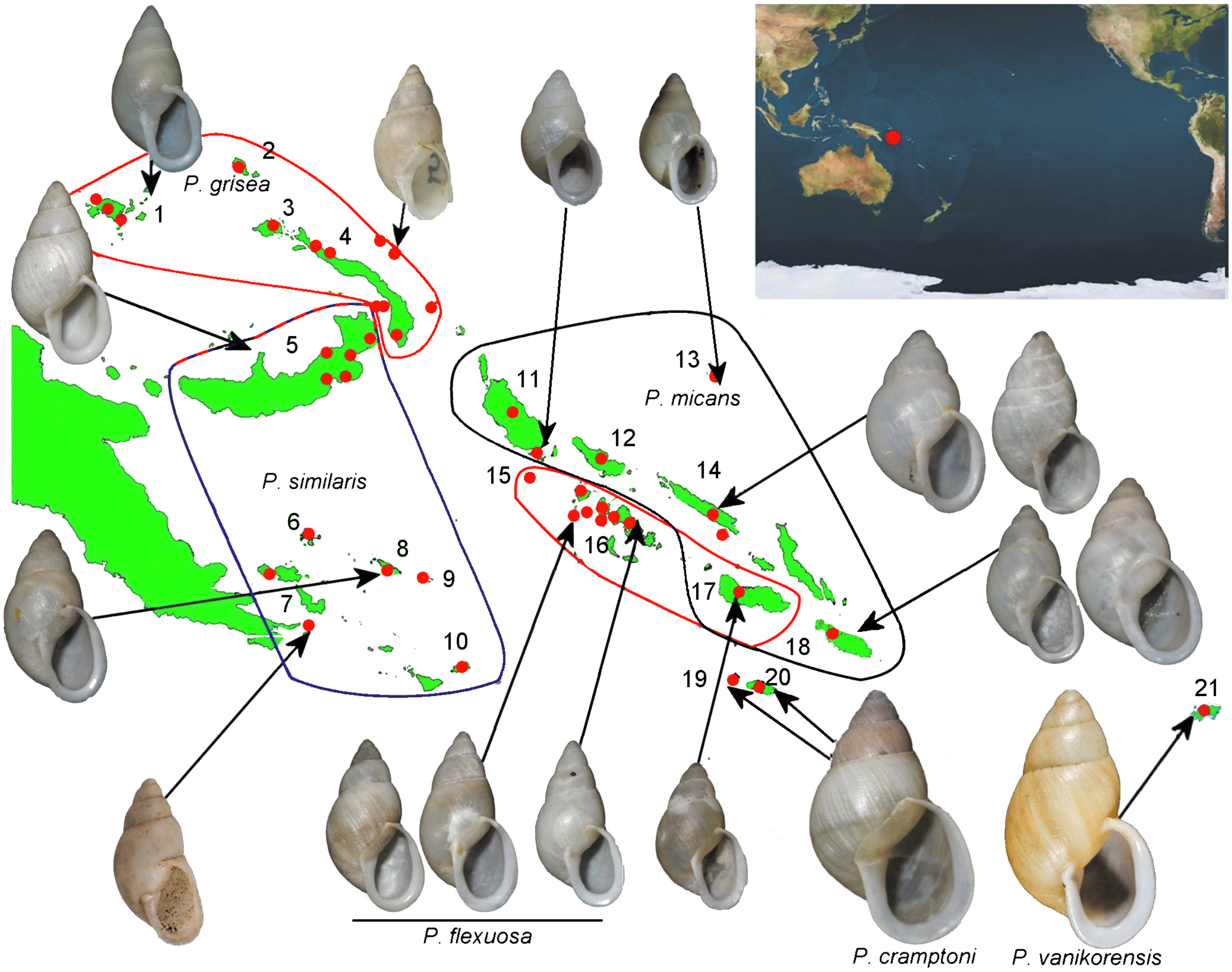


Figure 5–2. This is Figure 9.1.1 from Gerlach (2016), incorporated here with permission of author, and summarizes the distributions and shell phenotypes of the 6 species of *Partula* he recognized in Papua New Guinea and the Solomon Islands (Near Oceania) and in the Santa Cruz archipelago (Remote Oceania). Location key is as follows: 1-Manus, 2-Mussau, 3-New Hannover, 4-New Ireland, 5-New Britain, 6-Trobiands, 7-d'Entrecasteaux, 8-Woodlark, 9-Laughlans, 10-Louisades, 11-Bougainville, 12-Choiseul, 13-Ontong Java, 14-Santa Isabel, 15-Shortlands, 16-New Georgias, 17-Guadalcanal, 18-San Cristobal, 19-Bellona, 20-Rennell, 21-Santa Cruz.

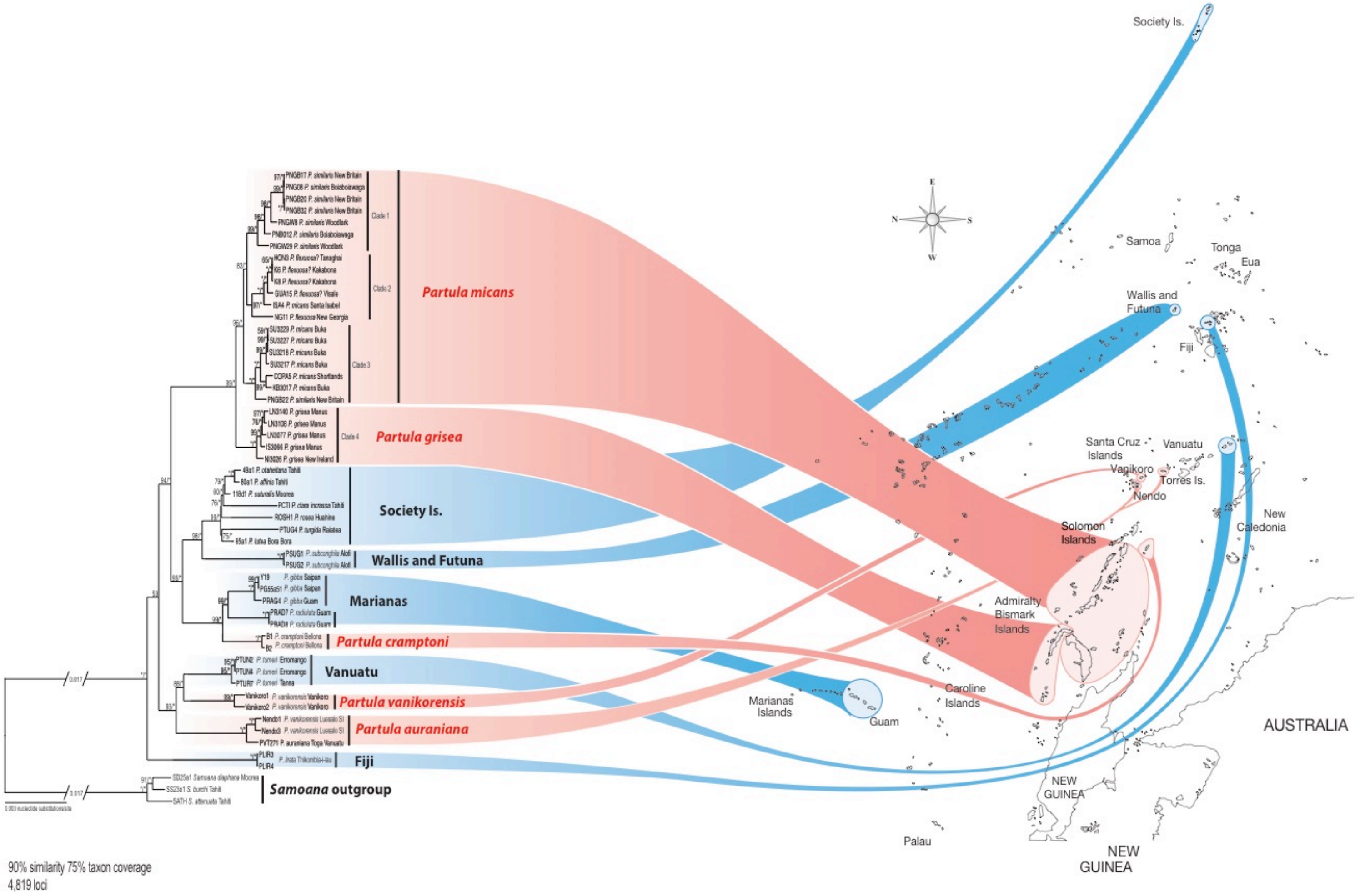


Figure 5–3. Maximum likelihood phylogenomic tree depicting range-wide relationships among partulid species for the ddRADseq 4,819 loci 90% similarity threshold clustering across 75% of individuals. The tree was rooted with three species of Society Islands *Samoana,*the sister genus of *Partula*. Values on tree nodes indicate Maximum likelihood bootstrap supports and Bayesian posterior probabilities (pp). Support values of 100% or 1.00 pp are indicated by an *. Near Oceania and Santa Cruz archipelago species are highlighted in red, other congeners are highlighted in blue. OTU labels utilize Gerlach's (2016) taxonomy for individual Near Oceania and Santa Cruz snails, but specimens from Guadalcanal, where two poorly-defined nominal taxa co-occur (Gerlach, 2016) were tentatively identified as *P. flexuosa*? Near Oceania and Santa Cruz taxa for which I am revising Gerlach's (2016) taxonomy (*P. similaris* & *P. flexuosa* to *P.micans*, and Nendo *P. vanikorensis* to *P. auraniana*) are renamed in the respective summary captions.

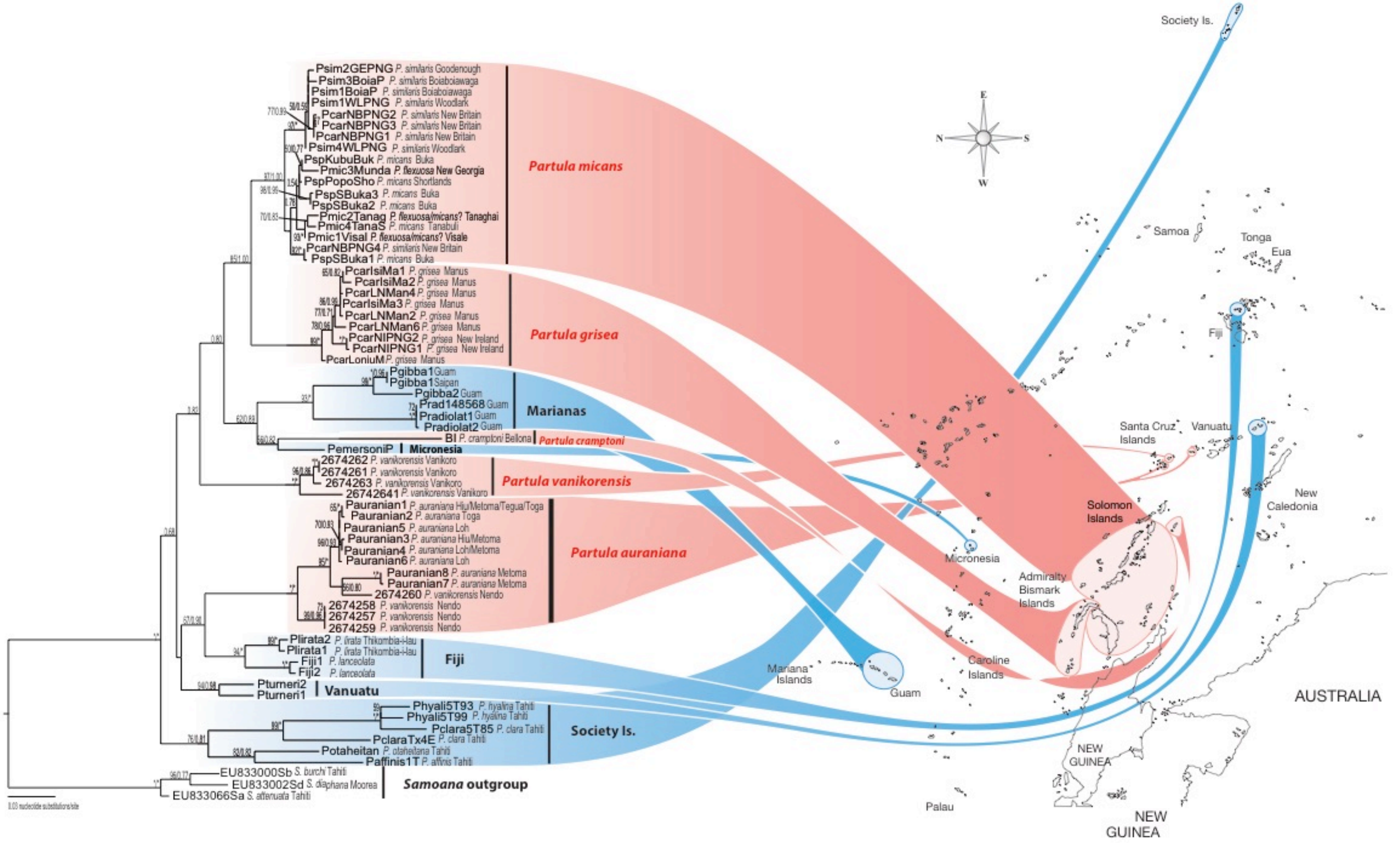


Figure 5–4. Bayesian phylogenetic tree depicting range-wide relationships among partulid species using a mitochondrial COI dataset. The tree was rooted with three species of Society Islands *Samoana*, the sister genus of *Partula* and posterior probability values ≥50 are given on their respective nodes. Near Oceania and Santa Cruz archipelago species are highlighted in red, other congeners are highlighted in blue. OTU labels utilize Gerlach's (2016) taxonomy for individual Near Oceania and Santa Cruz snails, but specimens from Guadalcanal, where two poorly-defined nominal taxa co-occur (Gerlach, 2016) were tentatively identified as *P. flexuosa*? Near Oceania and Santa Cruz taxa for which I am revising Gerlach's (2016) taxonomy (*P. similaris* & *P. flexuosa* to *P.micans*, and Nendo *P. vanikorensis* to *P. auraniana*) are renamed in the respective summary captions.

Figure 5–5. Sampling *Partula grisea* on NewIreland from coastal vegetation near Put Put Mission (left). One of the local children (on right) who helped with the sampling – note the shorefront in the background.

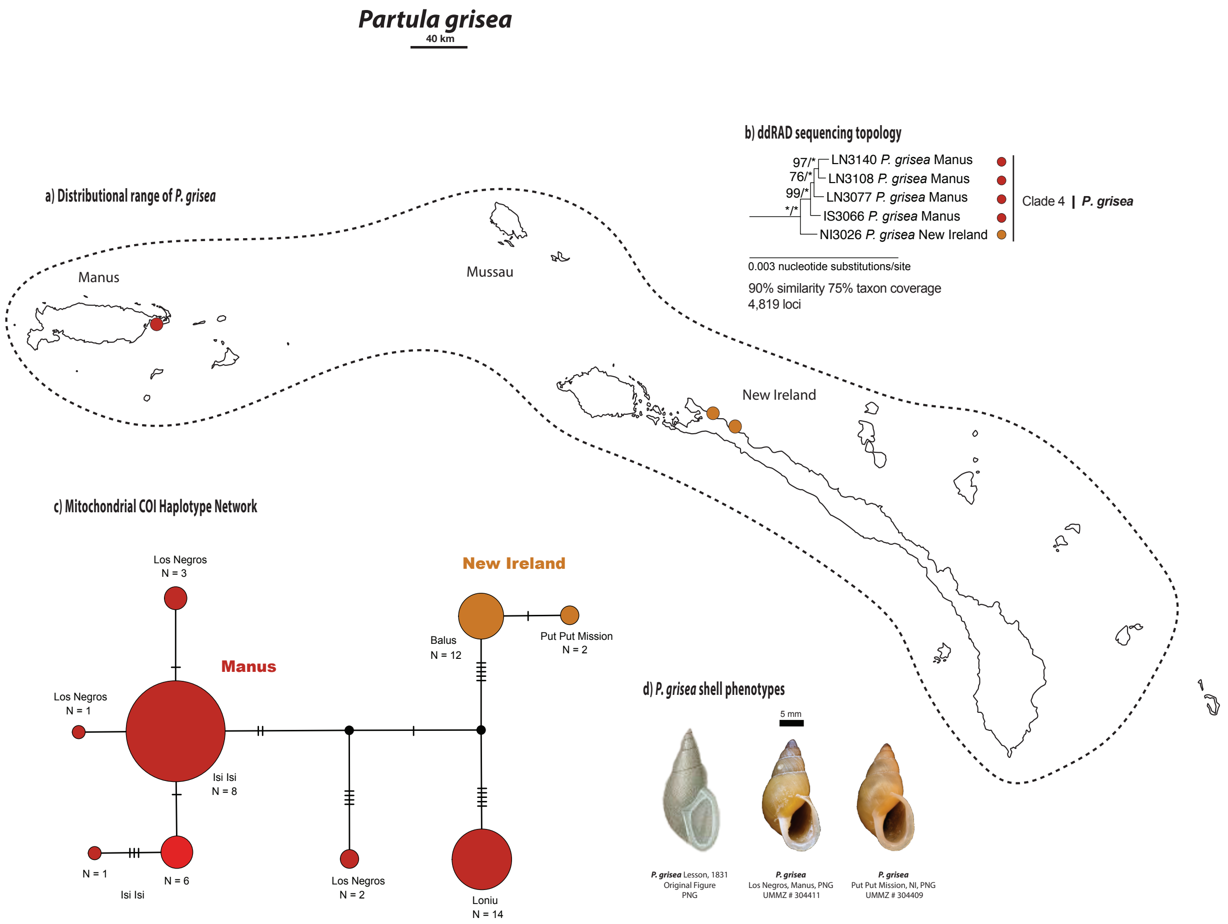
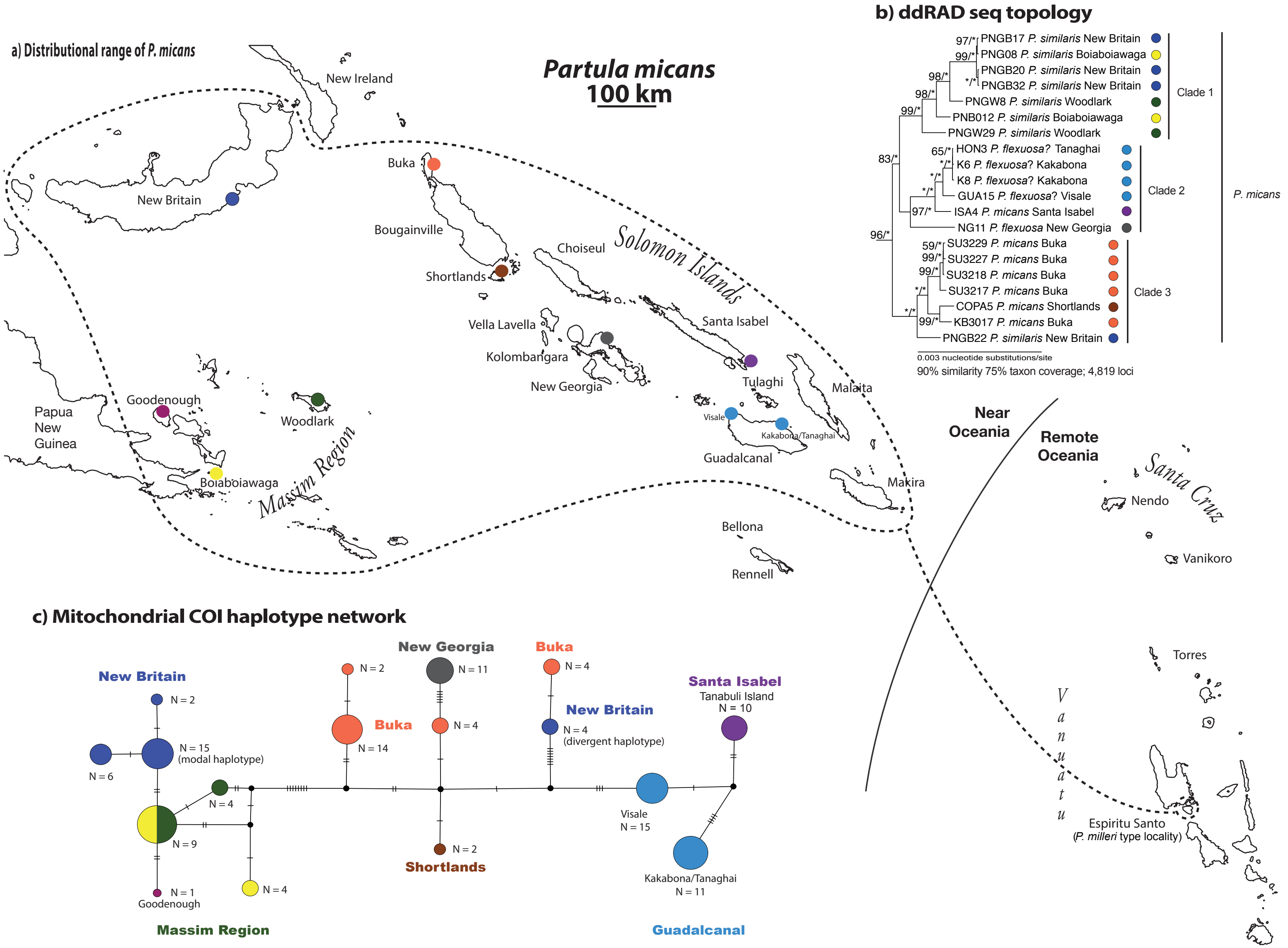


Figure 5–6. *Partula grisea* sampling sites, within-species phylogentic structure and shell phenotypes. a) Map showing sampling locations on Manus Island and New Ireland. b) Detail of the *P. grisea* ddRADseq clade in Figure 3. c) Statistical parsimony network of the 9 mitochondrial cytochrome c oxidase subunit I (COI) haplotypes (655-nucleotide fragments) obtained from Manus and from New Ireland samples of *Partula grisea*. Each terminal circle represents a single COI haplotype, sized according to its relative abundance, and shaded to reflect the island that the snails bearing it were sampled from. Branches connecting the haplotype circles are scaled to reflect the number of inferred substitutions separating them with smaller unlabeled circles representing inferred 'missing' intermediate haplotypes. d) Representative *P. grisea* shell phenotypes of the (now lost) type specimen as well as genotyped individuals from Manus and from New Ireland.



a) Distributional range of *P. micans*

b) ddRAD seq topology

c) Mitochondrial COI haplotype network

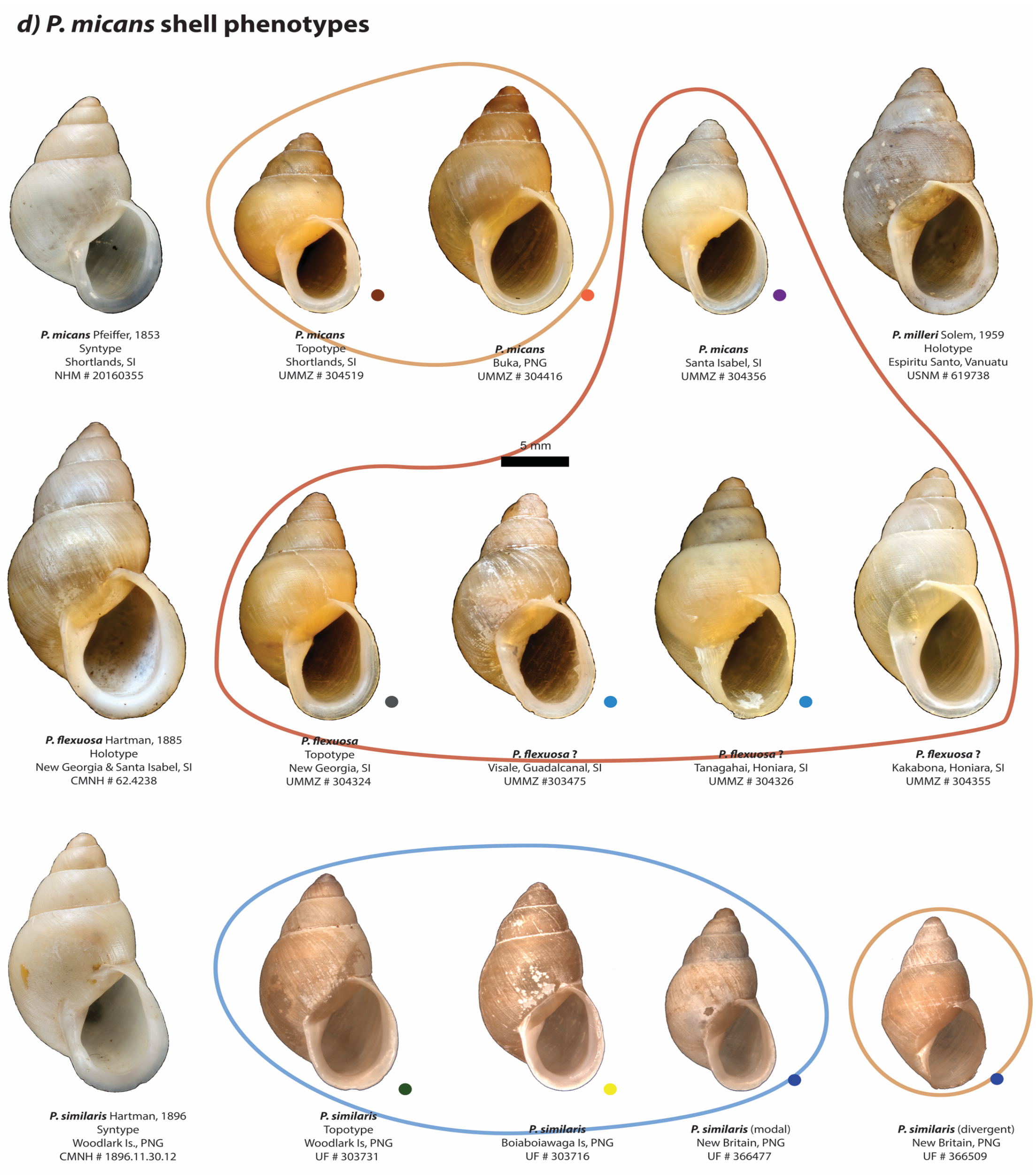


Figure 5–7. *Partula micans* sampling sites, within-species phylogentic structure and shell phenotypes. a) Map showing the sampling locations (color-coded by island) on Papua New Guinean archipelagos and on the main Solomon Islands archipelago. b) Detail of the *P. micans* ddRADseq crown clade in Figure 5-3, showing its three constituent tip clades and their respective among-island distributions. Support values of 100% or 1.00 pp are indicated by an *. OTU labels utilize Gerlach's (2016) taxonomy for individual snails, but specimens from Guadalcanal, where two poorly-defined nominal taxa co-occur (Gerlach, 2016) were tentatively identified as *P. flexuosa?* Near Oceania taxa for which I am revising Gerlach's (2016) taxonomy (*P. similaris* & *P. flexuosa* to *P. micans*) are renamed in the respective summary captions). c) Statistical parsimony network of the mitochondrial cytochrome c oxidase subunit I (COI) haplotypes (655-nucleotide fragments) obtained for genotyped *P. micans* snails. Each terminal circle represents a single COI haplotype, sized according to its relative abundance, and shaded to reflect the island that the snails bearing it were sampled from. Branches connecting the haplotype circles are scaled to reflect the number of inferred substitutions separating them with smaller unlabeled circles representing inferred 'missing' intermediate haplotypes. Point mutations are indicated by dashes. d) Representative *P. micans* shell phenotypes, including respective type specimens of the three regional congeners recognized by Gerlach (2016), *P. micans*, *P. flexuosa* and *P. similaris*, as well as *P. milleri*, synonymized with *P. micans* by Gerlach (2016). The shell phenotypes from genotyped snails are arranged according to Gerlach's (2016) taxonomy but the color-coded outlines indicate the taxonomically-incongruent individuals that grouped together in the three ddRADseq tip clades (7d).

Figure 5–8. Kibiri villagers (Munda, New Georgia Island, Western Province, Solomon Islands) sampling partulids from hibiscus bushes within meters of a house – see eaves in the top right of the right photo.

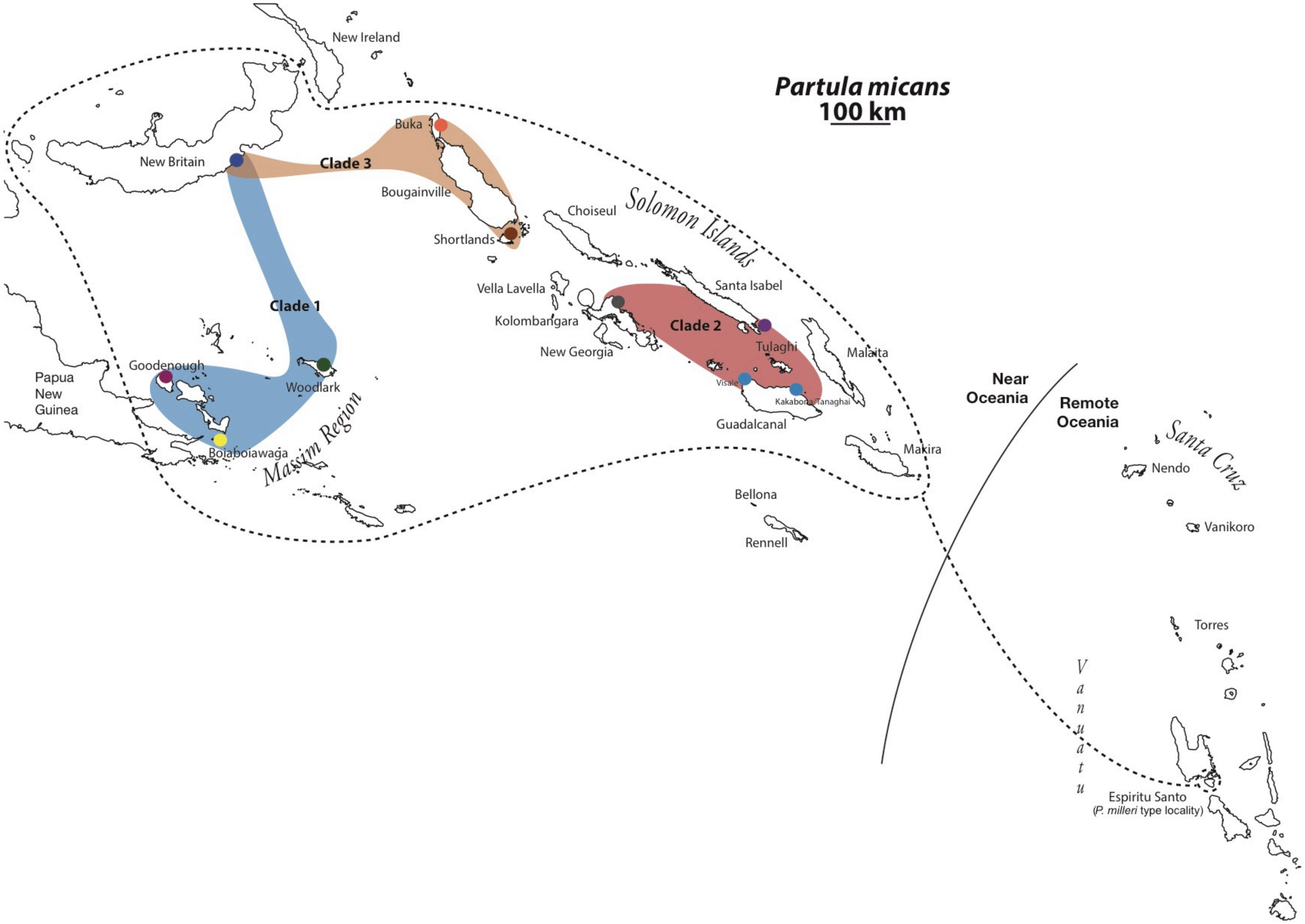


Figure 5–9. Inferred prehistoric regional interaction networks in Near Oceania from *Partula micans* ddRADseq topological data (Figure 5-7b). These are consistent with three regional subsets of interaction, one for each tip clade, linking Woodlark Island to Boiaboiawaga and New Britain; New Britain to Buka and Shortlands and New Georgia to Sanata Isabel and Guadalcanal.

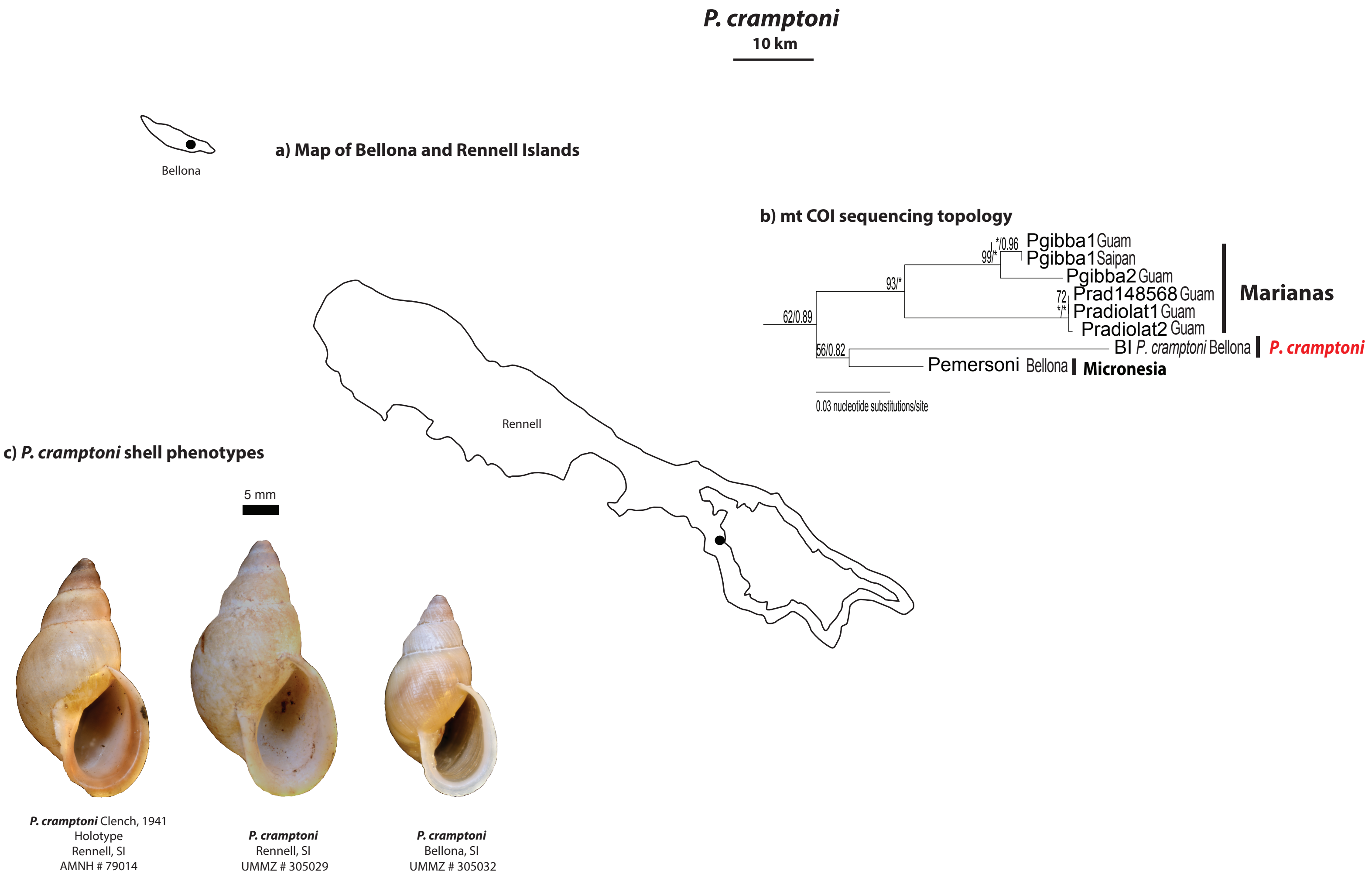
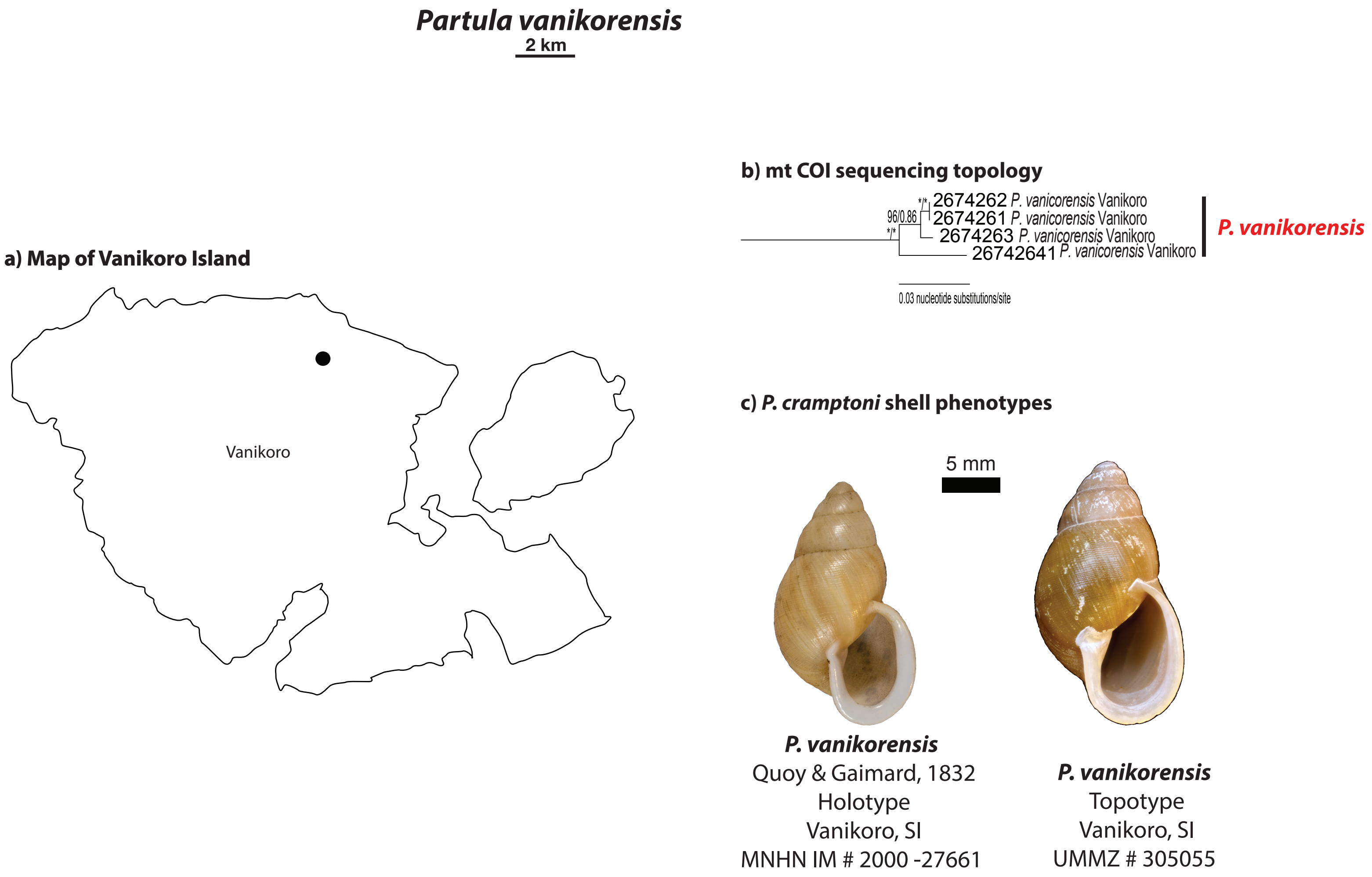


Figure 5–10. *Partula cramptoni* sampling sites, phylogentic relationships and shell phenotypes. a) Map showing sampling locations on Bellona and Rennel Islands (dead shells only found on the latter). b) Detail of the mt COI *P. cramptoni* phylogenetic realtionships presented in Figure 5-4. c) Representative *P. cramptoni* shell phenotypes including the holotype as well as a specimen each from Bellona and Rennell islands.



Partula vanikorensis

a) Map of Vanikoro Island

b) mt COI sequencing topology

c) *P. cramptoni* shell phenotypes

P. vanikorensis
Quoy & Gaimard, 1832
Holotype
Vanikoro, SI
MNHN IM # 2000 -27661

P. vanikorensis
Topotype
Vanikoro, SI
UMMZ # 305055

Figure 5–11. *Partula vanikorensis* sampling site, detail of mt COI clade and shell phenotypes. a) Map showing sampling locations on Vanikoro Island. b) Detail of the mt COI *P. vanikorensis* clade presented in Figure 5-4. c) Representative *P. vanikorensis* shell phenotypes including the holotype as well as a specimen from Vanikoro.

Figure 5–12. *Partula vanikorensis* in the interior forest of Vanikoro Island, Temotu Province (Santa Cruz Archipelago)

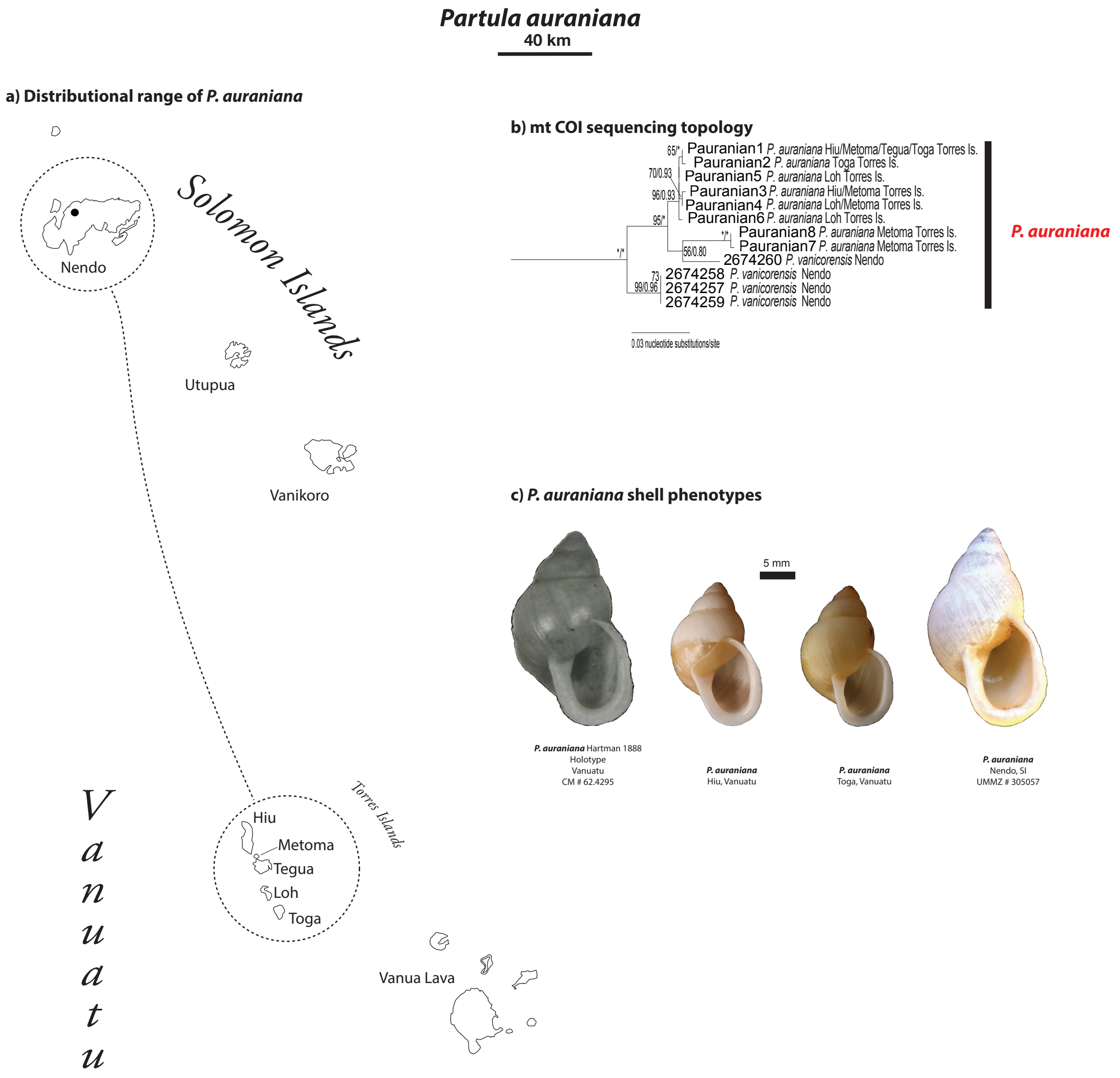


Figure 5–13. *Partula auraniana* sampling sites, within-species phylogentic structure and shell phenotypes. a) Map showing the sampling locations Nendo Island in the Santa Cruz archipelago and in the Torrs Archipealgo (Vanuatu). b) Detail of the *P. auraniana* mt COI clade in Figure 4, showing its among-island distribution. Support values of 100% or 1.00 pp are indicated by an *. OTU labels utilize Gerlach's (2016) taxonomy but specimens from Nendo are clearly *P. auraniana*, not *P. vanikorensis* and these are renamed in the summary caption. c) Representative *P. auraniana* shell phenotypes including the holotype from Vanuatu.

Figure 5–14. IUCN Certified Ranger Titus Godfrey holding field-collected *Partula auraniana* in the interior forest of Nendo Island, Temotu Province (Santa Cruz Archipelago).

Table 5-1. Sampling details for the partulids of Near Oceania and the Santa Cruz archipelagos. Boxes highlighted in yellow denote Kondo's 1966 unpublished study sites from the Solomon Islands (SI) and Papua New Guinea (PNG). In the column recording the number of individuals, "x" denotes that no *Partula* were found at the site.

Full Name	Country	Locality Name	Verbatim Locality & Habitat Description	Latitude	Longitude	Collector	Collection Date	Number of individuals
P. micans	SI	Visale, Guadalcanal Province		9.72° S	159.72° E	Ó Foighil, D	04/28/2012	39
P. micans	SI	Kibiri Village, Munda, New Georgia		8.332293° S	157.277699° E	Ó Foighil, D	12/10/2012	63
P. micans	SI	Gizo, New Georgia				Ó Foighil, D	12/2012	x
P. micans	SI	Tanaghai, Honiara		9.422708° S	159.902039° E	Ó Foighil, D	12/15/2012	17
P. grisea	PNG	Kavieng	Near Nusa Village Resort and along Nusa Parade road			Bick, C. ; Slapcinsky, J.	11/27/12	x
P. grisea	PNG	Balus	3 km E of Balus, 25 km SE of Kavieng, 7m elevation; Coastal forest on ginger	2.68598° S	150.98366° E	Bick, C. ; Slapcinsky, J.	11/28/2012	25
P. grisea	PNG	Put Put Mission	17 km SE of Kavieng, 12 m elevation; Coastal forest on ginger	2.64823° S	150.91999° E	Bick, C. ; Slapcinsky, J.	11/28/2012	4
P. grisea	PNG	Lorengau	Coastal forest, Lorengau town and along the highway			Bick, C. ; Slapcinsky, J.	11/28/12	x
P. grisea	PNG	Isi Isi Beach	1.6 km NW of Lorengau, 10 m elevation; Coastal forest	2.01745° S	147.2547° E	Bick, C. ; Slapcinsky, J.	11/30/2012	21
P. grisea	PNG	Loniu	0.4 km W of Loniu village, 16 m elevation; Coastal forest with ginger	2.07485° S	147.33277° E	Bick, C. ; Slapcinsky, J.	12/01/2012	16
P. grisea	PNG	Naringel Beach, Los Negros	9 m elevation; Coastal forest with ginger	2.08147° S	147.39328° E	Bick, C.	12/02/2012	92
P. grisea	PNG	Momote, Los Negros	6 km SW of Momote, 22 m elevation; Coastal forest with ginger	2.07594° S	147.37938° E	Bick, C.	12/02/2012	1
P. micans	PNG	Buka Town, Buka Island	Coastal forests near Buka Island airport			Bick, C. ; Slapcinsky, J.	12/03/2012	x
P. micans	PNG	Kubu, Buka Island	20 m elevation; Coastal forest on bluff	5.41326° S	154.68132° E	Bick, C. ; Slapcinsky, J.	12/05/2012	4
P. micans	PNG	Suhin Village, Buka Island	80 m elevation; Seepy area on bluff with ginger	5.22998° S	154.70938° E	Bick, C. ; Slapcinsky, J.	12/06/2012	71
P. micans	SI	Tanaghai, Honiara		9.422708° S	159.902039° E	Bick, C. ; Ó Foighil, D	06/01/2013	14
P. micans	SI	Kakabona, Honiara	Patchy forest next to river bank and White River bridge	9.422708° S	159.902039° E	Bick, C. ; Ó Foighil, D	06/01/2013	14
P. micans	SI	Tulagi	Searched all of the Eastern part of the main island, Ó Foighil also searched in this site by himself in 2012			Bick, C. ; Ó Foighil, D	06/03/2013	x
P. micans	SI	Songonagona Island, Tulagi	Coastal forest			Bick, C. ; Ó Foighil, D	06/04/2013	x

P. micans	SI	San Jorge Island	Near Kaola; around Kolamola village			Bick, C.	06/04/2013	x
P. micans	SI	Tanabuli Island/Pt., Tanabuli Island, Santa Isabel	Coastal forest near houses	8° 24.167' S	159° 49.250' E	Bick, C.	06/09/2013	18
P. micans	SI	Central Village, Poporang Island, Shortland Island	Shortland Province, Nila Island, Behind Catholic church, on hibiscus, interspersed with some shrubs (elev: 69m)	7° 05.359' S	155° 51.865' E	Bick, C.	07/04/2014	28
P. micans	SI	Copacabana Village, Poporang Island, Shortland Island	Shortland Province, 1 km east of Central Village, on hibiscus, Mary Laore's front yard (elev: 73m)	7° 05.494' S	155° 51.808' E	Bick, C.	07/04/2014	80
P. micans	SI	Mole Island	Choiseul Province, Catholic Mission			Bick, C.	07/06/2014	x
P. cramptoni	SI	Lake Tegano Village, Rennell Island	Only dead shells, patchy interior forest	11° 44.660' S	160° 25.755' E	Bick, C.	06/02/2015	4
P. cramptoni	SI	Nggonggona Village, Bellona Island	Patchy forests and gardens	11° 17.732' S	159° 46.769' E	Bick, C.	06/07/2015	8
P. cramptoni	SI	Pauta Village, Bellona Island	Patchy forests and gardens	11.286560° S	159.766821° E	Bick, C.	06/08/2015	2
P. vanikorensis	SI	Emua Village, Vanikoro Island	Interior forests in cultivated giant taro stands, Temotu Province	11° 42.278' S	166° 58.482' E	Bick, C.	06/24/2016	102
P. vanikorensis	SI	Vanikoro Island	Temotu Province			Bick, C.	07/03/2016	18
P. vanikorensis	SI	Luesalo, Nendo Island	Interior forests in cultivated giant taro stands in wet marsh; Temotu Province, (Santa Cruz Island) Island	10° 43.940' S	165° 50.463' E	Bick, C.	07/07/2016	18

Table 5-2. Summary of ddRADseq data for each partulid individual including the number of raw reads, number of loci passing the paralog filter with a sequencing depth >6, and mean depth of loci with sequencing depth >6 for 85, 90, and 95% similarity thresholds.

				85% similarity			90% similarity			95% similarity	
Species	Clade	sample	Raw reads	loci	depth		loci	depth		loci	depth
P. similaris	*P. micans* 1	PNB012	2,675,760	48,697	38.3		53,760	38.4		57,392	37.1
		PNG08	370,300	8,777	11.3		9,507	11.2		9,687	10.9
		PNGB17	950,283	22,570	32.4		23,741	32.1		24,351	31.4
		PNGB20	1,146,012	35,053	21.8		38,302	21.7		40,729	21.2
		PNGB32	1,349,229	37,286	23.4		41,342	23.3		44,310	22.8
		PNGW29	3,398,144	53,455	48.1		58,933	47.8		62,723	46.0
		PNGW8	3,871,664	57,669	44.3		64,332	44.5		69,591	43.5
	P. micans 3	PNGB22	1,141,698	36,814	19.8		40,435	19.6		43,078	19.4
P. flexuosa	*P. micans* 2	NG11	3,210,897	45,950	49.9		50,669	50.1		54,960	48.8
P. flexuosa/micans?		GUA15	2,721,623	36,231	56.6		39,728	57.1		42,801	55.4
		HON3	2,263,289	26,609	72.1		28,108	71.8		29,175	70.1
		K6	4,030,495	31,043	109.8		32,853	108.1		34,244	105.6
		K8	4,545,597	33,103	118.5		35,352	117.3		37,109	112.8
P. micans		ISA4	3,858,738	30,245	109.9		32,049	108.5		33,418	104.8
	P. micans 3	KB3017	1,174,508	32,904	19.6		36,804	20.3		39,707	20.1
		SU3217	3,907,872	50,352	57.0		55,661	56.9		60,496	55.5
		SU3218	6,393,291	38,641	143.5		41,264	141.4		43,623	135.1
		SU3227	4,615,462	52,163	65.0		57,825	64.9		63,328	63.4

		SU3229	4,438,013	48,776	68.7		53,841	68.9		58,979	66.8
		COPA5	1,075,419	31,093	21.6		34,070	22.0		36,273	21.6
P. grisea	*P. grisea*	IS3066	3,288,291	44,547	56.0		49,335	55.9		53,429	54.2
		LN3077	3,241,553	47,622	45.3		53,220	45.1		58,264	45.2
		LN3108	4,760,936	39,317	103.8		42,537	101.3		44,986	97.2
		LN3140	2,777,586	39,803	53.0		44,066	52.8		47,749	51.2
		NI3026	4,926,741	52,266	66.3		58,062	67.3		63,784	65.5
P. otaheitana		49a1	2,218,454	30,517	52.8		33,754	52.0		36,848	50.8
P. affinis		80a1	2,271,322	29,648	56.9		32,648	55.4		35,525	53.3
P. suturalis		118d1	2,015,712	27,720	54.2		30,488	53.4		33,366	50.9
P. clara incrassa		PCTI	1,417,747	35,114	27.9		38,559	27.7		41,238	27.0
P. rosea		ROSH1	1,962,303	24,819	63.6		26,065	62.8		26,799	61.1
P. turgida		PTUG4	2,651,654	50,744	35.5		55,870	34.9		60,374	33.8
P. lutea		65a1	2,235,354	28,391	62.0		30,225	60.9		31,958	57.8
P. subgonochila		PSUG1	4,977,681	47,620	80.7		52,049	80.6		55,003	77.4
		PSUG2	426,697	12,893	21.1		13,677	21.4		13,824	21.1
P. gibba		PG55a51	3,220,828	39,824	61.9		43,778	61.5		46,292	60.3
		PRAG4	796,536	30,021	14.5		33,193	14.5		35,332	14.0
		Y19	5,891,910	53,574	82.7		59,282	82.4		63,438	81.0
P. radiolata		PRAD7	957,677	30,440	18.8		33,445	18.7		35,640	18.1
		PRAD8	747,536	24,540	15.7		26,910	15.7		28,399	15.3
P. cramptoni		B1	2,744,600	26,562	79.8		28,007	79.0		28,748	77.2

		B2	2,925,185	28,945	85.3		30,779	84.3		32,188	81.2
P. turneri		PTUN2	274,845	7,753	10.6		8,385	10.5		8,499	10.3
		PTUN4	618,459	22,398	13.3		24,691	13.3		26,451	13.1
		PTUR7	165,507	5,374	9.0		5,534	9.0		5,510	8.8
P. vanikorensis		Vanikoro1	1,672,617	24,014	57.4		25,390	56.1		26,266	54.2
		Vanikoro2	2,487,549	27,525	72.0		29,242	70.4		30,232	68.3
P. auraniana		Nendo1	1,379,030	22,971	49.6		24,148	48.9		24,491	47.5
		Nendo3	1,953,391	24,383	67.5		25,770	66.3		26,266	64.2
		PVT271	1,390,541	24,363	44.7		25,621	44.2		26,172	43.0
P. lirata		PLIR3	804,236	22,554	25.9		23,803	25.7		24,453	25.3
		PLIR4	834,187	30,493	14.2		33,408	14.1		35,255	13.9
Samoana diaphana		SD25a1	2,179,667	35,922	36.1		38,034	35.4		39,108	34.2
S. burchi		SS23a1	2,342,640	37,531	47.8		39,944	46.9		41,101	44.9
S. attenuata		SATH	2,111,133	33,454	52.7		35,187	51.9		36,129	50.1

CHAPTER 6

Conclusions

The primary goal of my dissertation was to determine whether partulid tree snails could survive in the Anthropocene? The answer is guardedly yes! My findings have yielded valuable clues into the aspects of partulid tree snail biology and ecology that has allowed them to survive in modern Oceania outside of captivity. In Chapter 2-4 I have uncovered that rarity, higher clutch size, and microhabitat preference are important aspects that have allowed partulids to differentially survive on Tahiti. Higher clutch size is also an important aspect of survival in Guam and Saipan but was not as evident in Moorea. The riddle of Moorea is an interesting opportunity to pursue in the future regarding other aspects of life history and island ecology that allow partulid differential survival.

It is also of interest to note that on Tahiti, another survivor *Partula otaheitana* is now extirpated from Tahitian valleys and present only in montane forest refuges that are more than 1000 meters in altitude. Gerlach (2001) indicated that in this environment, the predator's activity is impaired by the cooler environment 5-15 °C versus 25-27 °C at sea level. So at least for the moment this abiotic condition limits the activity of *E. rosea* and provides *P. otaheitana* a reprieve from predation, but for how long? This question could possibly be a subject for another future study and although my dissertation did not involve a thorough investigation of the persistence of *P. otaheitana* on montane forest refuges in Tahiti, it is vital to understand all aspects of *Partula* differential survival in its range in order to make informed decisions about its conservation.

I have also uncovered evidence suggesting that a number of partulid tree snail species in a different part of their range, Near Oceania, have very atypical synanthropic and cryptic multi-archipelago ranges. This indicates the role of prehistoric humans in their distribution and to that end I have attempted to locate a source island population but that currently remains a mystery. This raises many compelling questions regarding their ecology and evolutionary life history. Specifically, what is it about their biology and/or ecology that make them transportable? What I have been able to establish from Near Oceania partulids thus far is that although they are human associated and have a wide-ranging distribution, it does not necessarily guarantee survival. The threat of habitat destruction also looms large in the future of conservation for these taxa, but it in order to do this its clear that the taxonomy of Near Oceania partulids, representing >10% of this highly endangered tree snail family, is urgently in need of revision.

Fecundity and Partulid Survival

In Chapter 2 I analyzed historical demographic data collected by H. E. Crampton (1916) over a century ago to understand the differential survival of two surviving Tahitian partulid tree snail species, *Partula clara* and *Partula hyalina*. The initial hypothesis that they were demographically abundant and widely distributed and will eventually be driven to extinction was refuted (Bick *et al*., 2016). My analysis of Crampton's 1916 survey shows that *Partula clara* and *Partula hyalina* were both widespread in Tahiti which is consistent with one prediction of my hypothesis. However, *P. clara* and *P. hyalina* did not meet the prediction of abundance they collectively represented <5% of the tree snails sampled by Crampton (1916) across the island as a whole (Bick *et al*., 2016) and in individual valleys (Bick *et al*., 2016). Based on this result and the fact that molecular phylogenies have shown that *P. clara* and *P. hyalina* are members of a founding lineage that is distinct from other Tahitian congeners (Lee *et al*., 2009, 2007) suggests some shared biological attribute aiding their differential survival. Fortunately, Crampton (1916) also documented instantaneous clutch sizes of thousands of gravid Tahitian partulids. My analysis of his instantaneous clutch size data determined that the two surviving Tahitian partulids, *P. clara* and *P. hyalina*, had higher instantaneous mean clutch sizes relative to their co-occuring congeners. I concluded that higher fecundities might be a contributing factor to their differential survival.

Chapter 3 extends on the initial finding in Chapter 2. It addresses inherent shortcomings in Crampton's data – instantaneous clutch sizes are not reproductive rates and fecundity is modulated by environmental heterogeneity – by calculating species-specific reproductive rates from captive populations. It also extends the study to include partulids on additional islands Moorea in the Society Islands and Guam and Saipan in the Mariana Islands – for which historical clutch size data and captive reproductive rates are also available. These results show that reproductive rate in captivity is strongly correlated with historical clutch size data obtained by Crampton from intact, wild populations, and that partulid survival in the Mariana and Society archipelagoes is strongly correlated with higher reproductive rates, although the strength of the correlation varies among islands.

Chapter 2 and 3 have emphasized the importance of higher fecundity as a mechanism for *Partula* survival and it may be a worthwhile venture to study the genetic underpinnings associated with their development and reproduction. If the genes associated with higher fecundity can be identified the next steps could involve modifying these genes with a genome editing tool such as CRISPR-Cas9 (Hsu, 2014; Cong, 2013). This would have broad conservation implications in terms of enhancing the fecundity for other partulid congeners with lower reproductive rates. Perhaps this is a practical initial option before they can be reintroduced into the wild.

Still, the outcomes in Chapter 3 also suggested that the linkage between higher reproductive output and survival in *Partula* does not apply to all of the island populations (Guam, Saipan, Moorea) and is unlikely to be the only determining factor in their survival. For instance, *Partula aurantia* and *Partula suturalis vexillum,* the two taxa with the highest mean instantaneous clutch sizes on Moorea were extirpated in the wild within a decade of *E. rosea* introduction (Murray *et al*., 1988). However, the sole surviving Moorean taxa, *Partula taeniata*, has an intermediate clutch size but also exhibited a higher birth rate in captivity relative to its extinct congeners. This taxon is also sister to the two Tahitian survivors, *P. clara* and *P. hyalina* (Lee *et al*., 2009) and all 3 have persisted for more than 40 years of *E. rosea* predation pressure. Interestingly, *P. clara* and *P. hyalina* have much higher reproductive rates in the wild and in captivity. So it is possible that there may be some other aspect of *P. taeniata's* biology that has enabled it to differentially survive.

On Guam, *P. radiolata* - one of the two survivors, has remarkably been able to maintain robust population densities around the island despite being exposed to a suite of introduced predators for over 6 decades. A previous study (Sischo & Hadfield, 2017) concluded that some aspect of its life history, possibly fecundity, or behavior is significant to its continued survival. In Chapter 3, my results do indicate that fecundity may be an important factor due to its highest mean instantaneous clutch size and the third highest reproductive rate in captivity though I still lack insight into their ecology and behavior. The unlikely survival of wild populations of *P. taeniata* on Moorea and *P. radiolata* on Guam have highlighted the importance and urgency in conducting detailed ecological and behavioral studies in not only these two taxa but also for other surviving wild *P. gibba* (Guam & Saipan), *P. taeniata* (Moorea), *P. hyalina* and *P. clara* (Tahiti) populations.

Microhabitat Preferences and Partulid Survival

The impact of introduced predators may also vary across island microhabitats; *e.g.*, in addition to larger clutch sizes, survival in the Guam avifauna is associated with the ability to nest in locations inaccessible to the brown tree snake (Wiles *et al.*, 2003). Although *P. clara* and *P. hyalina* stem from a single founding lineage (Lee *et al.*, 2009; Lee *et al.*, 2007) and share similarly high clutch sizes (Bick *et al.* 2016), they have not exhibited the same levels of survival in the presence of *Euglandina rosea*, the North American carnivorous land snail. Only a few Society Island *Partula* species have been able to endure predation pressure from *E. rosea*, most notably the white-shelled *P. hyalina*, which persists in a total of 31 Tahitian valleys.

Land snails are limited to shady areas such as valleys and deep forests (Prior, 1985), but those exhibiting high albedo light shell coloration are able to tolerate long periods of exposure to open sunlit environments (Ozgo, 2011; Chiba, 1999). Crampton (1916) described *Partula hyalina* as being the only Tahitian partulid that regularly occurs on edge habitats where it is exposed to prolonged direct sunlight, in addition to it also occurring in the more typical partulid shaded habitat within the forest. In Chapter 4 I corroborated the hypothesis that edge habitats form “solar refuges” for surviving *P. hyalina* where they will routinely experience significantly higher rates of solar radiation than the predator and the latter will actively avoid such conditions by rapidly migrating away into more shaded cover. I determined that surviving wild *P. hyalina* populations are exposed to significantly higher ambient solar irradiation levels than those endured by the alien predator *Euglandina rosea* foraging in forest edge and clearing habitats.

Any protective effect gained from being in a "solar refuge" though tends to disappear on overcast days.

Interestingly, the largest known surviving *P. hyalina* population occurs in our Tipaerui-Iti Valley Study site, characterized by discrete patches of vegetation with an extensive stand of wild red ginger, *Etlingera cevuga.* This plant species is commonly found near rivers in semi-open habitats but not in closed canopy forests and can grow up to 4 m in height (Brown, 1931). Previous surveys of 70 Tahiti-Nui valleys found that 75% of remnant *P. hyalina* populations occurred on this host species alone (Coote, 2007). This emphasizes the importance of cultivating stream edge *Etlingera cevuga* stands in the long-term survival of *P. hyalina* in Tahitian valleys.

Currently, conservation efforts concerning Society Island partulids entails the reintroduction of captive-bred *Partula* into the wild. The first experimental release was carried out in 1994 in an interior forest on the island of Moorea (Coote, 2004). An exclosure made of galvanized iron roof panels with an electric fence at the top and salt troughs at the base was set up as a barrier to keep the predator *E. rosea* from preying on the captive-bred *Partula* species. Despite all of these preventative measures *E. rosea* was still able to breach the security of the exclosure. Also, coupled with poor maintenance and monitoring difficulties the havoc caused by *E. rosea* encroachment resulted in only 8 individual surviving *Partula* out of the 320 that were released. The latest reintroduction started in 2016 and has either shown mixed results or it is still too early to tell. It is clear that these methods are not only expensive but indefinitely require high maintenance.

To mediate some of these challenges, my field study in Chapter 4 has identified conditions in which successful reintroductions might be achieved with minimal resources and significantly increase the feasibility and scale of future reintroduction efforts. The results of my field study also suggest that any scenarios of conservation efforts concerning *P. hyalina* should involve mapping out and actively maintaining and monitoring discrete patches of *E. cevuga* stands across the island, similar to Tipaerui-Iti, before reintroducing them into the wild. Specifically, this would entail trimming back encroaching tree canopies to create patchy sunlit environments within the stands that can be tolerated by *P. hyalina* but would be difficult for *E. rosea* to easily navigate. Another recommendation would be to proactively remove leaf litter within the stands to eliminate possible concealment habitats for *E. rosea* as implied by Meyer & Cowie (2011).

As previously pointed out by Ó Foighil (2009), the main goal of partulid conservation is to reintroduce them into the wild but the effectiveness of reintroducing them to environments still containing the extinction agent is debatable. Perhaps a controversial conservation strategy, but a potentially viable one that needs thorough consideration, would be to carry out reintroductions on predator free islands (Ó Foighil, 2009). Some potential island candidates for *Partula* reintroduction could be The Cook and Austral Islands primarily because it is an invasive predator free haven containing anthropogenic founder populations of *P. hyalina* (Ó Foighil, 2009; Lee *et al*. 2007). Therefore, it may not be an impractical approach to gradually reintroduce individuals to similar islands that are free of invasive predators to ensure their continued survival.

Chapter 4 also highlights that there are parallels between the persistence of endemic Tahitian *Partula* under severe selection pressure from an introduced continental predator and the fate of Guam's avifauna (Wiles *et al*., 2003). In both cases, endemic species with larger clutch sizes exhibited better survival. Guam's surviving endemic avifauna also display microhabitat differences (specifically in nesting habitat) that has allowed them to persist in the presence of the brown tree snake for multiple decades (60-70 years on Guam). On Tahiti, *P. hyalina* has been able to persist in the presence of *E. rosea* for more than 40 years and also exhibits a parallel pattern of greater clutch size and protected habitat and this general life history combination may also apply more broadly to surviving members of diverse endemic clades across Oceania.

Insights from Near Oceania

Chapter 5 had two interrelated biogeographic goals: 1) test the hypothesized prehistoric introduction of partulid tree snails to Papua New Guinean island archipelagos with genetic markers; 2) use the results to revise the taxonomy of these poorly-studied snails and to reconstruct prehistoric East-West Melanesian exchange networks. It required extensive sampling throughout the island archipelagoes of Papua New Guinea (PNG) and the Solomon Islands (SI), which also included the Remote Oceania Santa Cruz archipelago. I carried out multiple sampling expeditions in 2012-2016. Tissue samples obtained from collected specimens were genotyped using Next Generation Sequencing (NGS) double digested Restriction Associated DNA sequencing (ddRADseq) encompassing 4819 loci as well as a traditional targeted gene approach using a single mitochondrial COI (Cytochrome Oxidase I) gene. My phylogenetic results indicate that only 5 corroborated species of partulids are present in the region and that most of the described SI species are cryptic populations of a single human-associated (restricted to coastal villages, absent from native forest) partulid. In particular, only 3 nominal species are present in Near Oceania:

(1) *Partula grisea* (Lesson, 1830). In Gerlach's (2016) revisionary monograph of Partulidae, he synonymized *Partula carteriensis* (Quoy & Gaimard, 1832), recorded as being widely distributed throughout the Bismarck Archipelago (Rensch, 1937) with *Partula grisea* (Lesson, 1830) and restricted it to the northern part of the Archipelago. My phylogenetic analysis corroborated Gerlach (2016): I recovered it from only two of the three main Archipelago islands: present in New Ireland and Manus, but absent from New Britain (contains its sister species). *P. grisea* is common on Manus, less so in New Ireland, and restricted to coastal forest fringes on both islands. Mitochondrial genotyping of the samples from both islands show that, although they did not share haplotypes, *P. grisea* individuals on Manus and on New Ireland are genetically very similar and the island populations display very modest levels of genetic divergence.

(2) *Partula micans* (Pfeiffer, 1854). Only one species, *P. micans* is spread throughout both PNG extending from New Britain in the north and the Massim Islands in the south and to Guadalcanal in the SIs and westwards through its central and western provinces. Gerlach (2016) recently synonymized the 16 nominal species of *Partula* historically documented from this area to 3 species: *P. micans* Pfeiffer, 1854 (type locality: Shortland Islands), *P. flexuosa* Hartman 1885 (two potential type localities mentioned in the original description: San Jorge and Eddystone (Simbo) islands), and *P. similaris* Hartman 1886 (type locality: Woodlark (Muyua) Island).

Ó Foighil *et al*. (2011) previously genotyped *P. similaris* from its type locality. I then combined these findings with my newly genotyped specimens of *P. micans* collected from its type locality in the Shortland Islands and *P. flexuosa* collected from Tanabuli Island which is within ~25 km of San Jorge, its type locality. My phylogenetic results place their respective topotype populations in the same clade and do not corroborate the retention of a specific status for each of these 3 taxa. Therefore I propose synonymizing these 3 taxa to 1 taxon. *P. micans* is the oldest available name and therefore has taxonomic priority over *Partula flexuosa* and *Partula similaris*. My proposed taxonomic revision (with the exception of New Britain) largely agrees with work by early *Partula* expert Yoshio Kondo (unpublished 1971 manuscript) in that the collective range for *P. micans'* spanned the Massim Islands and Bougainville-to-Guadalcanal.

A notable feature of *Partula micans* is its strikingly aberrant synanthropic ecology, a characteristic that is unprecedented for *Partula*. In none of my field sites did I encounter *P. micans* in native forest habitats, but near coastal villages and settlements. This detail strongly implicates prehistoric human introduction as the dispersal mechanism (Ó Foighil *et al*., 2011). At present, the molecular data has provided insights regarding their regional distribution spanning multiple archipelagos, but the populations collected thus far lack evidence of a source population for Near Oceania partulids. One remaining possibility concerns *P. milleri*, described from Espiritu Santo island (Vanuatu) and has been recently synonymized with *P. micans* on conchological grounds (Gerlach, 2016). However, it is not clear if it is still extant (a French-led survey of the type locality failed to find it) or if it represents a source or founder relative to the PNG/SIs population. I plan on mounting a dedicated expedition to Espiritu Santo at a later date to investigate this further.

Although the distribution of *Partula micans* is remarkable it surprisingly was not abundant in many of the Solomon Island locations where I collected and often took many hours to search for them. Kondo (unpublished1966 field notes obtained from the Bishop Museum records) described a similar experience. I also revisited his 1966 sampling locales and was only successful in obtaining snails from half of those locations. Based on these field observations a word of caution is that even though *P. micans* has an extraordinary multi-archipelago distribution and appear to be synanthropic, it does not guarantee their survival. This is very important for consideration of their conservation status. Perhaps adopting somewhat similar considerations as the Society Islands partulids would be ideal for the long-term survival of *P. micans*. Wild stands of ginger are also found throughout forests in Near Oceania. Instead of cultivating hibiscus stands near homes that could facilitate maintaining tiny populations of *Partula* that will eventually go extinct, perhaps introducing them into wild ginger stands in interior forests may give them a better chance of survival.

(3) *Partula cramptoni* (Clench, 1941). This species is the only endemic described from the Rennell and Bellona archipelago. On Rennell Island, the type locality for *P. cramptoni*, with the exception of a few dead shells I was not able to recover any living snails after 4 days of searching and with extensive help from local people. This may be alarming because Rennell is heavily logged and also undergoing extensive mining developments. Currently I cannot confirm whether this species is still extant on Rennell Island. More exhaustive search for this species on Rennell should be carried out to sort out their conservation status. I was able to locate individuals in the nearby island of Bellona and my molecular phylogenetic analysis shows that they are very distinct from the other Near Oceania taxa and that its closest relatives are in Micronesia and the Mariana archipelagos.

Partula in the Santa Cruz archipelago

In the adjacent Remote Oceania Santa Cruz archipelago I attempted to locate a convincing source island population for *P. micans* in the islands Nendo and Vanikoro. I was able to rule out the Remote Oceania Santa Cruz archipelago as a source but the mystery of their origins still remains. Furthermore, I was able to identify 2 *Partula* taxa from this region and they are:

(1) *Partula vanikorensis* (Quoy & Gaimard, 1832). This species was first recorded in 1832 from Vanikoro Island and the type specimen has been kept in the collections at the *Muséum national d'histoire naturelle* in Paris. It has received scant scientific attention since then. I successfully encountered abundant populations in the interior forest on Vanikoro Island. Although Gerlach (2016) thought they were found on multiple islands, my phylogenetic findings indicated that they are endemic and distinctive to Vanikoro Island. As on Rennell Island, Vanikoro is presently undergoing intensive industrial logging and could quickly threaten the survival of these species. This adds a degree of urgency to the proposed taxonomic revision to help design a rational conservation program for these tree snails as this may be our last chance to study many of these partulid populations.

(2) *Partula auraniana* (Hartman, 1888). This species was originally described from Vanuatu but it is now extinct from its type locality. Lee *et al*. (2014) genotyped surviving individuals collected from the Torres Islands. I collected these individuals from Nendo Island the Santa Cruz group of the Solomon Islands. Unpublished field notes by Yoshio Kondo (1966) speculated that they were *P. auraniana*. In contrast Gerlach (2016), using conchological distinctions, identified them as *P. vanikorenis* and that they were highly variable. My molecular phylogeny clearly indicated that the Nendo specimens I collected are in fact *P. auraniana* and not *P. vanikorensis*. This confirms that *P. vanikorensis* is distinct and a Vanikoro Island endemic and interestingly reveals a multi-archipelagic range extension (~250km) for *P. auraniana* that includes Nendo Island as well as the Torres Group.

Control of the Rosy Wolf Snail *Euglandina rosea* and the New Guinea flatworm *Platydemus manokwari*

One final consideration related to the conservation of *Partula* throughout the Pacific is the eradication of introduced predators such as the Rosy Wolf Snail *Euglandina rosea* and the New Guinea flatworm *Platydemus manokowari*. Many of the control methods on Pacific oceanic islands have revolved around the eradication of mammalian invasions due to the fact that the ecological disturbances they cause are very conspicuous and well documented (Courchamp *et* *al*., 2003; Blackburn *et al*. 2004; Towns *et al*., 2006). Rats *Rattus sp*. (Jones *et al*., 2008) and cats *Felis catus* (Nogales, 2004) are usually the main predatory threats on Pacific oceanic islands (Myers *et al*., 2000; Phillips, 2010).

In order to control for these invasive predators physical methods have been employed ranging from the use of fencing, shooting, as well as trapping (Courchamp *et al*., 2003). Fencing exclosures have been shown to not be effective in controlling *E. rosea* in the Society Islands and requires experienced and dedicated staff to maintain it (Coote, 2004). Shooting and trapping have been successful on some Pacific Islands in eradicating mammalian herbivores, omnivores and carnivores but there are also many limitations associated with these methods that make it impractical for eradication of *E. rosea* and *P. manokowari* (Parkes, 1990; Courchamp *et al*., 2003). Both of these methods require a lot of manpower and resources to implement. The use of shooting in this context is unrealistic because the targets are small and *E. rosea* is particularly difficult to spot because the red/brown shell blends in well with the leaf litter (personal observation). Trapping is also a concern because it requires deploying attractive baits for target species but also making sure they are not attractive for non-target species (Courchamp *et al*., 2003), but there are no realistic baits that can be used to attract *E. rosea* because it mainly eats other live snails and slugs.

Other techniques like poisoning and pathogen introduction have also been utilized to control invasive mammalian species on Pacific Islands (Tyndale-Biscoe, 1994; Courchamp *et al*., 2003). The use of poison is very hazardous in that there is no discrimination of its impact on target and non-target species (Morris, 2001) and the potential for developing bait aversion (Hickling *et al*. 1999). Pathogen introduction can also be very risky because of its impact on non-target species and the potential for immunity evolution (Parkes *et al*., 2002 – Wildlife Research;

Courchamp *et al*., 2003). Therefore the use of these techniques may not be as ideal in the conservation of extant *Partula* in their natural range. Perhaps another suitably effective, although a very controversial approach, is the use of synthetic meiotic drive to disrupt the nuclease based genes needed for fertility (Burt & Trivers, 2009) in both *E. rosea* and *P. manokowari*. Fertile individuals can pass on a defective copy of the gene to their offspring and thereby making them infertile and eventually causing the population to crash (Esvelt & Gemmell, 2017). The main concern over this technique is the loss of control that the drive system will spread beyond the target area (unless that is the goal) and the ecological consequences associated with it require more understanding.

Another effective method, and perhaps the most relevant to the control of *E. rosea* and *P. manokowari*, is to set up refuge islands for the reintroduction of *Partula* and restricting human access. Countries like New Zealand have been at the forefront of establishing predator-free offshore island refugia for endangered endemics (Jamieson & Ryan, 1999; Simberloff, 2002; Rimmer, 2004; Bellingham *et al*., 2009). Perhaps the New Zealand model could be replicated to ensure partulid long-term survival at the moment while developing effective and safe approaches for the eradication of *E. rosea* and *P. manokowari* across Oceania.

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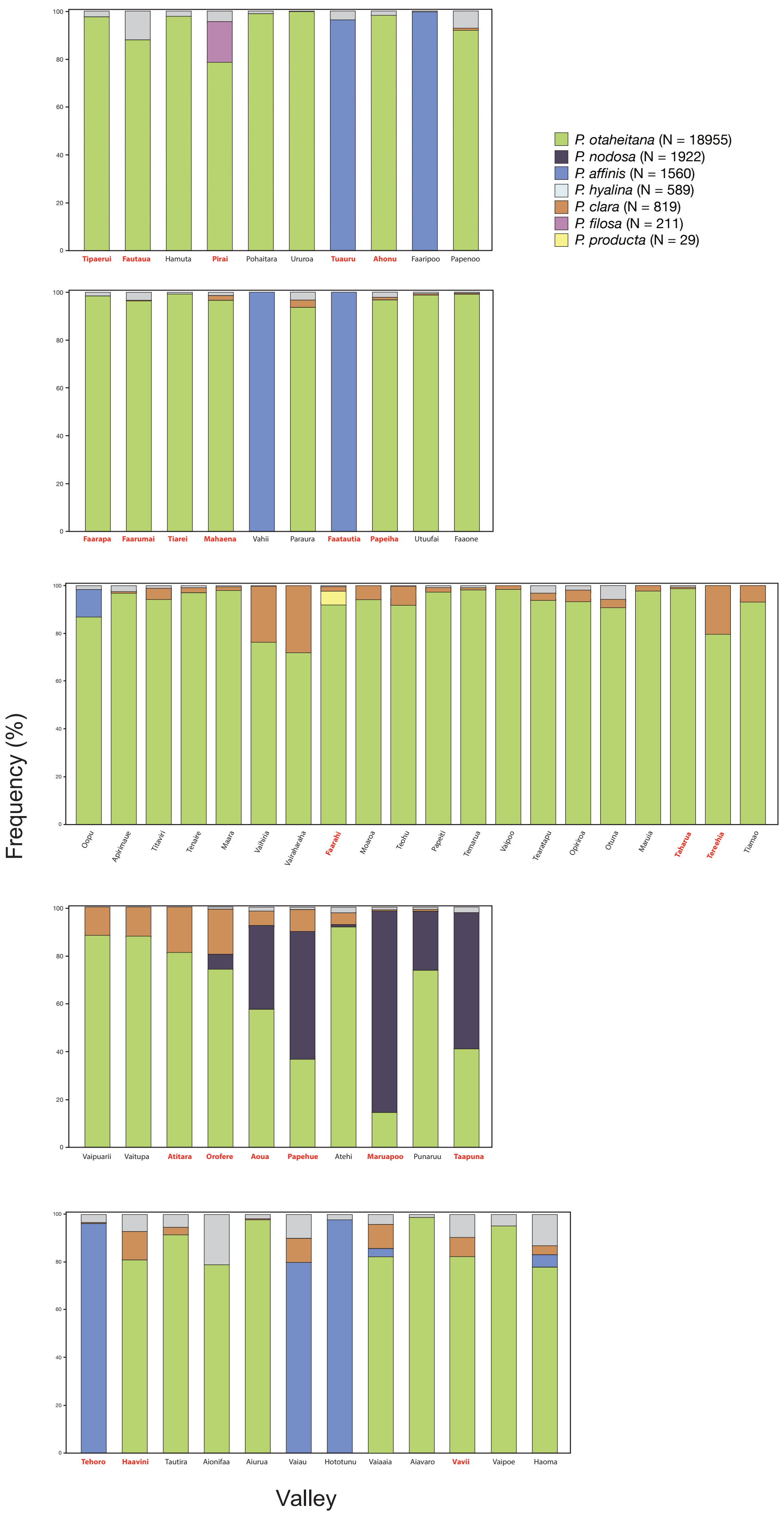
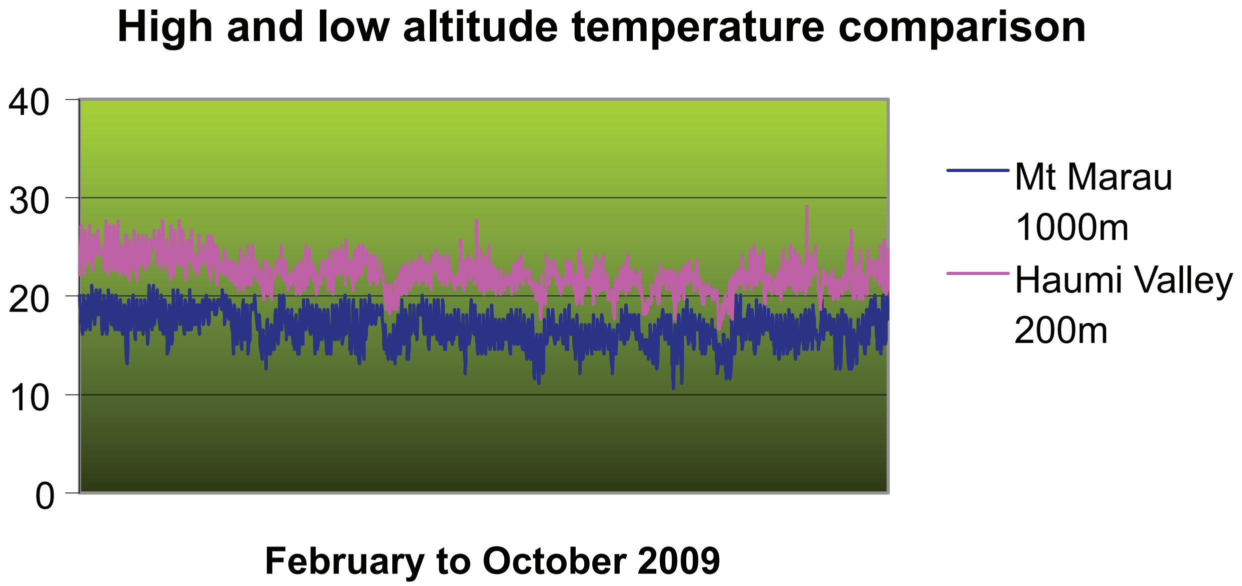
APPENDICES

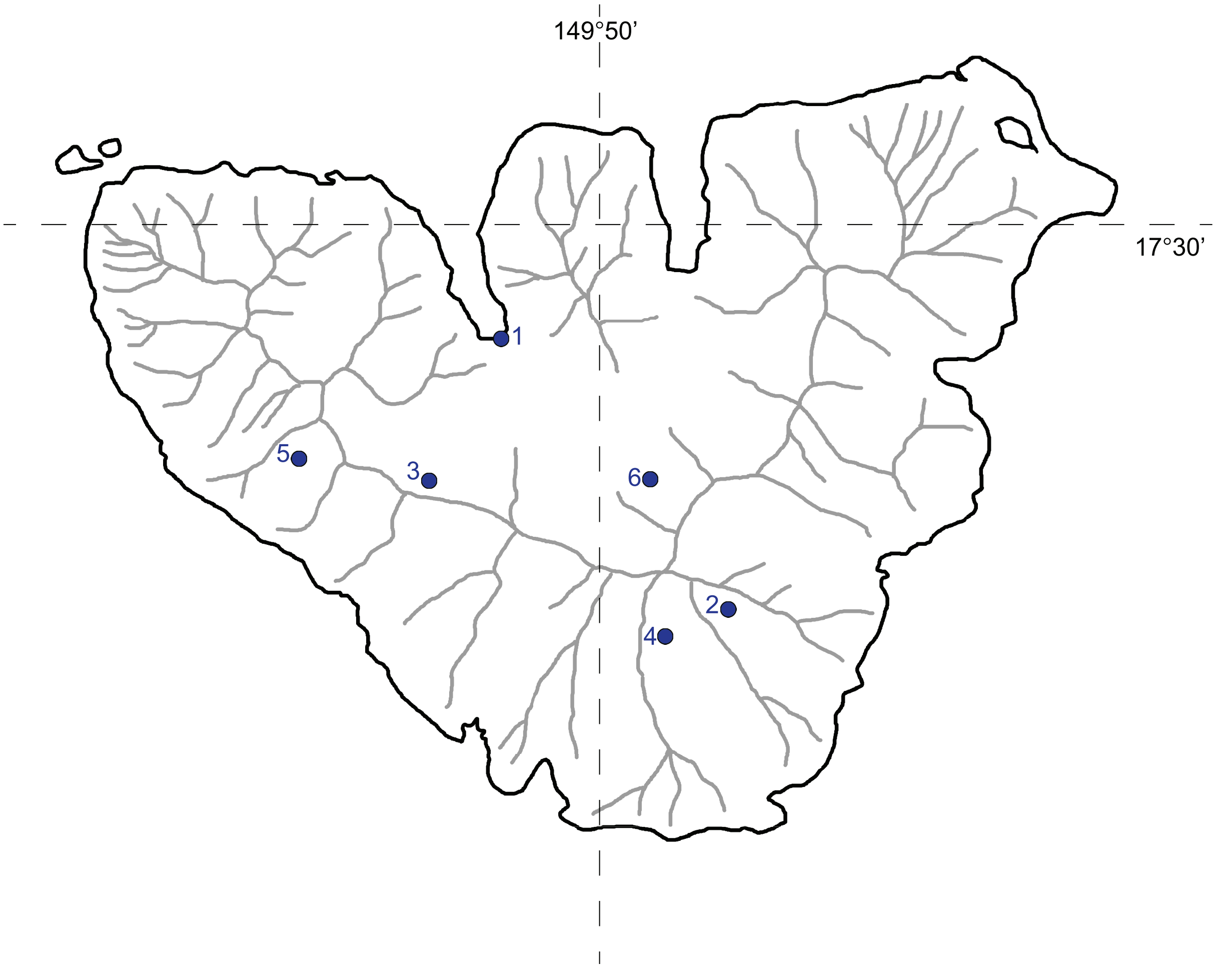
Appendix I. The relative composition of seven endemic *Partula* species in the 62 Tahitian valleys surveyed by Crampton (1916) during 1906–1909, arranged by island subdivision. The 23 valley names in red contain surviving partulids (see Table 2-1 for details).


P. otaheitana (N = 18955)
P. nodosa (N = 1922)
P. affinis (N = 1560)
P. hyalina (N = 589)
P. clara (N = 819)
P. filosa (N = 211)
P. producta (N = 29)
Frequency (%)
Valley
0
20
40
60
80
100
Tipaerui
Fautaua
Hamuta
Pirai
Pohaitara
Ururoa
Tuauru
Ahonu
Faaripoo
Papenoo
Faarapa
Faarumai
Tiarei
Mahaena
Vahii
Paraura
Faatautia
Papeiha
Utuufai
Faaone
Oopu
Apirimaue
Titaviri
Tenaire
Maara
Vaihiria
Vairaharaha
Faarahi
Moaroa
Teohu
Papeiti
Temarua
Vaipoo
Tearatapu
Opiriroa
Otuna
Maruia
Taharua
Tereehia
Tiamao
Vaipuarii
Vaitupa
Atitara
Orofere
Aoua
Papehue
Atehi
Maruapoo
Punaruu
Taapuna
Tehoro
Haavini
Tautira
Aionifaa
Aiurua
Vaiau
Hototunu
Vaiaaia
Aiavaro
Vavii
Vaipoe
Haoma

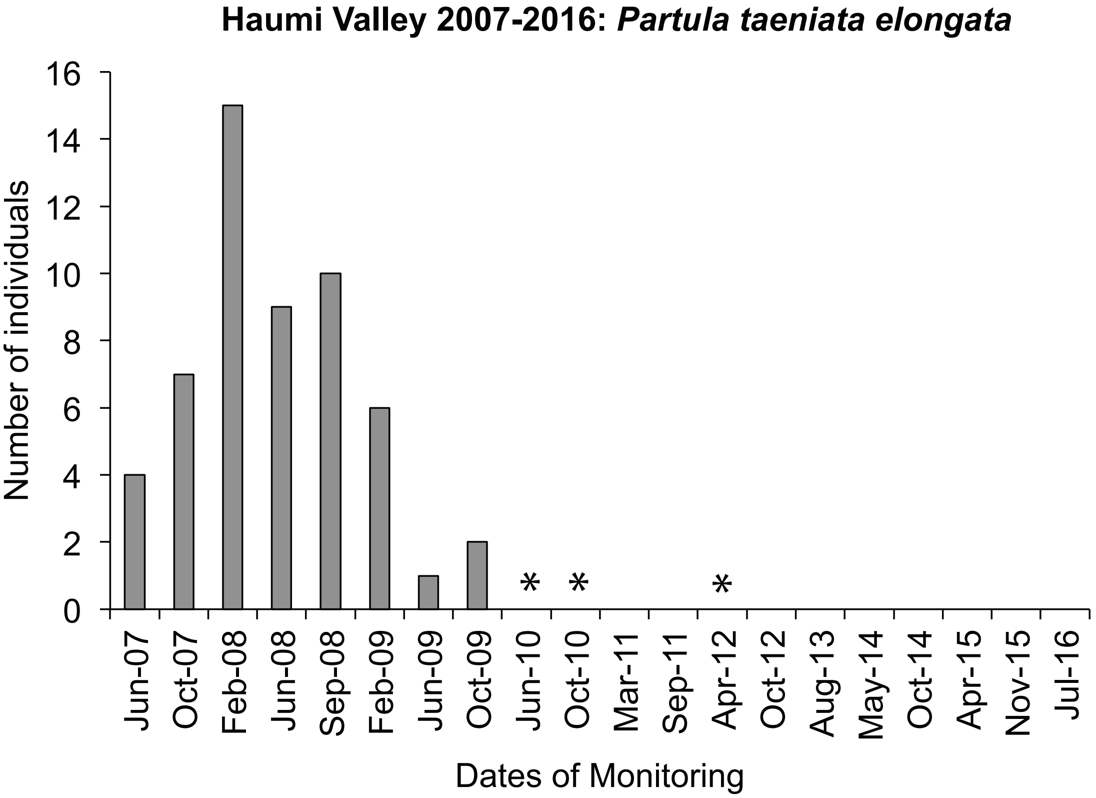
Appendix II. Summary of environmental temperatures logged at two Society Island partulid sampling locations over an 8-month period by Trevor Coote. The high altitude Mount Marau site is on the island of Tahiti and was the source of the (now expired) captive *Partula otaheitana* population (Figure 3-5). The lower altitude Haumi Valley site is 30 km away on the neighboring island of Moorea and retained a surviving population of *P. taeniata* until 2009.



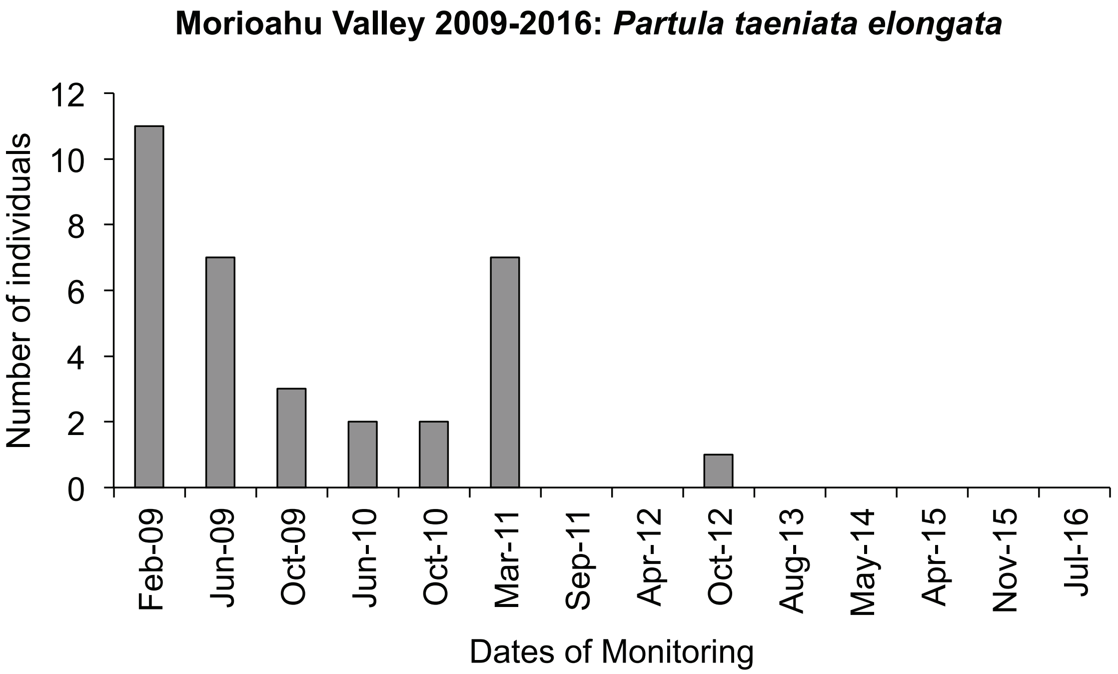
Appendix III. Map of the island of Moorea showing the locations of surviving populations of *Partula taeniata*. Location Key is as follows, 1: Opunohu Bay mangrove habitat (census data unavailable); 2: Haumi Valley; 3: Morioahu Valley; 4: Maatea Valley; 5: Moruu Valley; 6: Maramu Valley.



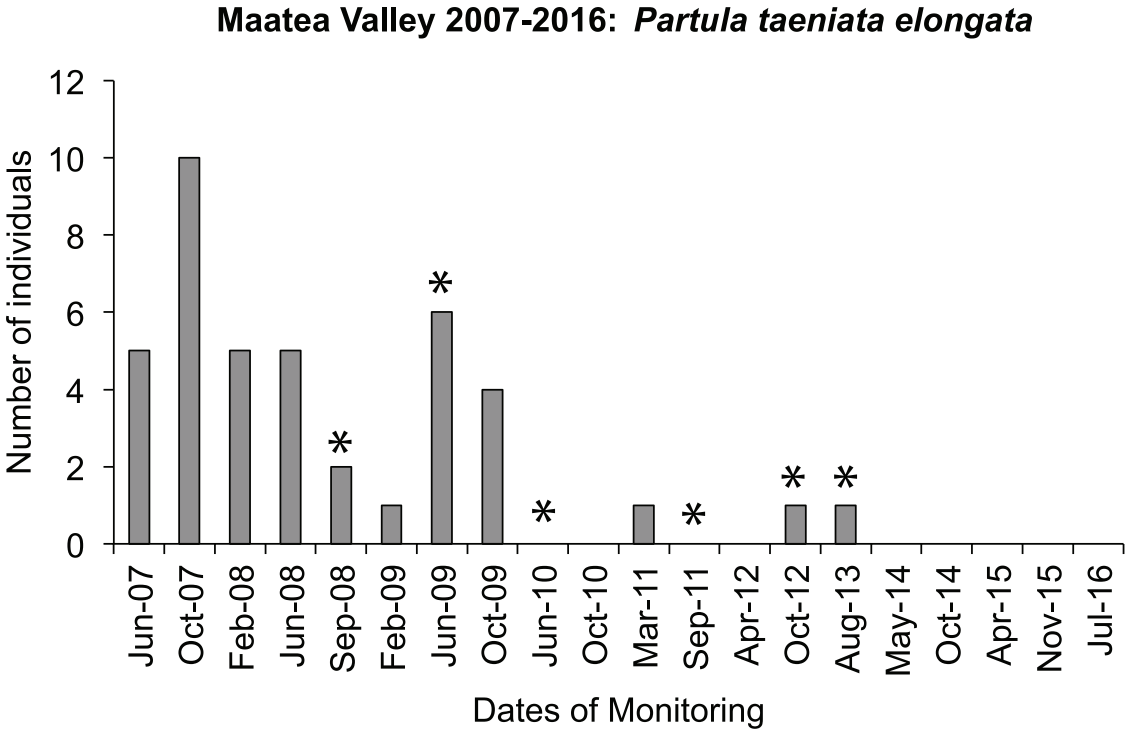
Appendix IV. Field census results of Haumi Valley *Partula taeniata elongata* population by Trevor Coote from 2007 to 2016. Last live individual was detected in 2009. Asterisks (*) indicate detection of live *Euglandina rosea*.



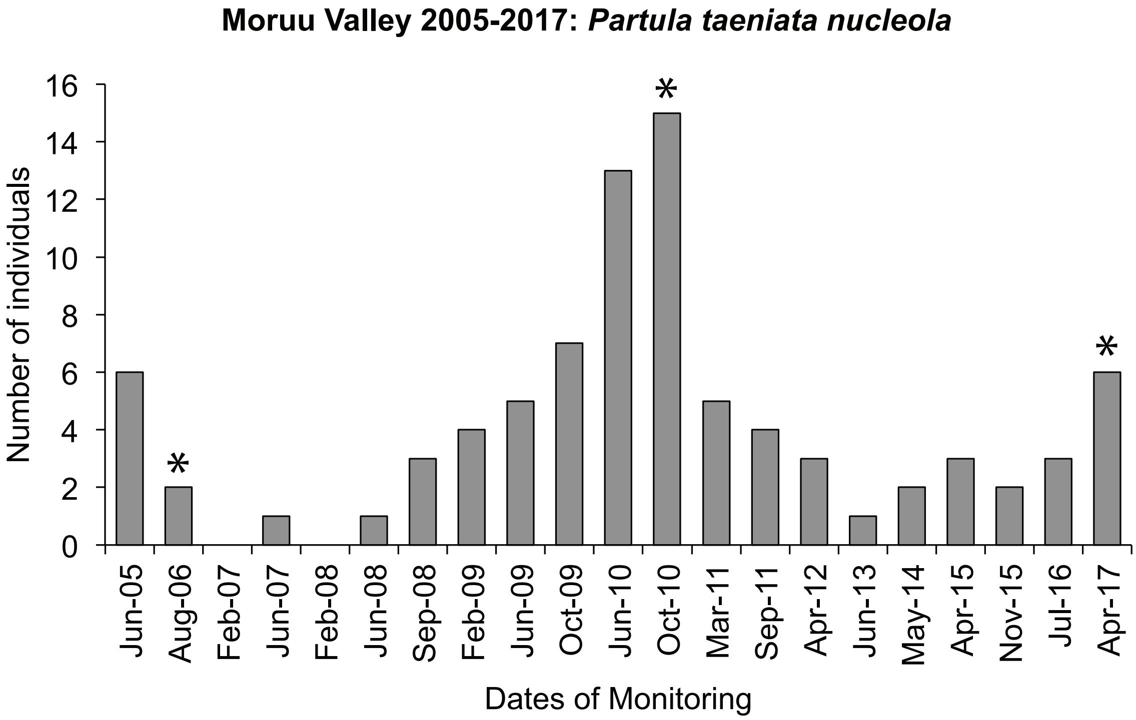
Appendix V. Field census results of Morioahu Valley *Partula taeniata elongata* population by Trevor Coote from 2009 to 2016. Last live individual was detected in 2012.



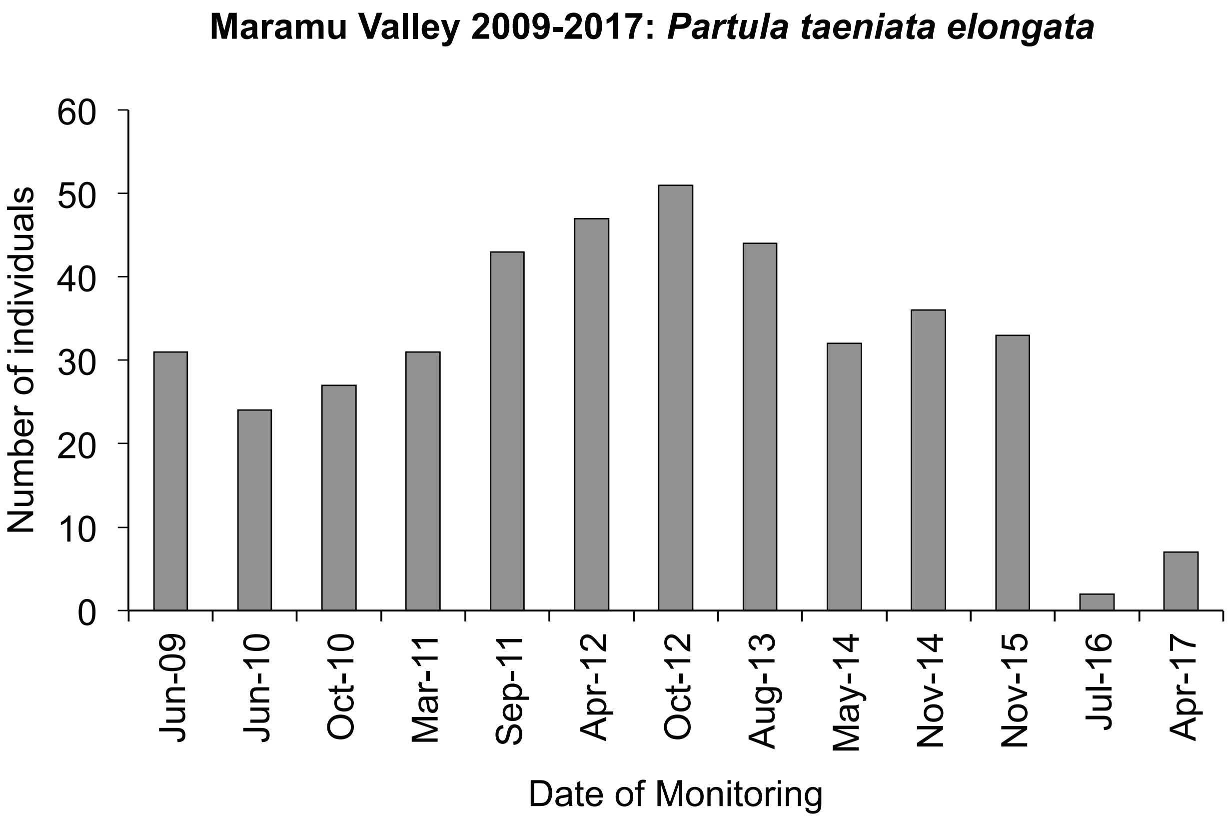
Appendix VI. Field census results of Maatea Valley *Partula taeniata elongata* population by Trevor Coote from 2007 to 2016. Last live individual was detected in 2013. Asterisks (*) indicate detection of live *Euglandina rosea*.



Appendix VII. Field census results of Moruu Valley *Partula taeniata nucleola* population by Trevor Coote from 2005 to 2017. Asterisks (*) indicate detection of live *Euglandina rosea*.

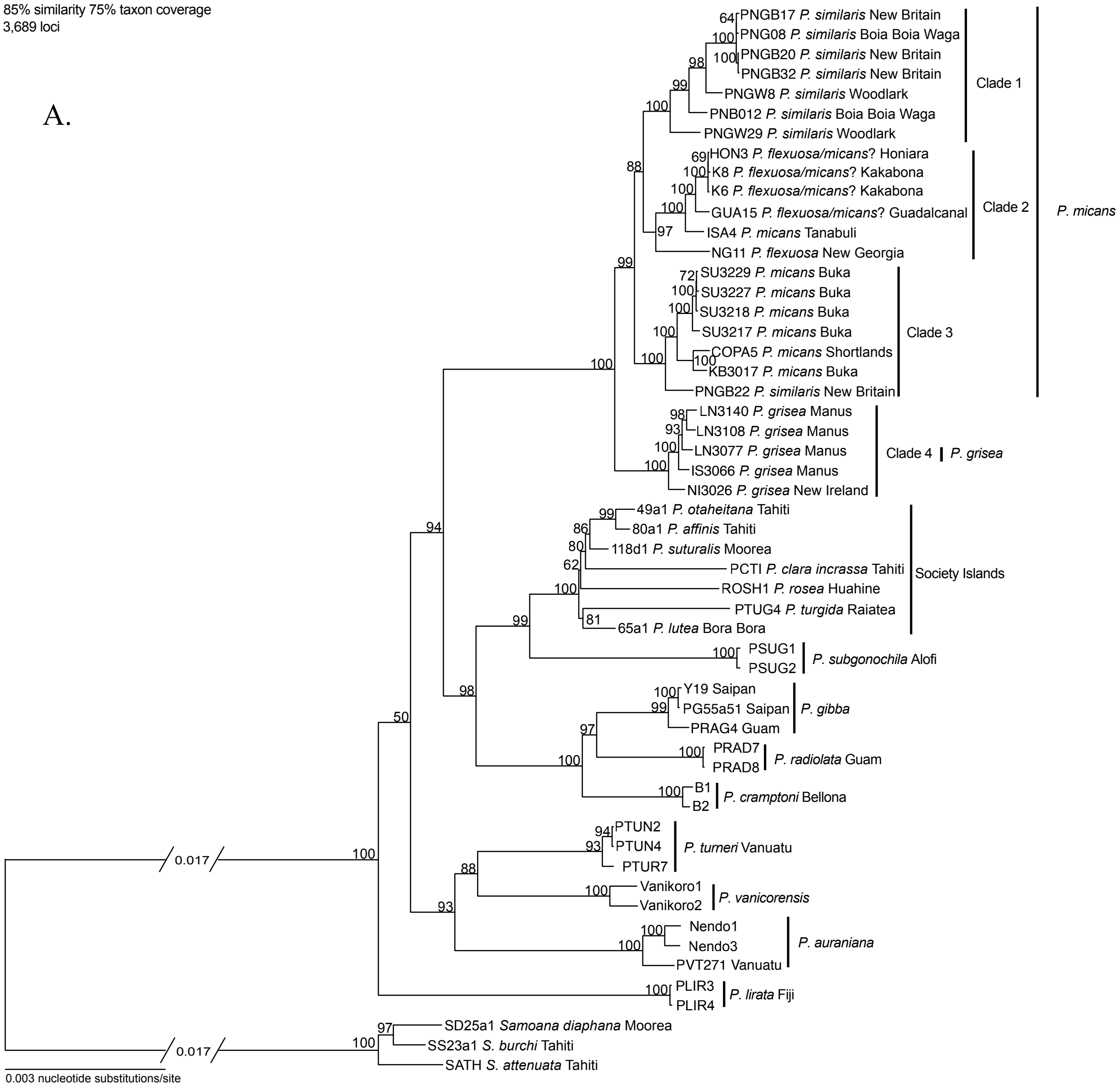


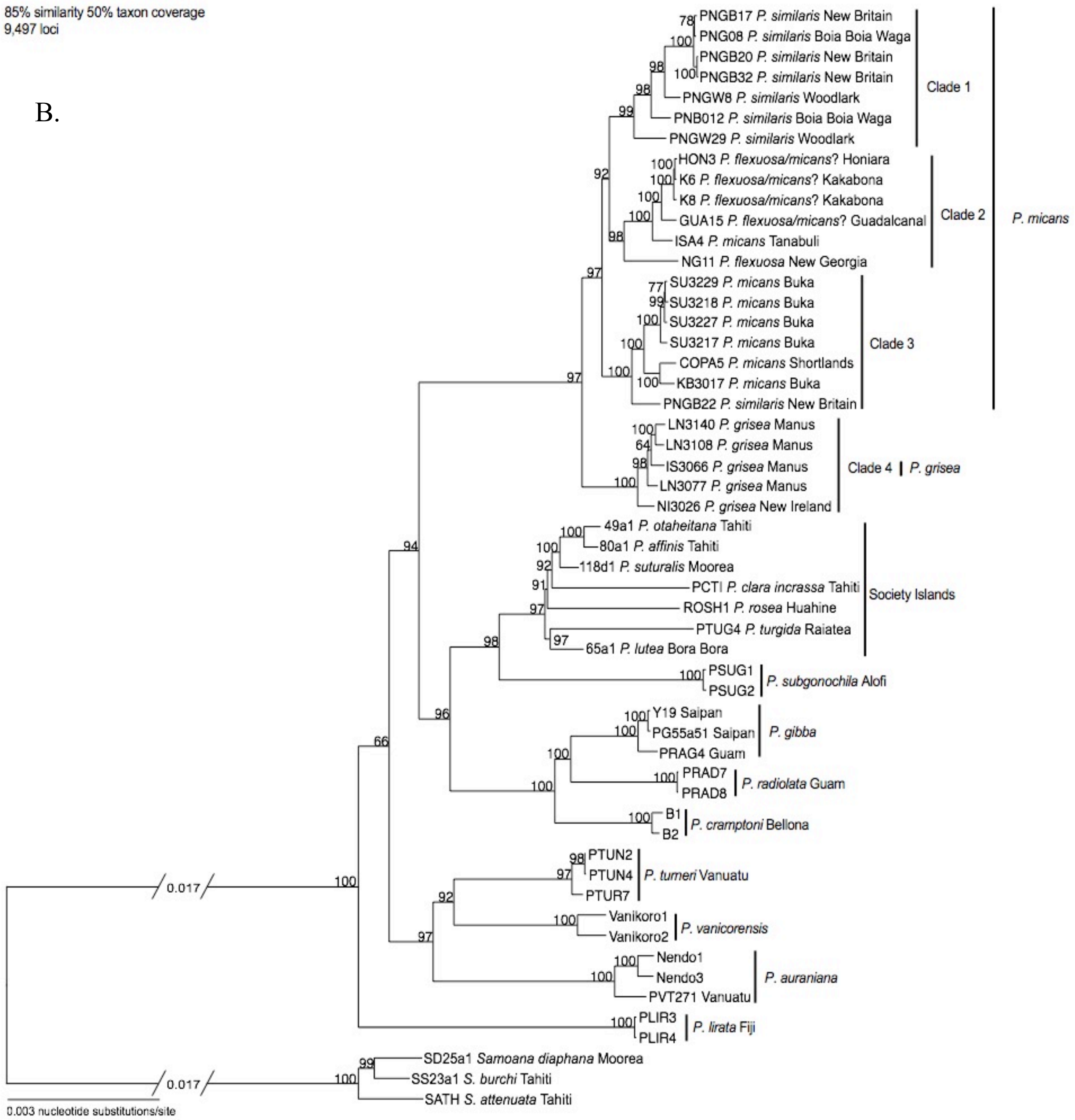
Appendix VIII. Field census results of Maramu Valley *Partula taeniata elongata* population by Trevor Coote from 2009 to 2017.



Appendix IX. Video clip of foraging *Eugladina rosea*.

Appendix X. Maximum likelihood phylogenomic trees depicting relationships among partulid species for the three similarity thresholds 85, 90, 95% clustering across 75, 50 and 25% of individuals (A) 85%, 75%, 3,689 loci (B) 85%, 50%, 9,497 (C) 85%, 25%, 23,977 (D) 90%, 50%, 10,735 (E) 90%, 25%, 27,026 (F) 95%, 75%, 4,971 (G) 95%, 50%, 15,396 (H) 95%, 25%, 39,946. Trees were rooted with three species of Society Islands *Samoana*, the sister genus of *Partula*. Values on tree nodes indicate Maximum likelihood bootstrap supports.




85% similarity 50% taxon coverage
9,497 loci
B.
PNGB17 P. similaris New Britain
PNG08 P. similaris Boia Boia Waga
PNGB20 P. similaris New Britain
PNGB32 P. similaris New Britain
PNGW8 P. similaris Woodlark
PNB012 P. similaris Boia Boia Waga
PNGW29 P. similaris Woodlark
Clade 1
HON3 P. flexuosa/micans? Honiara
K6 P. flexuosa/micans? Kakabona
K8 P. flexuosa/micans? Kakabona
GUA15 P. flexuosa/micans? Guadalcanal
ISA4 P. micans Tanabuli
NG11 P. flexuosa New Georgia
Clade 2
P. micans
SU3229 P. micans Buka
SU3218 P. micans Buka
SU3227 P. micans Buka
SU3217 P. micans Buka
COPA5 P. micans Shortlands
KB3017 P. micans Buka
PNGB22 P. similaris New Britain
Clade 3
LN3140 P. grisea Manus
LN3108 P. grisea Manus
IS3066 P. grisea Manus
LN3077 P. grisea Manus
NI3026 P. grisea New Ireland
Clade 4 | P. grisea
49a1 P. otaheitana Tahiti
80a1 P. affinis Tahiti
118d1 P. suturalis Moorea
PCTI P. clara incrassa Tahiti
ROSH1 P. rosea Huahine
PTUG4 P. turgida Raiatea
65a1 P. lutea Bora Bora
Society Islands
PSUG1
PSUG2
P. subgonochila Alofi
Y19 Saipan
PG55a51 Saipan
PRAG4 Guam
P. gibba
PRAD7
PRAD8
P. radiolata Guam
B1
B2
P. cramptoni Bellona
PTUN2
PTUN4
PTUR7
P. turneri Vanuatu
Vanikoro1
Vanikoro2
P. vanicorensis
Nendo1
Nendo3
PVT271 Vanuatu
P. auraniana
PLIR3
PLIR4
P. lirata Fiji
SD25a1 Samoana diaphana Moorea
SS23a1 S. burchi Tahiti
SATH S. attenuata Tahiti
78
100
98
100
98
99
92
100
100
100
100
98
97
77
99
100
100
100
100
97
100
64
98
100
100
100
92
91
97
97
98
100
94
100
100
100
100
96
100
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66
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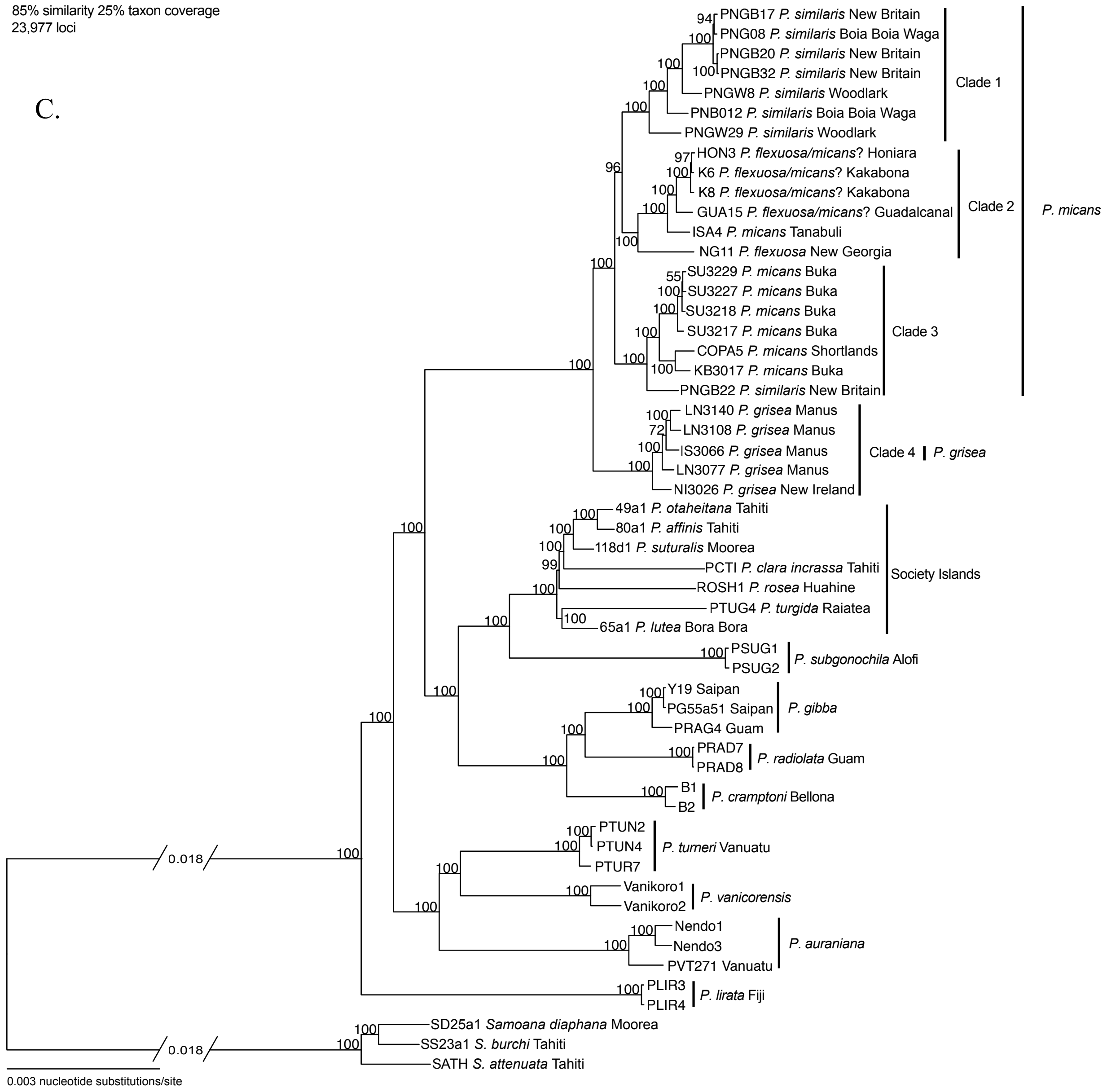
97
92
100
97
100
100
100
100
99
100
0.017
0.017
0.003 nucleotide substitutions/site


85% similarity 25% taxon coverage
23,977 loci
C.
PNGB17 P. similaris New Britain
PNG08 P. similaris Boia Boia Waga
PNGB20 P. similaris New Britain
PNGB32 P. similaris New Britain
PNGW8 P. similaris Woodlark
PNB012 P. similaris Boia Boia Waga
PNGW29 P. similaris Woodlark
Clade 1
HON3 P. flexuosa/micans? Honiara
K6 P. flexuosa/micans? Kakabona
K8 P. flexuosa/micans? Kakabona
GUA15 P. flexuosa/micans? Guadalcanal
ISA4 P. micans Tanabuli
NG11 P. flexuosa New Georgia
Clade 2
P. micans
SU3229 P. micans Buka
SU3227 P. micans Buka
SU3218 P. micans Buka
SU3217 P. micans Buka
COPA5 P. micans Shortlands
KB3017 P. micans Buka
PNGB22 P. similaris New Britain
Clade 3
LN3140 P. grisea Manus
LN3108 P. grisea Manus
IS3066 P. grisea Manus
LN3077 P. grisea Manus
NI3026 P. grisea New Ireland
Clade 4
P. grisea
49a1 P. otaheitana Tahiti
80a1 P. affinis Tahiti
118d1 P. suturalis Moorea
PCTI P. clara incrassa Tahiti
ROSH1 P. rosea Huahine
PTUG4 P. turgida Raiatea
65a1 P. lutea Bora Bora
Society Islands
PSUG1
PSUG2
P. subgonochila Alofi
Y19 Saipan
PG55a51 Saipan
PRAG4 Guam
P. gibba
PRAD7
PRAD8
P. radiolata Guam
B1
B2
P. cramptoni Bellona
PTUN2
PTUN4
PTUR7
P. turneri Vanuatu
Vanikoro1
Vanikoro2
P. vanicorensis
Nendo1
Nendo3
PVT271 Vanuatu
P. auraniana
PLIR3
PLIR4
P. lirata Fiji
SD25a1 Samoana diaphana Moorea
SS23a1 S. burchi Tahiti
SATH S. attenuata Tahiti
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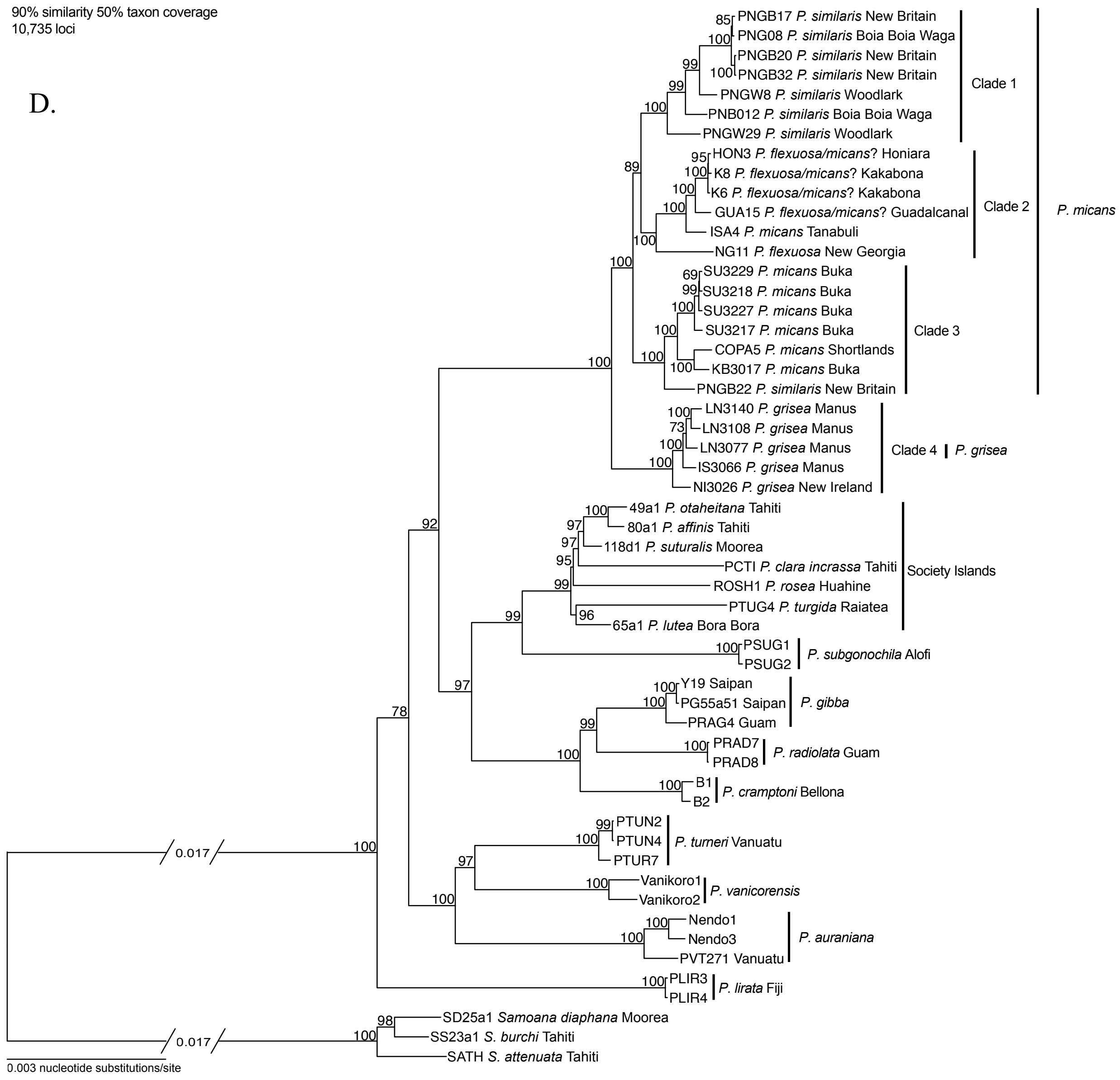
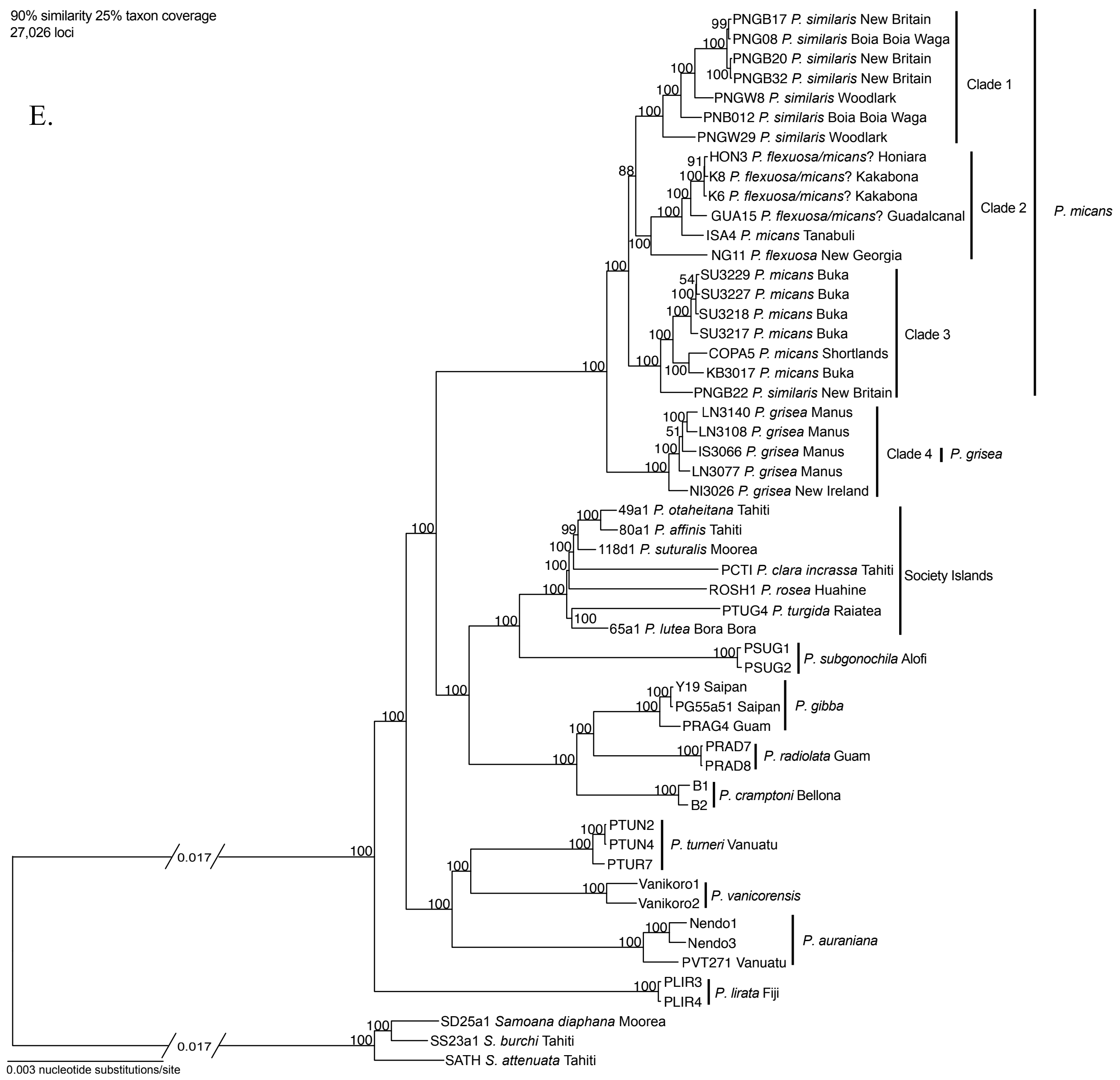
0.018
0.003 nucleotide substitutions/site


90% similarity 50% taxon coverage
10,735 loci
D.
85 PNGB17 *P. similaris* New Britain
100 PNG08 *P. similaris* Boia Boia Waga
99 PNGB20 *P. similaris* New Britain
100 PNGB32 *P. similaris* New Britain
99 PNGW8 *P. similaris* Woodlark
100 PNB012 *P. similaris* Boia Boia Waga
PNGW29 *P. similaris* Woodlark
Clade 1
89
95 HON3 *P. flexuosa/micans*? Honiara
100 K8 *P. flexuosa/micans*? Kakabona
100 K6 *P. flexuosa/micans*? Kakabona
100 GUA15 *P. flexuosa/micans*? Guadalcanal
100 ISA4 *P. micans* Tanabuli
NG11 *P. flexuosa* New Georgia
Clade 2
P. micans
100
69 SU3229 *P. micans* Buka
99 SU3218 *P. micans* Buka
100 SU3227 *P. micans* Buka
100 SU3217 *P. micans* Buka
100 COPA5 *P. micans* Shortlands
100 KB3017 *P. micans* Buka
PNGB22 *P. similaris* New Britain
Clade 3
100
100 LN3140 *P. grisea* Manus
73 LN3108 *P. grisea* Manus
100 LN3077 *P. grisea* Manus
100 IS3066 *P. grisea* Manus
NI3026 *P. grisea* New Ireland
Clade 4
P. grisea
92
100 49a1 *P. otaheitana* Tahiti
97 80a1 *P. affinis* Tahiti
97 118d1 *P. suturalis* Moorea
95 PCTI *P. clara incrassa* Tahiti
99 ROSH1 *P. rosea* Huahine
PTUG4 *P. turgida* Raiatea
96 65a1 *P. lutea* Bora Bora
Society Islands
99
100 PSUG1
PSUG2
P. subgonochila Alofi
97
100 Y19 Saipan
100 PG55a51 Saipan
PRAG4 Guam
P. gibba
99
100 PRAD7
PRAD8
P. radiolata Guam
100
100 B1
B2
P. cramptoni Bellona
78
99 PTUN2
100 PTUN4
PTUR7
P. turneri Vanuatu
97
100 Vanikoro1
Vanikoro2
P. vanicorensis
100
100 Nendo1
100 Nendo3
PVT271 Vanuatu
P. auraniana
100
0.017
100 PLIR3
PLIR4
P. lirata Fiji
98 SD25a1 *Samoana diaphana* Moorea
100 SS23a1 *S. burchi* Tahiti
SATH *S. attenuata* Tahiti
0.017
0.003 nucleotide substitutions/site

E.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PNG08 P. similaris Boia Boia Waga
PNGB20 P. similaris New Britain
100
PNGB32 P. similaris New Britain
100
PNGW8 P. similaris Woodlark
100
PNB012 P. similaris Boia Boia Waga
100
PNGW29 P. similaris Woodlark
Clade 1
91
HON3 P. flexuosa/micans? Honiara
100
K8 P. flexuosa/micans? Kakabona
100
K6 P. flexuosa/micans? Kakabona
100
GUA15 P. flexuosa/micans? Guadalcanal
88
ISA4 P. micans Tanabuli
100
NG11 P. flexuosa New Georgia
Clade 2
P. micans
100
54
SU3229 P. micans Buka
100
SU3227 P. micans Buka
100
SU3218 P. micans Buka
SU3217 P. micans Buka
100
COPA5 P. micans Shortlands
100
100
KB3017 P. micans Buka
PNGB22 P. similaris New Britain
Clade 3
100
100
LN3140 P. grisea Manus
51
LN3108 P. grisea Manus
100
IS3066 P. grisea Manus
100
LN3077 P. grisea Manus
NI3026 P. grisea New Ireland
Clade 4
P. grisea
100
49a1 P. otaheitana Tahiti
99
80a1 P. affinis Tahiti
100
118d1 P. suturalis Moorea
100
PCTI P. clara incrassa Tahiti
100
ROSH1 P. rosea Huahine
PTUG4 P. turgida Raiatea
100
100
65a1 P. lutea Bora Bora
Society Islands
100
PSUG1
PSUG2
P. subgonochila Alofi
100
100
Y19 Saipan
100
PG55a51 Saipan
PRAG4 Guam
P. gibba
100
100
PRAD7
PRAD8
P. radiolata Guam
100
100
B1
B2
P. cramptoni Bellona
100
100
PTUN2
100
PTUN4
PTUR7
P. turneri Vanuatu
100
100
Vanikoro1
Vanikoro2
P. vanicorensis
100
100
Nendo1
100
Nendo3
PVT271 Vanuatu
P. auraniana
100
PLIR3
PLIR4
P. lirata Fiji
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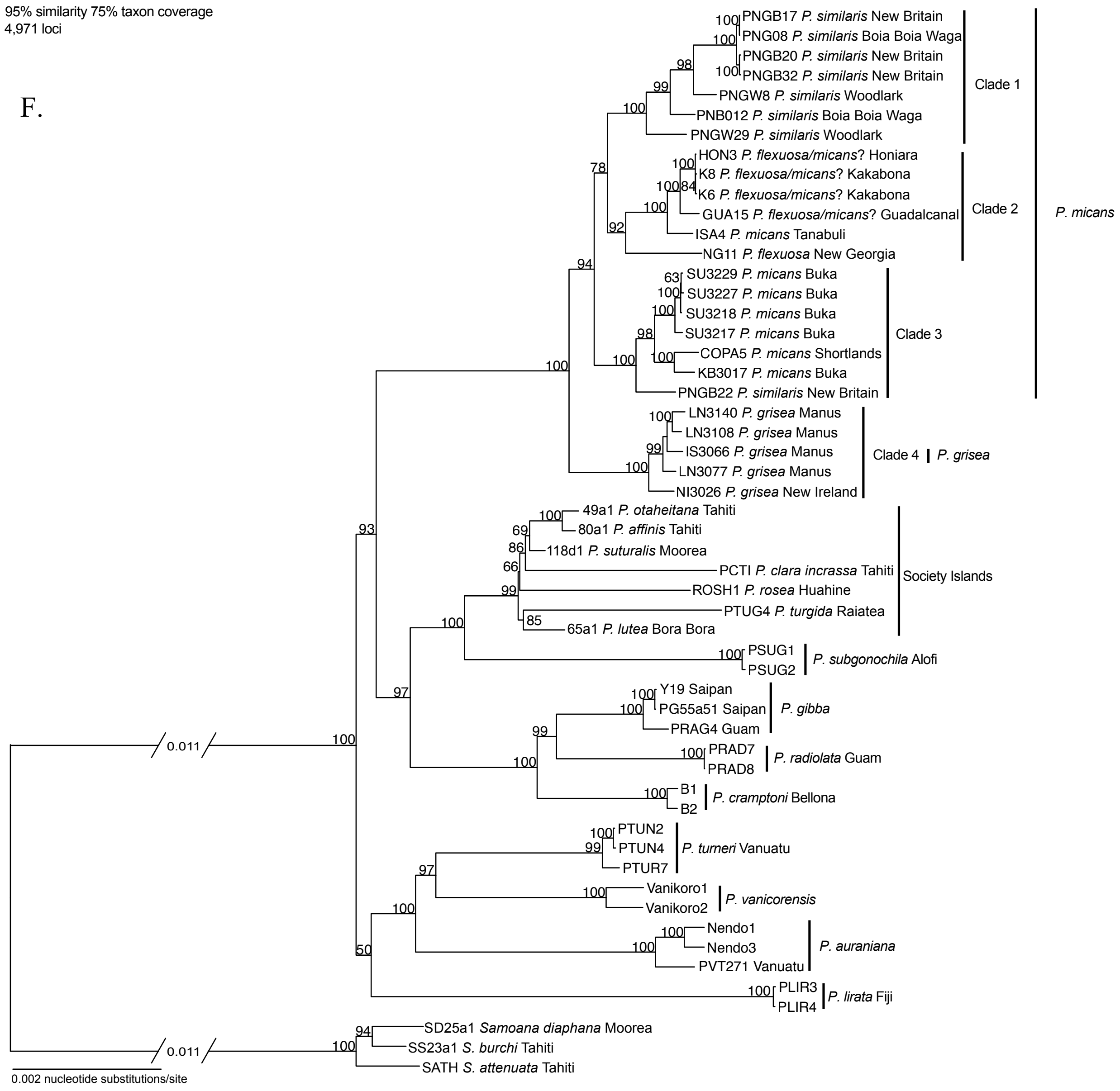
0.017
100
100
SD25a1 Samoana diaphana Moorea
SS23a1 S. burchi Tahiti
SATH S. attenuata Tahiti
0.003 nucleotide substitutions/site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4,971 loci
F.
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PNG08 P. similaris Boia Boia Waga
PNGB20 P. similaris New Britain
PNGB32 P. similaris New Britain
PNGW8 P. similaris Woodlark
PNB012 P. similaris Boia Boia Waga
PNGW29 P. similaris Woodlark
Clade 1
HON3 P. flexuosa/micans? Honiara
K8 P. flexuosa/micans? Kakabona
K6 P. flexuosa/micans? Kakabona
GUA15 P. flexuosa/micans? Guadalcanal
ISA4 P. micans Tanabuli
NG11 P. flexuosa New Georgia
Clade 2
P. micans
SU3229 P. micans Buka
SU3227 P. micans Buka
SU3218 P. micans Buka
SU3217 P. micans Buka
COPA5 P. micans Shortlands
KB3017 P. micans Buka
PNGB22 P. similaris New Britain
Clade 3
LN3140 P. grisea Manus
LN3108 P. grisea Manus
IS3066 P. grisea Manus
LN3077 P. grisea Manus
NI3026 P. grisea New Ireland
Clade 4
P. grisea
49a1 P. otaheitana Tahiti
80a1 P. affinis Tahiti
118d1 P. suturalis Moorea
PCTI P. clara incrassa Tahiti
ROSH1 P. rosea Huahine
PTUG4 P. turgida Raiatea
65a1 P. lutea Bora Bora
Society Islands
PSUG1
PSUG2
P. subgonochila Alofi
Y19 Saipan
PG55a51 Saipan
PRAG4 Guam
P. gibba
PRAD7
PRAD8
P. radiolata Guam
B1
B2
P. cramptoni Bellona
PTUN2
PTUN4
PTUR7
P. turneri Vanuatu
Vanikoro1
Vanikoro2
P. vanicorensis
Nendo1
Nendo3
PVT271 Vanuatu
P. auraniana
PLIR3
PLIR4
P. lirata Fiji
SD25a1 Samoana diaphana Moorea
SS23a1 S. burchi Tahiti
SATH S. attenuata Tahiti
0.011
0.011
0.002 nucleotide substitutions/site
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100
100
100
98
99
100
78
100
100
84
100
92
94
63
100
100
98
100
100
100
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99
100
93
100
69
86
66
99
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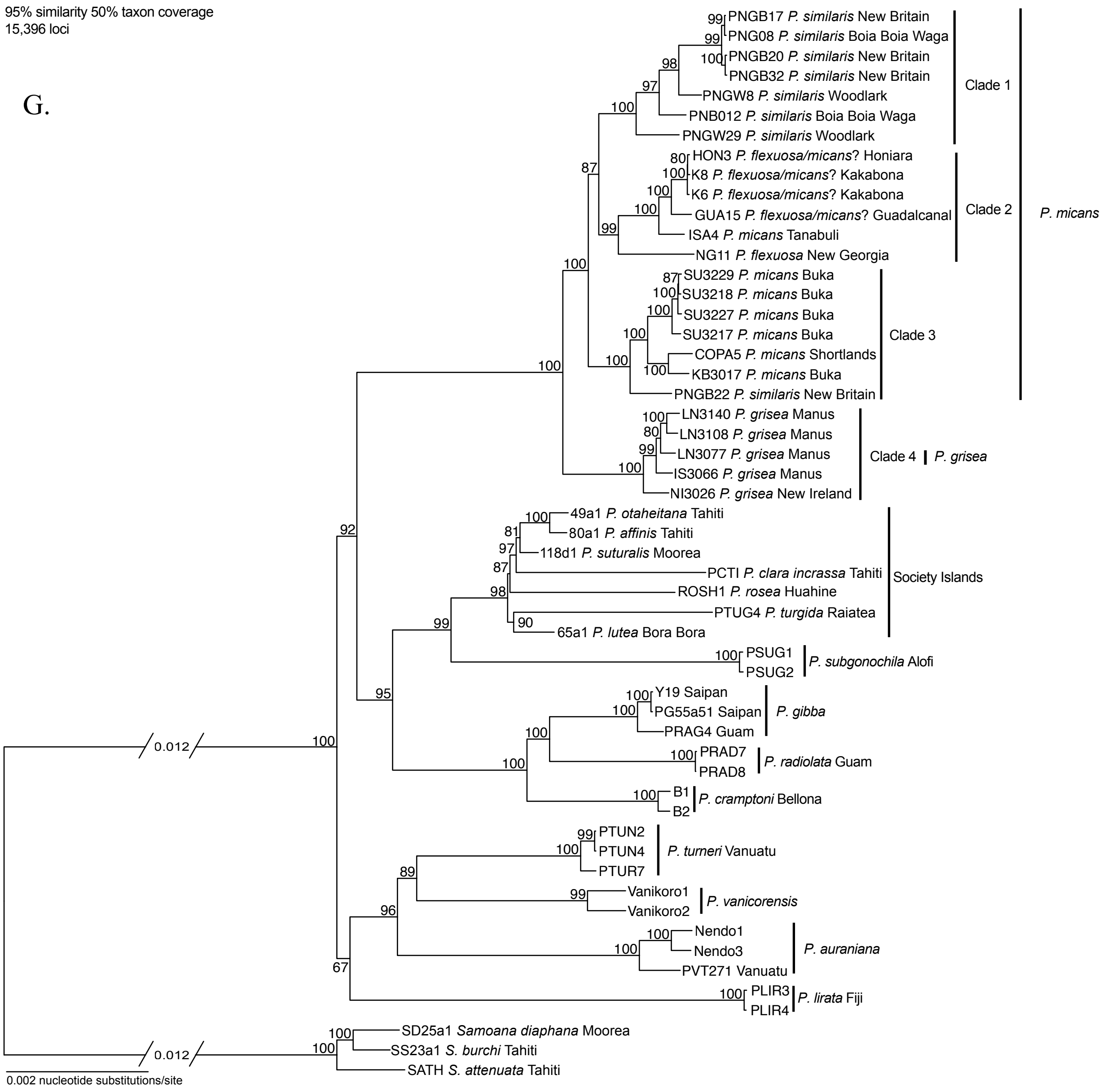
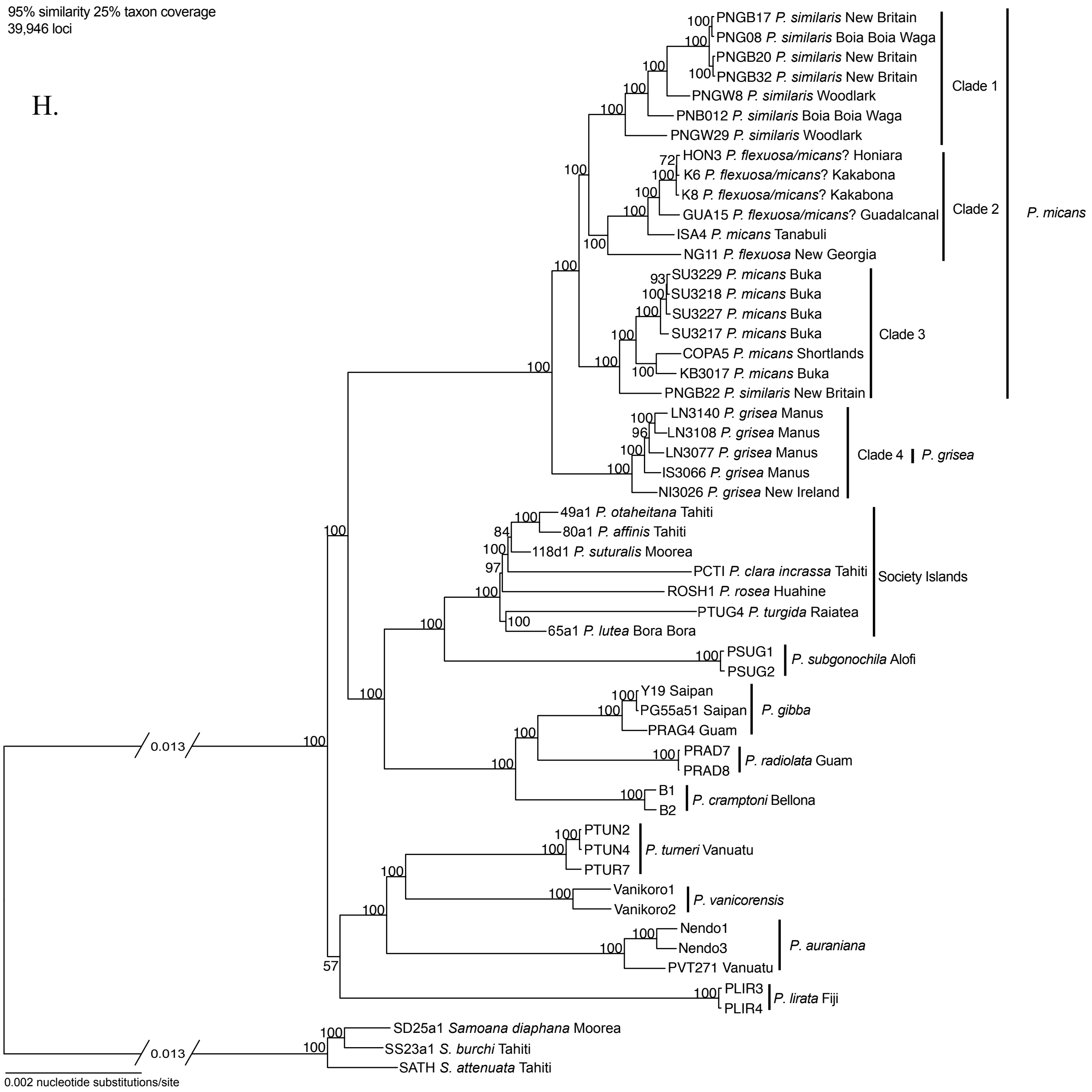
100
100
100
50
100
94
100


95% similarity 50% taxon coverage
15,396 loci
G.
PNGB17 *P. similaris* New Britain
PNG08 *P. similaris* Boia Boia Waga
PNGB20 *P. similaris* New Britain
PNGB32 *P. similaris* New Britain
PNGW8 *P. similaris* Woodlark
PNB012 *P. similaris* Boia Boia Waga
PNGW29 *P. similaris* Woodlark
Clade 1
HON3 *P. flexuosa/micans*? Honiara
K8 *P. flexuosa/micans*? Kakabona
K6 *P. flexuosa/micans*? Kakabona
GUA15 *P. flexuosa/micans*? Guadalcanal
ISA4 *P. micans* Tanabuli
NG11 *P. flexuosa* New Georgia
Clade 2
P. micans
SU3229 *P. micans* Buka
SU3218 *P. micans* Buka
SU3227 *P. micans* Buka
SU3217 *P. micans* Buka
COPA5 *P. micans* Shortlands
KB3017 *P. micans* Buka
PNGB22 *P. similaris* New Britain
Clade 3
LN3140 *P. grisea* Manus
LN3108 *P. grisea* Manus
LN3077 *P. grisea* Manus
IS3066 *P. grisea* Manus
NI3026 *P. grisea* New Ireland
Clade 4
P. grisea
49a1 *P. otaheitana* Tahiti
80a1 *P. affinis* Tahiti
118d1 *P. suturalis* Moorea
PCTI *P. clara incrassa* Tahiti
ROSH1 *P. rosea* Huahine
PTUG4 *P. turgida* Raiatea
65a1 *P. lutea* Bora Bora
Society Islands
PSUG1
PSUG2
P. subgonochila Alofi
Y19 Saipan
PG55a51 Saipan
PRAG4 Guam
P. gibba
PRAD7
PRAD8
P. radiolata Guam
B1
B2
P. cramptoni Bellona
PTUN2
PTUN4
PTUR7
P. turneri Vanuatu
Vanikoro1
Vanikoro2
P. vanicorensis
Nendo1
Nendo3
PVT271 Vanuatu
P. auraniana
PLIR3
PLIR4
P. lirata Fiji
SD25a1 *Samoana diaphana* Moorea
SS23a1 *S. burchi* Tahiti
SATH *S. attenuata* Tahiti
0.012
0.012
0.002 nucleotide substitutions/site
99
99
100
98
97
100
80
100
100
100
99
87
87
100
100
100
100
100
100
100
80
99
100
100
100
81
97
87
98
90
99
100
100
100
100
100
95
100
92
100
99
100
99
89
100
100
96
100
67
100
100


95% similarity 25% taxon coverage
39,946 loci
H.
100
PNGB17 *P. similaris* New Britain
100
PNG08 *P. similaris* Boia Boia Waga
100
PNGB20 *P. similaris* New Britain
100
PNGB32 *P. similaris* New Britain
100
PNGW8 *P. similaris* Woodlark
100
PNB012 *P. similaris* Boia Boia Waga
PNGW29 *P. similaris* Woodlark
Clade 1
72
HON3 *P. flexuosa/micans*? Honiara
100
100
K6 *P. flexuosa/micans*? Kakabona
100
K8 *P. flexuosa/micans*? Kakabona
100
GUA15 *P. flexuosa/micans*? Guadalcanal
ISA4 *P. micans* Tanabuli
100
NG11 *P. flexuosa* New Georgia
Clade 2
P. micans
100
93
SU3229 *P. micans* Buka
100
SU3218 *P. micans* Buka
100
SU3227 *P. micans* Buka
100
SU3217 *P. micans* Buka
COPA5 *P. micans* Shortlands
100
100
KB3017 *P. micans* Buka
100
PNGB22 *P. similaris* New Britain
Clade 3
100
LN3140 *P. grisea* Manus
96
LN3108 *P. grisea* Manus
100
LN3077 *P. grisea* Manus
100
IS3066 *P. grisea* Manus
NI3026 *P. grisea* New Ireland
Clade 4
P. grisea
100
49a1 *P. otaheitana* Tahiti
84
80a1 *P. affinis* Tahiti
100
118d1 *P. suturalis* Moorea
97
PCTI *P. clara incrassa* Tahiti
100
ROSH1 *P. rosea* Huahine
PTUG4 *P. turgida* Raiatea
100
100
65a1 *P. lutea* Bora Bora
Society Islands
100
PSUG1
PSUG2
P. subgonochila Alofi
100
100
Y19 Saipan
100
PG55a51 Saipan
PRAG4 Guam
P. gibba
100
100
100
PRAD7
PRAD8
P. radiolata Guam
0.013
100
100
B1
B2
P. cramptoni Bellona
100
PTUN2
100
PTUN4
PTUR7
P. turneri Vanuatu
100
100
Vanikoro1
Vanikoro2
P. vanicorensis
100
100
Nendo1
100
Nendo3
PVT271 Vanuatu
P. auraniana
57
100
PLIR3
PLIR4
P. lirata Fiji
100
SD25a1 *Samoana diaphana* Moorea
100
SS23a1 *S. burchi* Tahiti
0.013
SATH *S. attenuata* Tahiti
0.002 nucleotide substitutions/site