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# Biodiversity and Extinction of Hawaiian Land Snails: How Many Are Left Now and What Must We Do To Conserve Them—A Reply to Solem (1990)

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**Synopsis** Pacific islands, with their incredible biodiversity, are our finest natural laboratories for evolutionary, ecological, and cultural studies. Nowhere, in relation to land area, does land snail diversity reach that of the Pacific islands, with more than 6000 species, most of which are single island endemics. Unfortunately, land snails are the most imperiled group with the most recorded extinctions since the 1500s, and Pacific island snails make up the majority of those extinctions. In 1990, Dr. Alan Solem, a well renowned malacologist, with expertise in Pacific island land snails, posthumously published a plea to save the remaining Hawaiian land snails before they vanish forever. Now, more than 25 years later, we have finally begun to make inroads into answering the questions "How many Hawaiian land snails remain?" and "What will we need to save them?". Here we provide a belated reply to Solem (1990) and address these questions about Hawaiian land snails. We conclude by building on the actions suggested by Solem and that we feel are still needed to realize his hope of conserving Hawaii's remaining land snails specifically, but also our hope of conserving invertebrates more broadly.

## Introduction

. . . their loss will be the equivalent of the dodo and elephant bird extinctions . . . (Solem 1990).

More than 25 years ago Solem (1990) wrote those words as part of an impassioned plea for someone, all of us, to do something before the remaining Hawaiian land snails were lost forever. While he was specifically referring to land snails of Hawaii, the ideas and statistics published in that paper could have been repeated for each of the nearly 25,000 islands across the Pacific, and probably for most oceanic islands across the globe (Chiba and Cowie 2016) and oceanic island biotas, broadly (Keppel et al. 2014; Meyer et al. 2015). Only 5% of the earth's surface is insular, yet oceanic island biotas have historically been instrumental in helping develop the theories of biogeography, ecology, and evolution (Engler 1879; Wallace 1902; Gulick 1905; Skottsberg 1939; MacArthur and Wilson 1963; Simberloff 1974; Cain 1984; Graham et al. 2017; Whittaker et al. 2017). Even now, the study of Pacific island ecosystems still offers novel insights into processes that influence speciation (Gillespie and Roderick 2002; Baldwin and Wagner 2010; Cowie 1995; Brook 2010; Rundell 2011; Baker and Couvreur 2013; Claridge et al. 2017; Graham et al. 2017) and extinction events (Solem 1990; Steadman 1995, 2006; Lee et al. 2014; Régnier et al. 2015a, 2015b; Chiba and Cowie 2016; Graham et al. 2017). Although scientist have identified and described more than 14,000 plant and animal species (CEPF 2007, 2012) from across the Pacific islands, many remain to be discovered, even on the best studied archipelagos (Bouchet and Abdou 2003; Gargominy 2008; Evenhuis 2013; Richling and Bouchet 2013; Sartori et al. 2013; Ramage et al. 2017; Christensen et al. 2018) or rediscovered (Wood 2012; Yeung et al. 2015, 2018) with each biodiversity assessment.

Despite the vast numbers of plant and animal species endemic to Pacific Islands (Solem 1984; Allison and Eldredge 1999; Kier et al. 2009) there are no comprehensive reports of diversity, levels of endemism, or conservation assessments for most invertebrates (CEPF 2007, 2012; Zamin et al. 2010; Cowie et al. 2017; IUCN 2017), which make up the bulk of animal diversity (Mora et al. 2011). Invertebrates are notoriously poorly represented in conservation management and policies, mainly because of their perceived abundances, high diversity, lack of systematic information (New 1999; Ward and Larivière 2004; Cardoso et al. 2011), and dearth of established monitoring protocols needed to track and assess biodiversity (Uys et al. 2010). Such underrepresentation of invertebrates is reflected in biodiversity research broadly, with the biodiversity research community failing to study the neglected majority in proportion to their diversity or imperiled status (Dunn 2005; Donaldson et al. 2016; Titley et al. 2017). Yet, without this fundamental understanding of biodiversity, it is impossible to develop effective conservation priorities, especially in biodiversity hotspots like Pacific Islands, and we remain in danger of losing the organisms that make up the bulk of the biodiversity, and that are most vital to the ecosystem services and functions on which we rely (Kellert 1993; Cardoso et al. 2011; Mace et al. 2012; Ceballos et al. 2015).

## Pacific Island land snails

Nowhere, in relation to land area, does land snail diversity reach that of the Pacific islands (Cowie 2002). The approximately 25,000 islands of the Pacific are home to more than 6000 land snail species, most of which are single island/archipelago endemics (Cowie 2000, 2002; Koppers 2009). The Hawaiian Islands, one of the better studied archipelagos, harbors over 750 land snail species, and all but three species are endemic (Cowie et al. 1995). Spectacular diversity, in terms of species, ecosystems, and geology, is the hallmark of what has made Pacific islands grand natural laboratories for evolutionary, ecological (Carson 1987, 1992; Whittaker 1998; Cowie and Holland 2008), and more recently—restoration and conservation research (Graham et al. 2017; Wood et al. 2017). Insular snails, because of their long evolutionary history, adaptation in isolation, high endemicity, and tendency for passive trans-oceanic dispersal, have achieved extraordinary diversity (Gittenberger et al. 2006; Holland and Cowie 2009). They contribute substantially to island habitats providing key ecosystem services, including soil development (Lavelle et al. 2006), litter decomposition and nutrient cycling (Jennings and Barkham 1976; Theenhaus and Scheu 1996; Meyer et al. 2013), and serve as flagship indicator species (Schlegel et al. 2015), key to watershed maintenance (Mascaro et al. 2008; Daily et al. 2009; Lara et al. 2009).

Unfortunately, Pacific island land snails account for 40% of the 743 documented animal extinctions included in the IUCN Red List, and the majority of these are recorded from three well studied island areas, French Polynesia, Mascarene Islands, and the Hawaiian Islands (IUCN 2016; Cowie et al. 2017). The latter point punctuates the high probability that these recorded extinctions are a vast underestimate of the true crisis facing snails, and other invertebrates across the islands (Régnier et al. 2015a, 2015b), and these extinctions show no sign of abating (Hawksworth and Cowie 2013; Richling and Bouchet 2013; Cowie et al. 2017). However, all is not lost, nor are all these extinctions inevitable (Safina 2018; Stokes 2018). There is still time, and diversity left to discover and conserve (Ceballos et al. 2015). There remains a glimmer of hope that even presumably extinct taxa may still be rediscovered (Yeung et al. 2015, 2018; Hirano et al. 2018) along with the vast diversity we have yet to uncover—we only have to look.

## Hawaiian land snails

Hawaii supports one of the world's most spectacular radiations of land snails (Solem 1983, 1984; Cowie 1996), with a disharmonic fauna composed of 10 of the approximately 100 gastropod families with terrestrial members (Cowie et al. 1995; Mordan and Wade 2008; Bouchet et al. 2017). The real number of Hawaiian species is difficult to ascertain, since until very recently, most had not been studied in a comprehensive systematic manner for more than half a century. Based on a review of the literature and museum material, Solem (1990) estimated there to be 1461 endemic taxa, including species, subspecies, and varieties with no recognized taxonomic status. This was a substantial overestimate when compared with Cowie et al. (1995), which recognized 752 species and is considered the most rigorously verifiable estimate currently available (Johnson 1996). However, the true diversity lies somewhere between these two estimates. Despite such uncertainty, even the most conservative estimates indicate that Hawaii is an incontrovertible gastropod diversity hotspot. Even more spectacular is that >99% of the species are endemic, nearly all to single islands (Cowie et al. 1995), and many to a single mountain range within the islands (Pilsbry and Cooke 1914–16).

More than a century ago, C.M. (Monte) Cooke, Jr. (Bishop Museum malacologist 1902–1948), recognized the plight of Hawaiian land snails, and prior to his death in 1948, in cooperation with H.A. Pilsbry (Academy of Natural Sciences malacologist) and a handful of other malacologists, dominated the study of Pacific island land snails, particularly the Hawaiian fauna (Kondo and Clench 1952). Much of what we know about the numerous extinct, and few remaining species can be attributed to these early works, without which we would have lost not only the species, but any knowledge of their existence. Although they carried out detailed monographic work on some of the families in Hawaii, no comprehensive taxonomic treatment of the fauna exists (Solem 1990). Prior to Cowie et al. (1995), the most complete summary of the fauna was by Zimmerman (1948), an entomologist. The last major taxonomic treatment of any Hawaiian snail family, Achatinellidae, was published in 1960 by Cooke and Kondo (1960), and focused primarily on other Pacific island taxa, with major Hawaiian members included. Prior to Cooke and Kondo's (1960) publication, Baker (1940) produced a monograph on Pacific island Helicarionidae with accounts of several Hawaiian species. The decades after 1960 were considered a period of malacological silence for land snail research in Hawaii, with little to no systematic work being published (Solem 1990). This began to change in 1981, when conservation efforts (Hadfield and Mountain 1980; see also USFWS 1981) and increased publicity (Hart 1975, 1978; Whitten 1980) led to the listing of the entire genus *Achatinella* as endangered under the US Endangered Species Act (USFWS 1981). This sparked renewed interest in Hawaiian tree snails, but focused attention only on the subfamily Achatinellinae, which constitutes less than 14% of the entire Hawaiian land snail fauna. This narrowly focused interest led to them being one of only two Hawaiian land snail groups that have been the subject of molecular systematic studies or conservation assessments over a 30-year period, the others being succineids (Rundell et al. 2004; Holland and Cowie 2009; Yeung et al. 2018), and amastrids (Régnier et al. 2015b).

Twenty-eight years ago, Alan Solem, a renowned malacologist from the Field Museum, recognizing the plight of Hawaii's land snails, urged the conservation and malacology community to take measures to save them before they are lost forever, imploring that "... their loss will be the equivalent of the dodo and elephant bird extinctions, the only island restricted families of vertebrates to become extinct in historic times" (Solem 1990, 34). Therein he provided the conservation status for each of the families and grimily estimated that 50% extinction of the fauna was "wildly optimistic" considering the nearly complete lack of comprehensive surveys since the 1930s and argued that 65–75% of the fauna was already lost. He also provided some recommendations for immediate conservation actions, less the remaining 25–35% of the Hawaiian land snail fauna become the next generation's dodo.

Solem proposed actions necessary for conservation in four phases: (1) use the extensive collections in natural history museums to develop a baseline of the identity, historical distribution, and abundance of species; (2) use these data to organize and carry out extensive field surveys to identify the remaining taxa and their habitats; (3) develop approaches to protect and expand suitable habitat by identifying immediate threats to the remaining taxa and their habitats; and (4) complete systematic revisions of all 10 families to serve as a basis for conservation and further research. To these we add a fifth phase, changing peoples' perceptions and appreciation of invertebrates, which is critical for saving the lesser known and underappreciated faunas of Pacific Islands, and beyond—those spineless creatures that rule the world (Collen et al. 2012).

## Museum collections

Conservation of plants and animals requires accurate knowledge of biodiversity and taxonomy (Cardoso et al. 2011) and critical to developing this knowledge and making conservation management decisions are natural history museum collections (Suarez and Tsutsui 2004; Drew 2011; Tewksbury et al. 2014; Page et al. 2015; Monfils et al. 2017). Efforts to digitize collections over the last decade have increased the amount of data available to the community and with the information (e.g., field notes, images of habitats, locality information) that accompanies each specimen, researchers are now able to better target areas of historical diversity and assess habitat suitability for present and future population viability (Tewksbury et al. 2014; Monfils et al. 2017; Rapacciuolo et al. 2017). Since much of the Hawaiian land snail fauna has not been studied since the 1930s, museum collections, such as those in the Malacology Center at the Bishop Museum, contain the last records of species and these records not only provide the historical distribution of land snails for targeted surveys, but allows researchers to develop search images and identify species found during surveys, many of which have not been seen since their original descriptions.

The Bishop Museum malacology collection is the most comprehensive Pacific Island land snail collection with nearly 4 million specimens from 28 island groups across Polynesia, Micronesia, and Melanesia. Almost half of these holdings are of Hawaiian land snails, most collected before 1940, and over 500 species representing extinct or critically imperiled taxa. Unfortunately, less than 15% of the collection had been digitized (including updated taxonomy, taxa identification, locality, collector information, and collection date) until funding provided by the National Science Foundation's Collections in Support of Biological Research Program in 2015 was acquired to digitize the entire Bishop Museum land snail collection. To date, 40% of the collection has been digitized, making the taxonomic and biogeographical data widely accessible and yielding insights for taxonomic revisionary work, and guiding surveys for remaining taxa, several of which have resulted in rediscoveries of species that have not been seen for more than 50 years (Yeung et al. 2015, 2018).

## Comprehensive surveys

Anthropogenically induced changes, primarily habitat destruction, invasive species, and climate change have relegated much of the remaining fauna to high elevation refugia in protected forest and/or natural area reserves (NAR) (Pilsbry and Cooke 1914–16). Solem (1990, 36) suggested that "the higher mountain slopes of the Hawaiian Islands offer an almost unlimited field of study ... of land Mollusca," and urged researchers to carry out this critical work. Revisiting areas that once harbored native species, and exploring remote sites that were mostly inaccessible half a century ago is critical to providing an updated baseline documenting the existence and habitats of the remaining native land snails.

Embarrassingly, few comprehensive surveys were carried out for the non-Achatinellinae fauna during the first two decades following Solem's plea, in part because of the assumption that most were already gone. Field surveys during the 1990s primarily targeted the already federally protected *Achatinella* spp. and other members of the subfamily, leading to the federal listing of three additional species in 2013 (*Partulina semicarinata*, *P. variabilis*, *Newcombia cumingi*). In the early 2000s, Hawaiian succineids (42 species) were the focus of ecological, phylogenetic, and biogeographical studies (Brown et al. 2003; Rundell and Cowie 2003; Rundell et al. 2004; Holland and Cowie 2009; Meyer 2012). Other surveys during this period were opportunistic (e.g., Cowie et al. 1995; Miller et al. 1995; Evenhuis et al. 1996; Moretzsohn and McShane 2003) and usually part of wider environmental impact assessments (EIAs). In many of these EIAs, the micromollusc community (snails with a shell height or diameter less than 5 mm) and/or epigeal (ground-dwelling or in leaf-litter) species were only identified to the genus level and survey techniques employed (i.e., visual searches) targeted primarily larger sized arboreal snails (Durkan et al. 2013). Thus, significant components (and entire families) of the Hawaiian land snail fauna were missed during these surveys, EIAs, and the development of natural area management plans. For example, prior to 2008, *Kaala subrutila*, an epigeal land snail endemic to the highest summit on the island of Oahu, Mt. Kaala, had not been recorded alive since its original description in 1940 (Curry and Yeung 2013), and was not listed among the "rare and endangered species" in the Mt. Kaala NAR (1990) management plan despite being the only member of a monotypic genus restricted to the reserve.

In 2011, we, along with collaborators received a National Science Foundation award to conduct the most comprehensive Hawaiian land snail survey in the last 60 years. Surveys of more than 950 sites across the six largest main Hawaiian Islands (Kauai, Oahu, Maui, Molokai, Lanai, Hawaii Is.) have targeted locations historically recorded as harboring native species, as well as, new remote locations; yielding more than 200 species of snails in nine families, including several new species. Morphological, molecular systematic, and biogeographical analyses are being used to update taxonomy and clarify systematic relationships among recorded taxa. Here, we provide the first comprehensive update on the conservation status of the 10 families since Solem (1990). Taxonomy and the recognized number of species (in parentheses) follow Cowie et al. (1995), but where appropriate we provide updated familial nomenclature (italics with species numbers in brackets) following Bouchet et al. (2017).

### Hydrocenidae (2) and Punctidae (1)

The Hawaiian hydrocenids and punctids are among Hawaii's smallest micromolluscs and were considered extirpated from low and mid elevational areas by Solem (1990). No hydrocenids have been recorded at any elevational range since the 1930s and both Hawaiian species are probably extinct. *Punctum horneri*, the only punctid described from Hawaii, is still extant. We also found several undescribed species, and recognized that one species previously mistaken for a native Hawaiian punctid is in fact *Paraloama servilis* (Christensen et al. 2012), an introduced species. As predicted, nearly all of these punctid species were recorded in high elevation forests and occurred in low densities (less than five individuals at a given site).

### Pupillidae (56; *Vertiginidae* [55], *Pupillidae* [1])

Solem (1990) thought that several species in the genus *Pronesopupa* were still common and persisting in low elevation, non-native forest, and that some *Nesopupa* and *Lyropupa* species may still remain in upland native forests. Recent surveys have confirmed this pattern, and preliminary conchological and molecular assessments have tentatively identified 23 endemic taxa. *Pronesopupa* species can still be found in low elevation, non-native forests as well as high elevational areas, and as Solem predicated, *Nesopupa* species were recorded in upland native forests but were also found in low elevational areas with *Pronesopupa*. However, no individuals that could be referred to the genus *Lyropupa* were recorded, and the entire genus is presumed extinct in Hawaii. Interestingly, several species with unknown native provenance were recorded, and have phylogenetic affinities closer to North American *Vertigo* spp., a genus not reported from Hawaii. Several of these unidentified pupillids were found in remote, high elevation areas among leaf litter, and are conchologically similar to the endemic Hawaiian *Lyropupa* species. As such, it is possible that they are indeed undescribed native taxa belonging to this genus. Surprisingly, we found many more populations of pupillids than initially expected, indicating that they are still moderately abundant, or the diversity has been substantially underestimated.

### Succineidae (42)

The Hawaiian Succineidae are among the few families reportedly doing relatively well (Solem 1990; Rundell et al. 2004; Holland and Cowie 2009), with many succineid species abundant in higher elevational forests across all the islands. We recorded 29 species from the six largest Hawaiian Islands, many in high abundances. This represents more than half of the known diversity, which like many families is probably underestimated, and fewer than half of these have been identified to described species. Systematic revisionary studies, and research on the overall biology of this family in Hawaii may yield greater insights into why some lineages are doing better than others, and provide the foundation for conservation management strategies.

### Zonitidae (10; *Gastrodontidae* [3], *Vitrinidae* [1], *Oxychiliidae* [6]) and Helicarionidae (60; *Euconulidae* [60])

Solem (1990) provided scant details regarding the remaining diversity of the Hawaiian Zonitidae and Helicarionidae, citing the difficulties in delineating and identifying the various species within each of these limacoid families. While the live animals, especially the helicarionids, have interesting coloration and patterns resulting from the body, empty shells for both families are rather uniform in color with few taxonomically informative characters. Further limiting a meaningful assessment of the zonitids was the limited records in museum collections, which may reflect the actual historical abundance and distribution of species within this family, or dramatic losses. Recent surveys yielded only four zonitid species from 20 sites, less than 2% of all sites surveyed. In contrast, Solem assumed that the helicarionids were faring well based on his observation that members of this family were abundant on other Pacific islands. We identified 70 genetically distinct lineages of helicarionids, a 17% increase over the recognized Hawaiian diversity. Nearly 40% of these lineages have been identified as a previously described species, and many of the remaining taxa likely represent cryptic diversity. While it is possible that some of these unidentified species will be matched to known species, the pattern indicates that diversity has been substantially underestimated. As such, we have still lost a considerable portion of the diversity and much of it before it was described. Nonetheless, this remains one of the most diverse families, with one of the widest distribution in the islands.

### Helicinidae (14)

Neal (1934) recognized 14 species of helicinids, distributed across the six main Hawaiian Islands. Solem (1990), primarily because of vulnerability related to their epigeal habits, suggested that the family was extirpated from the islands. However, Meyer (2006) recorded a population of an unidentified helicinid species on Oahu, and subsequent surveys have recovered eight additional species, some from multiple populations, but only from the islands of Oahu, Maui, and Kauai.

### Endodontidae (33)

The endodontids have suffered the greatest losses after the Amastridae. Although there are only 33 described species from Hawaii, there were an estimated 300 undescribed species in the Bishop Museum collections (Solem 1990). At the time, Solem predicted that less than 5% of known diversity was likely to be found in high elevation refugia. Unfortunately, this was an overestimate, as three species have been recorded in recent surveys, *Cookeconcha hystricella* and two undescribed species. Sadly, extensive surveys have failed to find additional species or populations, and this family has been nearly extirpated from the islands. Unless management plans are developed and funding provided to implement them, these remaining species will likely disappear in the next decade.

### Amastridae (325)

The Amastridae is the most diverse and the only endemic land snail family in Hawaii, as well as, the only extant endemic plant or animal family in the islands. Estimates of extinction indicate that 2% or less of the fauna remains, resulting from extinction rates in the last century that may have reached 5–10% per decade (Régnier et al. 2015b). Amastrids were thought to be completely extirpated from the island of Kauai and only a few remnant populations of a handful of species were thought to remain on Oahu. However, recent surveys have recorded 22 extant species (Yeung et al. 2018), most consisting of single, small populations hanging on in highly threatened habitats on Oahu, Kauai, Maui, Molokai, and Hawaii Is. Some species exist only in captively reared populations, which is work being done without direct funding. Although, like many groups, hope remains, as at least one species was recently re-discovered in a remote gully on Molokai, and there are likely other species yet to be discovered. But extensive surveys are required to locate these remaining species before they are gone forever.

### Achatinellidae (209)

The Achatinellidae is the second largest family of land snails in Hawaii, with two endemic subfamilies—the Achatinellinae and Auriculellinae. The larger more charismatic Achatinellinae have received more study and conservation protection than any other Hawaiian snail group, while the smaller Auriculellinae and the other subfamilies containing even smaller sized snail species with distributions beyond Hawaii have received far less attention. Despite being so well studied, having the most charismatic among them now protected, Solem (1990) predicted that the *Achatinella* were mostly extinct, but the status of the smaller sized species within the Hawaiian Achatinellidae was uncertain. Like most Hawaiian land snail families, our recent surveys indicate that a substantial portion of the achatinellid diversity has indeed been irretrievably lost, yet recent rediscoveries of species thought to be extinct and the identification of several cryptic species means that there is still time to act and do what is needed to protect the jewels of the Pacific.

## Protecting the remaining taxa

The first two phases, assessing museum collections and comprehensive surveys, were estimated to require several years of work each and the protection and expansion of suitable habitat would last the longest with decades of work required (Solem 1990). Once areas harboring native land snails were recognized, researchers and conservation managers could identify immediate threats to these areas and start the long term and difficult process of restoring and protecting these habitats. As Solem (1990, 34) concluded, there are still species extant, although precariously, and that "time is very late, and much remains to be done".

Since 1990, there has been increased development and organization of conservation and resource partnerships that connect private, state, and federal landowners to protect Hawaii's ecosystems (e.g., The Nature Conservancy; Puu Kukui Watershed Preserve, PKW; Hawaii Association of Watershed Partnerships; Oahu Army Natural Resources Program, OANRP). Within these past 5 years, these organizations have begun to work more closely with the State's Department of Land and Natural Resources (DLNR) following the creation, in 2013, of the Snail Extinction Prevention Program (SEPP), established to protect Hawaii's imperiled snail fauna and to provide habitat protection, where possible. With federal, state, and non-governmental agencies now acknowledging the plight of these species, beyond just the charismatic Oahu Tree Snails, we have now just begun habitat conservation and recovery planning for dozens of species.

In the late 1990s, two snail enclosures built in protected forest reserves and watershed preserves were built on the island of Oahu to protect endangered snails (specifically *Achatinella* spp.) from predators (Natural Area Reserves Program 2016). The DLNR and OANRP cleared these two areas of invasive plants and animals and planted native host plants within these enclosures. With the recent collaborations among conservation agencies, four additional enclosures on Oahu and one each on Maui and Lanai have been built within the last 6 years. Although the federally listed species are the primary focus for the development of these enclosures, organizations such as SEPP, OANRP, and PKW are including in these enclosures other land snail species that our data indicate are endangered, threatened, and/or vulnerable. With these artificial islands of refuge, some species of captively reared land snails are already being reintroduced into the wild, giving some a fighting chance of survival for at least a few more decades. However, increased funding support is necessary to maintain and expand existing enclosures and additional protected areas for land snails are needed on all islands.

## Systematic revisions

Systematic work on most Hawaiian land snails had stalled since 1960, but renewed interests fueled by NSF and USFWS funding has allowed us to rejuvenate monographic works for each of the families, starting with the Achatinellidae. Systematics is where taxonomy meets phylogeny—where we begin to name and classify taxa and understand how they relate to each other. With each comprehensive taxonomic monograph or revision, the taxa within a group become better defined and their distributions and habitats are more accurately delineated. Assessments of threatened taxa, and determination of extinction cannot be completed if we lack core biological knowledge (e.g., habitat requirements, life history) of species, and species that are taxonomically and phylogenetically more studied are also generally better known biologically (Diniz-Filho et al. 2013; von Staden et al. 2013; Mace 2004). A prime example of this within the Hawaiian land snail fauna is the conservation of the Achatinellinae, which includes the federally protected *Achatinella* genus and several *Partulina* and *Newcombia* species. Over the last few decades focusing the bulk of research and conservation funds on this small group, which are indisputably beautiful, has already provided important contributions to evolutionary theory and conservation practices. The bulk of knowledge on Hawaiian land snail biology beyond taxonomy is derived almost exclusively from this group, but with such a continued narrow taxonomic focus our knowledge will grow, possibly at the expense of losing the other 650 species, which are arguably equally beautiful and important. While our currently funded revisionary work focuses on this same family, it is primarily aimed at illuminating the forgotten members, and emphasizing an approach to be applied to other land snail families.

With the discovery of numerous undescribed species in almost all Hawaiian land snail families, it is clear that the fauna has been vastly understudied, highlighting the desperate need for, and importance of, this type of basic biodiversity and taxonomic work to inform the way forward as we are confronted with such substantial biodiversity loss in coming decades. Without updated systematic revisions to guide future conservation activities, the first three phases of land snail conservation will eventually become unlinked. And one of the first major steps we must take is to begin filling in the broad knowledge gaps for the non-achatinellinine snails.

## Changing public perception—beyond the creepy, crawly, slimy things

Something not mentioned by Solem (1990), but that we, and others, feel is critical in determining the likelihood of many species' surviving beyond the next decade, is the reality that those that will survive will be those that we choose to protect (Batt 2009). As such, understanding of human preferences, how they are formed, and what can be done to shape them must be integrated into any conservation strategy. Disparity in human preferences driven by perceptions of the "attractiveness" or similarity of organisms to humans is very much at the heart of why some groups of animals (and plants) are the subject of intense biodiversity, conservation, and systematic studies, while others, despite being numerically dominant, more ecologically relevant, and/or more critically endangered are ignored (Stokes 2007; Patrick and Tunnicliffe 2011; Brambilla et al. 2013; Colléony et al. 2017). This bias is evident when looking at the distribution of funding allocated by the USFWS (2015) to vertebrates, invertebrates, and plants. In 2015, more than a billion dollars (US$) were spent on about 500 species of vertebrates, nearly $2 million per species. At the same time, only $126,000/species was spent on approximately 300 species of invertebrates and <$70,000/per species for plants (~700 species). This trend is consistent across years over the last decade in US federal spending on endangered species. Similar patterns can be found at the state level as well, with spending on vertebrates being 12× that of invertebrates (USFWS 2015). A vertebrate-centric bias is not a new phenomenon, and we suspect has been a grievance articulated by invertebrate researchers, especially entomologists (except those studying large, charismatic butterflies), since humans formally began studying life. However, the consequences of a vertebrate-centric bias on scientific research, conservation funding, and the publics' appreciation and understanding (Prokop et al. 2008; Donaldson et al. 2016; Titley et al. 2017; Troudet et al. 2017) of animals have in recent decades taken on a new urgency as predictions of species losses during the Anthropocene grow ever grimmer (Kellert 1993; Ceballos et al. 2015; Régnier et al. 2015b).

It has been suggested that human preferences for certain animals (e.g., apes, pandas, elephants, lions) was determined early in the evolution of our species, with phylogenetically and behaviorally similar animals being perceived as less "ugly" (Prokop and Randler 2018), and such predispositions emerging early in childhood (Borgi and Cirulli 2015). Additionally, animals that are harmful to humans also perform poorly in the proverbial biodiversity beauty contests, with parasites, snakes, and spiders finishing in the bottom, but butterflies and birds often crowned winners (Vetter 2013; Schlegel et al. 2015). However, there is also a large culturally learned component of perceptions and attitudes, both negative and positive, toward certain animals (Prokop and Randler 2018). Emerging research, and our own anecdotal experiences, indicate that education, exposure, and opportunities to interact with animals traditionally viewed as less charismatic or attractive (i.e., most invertebrates) can ameliorate biases that manifest themselves as fear, disgust, and ultimately a lack of perceived conservation value of these taxa (Clark et al. 2014; Schlegel et al. 2015; Donaldson et al. 2016; Curtin and Papworth 2018). Here, we join the growing chorus of conservationists (Mascia et al. 2003) calling for increased efforts to shape public perception in an effort to overcome vertebrate-centric biases driven in large part by early educational and natural history experiences (Schlegel et al. 2015), which in turn has fundamental consequences for conservation research and funding (Czech et al. 1998; Martín-López et al. 2009; Titley et al. 2017).

A shift in public opinion and perceptions can be accomplished through multiple approaches, many of which are already supported and encouraged through major funding agencies and include curriculum development, informal education, involvement of citizen scientists, and integrating cultural knowledge and traditions with science. With formal curriculum development in primary schools in collaboration with educators, we can increase young children's exposure to the importance and values of animals beyond the typical classroom pets (Schlegel et al. 2015). Outreach efforts through museums, zoos, and non-profits aimed at increasing awareness of local plants and animals have been shown to drive a greater appreciation for their value (Silvertown 2009; Ballard et al. 2017). Activities through these organizations can include development of exhibits, participation in science awareness and engagement days, and training for citizen science events (Ballard et al. 2017; McKinley et al. 2017). In turn, development of electronic keys and guides to local species can be used by schools, resource, managers, and the general public in the wider adoption of citizen science initiatives (Stevenson et al. 2003).

With these informal training opportunities, researchers can engage the entire educational pipeline from GK-12 to college interns and beyond. When engaging the entire community, which includes integrating cultural understanding from cultural practitioners, we can all gain a wider appreciation for nature and hopefully, invertebrate conservation (Clark et al. 2014). In the political arena, we need leaders representing the interests of invertebrate conservation to serve in local offices or on advisory boards, or indirectly by educating those serving in such positions through engagement with scientific research (Parsons 2001; Ascher 2004) and integration of science into public policy (Durand and Vázquez 2011).

## Conclusion

More than 25 years have passed since Solem (1990) suggested that the remaining Hawaiian land snails were doomed unless immediate actions were taken. He laid out several suggestions, to which we now add a critical component in hopes of spurring others to take this approach, not just for land snails, but for other members of the forgotten majority. While continued and expanded research into species discovery, systematics, and conservation is necessary, especially for underrepresented groups like snails, worms, and non-butterfly insects, we feel strongly that all researchers engaged in these activities need to expand efforts to increase the publics' awareness and appreciation for invertebrates. Such efforts are a crucial component of the complex dynamic that determines not only public policy, but also research funding and support for conservation (Martín-López et al. 2009).

Shifting the general view of snails from being "icky" and "slimy" things that one pours salt on in the garden, to one of understanding and appreciation for their intrinsic beauty and importance as an integral part of nature is critical if we hope to save most species. Several emerging studies indicate that this shift is possible and that scientific information can and does drive such changes (Lindemann-Matthies 2005; Martín-López et al. 2009; Patrick and Tunnicliffe 2011; Colléony et al. 2017; Curtin and Papworth 2018). Although much of what Solem predicted has come to pass, like him, we feel that there is still hope, there is still time, and with renewed efforts and a more equitable taxonomic focus we can change the trajectory of biodiversity loss, preserving the legacy of the lesser known fauna for the future.

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