THE DISTRIBUTION AND DEMOGRAPHY OF RELICT PARTULIDAE ON MO'OREA, FRENCH POLYNESIA: Back from the Brink of Extinction?

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Abstract. This study re-examined partulid distribution and microhabitat structure on Mo'orea, French Polynesia. It was an assessment of the impact of introductions on endemic species and its purpose was to resurvey previously recorded populations, thoroughly document demographics of remaining populations, and characterize the environments in which they exist. The resultant findings contribute to over a century of extensive studies on wild populations of Mo'orean Partulidae and help to address questions regarding the survival of refugia populations, the resilience of rare and endemic species, and their abilities to recover from near-extinction devastation.

Key words: biodiversity; biological control; conservation; community structure; endemism; Euglandina; *extinction; Moorea, French Polynesia; Partulidae; predation;*

INTRODUCTION

For centuries, studies of island biota have contributed greatly to our understanding of general principles in evolutionary biology and ecology (Darwin 1859, Mayr 1942, Powell 1997, Clarke and Murray 1971). Island ecosystems are unique in that their geographical isolation, plethora of empty ecological niches, and lack of natural predators, in addition to the opportunity for successive reinvasions, create an environment that is conducive to speciation and the adaptive radiation of endemic terrestrial species (Murray *et al.* 1993). The relative climatic stability and short natural history of tropical oceanic island systems in particular, allow us to conduct studies on organisms that likely have not been subject to mass extinction events or large-scale climatic change, and have instead experienced extended periods of undisturbed evolution (Clarke and Murray 1969). Thus, although these systems are typically relatively simple when compared to temperate, continental systems, the flora and fauna within them are often more complex in terms of speciation and niche differentiation (Clarke and Murray 1969). This high instance of endemism on islands is responsible for making significant contributions to biodiversity, the conservation of which is vital for medicinal, cultural, and intrinsic reasons (Cowie 2001, Myers *et al.* 2000).

Due to the lack of large herbivores and other natural predators, flora and fauna endemic to islands are particularly defenseless against the introduction of alien species (Hickman 1999, Lee *et al.* 2009). This vulnerability, in conjunction with small population sizes and extreme isolation result in a much higher rate of extinction for island species as compared to continental ones (Atkinson 1989, Cowie 1992, Diamond 1984). Accidental introductions, the use of biological control agents, and other invasions have caused the extinction of countless endemic island species around the world, and continue to pose a threat to existing vulnerable species today. It is estimated that introduced mammals have been involved in over 60 percent of extinctions worldwide and that over 90 percent of the extinctions of reptiles, amphibians, land birds, and freshwater birds that have occurred since 1600 have been of island forms (Atkinson 1989). Furthermore, more than three fourths of the world's major island groups have indigenous species in danger of extinction due to human destruction of habitat and alien introductions (Atkinson 1989). This alarming statistic prompts a call for immediate conservation efforts, however the full impact that a specific alien introduction has – both direct and indirect – on an island's existing flora and fauna cannot be fully determined, and as the introduction rate to islands continues to increase, protecting endemic species from alien invasion is becoming ever more challenging and complex.

Island biotas contain an unusually high proportion of taxa with long-distance dispersal abilities since all clades present on tropical islands were dispersed there by way of air, ocean, or human introduction (Hickman 1999). In particular, land snail fauna of the Pacific islands have been the focus of many studies on overseas dispersal, speciation, and ecological diversification (Murray *et al.* 1993). About 60% of Pacific land snails are minute, while the same size class comprises just over a quarter of continental land snail fauna. According to Vagvolvyi (1975), this striking size disparity indicates the aerial dispersal of the Pacific land snail fauna, as small size and minimal weight prove advantageous for air-borne colonists and snails hitching rides concealed in the plumage of marine birds.

The nine species of Mo'orean Partulidae (of the genera *Partula* and *Samoana*) have been the focus of extensive studies on evolution, adaptive radiation, and phylogenetics over the last century (Garrett 1884, Crampton 1932, Lee *et al.* 2009), and are just one example of minute Pacific land snails unique to a single island archipelago (see Appendix A). Mo'orea is a high island of volcanic origin, roughly 1.2 million years old (Jackson 1976), and is located just 16 kilometers northwest of Tahiti in the Society Island chain of French Polynesia (at 17° 32'S and 149° 50'W) (Clarke and Murray 1971, Murray, E. 1993).

Figure 1. A map of the primary islands in the Society Island chain. Mo'orea is shown in black.

The seven partulids endemic to Mo'orea show great morphological diversity and studies indicate that they radiated from a single colonization that occurred farther up the island archipelago roughly 1.5 million years ago (Johnson *et al.* 1986a, Johnson *et al.* 1986b). In addition to their scientific importance, certain varieties of Partulidae hold cultural significance in the region's heritage (Murray *et al.* 1988, Pearce-Kelly *et al.* 1997). However, like many species endemic to Pacific islands, habitat destruction and human-mediated introductions threaten to push the Mo'orean partulids to extinction.

In 1967, the giant African snail *Achatina fulica* (Bowditch) (Encyclopedia of Life, 2010) was introduced to Tahiti as a food source intended for human consumption. *A. fulica* quickly spread to Mo'orea and its herbivorous diet caused it to become a severe agricultural pest (Clarke *et al.* 1984), prompting the introduction of the predatory snail *Euglandina rosea* (Ferussac) (Encyclopedia of Life, 2010) - also known as the rosy wolfsnail - to an orange plantation on Mo'orea in 1977 (Murray, E. 1993). The Service de l'Economie Rurale and the Division de Recherche Agronomique selected *E. rosea* as a biological control agent because of its demonstrated ability to track and consume *A. fulica* without harming agricultural crops (Chiu and Chou 1962), and because of its use in prior biological control efforts in several locations including Hawaii, Mauritius, and Guam (Griffiths *et al.* 1993). Chiu and Chou (1962) found *E. rosea* to be the "most promising predator of the giant African snail," and although there was a clear trend in prey selection towards host snails of smaller size, the study strongly supported the use of *E. rosea* as a means of controlling *A. fulica* without any examination of the potential effects that the introduction of *E. rosea* could have on other, smaller snail species. Later work by Griffiths *et al.* (1993) concluded that *Achatina* spp. were not a major prey item for *E. rosea* in the field due to a strong demonstrated preference for smaller prey, making *E. rosea* an ineffective biological control agent for *A. fulica*, when smaller snail species are present. Thus, *E. rosea* was a potentially devastating predator for native island snails such as the *Partula* spp. and *Samoana* spp. of Mo'orea.

Euglandina rosea is thought to have contributed to the extinction of native gastropod species in Mauritius and to the decline of *Partula* spp. in Guam (Griffiths *et al.* 1993). Severe habitat devastation due to human development also contributed to the decline of the native land snail species in these and other places. As a result, when *E. rosea* was introduced to Mo'orea, a strong causation had not yet been demonstrated between the introduction of *E. rosea* and the decline – sometimes to extinction – of land snail species native to Pacific islands (Griffiths *et al.* 1993). Additionally, there were no extensive follow-up studies to provide evidence of *E. rosea*'s efficacy in the field as a biological control agent for *Achatina fulica* before its introduction to the island of Mo'orea. This lack of thorough documentation was one factor that allowed for the catastrophic decline of the partulids of Mo'orea. Upon its introduction near the town of Paopao, *E. rosea* spread rapidly throughout the island at an estimated rate of about 1.2 kilometers per year (Clarke *et al.* 1984, Coote *et al.* 1999), preying on native and introduced land snails to support its growing populations. While a significant decrease in *A. fulica* abundance was recorded on Mo'orea following the introduction of *E. rosea*, a similar decline was recorded at the same time on the island of Huahine – where *E. rosea* had not been introduced – indicating that the decline of *A. fulica* on Mo'orea may have been part of a larger trend encompassing the entire Society Island chain, rather than a direct result of the introduction of *E. rosea* (Griffiths *et al.* 1993).

Prior to the introduction of *Euglandina rosea*, the *Partula* spp. and *Samoana* spp. of Mo'orea had a combined range that nearly covered the entire island (Clarke and Murray 1969). However, by 1987, just ten years after its introduction to the island, *E. rosea* had extended its range to include this habitat almost in its entirety (Clarke and Murray 1969). In 1982, Clarke, Murray, and Johnson were unable to find any *Partula* individuals in areas already inhabited by *E. rosea* and an extensive follow-up survey of 16 valleys on Mo'orea was conducted by James and Elizabeth Murray on behalf of the International Union for the Conservation of Nature, to find, document and sample remaining populations of *Partula* (Murray, E. 1993). Tragically, in spite of great experience and particular attention to detail, the researchers completed their survey without finding a single individual and concluded that the genus *Partula* was completely extinct on Mo'orea (Murray, E. 1993).

In response to the rapid decline of *Partula spp.* throughout the Pacific, an international conservation effort was launched in 1986 and populations of 33 different species of *Partula* were collected to be kept in captivity in 18 zoos and laboratories around the world (Coote *et al.* 1999, Coote *et al.* 2004, Cowie 1992, Pearce-Kelly *et al.* 1997). The ultimate goal of keeping otherwise extirpated populations in captivity is to ensure they maintain the ability to produce viable offspring, maintain sufficient genetic heterozygosity, and eventually to successfully release them back into their native habitats to persist in perpetuity. Captive populations of *Partula* are still being kept in hopes that over-predation and unstable oscillations of a natural predator-prey cycle will actually push *Euglandina rosea* to extinction on Mo'orea, allowing for safe reintroduction of the endemic *Partula* species (Murray *et al.* 1988). In 1994, populations of three *Partula* species endemic to Mo'orea were experimentally released into a predator-proof exclosure located within suitable natural habitat (Coote *et al.* 2004). Although *E. rosea* individuals were able to breach the exclosure on multiple occasions, decimating the *Partula* populations within it, the study still had findings of momentous importance. In spite of invasions of *E. rosea*, the *Partula* populations released in the experimental exclosure reached sexual maturity and produced viable offspring that retained a high level of genetic variability, indicating the success of the captive breeding programs that they stemmed from (Coote *et al.* 2004, Hickman 1999).

Since the supposed extinction of Mo'orean Partulidae in 1987, *Euglandina rosea* populations have experienced drastic decline and small relict populations of *Partula* spp. have been discovered (Coote *et al.* 1999). Demographic documentation on these remnant populations is lacking, and future research could make important contributions to our understanding of how endemic species might recommence adaptive radiation and speciation following a devastating disturbance. The purpose of this study was to start that documentation process and to explore possible reasons for selective survival. It re-examined Mo'orean partulid distribution, documented demographics of wild populations, and characterized the environments in which they were found.

METHODS

Site selection

The selection of study sites was heavily influenced by decades of prior work on the distribution of Partulidae on Mo'orea. These surveys, including the work of Murray, Clarke, and Johnson in the 1960's and 1980's, Burch in the 1970's, and Hickman, Coote, and Meyer in the last two decades, have documented the decline of Partulidae on Mo'orea resulting from habitat destruction and the spread of the predatory snail *Euglandina rosea*. The locations and characteristics of a few relict populations were also recorded. Maps from multiple studies documenting partulid distribution from the last half century were simplified and overlaid to aid in site selection (see Appendix B).

Twenty four study sites were selected in total for this study (fig. 2). Five previously identified relict populations were selected to be reexamined – four high elevation sites including the 1994-1998 site of experimental reintroduction, and one coastal site near 'Opunohu Bay. Nine more mid to high

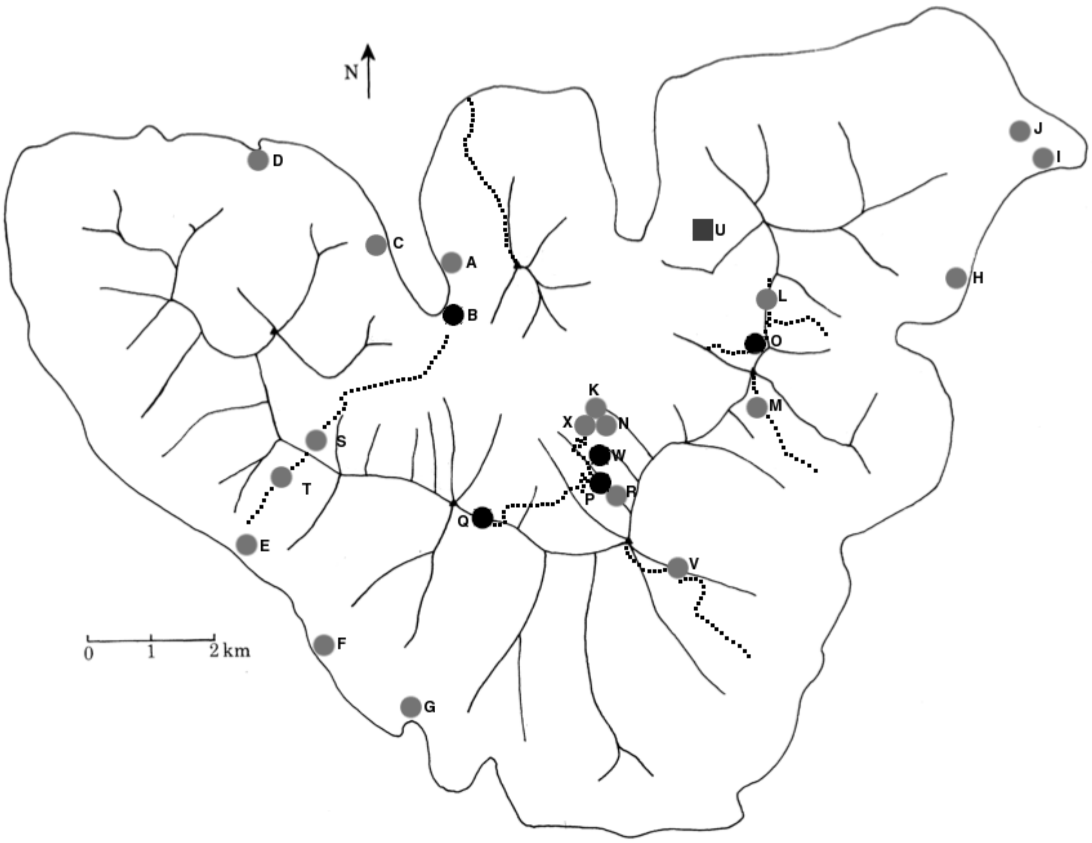

Figure 2. A map of the island of Mo'orea showing study site locations. Dotted lines represent search paths. The 1977 introduction site (U) of *E. rosea* is indicated with a square and previously documented relict populations are represented in black (B, P, Q, O, W).

elevation study sites spread across the island's mountain ridges were chosen for the existence of seemingly similar habitat, reasonable accessibility, and scattered dispersal within historically documented ranges of Partulidae. Additionally, an island-wide survey of coastal habitat was conducted and nine locations similar to the site in the back of 'Opunohu Bay were selected. The final study location was the primary site of introduction for *Euglandina rosea* in 1977.

Site surveys and habitat characterization

Using past studies and the hypotheses being tested as a foundation for distinguishing pertinent environmental and demographic variables, nine factors were chosen to document the characteristics of individual *Partula* and *Samoana* populations found throughout the course of this study, and eight factors were chosen to document the study site habitats.

Latitude and longitude coordinates were recorded using a handheld GPS unit to mark the location of each study site and of each individual snail that was included in this study, allowing for more accurate mapping and population characterization. Air temperature, canopy cover density, and approximate site size were also recorded and the elevation of each site was estimated using GPS coordinates and a contour map. Observations regarding site flora and fauna, ground cover, and weather were also taken, as well as a 50ml soil sample for further analysis. Some sites had natural boundaries and sparse vegetation, allowing for a more thorough search, while others were large and covered with dense vegetation. A timed effort approach was used to address such variation. Sites were initially searched for the equivalent of 45 minutes. When initial searches proved fruitless, approximate search areas were recorded in the field and GPS tracking information was later used for area confirmation upon returning to the lab.

Initial searches in which partulids were found were followed by a more close examination to locate other individuals and provide a more accurate indication of population composition, size, density, and area. The type of plant upon which each snail was found was identified and recorded in addition to the location of each snail on its host plant and its height off of the ground. Surface temperatures and snail behaviors were also recorded when possible. These more thorough surveys collected sufficient data to roughly estimate population demographics. Searching continued until physical, temporal, climatic, or other limitations were reached, or after an hour of fruitless searching. At each site, the presence or absence of live *Euglandina rosea*, *Achatina fulica*, and other terrestrial snails were recorded and empty shells were collected.

Identification of study organisms

Pictures vouchers were taken of each study snail (see Appendix C) and all individuals were assigned numbers for identification and documentation purposes. The shell length, shell width, and growth state (juvenile, adult, or subadult), of individual Partulidae was also recorded. Adult and subadult study organisms were identified based on picture vouchers, the historical range of each species of Mo'orean Partulidae and shell banding morphology guides (Crampton 1932, Johnson *et al.* 1993). Host plants including *Acrostichum aureum* L., *Angiopteris evecta* (J.R. Forster) Hoffmann, *Cyclophyllum barbatum* (G.Forst.) N.Hallé & J.Florence, *Freycinetia demissa* Benn., and *Syzygium malaccense* (L.) Merr. & L.M. Perry (Encyclopedia of Life, 2010) were identified using plant and picture vouchers, and were confirmed by Dr. Brent Mishler, Director of the University and Jepson Herbaria. Plant voucher specimens are deposited in the University and Jepson Herbaria at the University of California at Berkeley. *Euglandina rosea*, *Achatina fulica*, and partulid shell vouchers were also taken, their identities later confirmed by Malacologist Carole Hickman and Erin Meyer of the University of California at Berkeley. Snail shell voucher specimens and partulid picture vouchers are deposited in the University of California Museum of Paleontology.

Soil analysis

To test the hypothesis that relict partulid populations survived *E. rosea* predation due to soil conditions unfavorable for the carnivorous snail, soil samples from each site were analyzed for moisture content, salinity, and pH. Each of the 50ml soil samples were weighed after collection and dried for 5 days to eliminate moisture. The samples were then weighed again to measure original water content. Each soil sample was then ground with a mortar and pestle into a fine powder and a standard 5:1 dilution was made using distilled water. After being shaken for an hour, the resultant solution was tested for pH, temperature, and conductivity. Salinity was later calculated from those readings.

RESULTS

Identification of study organisms

A total of 187 partulid snails were documented in this study. Of these, 64 were juveniles and were not identified further than the family Partulidae. The remaining snails consisted of 43 subadults and 80 adults. 9 were identified as *Samoana* (4 *S. diaphana* and 5 *S. attenuata*) and 114 were identified as *Partula* (4 *P. mirabilis*, 15 *P. suturalis*, and 91 *P. taeniata*). 4 *Partula* individuals did not resemble any of the shell banding and morphology types illustrated and described in Crampton's 1932 manuscript and were left unidentified beyond the genus level.

Site surveys and habitat characterization

Live partulid snails were found at eight of the twenty four sites included in this study. They ranged in elevation from sea-level to about 520 meters. The heights at which partulids were found from the ground varied between species and within them (see Figure 4). The generalist species *P. taeniata* and *P. suturalis* had the largest and most variable height ranges of all the species documented in this study. The height ranges for *S. attenuata* and *S. diaphana* individuals documented in this study did not overlap very much at all, though the two species were often found living together on the same trees. Despite this trend, there was not statistically significant evidence for a difference in variance of height between partulid species (ANOVA, F=2.169, p=0.077).

The partulid snails documented in this study did show plant preference (Chi-square, D.F. = 4, $X^2 = 81.3$), but plant preference varied by partulid species and by study site (Chi-square, D.F. = 12, $X^2 = 129$). All but three of the *P. taeniata* in the 'Opunohu site were found on *A. aureum* and all but one of the *Samoana*

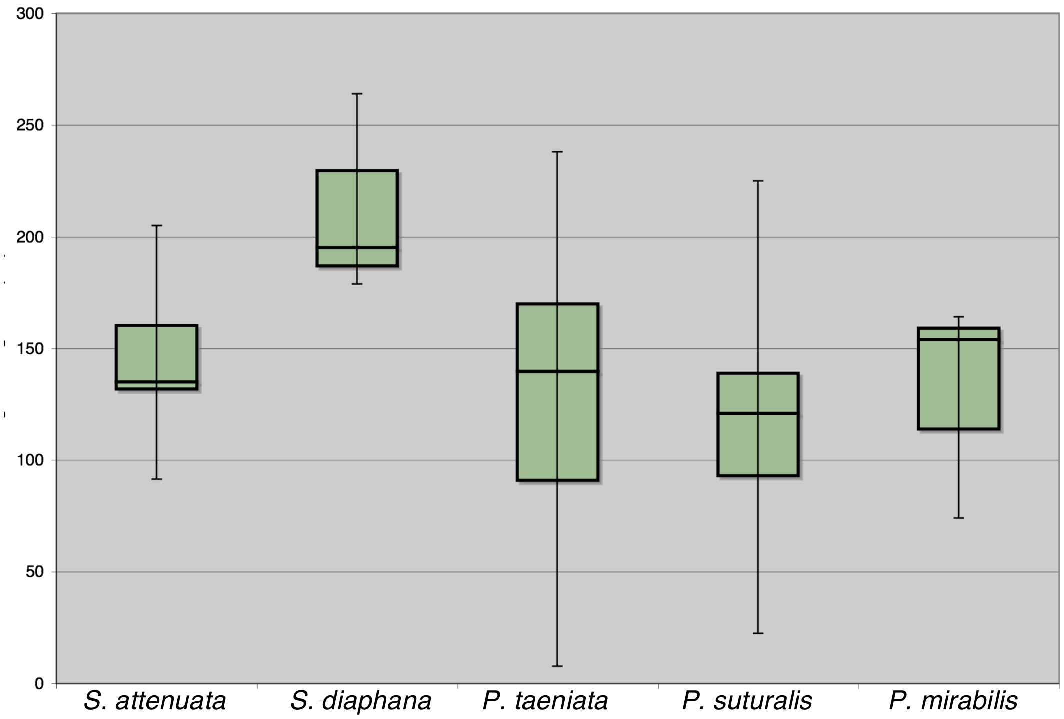

Figure 4. Height of individual partulids from the ground in cm. Box plots show 25th percentile, median, and 75th percentile by species and whiskers represent max and min heights.

individuals (including both species) were found on *C. barbatum*. Only a total of 4 individuals were found on *Freycinetia demissa* and only 3 were found on *Hibiscus tiliaceus*, two plants previously known as partulid favorites (see Figure 5).

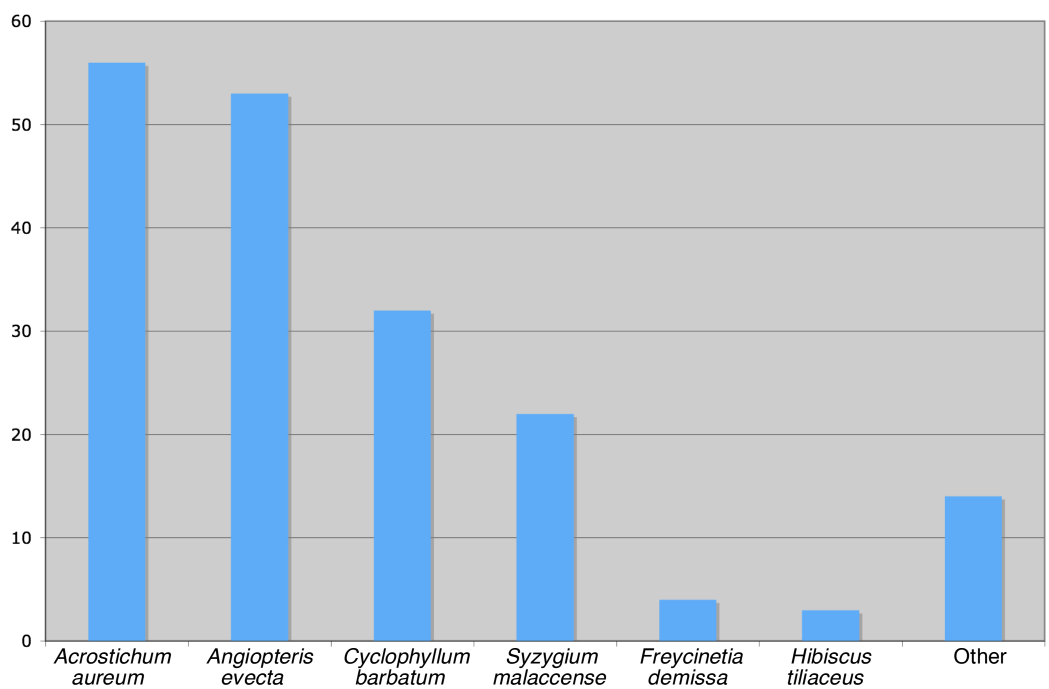

Figure 5. Number of partulid individuals found by species of host plant. The category 'other' includes rare vegetation, sticks, roots, soil, and dead organic matter.

Soil analysis

There was no statistically significant difference in soil pH (T-test, t-value = 0.411), moisture (T-test, t-value = 0.300), or salinity (T-test, t-value = 0.345) between sites that had live partulid snails and sites that did not. Coastal study sites other than the 'Opunohu site were not included in this analysis as they were unrepresentative of potential habitat within partulid range and were skewing statistical results.

The 'Opunohu population

The coastal 'Opunohu population that was documented in this study consisted of 59 *Partula* individuals within a search area of about 800 square meters. The population density was 0.07 snails/m^2, or roughly one snail per every 13 square meters. The vegetation at this study site consisted almost solely of *Hibiscus tiliaceus* and *Acrostichum aureum*, also known as the mangrove fern. All partulids found in this area were located on mangrove fern, with the exception of 3 – one of which was found on a dead hibiscus leaf that had fallen into a clump of mangrove fern, and two that were found on tree ferns. Of the 59 total snails found in this population, 19 were juveniles, 16 were *P. taeniata* subadults, and 24 were *P. taeniata* adults. 4 tissue and specimen samples were taken in 2010 by the biocode project and DNA analysis identified them all as *P. taeniata*. The individuals in this population show a variety of shell banding and color morphology, many of which fit Crampton's *P. taeniata* drawings. However, many of them show banding that neither follows the body whorl, nor the shell striations and instead runs mouth to apex, along all the whorls. This morphology has not been previously documented.

There was a notable presence of microgastropods at the 'Opunohu study site, but no sign of *Euglandina rosea* or *Achatina fulica* presence. There was a significant coconut crab population in the area, which resulted in the lack of leaf litter and ground cover.

The 'Opunohu study site was surrounded on two sides by waterways and by roads and drainage ditches on the other two sides. However, although the site is on public land, bulldozing by a nearby shrimp farm threatened to destroy some of this already limited partulid habitat. GPS points were taken to document the progress of such destruction (see Figure 3).

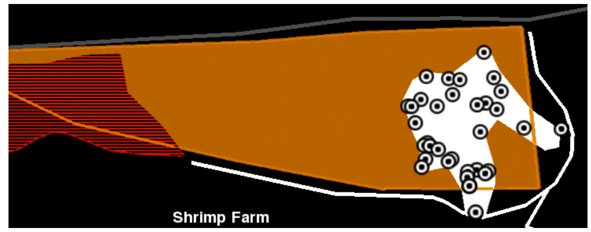

Figure 3. A map of the 'Opunohu study site. The search area is shown in white, with bullsyes representing partulid individuals. The solid filled area is public land and the striped area is bulldozed land. Waterways are shown as white lines. Grey lines represent roads and drainage ditches.

Euglandina rosea presence

Only two live *E. rosea* individuals were found throughout the course of this study. One was in an area with a high instance of live *Achatina fulica*, suggesting that the African snails may be its food source. 43 empty *E. rosea* shells were found and their locations documented using GPS coordinates. No *E. rosea* presence was detected at any of the sites containing live partulid snails.

DISCUSSION

Habitat characterization and plant preference

While physical and biotic factors varied greatly throughout the sites documented in this study, there seemed to be some very clear basic requirements for partulid life. Mo'orean Partulidae enjoy partial to full shade cover and relatively humid environments in areas that receive rain regularly. To maintain a significant population size, there must be a substantial number of adequate host plants that are close enough together for their leaves to be physically touching. A lack of live *E. rosea* predators within close proximity of partulid snails also substantially increases their chances of survival. Elevation was not restrictive on partulid distribution and live individuals were found at low, medium, and high elevation sites. Anthropogenic effects and habitat fragmentation are important factors to consider when evaluating the quality of habitat for partulid existence. Because these snails operate on such a small scale, the range of each individual is quite limited over its lifetime and habitat destruction can often mean the extirpation of entire populations.

Plant preference differed between species and study sites. *Samoana* individuals exhibited a strong preference for *Cyclophyllum barbatum*, however a more thorough study and larger sample size is necessary to make a definitive case for this behavior. There were not enough *P. mirabilis* or *P. suturalis* individuals documented in this study to detect any plant preference. *P. taeniata* showed a clear preference for *Acrostichum aureum* at the ʻOpunohu site despite the presence of several *Hibiscus tiliaceus* trees. At mid and high elevation sites, *P. taeniata* were much more abundant on *Angiopteris evecta* plants than *Freycinetia demissa, Syzygium malaccense, Cyclophyllum barbatum*, and other flora. In spite of these preferences, however, *P. taeniata* has shown the ability to thrive on several different types of vegetation and has been deemed a generalist species, along with *P. suturalis*. Of the seven species of *Partula* endemic to Mo'orea, these two species had the largest historical ranges and this study has shown they may have been considerably more successful at surviving *E. rosea* predation than their five specialist sister species, which showed a preference for *Freycinetia demissa* (Murray *et al.* 1993). According to a 2004 study by Davies, Margules, and Lawrence, rare and specialized species are much more vulnerable to extinction than are common generalist species. Continued surveys of Mo'orean Partulidae that pay attention to this generalist/specialist species delineation could add greatly to our understanding of the selective predation that these organisms underwent in the 1970's and 1980's, and help to explain why some populations survived and the vast majority did not.

Identification of study organisms

This study found populations of both of the *Samoana* species (*S. attenuata* and *S. diaphana*) originally documented by Crampton in the early 1900's currently surviving in the wild. Populations of three (*P. taeniata*, *P. suturalis*, and *P. mirabilis*) of the seven species of endemic *Partula* were also found in the wild. However, most of the sites included in this study fell outside the ranges of *P. mooreana*, *P. exigua*, *P. tohiveana*, and *P. aurantia*, as documented in the 1930's and 1960's. Therefore, a more thorough survey of the island is necessary before a definite conclusion can be drawn regarding the existence of these four remaining species of endemic Mo'orean *Partula* in the wild. Some of the individual snails documented in this study did not resemble any of Crampton's original drawings and descriptions, nor any of those of Clarke, Johnson, and Murray's. This may be the result of hybridization, mutation, or speciation, but only DNA analysis could provide further information on these mystery snails.

Soil analysis and physical boundaries

This study investigated some of the factors that may have been responsible for the selective survival of partulid populations on Mo'orea. Soil pH, moisture, and salinity have not been examined in past work on Mo'orean Partulidae, but the results of this study refute the hypothesis that these variables were major factors in shielding surviving partulid populations from *Euglandina rosea* predation. This study examined multiple coastal sites that seemed to provide comparable habitat to the ʻOpunohu site, which is home to the last known coastal population of Mo'orean partulids. However, although most of these sites had similar soil conditions to the ʻOpunohu site, none of them harbored partulid populations. Of the eight partulid populations that were documented throughout the course of this study, only two of them – Site B (the ʻOpunohu site) and Site X - were surrounded by clear physical barriers. The ʻOpunohu site is completely surrounded by waterways, drainage ditches, and roads, physical barriers may have played an integral role in protecting this partulid population from predation. The presence of coconut crabs throughout the site may also be a contributing factor for survival, as they prevent the accumulation of leaf litter and may pose a further threat to *Euglandina rosea* eggs and live *E. rosea*, which are commonly found in leaf litter and on exposed soil. The entirety of study Site X was located on the top of a very large boulder that lacked vegetation connecting to the forest floor. This may have served as another type of physical barrier that protected the partulid population living atop the boulder from *E. rosea* predators below.

The ʻOpunohu population

The ʻOpunohu population is different from the other seven documented in this study because of its coastal location. Most of the coastline of Mo'orea is now heavily influenced by human development and the ʻOpunohu site is no different. Although located on public land, a nearby shrimp farm has taken to bulldozing the area for purposes unknown, threatening the persistence of the nearby partulid population. Upon initial inspection of the site, cleared areas were photographed and GPS coordinates were recorded to document the bulldozed area. The site map and pictures were sent to partulid experts and government representatives in hopes that a terrestrial reserve might be established to protect this partulid population. However, after the completion of this study, we returned to this site and noticed much more extensive destruction had taken place. The *Hibiscus tiliaceus* L. (Encyclopedia of Life, 2010) trees that provided canopy cover for the area had mostly been cut down and much of the resultant debris landed on the mangrove fern plants, upon which the partulid population almost exclusively resided. Some mangrove ferns had been uprooted and many ferns were removed from the area. The *Hibiscus tiliaceus* canopy provided crucial protection from the sun, and in its absence, mangrove ferns that were still standing despite the debris were browning and becoming very dry. We were unable to find any *Partula* individuals and a more thorough search is necessary to document the decline, and perhaps recovery of this population. Future studies on the progress of this destruction are imperative if there is any hope for the establishment of a terrestrial reserve in this location and the option of relocation of remaining Partula individuals should be considered in the event of continued destruction. This could pose opportunities for interesting case studies on the resilience of Mo'orean Partulidae and their abilities to survive habitat destruction and relocation. Such information would provide important insight for future conservation efforts.

Euglandina rosea presence

Throughout the course of this study, only two live *E. rosea* individuals were found, both in the absence of partulid populations. Many intact *E. rosea* shells were found, however, indicating relatively recent death. *E. rosea* numbers have certainly dropped significantly since the late 1980's, but some populations still persist in places with sufficient food sources mostly comprised of *Achatina fulica*. There is ongoing research on E. rosea's ability to survive preying primarily on the island's microgastropods, but nothing has been published yet on this topic. The ability of the Mo'orean Partulidae to recover from near-extinction will depend heavily upon the continued presence of *E. rosea* on the island. In the absence of *E. rosea*, partulid snails could potentially make a significant comeback, however the two groups could alternatively follow a classic predator/prey cycle if *E. rosea* is able to persist on Mo'orea. There is no documentation of E. rosea's current distribution on Mo'orea, but such research will be absolutely necessary in determining the plausibility of eradication efforts and of the release of captive partulid populations back into the wild.

Future research

In addition to the studies already suggested, more thorough documentation of the distribution and persistence of relict populations on Mo'orea could give us great insight into the ability of endemic island species to survive the introduction of invasive species and recover from near-extinction. Because host plant preference has been exhibited to varying degrees by some species of partulids, a study on the changing vegetation in prime partulid habitat on Mo'orea would also be interesting when compared to past, current, and future ranges of these snails. Research on *E. rosea*'s ability to detect prey on different types of host vegetation and at varying heights from the ground would also provide a missing component to our efforts to determine which factors allowed for the selective survival of relict populations of Mo'orean Partulidae. This research could provide important scientific support for efforts to safeguard the limited remaining habitat on Mo'orea from human destruction and to prevent future introduction of alien species.

Some work has already been done on the deterioration of terrestrial gastropod shells in varying conditions over time (Pearce, 2008). However, similar studies specific to partulid, *Euglandina*, and *Achatina* shells would allow us to make more accurate estimates as to how much time has passed since snail death occurred. Subsequently, timelines could potentially be constructed showing the presence and absence of these three families of snails, and approximate times of extirpation for past populations. Recent historical data on relict populations could also be extrapolated from such a study.

DNA analysis could also help to determine how much genetic diversity has been lost or maintained since the near extinction of the endemic Partula species, and could indicate increased instances of hybridization and bottleneck effects due to extensive population reduction and decreased ranges of these species, which were long thought to be in the process of speciation. Countless endemic, island species have already been driven to extirpation, several more are currently facing extinction, and still more are in rapid decline. Such studies will potentially provide crucial information for future efforts to aid in the recovery and conservation of these and other rare and endemic species. The retention of the world's biodiversity is vital for medicinal, cultural, recreational, and intrinsic reasons, and the continuing study of invasive species, evolutionary biology, predator-prey cycles, bio-control, and conservation are important for its preservation.

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APPENDIX A

1916-1932 H.E. Crampton identifies and classifies 11 species of *Partula* on Mo'orea (*P. solitaria, P. exigua, P. tohiveana, P. olympia, P. aurantia, P. mirabilis, P. mooreana, P. suturalis, P. dendroica, P. taeniata*).

1953 Crampton & Cooke identify *Partula diaphana* on Mo'orea.

1962 J. Murray & B. Clarke take the first of a series of island-wide *Partula* collections on Mo'orea.

1967 Introduction of *Achatina fulica* to Tahiti. Murray & Clarke take a second island-wide distributional survey.

1968 Yoshio Kondo taxonomically reclassifies *Partula diaphana* and *Partula solitaria* to the genus *Samoana* as *Samoana diaphana* and *Samoana solitaria*. Murray & Clarke take a third island-wide survey and document the populations found from 1962-1968 in highly detailed maps.

1970 Museum samples taken by J. Burch.

1973 Kondo renames *Samoana solitaria* as *Samoana attenuata.*

1977 Introduction of the predatory snail *Euglandina rosea* to an orange plantation near Paopao, Mo'orea by the Service de l'Economie Rurale and the Division de Recherche Agronomique.

1980 James Murray & Bryan Clarke designate *P. tohiveana* and *P. olympia* as a conspecific pair, as well as *P. suturalis* and *P. dendroica*.

1980-1982 J. Murray & Clarke re-examine *Partula* distribution on Mo'orea, documenting their decline. No individuals are found in territories to which *Euglandina* has already spread.

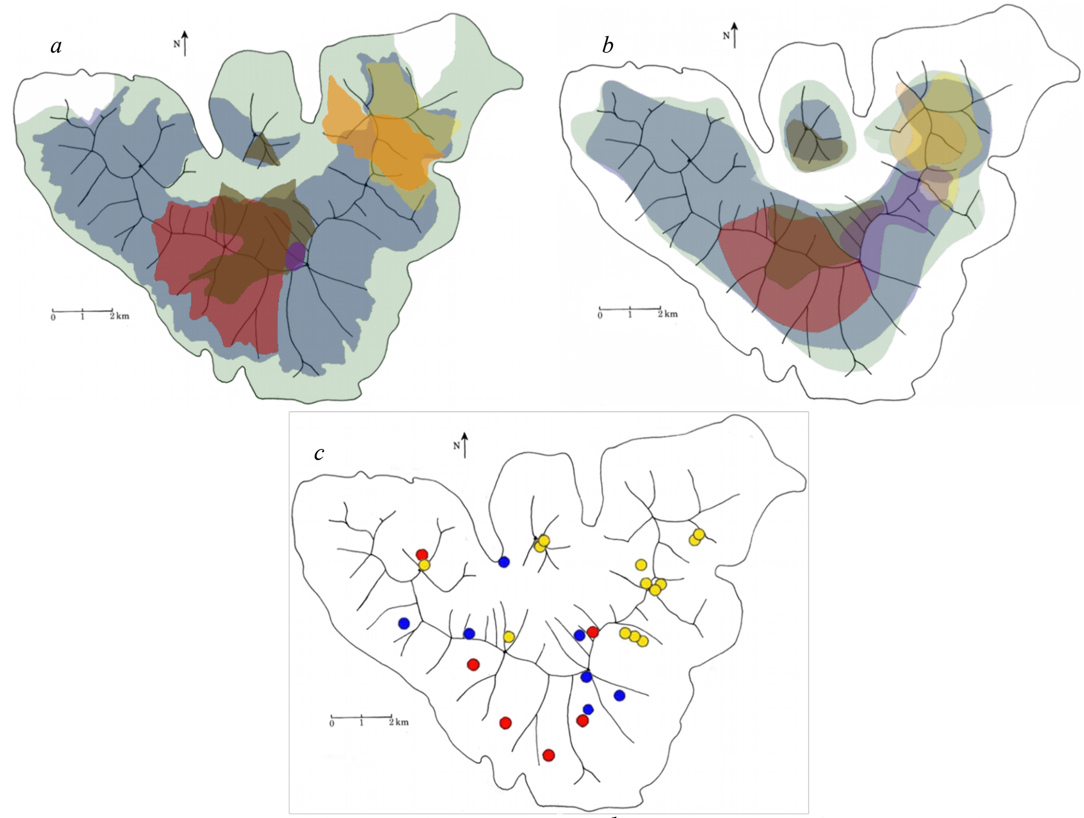
1987 James Murray & Elisabeth Murray extensively survey 16 valleys on Mo'orea without finding a single individual. *Partula* endemic to Mo'orea are thought to be extinct.

2009 7 of 9 (2 of the genus *Samoana* and 6 of the genus *Partula)* original partulid species are found on Mo'orea by T. Lee, J. Burch, T. Coote, P. Pearce-Kelly, C. Hickman, J-Y Meyer, and D. Ó Foighil.

2010 Olivier Gargominy takes 4 *Partula taeniata* tissue samples and 4 specimen samples from the coastal Opunohu Bay population for the Mo'orea Biocode Databases.

Appendix A. Timeline of the Mo'orean Partulidae: Taxonomic changes, invasive introductions, and distributional surveys since Crampton's first documentation

APPENDIX B



Appendix B. Mo'orean partulid distribution prior to the introduction of *E. rosea* and locations of relict populations that have since been discovered and documented.

A. Ranges of Mo'orean *Partula spp.*, Crampton, 1932; *P. aurantia* is shown in orange, *P. exigua* is shown in yellow, *P. mirabilis* is shown in brown, *P. mooreana* is shown in red, *P. suturalis* is shown in blue, *P. taeniata* is shown in green, and *P. tohiveana* is shown in purple.

B. Ranges of Mo'orean *Partula spp.*, Murray, Johnson, and Clarke, 1962-1968; *P. aurantia* is shown in orange, *P. exigua* is shown in yellow, *P. mirabilis* is shown in brown, *P. mooreana* is shown in red, *P. suturalis* is shown in blue, *P. taeniata* is shown in green, and *P. tohiveana* is shown in purple.

C. Museum samples taken by J.B. Burch in 1970 are shown in yellow; Captive Zoo Samples from 1980-1985 are shown in red; Relict Wild populations sampled by Lee, *et al.* from 2002-2006 are

APPENDIX C

Appendix C. Five Speceis of Mo'orean Partulidae.

A. *Samoana attenuata*
B. *Samoana diaphana*
C. *Partula suturalis*
D. *Partula mirabilis*
E. *Partula taeniata*
F. *Partula taeniata*
G. Unknown
H. Unknown
I. Unknown

* *Partula mirabilis* picture (D) used with permission, courtesy of John Slapcinsky of the Florida Museum of Natural History