



Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction

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Abstract: *The International Union for Conservation of Nature (IUCN) Red List includes 832 species listed as extinct since 1600, a minuscule fraction of total biodiversity. This extinction rate is of the same order of magnitude as the background rate and has been used to downplay the biodiversity crisis. Invertebrates comprise 99% of biodiversity, yet the status of a negligible number has been assessed. We assessed extinction in the Hawaiian land snail family Amastridae (325 species, IUCN lists 33 as extinct). We did not use the stringent IUCN criteria, by which most invertebrates would be considered data deficient, but a more realistic approach comparing historical collections with modern surveys and expert knowledge. Of the 325 Amastridae species, 43 were originally described as fossil or subfossil and were assumed to be extinct. Of the remaining 282, we evaluated 88 as extinct and 15 as extant and determined that 179 species had insufficient evidence of extinction (though most are probably extinct). Results of statistical assessment of extinction probabilities were consistent with our expert evaluations of levels of extinction. Modeling various extinction scenarios yielded extinction rates of 0.4–14.0% of the amastrid fauna per decade. The true rate of amastrid extinction has not been constant; generally, it has increased over time. We estimated a realistic average extinction rate as approximately 5%/decade since the first half of the nineteenth century. In general, oceanic island biotas are especially susceptible to extinction and global rate generalizations do not reflect this. Our approach could be used for other invertebrates, especially those with restricted ranges (e.g., islands), and such an approach may be the only way to evaluate invertebrates rapidly enough to keep up with ongoing extinction.*

Keywords: Amastridae, conservation bias, conservation status, extinction, Hawaii, IUCN Red List, taxonomic impediment

La Extinción de una Familia Hiperdiversa de Caracoles Terrestres Endémicos de Hawái y las Implicaciones de la Subestimación de la Extinción de Invertebrados

Resumen: *La Unión Internacional para la Conservación de la Naturaleza (UICN) incluye a 832 especies enlistadas como extintas desde 1600, una fracción minúscula de la biodiversidad total. Esta tasa de extinción es del mismo orden de magnitud que la tasa de fondo y se ha utilizado para minimizar la crisis que sufre la biodiversidad. Los invertebrados comprenden el 99% de la biodiversidad, y aún así sólo se ha evaluado el estado de un número insignificante. Evaluamos la extinción de la familia de caracoles terrestres hawaianos Amastridae (325 especies, de las cuales la UICN enlista a 33 como extintas). No utilizamos el criterio estricto de la UICN, bajo el cual la mayoría de los invertebrados estarían considerados como faltos de datos, sino*

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Paper submitted August 25, 2014; revised manuscript accepted March 26, 2015.

un criterio más realista que compara las colecciones históricas con censos modernos y el conocimiento de expertos. De las 325 especies de Amastridae, 43 fueron descritas originalmente como fósiles o sub-fósiles y se supuso que se encuentran extintas. De las 282 restantes, evaluamos a 88 como extintas y 15 como existentes y determinamos que 179 especies tenían evidencia insuficiente de su extinción (aunque probablemente se encuentren extintas). Los resultados de las valoraciones estadísticas de las probabilidades de extinción fueron consistentes con la evaluación de nuestros expertos de los niveles de extinción. La modelación de varios escenarios de extinción resultó en tasas de extinción del 0.4-14.0% de la fauna de la familia Amastridae por década. La verdadera tasa de extinción de esta familia no ha sido constante; en general ha incrementado con el tiempo. Estimamos que un promedio realista de la tasa de extinción es de aproximadamente 5% por década desde la primera mitad del siglo XIX. En general, la biota de las islas oceánicas son especialmente susceptibles a la extinción y las generalizaciones de la tasa global no reflejan esto. Nuestra estrategia podría usarse para otros invertebrados, especialmente aquellos con extensiones restringidas (p. ej.: las islas), y dicha estrategia puede ser la única forma de evaluar a los invertebrados lo suficientemente rápido para seguir el ritmo de las extinciones actuales.

Palabras Clave: Amastridae, estado de conservación, extinción, Hawái, impedimento taxonómico, Lista Roja UICN, sesgo de conservación

Introduction

Since the 1980s or so, the terms *biodiversity crisis* (Novacek 2001) and *sixth extinction* (Leakey & Lewin 1996) have been used increasingly in scientific, political, and media discourse. These issues have been explored largely by ecologists focused on mammals and birds, and invertebrates have received much less attention despite their constituting as much as 99% of animal species richness (Ponder & Lunney 1999). Measures of biodiversity decline are based essentially on knowledge of vertebrates.

Many data that can be used to assess invertebrate conservation status are unpublished, locked in museum collections and in taxonomists' personal knowledge and collections. Museum collections, accumulated over long periods, are key sources of temporal and spatial distribution data for many invertebrate groups (Ponder et al. 2001). Thus, the process for assessing the status of most invertebrates differs greatly from that for birds and mammals, for which field observations by large networks of specialists (primarily ecologists) are rapidly translated into formal assessments. The contrast is reflected by the International Union for Conservation of Nature (IUCN) Specialist Groups: 12 for invertebrates, none at the species level; 71 for vertebrates, several at the species level. As of 2008, all mammals and birds had been formally assessed (Vié et al. 2009) and their status recorded in the IUCN Red List (IUCN 2014), the preeminent vehicle for global conservation status assessment (Rodrigues et al. 2006).

In contrast, sparse assessment of invertebrates is due to their vast diversity and the disproportionately tiny cadre of specialists who study them (primarily taxonomists) (the so-called taxonomic impediment [Carvalho et al. 2007]), a result, in part, of the non-charismatic nature of most invertebrates. Even if they were perceived as charismatic, they are too numerous to be studied individually. And because the vast majority of publications on invertebrates comprises original descriptions and

revisionary or phylogenetic works, it is almost exclusively taxonomists, not ecologists, who generate data for invertebrate conservation. But assessing a species for the IUCN Red List requires considerable information on range, demography, trends, surveying effort, population size, etc., information that is lacking for most invertebrates, which hence prevents their assessment. Nonetheless, museum information can be used to assess extinctions, just not readily according to the IUCN criteria, although it has been attempted for groups for which much appropriate information is available (e.g., Willis et al. 2003).

Thus, the IUCN Red List contains only 733 animal species and 99 plant species listed as extinct since around 1600, a minuscule fraction of total biodiversity, commonly estimated at 5–10 million species (May 2011; Mora et al. 2011; Costello et al. 2013). This extinction rate (around 2 species/year) is of the same order of magnitude as the natural background rate based on the fossil record (May et al. 1995). Such statistics are used by environmental skeptics to downplay the loss of biodiversity (Lomborg 2001).

However, among animals, the focus on birds and mammals and the proportionately negligible assessment of invertebrates masks a real crisis. Although assessment of extinction for all invertebrates is impossible, it may be possible for certain, perhaps representative, groups. Such assessments might permit broad extrapolation and more realistic evaluation of true overall extinction levels.

Mollusks are such a group. Despite the relative lack of focus on invertebrates, almost as many mollusks (311) are listed as extinct by IUCN (2014) as all chordates combined (338); most (282) are gastropods and half of these (138) Pacific island land snails. Nonetheless, almost twice as many mollusks as are listed as extinct on the IUCN Red List are considered extinct by mollusk specialists (Régnier et al. 2009), yet the number assessed remains a tiny fraction of the 80,000–100,000 described species and perhaps up to 200,000 real species (Strong et al. 2008).

Most mollusks have shells, which remain after death, providing a record of past faunas (Christensen & Kirch 1986). Thus, studies of Pacific island land snails have documented extensive recent extinction of previously undescribed species (e.g., Abdou & Bouchet 2000; Bouchet & Abdou 2001; Richling & Bouchet 2013). This fauna may have declined to about 50% of its former diversity (Lydeard et al. 2004).

Hawaiian land snails have been subject to drastic human-mediated extinction. Polynesians first colonized the islands about 800–1000 years ago (Kirch 2011; Rieth et al. 2011), causing local species extirpations and probably extinctions, but when Europeans arrived (1778) the extinction rate increased dramatically (Christensen & Kirch 1986). Once numbering at least 750 species (Cowie et al. 1995), at least 65% may now be extinct (Solem 1990; Lydeard et al. 2004). Notably, the endemic Hawaiian family Amastridae, the most species-rich in the archipelago (Cowie et al. 1995) and the only extant plant or animal family endemic to the Hawaiian Islands, may have declined from 325 species to approximately 10 species (Lydeard et al. 2004), yet the IUCN Red List evaluates only 33 as extinct. Almost all amastrids are or were restricted to single islands (Cowie et al. 1995), most to just one of the main volcanos on an island and often to one or a few adjacent ridges or valleys.

Our immediate goal was to evaluate the conservation status of amastrids more rigorously than previously by assembling information from the literature, museum collections, people with knowledge of amastrids, and targeted field work. Our broader goal was to demonstrate that incorporating extensive expert knowledge and opinion into assessments of lesser known invertebrates generates a more realistic estimate of extinction rates in these taxa than strict adherence to the IUCN approach, which seriously underestimates the true rates.

Methods

Data Collection

We reviewed the original descriptions of all amastrid species (referenced by Cowie et al. [1995]) and considered species described as “fossil” or “subfossil” without more recent material as extinct. We then focused on the remaining species.

We reviewed the extensive amastrid collections and archived field notes of former collectors in the Bishop Museum (Honolulu) to identify the last specimens collected of each species, ascertain whether they were collected alive or as empty shells, and record where and when they were collected.

We then reviewed data from our own recent (2004–2013) surveys, which targeted all land snails, not amastrids specifically. We surveyed 481 sites on the 6

largest Hawaiian Islands, from sea level to the upper limits of land snail habitat (approximately 2100 m). We searched each site for at least one person hour. At many sites, we collected leaf litter and soil, which we searched under a microscope for especially small snails. This is the most comprehensive and temporally focused land snail survey effort ever undertaken in the Islands. We also drew on our own expert knowledge and interviewed others (see Acknowledgements) who have worked or are working in the field or have historical knowledge of the fauna. We asked which species they considered extant and which had become impossible to find and were supposed extinct.

Based on the above information, we undertook limited field work on the island of Oahu, specifically targeting a few species that we thought might be extant. We intended to use these as case studies to test the robustness of our assessments. We undertook three field trips in the Waianae Mountains and two in the Koolau Mountains, the latter primarily in attempts to locate two species formerly widely distributed there, readily collected into the 1950s and extant in the early 1960s: *Amastra turritella* and *Amastra tristis*.

Data Analyses and Interpretation

The core of the analyses involved comparison of the historical museum data with the recent expert data, primarily our own field data and knowledge but also information from the other experts and collectors. We compared all localities where amastrids had been collected historically with all localities surveyed since 2004 (Fig. 1). If a species had not been found since 2004 (expert database) at any recently surveyed location where it had formerly been recorded (museum database), we considered the species extinct (with one exception—see Results). The 2004 threshold was the year our extensive surveys began (expert database). Many localities have been searched several times since then, so for species not found there was little doubt that the last individual had died. Our approach differs from IUCN’s in that we used a clear cut-off for when a species should be declared extinct. For the IUCN to consider a species extinct, “exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range are required, as well as a date of extinction, possible causes of extinction and a description of the searches done to find the species” (IUCN 2001).

A difficulty with our approach was that the historical locality descriptions were verbal, whereas the modern localities were located primarily by GPS coordinates. Although many locations could be precisely relocated based on site descriptions, others could not. However, for some sites, the number and distribution of sites surveyed since 2004 were sufficiently dense in the region

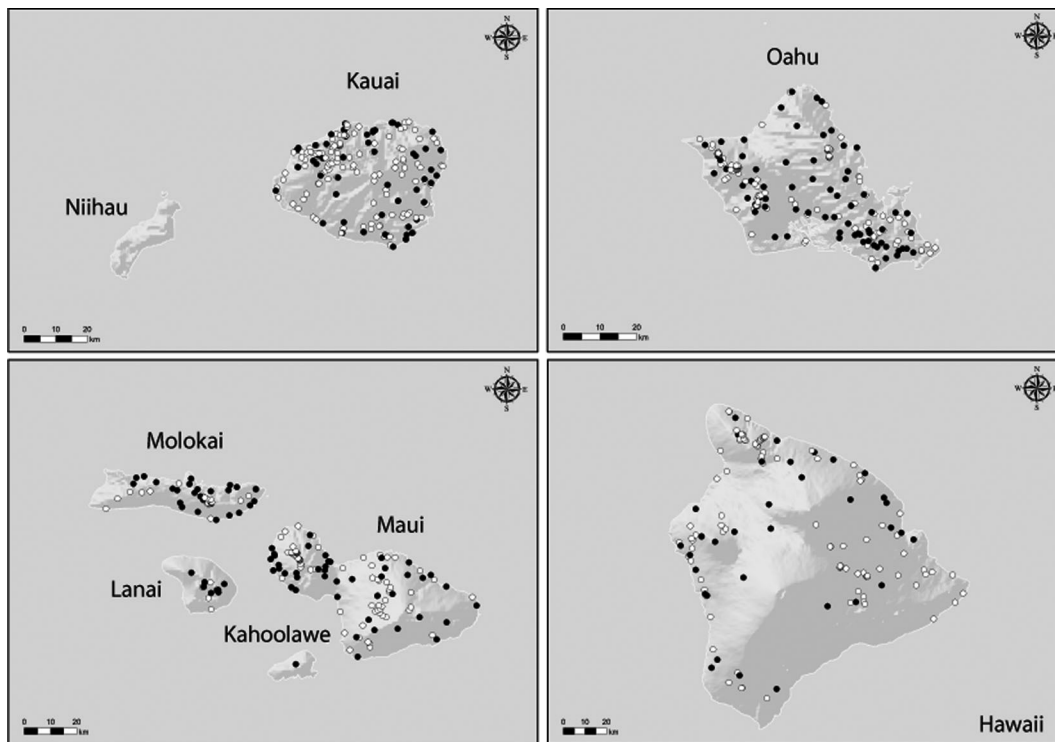


Figure 1. The Hawaiian Islands showing locations of historical collections of amastrids (filled circles) and locations of field surveys that took place 2004–2013 (open circles).

of the historical site that if amastrids were extant, it could reasonably be expected that they would have been found, and when they were not, extinction at the locality could be inferred. However, there remained other historical sites that could not be determined as corresponding precisely or even roughly to a modern locality or for which modern surveys did not cover the area adequately. We assessed most of the species at these sites as impossible to assess; we had insufficient evidence of their extinction.

We also assessed extinction probabilities based on collection years following Lee's (2014) numerical method for species with few records. We did this so we could determine whether our expert results were consistent with the results of this more complex statistical approach. We applied this method to species we assessed as extinct or extant but not to those classified as impossible to assess. Two priors are required for this method: a prior probability of seeing the species given it is extant (i.e., detectability) and a "prior probability that the species is still extant $P(X_T)$ " based on "the severity, duration and geographic scope of threats" to the species (Lee 2014). The prior probability of seeing the species, given it is extant, is S/T_N , where S is the total number of sightings and T_N is the number of years from the first to the last sighting. In her example (a bird), Lee (2014) used a prior for $P(X_T)$ provided by Birdlife International. Such a prior cannot be assessed for 325 poorly known land snail

species. We therefore applied the deterministic estimate $P(X_T) = T_N/T$, where T is the number of years from the first sighting to the year for which the estimate that the species is extant is being made, as suggested by Thompson et al. (2013) for such cases. We applied this method to species we had evaluated as extinct to obtain the probability that they were in fact still extant in 2013. We also applied it to the species we considered extant to obtain a probability that they were indeed extant. Arbitrarily, we used the year 2025 as if that were the year when we were doing the analysis because if we tried to determine the probability that a species was extant in 2013 (as for species evaluated as extinct) but input a sighting in 2013, Lee's model would fail.

Results

Of the 325 species, we evaluated 131 as extinct, including those previously listed by IUCN (2014) and additional fossil and subfossil species. For 179 species, we had insufficient evidence of extinction because the historical sites or surrounding areas may not have been recently surveyed. With more data and application of the IUCN (2001) criteria, these might be assessed as critically endangered (probably extinct). We categorized 15 species as extant. With more data they might be evaluated as endangered or critically endangered under criterion B2biii,

which relates to their decreasing area of occupancy, extent of occurrence, and quality of habitat.

These 15 species were recorded during recent field work, including our field work specifically targeting amastrids in the Waianae Mountains of Oahu (*Amastra cylindrica*, *Amastra micans*, *Amastra spirizona*, *Laminella sanguinea*, *Leptachatina cerealis*, *Leptachatina crystallina*, *Leptachatina gracilis*, *Leptachatina gummea*, *Leptachatina persubtilis*, *Leptachatina popouwelensis*), on Kauai (*Leptachatina cuneata*, *Leptachatina cylindrata*), on Maui (*Laminella aspera*, *Leptachatina nitida*), and on the island of Hawaii (*Leptachatina lepida*). This last species was included because when it was last seen (by R.H.C. 1992-1999) it was relatively widespread, and although the area has not been surveyed more recently it is considered highly unlikely that it is extinct. However, in our two field trips specifically targeting *A. turritella* and *A. tristis* we found no amastrids, alive or dead. These 2 species were widespread and relatively easily collected until the 1950s. (There are more lots of *A. turritella* in the most Bishop Museum than of any other amastrid [>478 lots collected up to 1962], and there are 348 lots of *A. tristis*.)

Of the 131 species evaluated as extinct, the statistically assigned probability of still being extant was <0.01 for 111 species, <0.1 for 16 species, and 0.1-0.3 for 4 species (Supporting Information), results generally consistent with the results from our non-statistical expert evaluations. For the 15 species evaluated as extant, the probabilities of being extant in 2025 were 0.38-0.93 (Supporting Information), also consistent with the results from our expert evaluations, especially because the lowest probabilities of still being extant were for species last seen in the late 1990s (*L. lepida*) and early 2000s rather than more recently.

Discussion

Our approach to assessing extinction increased the number of amastrids considered extinct from 33 (IUCN 2014) to 131, from 10% to 40% of amastrid diversity. Probabilistic analysis of collection and sighting records was consistent with these results. Even this number is considered an under-estimate because an additional 179 species may be extinct but cannot be assessed definitively. Thus, 310 of the 325 species (95%) may be extinct.

Costello et al. (2013) considered a current global biodiversity extinction rate of $<1\%$ per decade as the most realistic estimate. Our results permitted us to hypothesize various extinction rate scenarios for the amastrids. Some of the 43 fossil and subfossil species perhaps went extinct naturally before human arrival (approximately 800-1000 years ago [Kirch 2011; Rieth et al. 2011]), but this cannot be determined currently. If all 325 species were extant when humans arrived, we can base our hypotheses 1 of 2

suppositions regarding how many have gone extinct subsequently: conservatively, 131 species have gone extinct (i.e., those we evaluated confidently as such) or, perhaps more realistically, all but the 15 species known to be extant (i.e., 310) have gone extinct. Under these 2 basic scenarios and an unrealistic constant extinction rate, the extinction rates per decade since 1000 (the more conservative date for human arrival) are, respectively, 0.4% of the fauna (approximately 1.3 species/decade) and 0.95% (approximately 3 species/decade).

However, extinction rates have not been constant but are probably related to 4 phases of habitat destruction or modification and non-native species introduction. First, there was considerable habitat destruction by Polynesians before European arrival in 1778 (Ladefoged et al. 2009), undoubtedly causing local extirpations and some extinctions (Christensen & Kirch 1986). Polynesians introduced the Polynesian rat (*Rattus exulans*), which may have caused destruction of lowland forests (Athens 2009), although snails now seem to constitute a minimal part of its diet (Shiels et al. 2013). Polynesian pigs have been thought by some to have remained closely domesticated, causing little ecological harm, although highly damaging modern feral pigs are predominantly descended from them rather than European pigs (Nogueira et al. 2007).

Following European arrival, introduction of ungulates, notably goats and European pigs (Cox 1999), extended the destruction more widely to inland and higher elevation areas. The introduction and rapid spread of *Rattus norvegicus* and *Rattus rattus* (Atkinson 1977), which readily feed on snails, causing negative population level impacts (Hadfield 1986; Hadfield & Saufler 2009), probably affected amastrids. Introduced chameleons may more recently be having an impact (Chiaverano & Holland 2014). Feral pigs destroy host plants of various amastrids (Chung & Miyano 2001).

By the end of the nineteenth century, cattle ranching and pineapple and sugarcane cultivation led to much more habitat destruction. Mathematical modeling shows a rapid rate change in land snail extinctions globally around this time, with the change probabilistically centered around 1895 (Régnier et al. 2015).

Following WWII, rapidly increasing military, commercial, and tourism activity, as well as increased urbanization, led to more habitat destruction and alien species introductions. Notable were the predatory snails introduced in the 1950s, in particular *Euglandina rosea* but also *Gonaxis* spp., in misguided efforts to control the giant African snail (*Achatina fulica*) introduced in the 1930s (Cowie 2001). *E. rosea* in particular probably took a major toll on amastrids, as on achatinellid tree snails (Hadfield et al. 1993; Cowie 2001; Hadfield & Saufler 2009). Though speculative, other introduced snails, notably subulinids, may have out-competed amastrids (Cowie et al. 2008). New snail species introductions

continue (Cowie et al. 2008; Hayes et al. 2012). Introduced ants (there are no native ants) may also prey on snails (Solem 1990), and the introduced flatworm *Platydemus manokwari*, although not abundant in Hawaii, is a voracious snail predator (Sugiura 2010). In the early 1960s, it remained possible to collect amastrids in relatively low elevation forest (as observed by C.C.C.; Y. Kondo field notes in the Bishop Museum), whereas now none is known to occur below approximately 800 m. Low elevations now support non-native plants almost exclusively. Replacement of native plants by non-native invasive species, which may not provide habitat or food for many native snails (as observed by D.J.D.C.) and can lead to increased soil drying and changes in nutrient composition and litter density (Tuttle et al. 2009; Chau et al. 2013), has been an important factor in the decline of native snails.

Threats to native Hawaiian land snails are thus well understood and have probably intensified over the last 50–100 years (Hadfield 1986; Solem 1990; Hadfield & Saufler 2009). We therefore evaluated extinction rates under three additional scenarios superimposed on our extremes of 131–310 species having gone extinct during the last 1000 years (i.e., extinctions beginning only after 1778, 1895, and 1945) (Fig. 2). These are over-simplistic scenarios because the rate was probably continually increasing (exponential-like curves in Fig. 2), although a steadily increasing rate is also an oversimplification. It is more likely that there were step-wise rate increases. For example, early habitat modification by Polynesians probably only affected low- and some mid-elevation species, and if the rapid rate of modification stabilized somewhat the extinction rate may have declined (although agricultural expansion increased into at least the late seventeenth century [Ladefoged et al. 2009]). Whether such a decline in the extinction rate also happened between the much shorter periods 1778–1895 and 1895–1945 seems less likely, and while *E. rosea* introduced in the 1950s has been considered the final blow to arboreal snail species (Hadfield 1986), the generally ground-dwelling amastrids were probably mostly gone by 1951, when the last individual of the genus *Carelia* was seen alive. The amastrid extinction rate may now be very low because there are probably almost no species left to go extinct. We cannot know the true form of the curve, but the scenarios in Fig. 2 provide schematic assessments that at least bound the real rates and give some sense of the more likely rates.

The rates range from 0.4% of the amastrid fauna per decade (131 species extinct, beginning in 1000) to 14.0% per decade (310 species extinct, beginning in 1945). Because extensive modern field work has found only 15 species, we lean toward the higher number of extinctions, and because most known species (except those described as fossils or subfossils) were described from presumably live or recently dead shells, we lean toward about 1850 as the date when the extinction rate really

began to increase, especially among arboreal species affected by predation by *R. rattus* (introduced after 1840 [Atkinson 1977]) and *E. rosea* (introduced in the 1950s). This suggests an average extinction rate of approximately 5%/decade over the last 150–200 years.

Our most conservative extinction rate estimate is thus in line with the global estimate of <1%/decade of Costello et al. (2013). A rate of approximately 5% for the amastrids is more realistic, but still perhaps somewhat conservative. Such extinction levels globally will lead to loss of >50% of species within 150 years (Costello et al. 2013). This may be what has already happened to the amastrids.

The amastrids, and perhaps other Hawaiian land snail groups, may be exceptional instances of such high extinction levels. However, oceanic island snails are particularly susceptible to extinction generally (Coote & Loève 2003; Régnier et al. 2009) and some groups, notably the highly diverse endodontids throughout the Pacific, have an extinction rate as extreme as that of the amastrids (Solem 1976; Sartori et al. 2013). Other island taxa, notably birds (Duncan et al. 2013), also have had high levels of extinction. Less is known of insect extinctions (Hembry 2013), although most native island insects are now restricted to small remnants of their original ranges and are generally considered threatened (New 2008). Plants seem less extinction prone than animals (Sax & Gaines 2008), although on islands, including the Hawaiian Islands, many are seriously threatened (Caujape-Castells et al. 2010). In general, island biotas are more susceptible to extinction than continental biotas (Frankham 1998; Simberloff 2000; Vermeij 2004).

Generalizing global extinction rates may therefore be dangerous because they may not acknowledge the particular susceptibility of island biotas. By combining estimates of extinctions on islands and continents, global mean rates will drastically under-estimate actual rates on islands. Because islands harbor a highly disproportionate number of narrow (often single island or narrower) endemic species per unit area than continents, subsuming island extinction rates under global estimates may downplay the vulnerability of island biotas and de-emphasize their conservation needs.

We hypothesize that because more amastrid species were described from Oahu (118) than other islands (Kauai is next with 56) (Cowie 1995), more species remain extant on Oahu. Indeed 10 of the 15 extant species are from Oahu. We also hypothesize that the extant species were probably among the most abundant amastrids historically and therefore are represented by many museum collection lots. The 10 amastrid species represented by the largest numbers of Bishop Museum lots (219–478 lots) are all from Oahu, which also reflects the historical collecting bias in favor of Oahu, roughly 10 times more than on any other island (Cowie 1995). Nonetheless, four of these species (*A. cylindrica*, *A. spirizona*, *L. sanguinea*, *L. gummea*) are still extant and

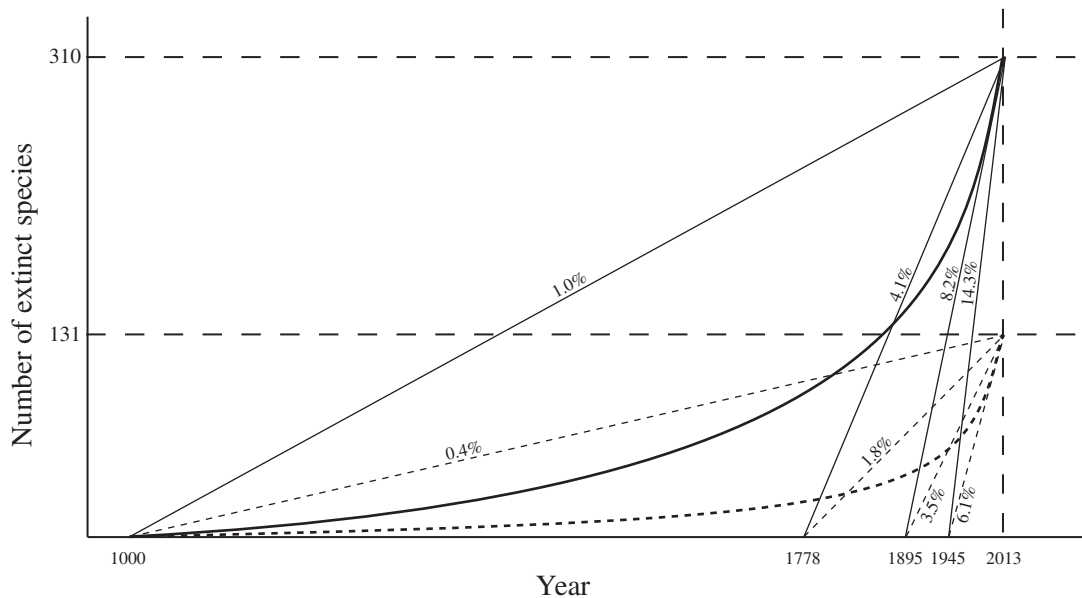


Figure 2. *Amastrid* extinction rates under 2 basic scenarios of either 136 or 310 species going extinct since the arrival of Polynesians around the year 1000 (see text for explanation of numbers). Straight lines (dashed for 136, solid for 310) show constant per decade extinction rates as a percentage of the total fauna available for extinction (325 species) depending on whether extinction began in 1000, 1778, 1895, or 1945 (see text for explanation of years). Curved lines are hypothetical, overly simplistic indications that extinction rates were not constant from 1000 but increased over time, dramatically so in the twentieth century (see text for more discussion of the curves).

among the ten extant species on Oahu, suggesting that indeed the more abundant species have fared better. Furthermore, we hypothesize that the small egg-laying species (*Leptachatina*) have fared better than the large live-bearing species (*Amastra*, *Carelia*, *Laminella*, etc.). In fact 10 of the 15 extant species are *Leptachatina* spp. That *Leptachatina* spp. are poorly represented (2 species) among the 10 with the largest representation in the Bishop Museum is probably because historical collectors probably focused more on Amastrinae than on the smaller and more uniformly brown Leptachatininae.

Most amastrids were ground dwelling. However, based on our field observations, the 3 *Amastra* species remaining are arboreal, which may be because of low levels of predation in trees (although rats and *E. rosea* will forage in trees), whereas all the extant *Leptachatina* species are ground dwelling. Nonetheless, all amastrid populations remain precarious, and all 15 extant species should be considered critically endangered. For example, the only two known populations of *A. spirizona*, in the Waianae Mountains, have been monitored for some years and are declining continually (V. Costello, personal communication). Our field work targeting Koolau Mountains amastrids, although limited, confirmed the results of previous extensive field work by one of us (D.J.D.C.), also specifically targeting amastrids, that no live amastrids have been found there since the 1970s. Without efforts specifically directed at conservation of these remaining

species, they will probably follow the fate of the vast majority of amastrids.

The IUCN Red List is not a good catalog of invertebrate extinctions. Its primary purpose, however, is to focus attention on extant species needing conservation action. Although strict adherence to the IUCN criteria for categorizing species according to threat level works well for mammals and birds, it cannot deal adequately with the immense diversity of invertebrates. Ours is a complementary approach for broadly assessing large and poorly known invertebrate groups.

As for any approach there are some caveats regarding ours, notably in the possibility and consequences of incorrectly reporting a species as extinct (e.g., Collen et al. 2010). However, for many invertebrates serious under-reporting of extinction may have even more serious consequences than over-reporting, especially regarding the true perception of the biodiversity crisis. Regarding amastrids specifically, we have little knowledge of their biology, for most of them we have only localities and collection dates. Nonetheless, this lack of knowledge is probably not a serious flaw in differentially assessing amastrid species because they share many characteristics, all being oceanic island species endemic to one archipelago and prone to the same causes of extinction.

An approach to assessing extinction such as ours could be used for other invertebrates with good historical records, especially those with restricted ranges such as islands, and may be the only reasonable way to

assess threats to such invertebrates rapidly enough to provide reasonably accurate approximations that could be used for conservation planning in the absence of more rigorous assessments based on the unattainable IUCN standard.

Acknowledgments

We thank R. Kawamoto for help in the Bishop Museum collections and archives, V. Costello, M. Severns, and K. Wood for sharing their knowledge and data, V. Costello for facilitating field work, students and colleagues who participated in surveys, B. Lefeuvre for help with maps, and T. Lee for discussion of how to adapt her method of inferring extinction. C.R. was supported by the Ars Cuttoli Foundation. R.H.C. was supported by a visiting curatorship at the Muséum national d'Histoire naturelle, facilitated by P. Bouchet and V. Héros. Surveys were supported by NSF grant DEB-1120906 and by grants from the U.S. Department of Agriculture, CAPS program, and from the Oahu Army Natural Resources Program.

Supporting Information

Tables of probabilities of being extant in 2013 for species evaluated as extinct (Appendix S1) and of being extant in 2025 for species evaluated as extant (Appendix S2) and a summary table of data for all the species we evaluated (Appendix S3) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Abdou A, Bouchet P. 2000. Nouveaux gastéropodes Endodontidae et Punctidae (Mollusca, Pulmonata) récemment éteints de l'archipel des Gambiers (Polynésie). *Zoosystema* **22**:689–707.
- Athens JS. 2009. *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. *Biological Invasions* **11**:1489–1501.
- Atkinson IAE. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pacific Science* **31**:109–133.
- Bouchet P, Abdou A. 2001. Recent extinct land snails (Euconulidae) from the Gambier Islands with remarkable apertural barriers. *Pacific Science* **55**:121–127.
- de Carvalho MR, et al. 2007. Taxonomic impediment or impediment to taxonomy? A commentary on systematics and the cybertaxonomic-automation paradigm. *Evolutionary Biology* **34**:140–143.
- Caujape-Castells J, et al. 2010. Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology Evolution and Systematics* **12**:107–129.
- Chau MM, Walker LR, Mehlreter K. 2013. An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. *Biological Invasions* **15**:355–370.
- Chiaverano LM, Holland BS. 2014. Impact of an invasive predatory lizard on the endangered Hawaiian tree snail *Achatinella mustelina*: a threat assessment. *Endangered Species Research* **24**: 115–123.
- Christensen CC, Kirch PV. 1986. Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. *Bishop Museum Occasional Papers* **26**:52–80.
- Chung D, Miyano L. 2001. Field survey of the land snails of Puu Hapapa and Waieli Gulch, Waianae Mountains, Oahu. Division of Forestry and Wildlife, State of Hawaii, Honolulu.
- Collen B, Purvis A, Mace GM. 2010. When is a species really extinct? Testing extinction inference from a sighting record to inform conservation assessment. *Diversity and Distributions* **16**:755–764.
- Coote T, Loève E. 2003. From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. *Oryx* **37**:91–96.
- Costello MJ, May RM, Stork NE. 2013. Can we name Earth's species before they go extinct? *Science* **339**:413–416.
- Cowie RH. 1995. Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution* **49**:1191–1202.
- Cowie RH. 2001. Can snails ever be effective and safe biocontrol agents? *International Journal of Pest Management* **47**:23–40.
- Cowie RH, Evenhuis NL, Christensen CC. 1995. Catalog of the native land and freshwater molluscs of the Hawaiian Islands. Backhuys Publishers, Leiden.
- Cowie RH, Hayes KA, Tran CT, Meyer III WM. 2008. The horticultural industry as a vector of alien snails and slugs: widespread invasions in Hawaii. *International Journal of Pest Management* **54**:267–276.
- Cox GW. 1999. Alien species in North America and Hawaii. Island Press, Washington.
- Duncan RP, Boyer AG, Blackburn TM. 2013. Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Sciences* **110**:6436–6441.
- Frankham R. 1998. Inbreeding and extinction: island populations. *Conservation Biology* **12**:665–675.
- Hadfield MG. 1986. Extinction in Hawaiian achatinelline snails. *Malacologia* **27**:67–81.
- Hadfield MG, Miller SE, Carwile AH. 1993. The decimation of endemic Hawaiian tree snails by alien predators. *American Zoologist* **33**:610–622.
- Hadfield MG, Sauffer JE. 2009. The demographics of destruction: isolated populations of arboreal snails and sustained predation by rats on the island of Moloka'i 1982–2006. *Biological Invasions* **11**:1595–1609.
- Hayes KA, Yeung NW, Kim JR, Cowie RH. 2012. New records of alien Gastropoda in the Hawaiian Islands: 1996–2010. *Bishop Museum Occasional Papers* **112**:21–28.
- Hembry DH. 2013. Herbarium specimens reveal putative insect extinction on the deforested island of Mangareva (Gambier Archipelago, French Polynesia). *Pacific Science* **67**:553–560.
- IUCN (International Union for Conservation of Nature). 2001. IUCN red list categories and criteria. Version 3.1. IUCN, Gland, Switzerland.
- IUCN (International Union for Conservation of Nature). 2014. The IUCN red list of threatened species. Version 2014.3. IUCN, Gland, Switzerland. Available from <http://www.iucnredlist.org/> (accessed February 2015).
- Kirch PV. 2011. When did the Polynesians settle Hawai'i? A review of 150 years of scholarly inquiry and a tentative answer. *Hawaiian Archaeology* **12**:3–26.
- Ladefoged TN, Kirch PV, Gon III SM, Chadwick OA, Hartshorn AS, Vitousek PM. 2009. Opportunities and constraints for intensive agriculture in the Hawaiian archipelago prior to European contact. *Journal of Archaeological Science* **36**:2374–2383.
- Leakey RE, Lewin R. 1996. The sixth extinction. Biodiversity and its survival. Weidenfeld and Nicolson, London.

- Lee TE. 2014. A simple numerical tool to infer whether a species is extinct. *Methods in Ecology and Evolution* **5**:791–796.
- Lomborg B. 2001. *The skeptical environmentalist: measuring the real state of the world*. Cambridge University Press, Cambridge.
- Lydeard C, et al. 2004. The global decline of nonmarine mollusks. *BioScience* **54**:321–330.
- May RM. 2011. Why worry about how many species and their loss? *PLoS Biology* **9** (e1001130) DOI: 10.1371/journal.pbio.1001130.
- May RM, Lawton JH, Stork NE. 1995. Assessing extinction rates. Pages 1–24 in JH Lawton, RM May, editors. *Extinction Rates*. Oxford University Press, Oxford.
- Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B. 2011. How many species are there on Earth and in the ocean? *PLoS Biology* **9**(e1001127) DOI: 10.1371/journal.pbio.1001127.
- New TR. 2008. Insect conservation on islands: setting the scene and defining the needs. *Journal of Insect Conservation* **12**:197–204.
- Nogueira SSC, Nogueira-Filho SLG, Bassford M, Silvius K, Fragoso JMV. 2007. Feral pigs in Hawai'i: using behavior and ecology to refine control techniques. *Applied Animal Behaviour Science* **108**:1–11.
- Novacek MJ. 2001. *The biodiversity crisis: losing what counts*. New Press, New York.
- Ponder WF, Carter GA, Flemons P, Chapman RR. 2001. Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology* **15**:648–657.
- Ponder WF, Lunney D. 1999. The other 99%: the conservation and biodiversity of invertebrates. The Royal Zoological Society of New South Wales, Mosman.
- Régnier C, Fontaine B, Bouchet P. 2009. Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conservation Biology* **23**:1214–1221.
- Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine, B. 2015. Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences* **112**(25):7761–7766.
- Richling I, Bouchet P. 2013. Extinct even before scientific recognition: a remarkable radiation of helicoid snails (Helicinidae) on the Gambier Islands, French Polynesia. *Biodiversity and Conservation* **22**:2433–2468.
- Rieth TM, Hunt TL, Lipo C, Wilmshurst JM. 2011. The 13th century polynesian colonization of Hawai'i Island. *Journal of Archaeological Science* **38**:2740–2749.
- Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffmann M, Brooks TM. 2006. The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution* **21**:71–76.
- Sartori AF, Gargominy O, Fontaine B. 2013. Anthropogenic extinction of Pacific land snails: a case study of Rurutu, French Polynesia, with description of eight new species of endodontids (Pulmonata). *Zootaxa* **3640**:343–372.
- Sax DF, Gaines SD. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences* **105**:11490–11497.
- Shiels AB, Flores CA, Khamsing A, Krushelnycky PD, Mosher SM, Drake DR. 2013. Dietary niche differentiation among three species of invasive rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*). *Biological Invasions* **15**:1037–1048.
- Simberloff D. 2000. Extinction-proneness of island species - causes and management implications. *Raffles Bulletin of Zoology* **48**:1–9.
- Solem A. 1976. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part 1. Family Endodontidae. Field Museum of Natural History, Chicago.
- Solem A. 1990. How many Hawaiian land snail species are left? and what we can do for them. *Bishop Museum Occasional Papers* **30**:27–40.
- Strong EE, Gargominy O, Ponder WF, Bouchet P. 2008. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* **595**:149–166.
- Sugiura S. 2010. Prey preference and gregarious attacks by the invasive flatworm *Platydemus manokwari*. *Biological Invasions* **12**:1499–1507.
- Thompson CJ, Lee TE, Stone L, McCarthy MA, Burgman MA. 2013. Inferring extinction risks from sighting records. *Journal of Theoretical Biology* **338**:16–22.
- Tuttle NC, Beard KH, Pitt WC. 2009. Invasive litter, not an invasive insectivore, determines invertebrate communities in Hawaiian forests. *Biological Invasions* **11**:845–855.
- Vermeij GJ. 2004. Ecological avalanches and the two kinds of extinction. *Evolutionary Ecology Research* **6**:315–337.
- Vié JC, Hilton-Taylor C, Stuart SN. 2009. *Wildlife in a changing world— an analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Willis F, Moat J, Paton A. 2003. Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern tropical Africa. *Biodiversity and Conservation* **12**:1537–1552.