

Article

Extinction through Climate Change: Review of Evidence and Analysis of Two Land Snails from the Seychelles Islands

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Abstract: Several extinctions have already been attributed, at least in part, to global warming, as climate change constitutes a serious threat for species living in isolated ecosystems and thus unable to track habitat changes. However, in all these cases extinction was due to human impacts, often directly but generally also through exotic invasive species. For two arboreal land snails in Indian Ocean islands a link has been proposed with decreasing rainfall. The decline (but probably not extinction) of *Pachnodus velutinus*, a specialist of moist forests on the summits of northwestern Mahé, was most likely caused instead by invasive plants altering its habitat and alien predators decimating the population in the small remaining moist forests. An alternative explanation assuming genetic swamping through hybridization with a species from lower elevations has no basis, as the presumed hybrid constitutes a distinct species able to survive in the altered, dryer habitat. On Aldabra Atoll, the endemic *Rhachistia aldabrae* was claimed to have been the first extinction due to climate change, but is still extant. No relationship can be detected between number of sightings and annual rainfall, although a weighted measure that takes into account rainfall in previous years suggests a limited impact of weather. Analysis of the sighting record in various ways yields a probability of survival over time that never dropped below 0.3. The decline was caused instead by intense impacts of exotic invasive species. Alternative shortcuts to evaluate extinction rates among poorly known species are shown to be unreliable. Although no contemporary extinction can still be attributed to climate change, indirect and synergistic impacts on biodiversity are expected, especially through promoting biological invasions.

Keywords: climate change; exotic invasive species; extinction; islands; land snails; Seychelles; sighting record

1. Introduction

How many species have gone extinct so far due to anthropogenic climate change? This may seem a tough question, given that it is hard to count absences in the darkness of long neglected impacts. There is no doubt that global warming constitutes a threat for many species [1–6], especially those on small islands [7–10] or island-like ecosystems [11]. In isolated ecosystems, there may be no place to go when local habitats become

altered beyond natural resilience. However, it is still unclear how biodiversity responds to climatic stressors [12]. Thus, although the threat is quite real and undeniably enormous, there can be no clear answer yet.

Even so, there have already been several claims of species extinctions caused by human modification of climate. Some of these have benefited from wide coverage by both scholarly journals and public media, but the evidence is simply not there—in all cases, direct human impact or the effects of exotic invasive species are the causal agents. Herein I show this by reviewing all cases of species extinction allegedly caused, at least in part, by climate change in the Red List [13].

There are, however, two cases that need a careful assessment, involving the apparent extinctions of land snails endemic to single islands in the Seychelles (western Indian Ocean). The decline of *Pachnodus velutinus* in the moist forest close to the summits of northwestern Mahé and *Rhachistia aldabrae* on Aldabra Atoll have been attributed to decreasing rainfall; in the former, also to genetic swamping through hybridization [14,15]. None of these scenarios agree with the data, as I show through findings in the field in the first case, and estimating the probability of extinction given the sighting record in the second. In both cases the rainfall record was taken into account; declines must be attributed instead to the impacts of exotic invasive species.

The importance and urgency of climate change research cannot be dismissed, yet there is a need for better science. No species has yet gone extinct through climate change, largely due to other impacts being stronger and more immediate; exotic invasive species are paramount, for two reasons: their spread and impacts are likely to increase as a consequence of climate change [16–20], and they may already account for the largest contribution to recent extinctions.

2. Materials and Methods

Cases to be analyzed are those species mentioned in the ecological literature and the IUCN Red List [13] as extinct, and attributed at least in part to climate change and severe weather. The literature was searched for references relevant to the specific extinction processes.

Field work was carried on 18 October 1993 on Mahé (Seychelles), searching for *Pachnodus* land snails along the path from Val Riche to the summit of Mount Copolia, in Morne Seychellois National Park. A personal collecting permit was granted by the Department of Environment of the Republic of Seychelles. All collected specimens are preserved in the author's museological collection (numbers CRA-4493 and CRA-4495). Species identification was based on both external features and dissection of genitalia. Broken shells were attributed to predation on the basis of experience with many other instances involving a variety of prey and predator species.

In the two cases where climate change has been explicitly invoked in a mechanistic way, local weather time series were examined for support to such hypotheses. Rainfall data for Mahé Island are from the station at Victoria [21]; those for Aldabra Atoll are from the station at Picard [22–23].

Polynomial regressions were calculated with the spreadsheet available from [24]. For the single case where an analysis of the sighting record has been presented, the original data and prior settings (Table 1) were introduced into the spreadsheets provided by [25,26].

3. Results and discussion

3.1. A variety of claims

Although most recorded (and inferred) extinctions have occurred on islands [9,27,28], assessing extinction rates is quite complex. For most species data are scarce, so it is exceedingly difficult to know population size and trend, and conservation status is often determined on the basis of unclear evidence. As a case in point, no less than 41 species extinctions have been attributed at least in part to climate change and severe weather [13,15]. The evidence, however, is missing for any link with anthropogenic climate change.

3.1.1. Oceanic island extinctions

Among the Hawaiian honeycreepers [29,30], the O'ahu and Lana'i akialoas, *Akialoa ellisiana* (Gray, 1860) and *A. lanaiensis* (Rothschild, 1893) are known from just three specimens each, all collected in the 19th century, although they may have been seen later on, before 1940. The Kaua'i akialoa, *A. stejnegeri* (Wilson, 1889) lasted until 1969, being wiped out by habitat destruction, invasive predators and imported disease. Two more recent avian extinctions on Kaua'i were due to the same causes: the Kaua'i O'o, *Moho braccatus* (Cassin, 1855) was common until the early 20th century, but in 1981 a single pair remained and the last call was heard in 1987; and the kamao, *Myadestes myadestinus* (Stejneger, 1887), once the island's most common forest bird, was last seen in 1985 (with an unreported sighting in 1991). Among Hawaiian bellflowers [31], *Delissea niihauensis* H. St. John, from Ni'ihau, has not been observed since 1870, and *Cyanea sessilifolia* (O. Deg.) Lammers, from O'ahu, was last recorded in 1946; the latter was heavily attacked by a plethora of invasive species. These seven species disappeared before climate change was perceived.

In other remote islands comparable cases occurred. The Reunion starling, *Fregilupus varius* (Boddaert, 1783) was last seen in the 1850s; it was so tame it was hunted with sticks; its habitat was ravaged by fire, felling and invasive mammals [32]. Two more recent extinctions are well understood: hungry humans captured all Wake Island rails, *Hypotaenidia wakensis* Rothschild, 1903 during World War II [33], and the Little Swan Island hutia, *Geocapromys thoracatus* (True, 1888) was readily eaten away by introduced cats in the early 1950's [34]. Also killed fast, but with a more prolonged agony, the Cape Verde giant skink, *Chioninia coctei* (Duméril & Bibron, 1839) was last seen in the wild in 1898, victim of predation by rats, cats and dogs; the final blow came from uncontrolled captures for the pet trade, although this allowed survival in captivity until 1940 [35].

For many other species, all we know is that they once existed. The millipede *Orthomorpha crinita* Attems, 1900 is known from a single specimen collected in 1894 in

Mahé [36]. This largest of the Seychelles Islands has lost virtually all of its native lowland forests. The cockroach *Margatteoidea amoena* (Bolívar, 1924) is known only from tiny Desroches Island in the Amirantes; it has not been recorded since 1905 [37], as the dense native forest was changed to copra plantation [38]. The small tree *Miconia abscondita* Majure, Judd & Skeeon 2015 was described on the basis of a collection dating from 1926 in southern Haiti; it probably disappeared through fire, felling and charcoal production [39]. Two beetles from the Azores are also listed [40]: the weevil *Neocnemis occidentalis* Crotch, 1867 was known only from a small forested area in Santa Maria, and the flightless carabid *Bradycellus chavesi* Allaud, 1919, known from a single specimen collected in Sao Miguel; as a considerable fraction of the endemics living on this archipelago, the almost complete destruction of the native forests and the impact of alien species are unequivocal causes. We can only guess at what has been lost without anyone recording its existence.

In two instances climate change or unusual weather might have struck a deathblow. The bellflower *Cyanea dolichopoda* Lammers & Lorence was discovered in 1990 in a remote site on Kaua'i. Only one mature specimen and three juveniles were sighted, and in 1992 they were swept by a landslide [41]. Whatever the proximal cause of this local disaster, the species had long been driven to a critical point by a plethora of local human impacts. This is the case of at least 34 of the 126 known species of the Hawaiian endemic genus *Cyanea* [42]. The Laysan rail, *Zapornia palmeri* (Frohawk, 1892) fell victim to habitat degradation by rabbits and guinea pigs, and predation by rats introduced also during World War II. However, two introduced populations on low-lying islet were spared... until they were wiped out by storms [43] —this just shows that the previous absence of the bird on those islets had a good reason.

Altogether, and in spite of various claims, none of these insular extinctions can be attributed to climate change.

3.1.2. Continental extinctions

On continents, changing weather has been invoked in several extinctions. In spite of previous hypotheses involving global atmospheric changes [44], it is now clear that the widespread decline of amphibians is causally linked to the human-induced expansion of chytridiomycosis [45,46]. Still, nine anuran extinctions are listed as due in part to climate change: Wyoming toad, *Anaxyrus baxteri* (Porter, 1964), Jambato toad, *Atelopus ignescens* (Cornalia, 1849), longnose stubfoot toad, *Atelopus longirostris* Cope, 1868, Pass stubfoot toad, *Atelopus senex* Taylor, 1952, McCranie's water frog, *Craugastor chrysozetetes* (McCranie, Savage & Wilson, 1989), Sierra de Omoa streamside frog, *C. omoaensis* (McCranie & Wilson, 1997), Corquin robber frog, *C. anciano* (Savage, McCranie & Wilson, 1988), Heredia robber frog, *Eleutherodactylus escoces* (Savage, 1975), and Monte Verde golden toad, *Incilius periglenes* (Savage, 1967). It is unclear why a hypothetical, unidentified impact persists in conservation assessments even when the smoking gun has been unequivocally identified.

Equally remarkable is the mention of climate influence on other continental extinctions. In three instances, the cause of extinction was directly linked to human activities. The Pampean fox, *Dusicyon avus* (Burmeister, 1866) was once common in

southern South America, but vanished just over three centuries ago. At that time the original grasslands experienced deep changes [47]. The canid's habitat was trampled by vast herds of feral ungulates, and horses allowed humans to move and hunt faster than ever before. The South African bluebuck, *Hippotragus leucophaeus* (Pallas, 1766) was greedily hunted to oblivion around 1800. It might have been already rare and spatially limited [48], but it would most likely be still extant had it not been exterminated along with the human communities who shared its habitat [49,50]. The Australian Paradise parrot, *Psephotellus pulcherrimus* (Gould, 1845) was last seen in the 1940s, having suffered intense predation by introduced mammals and humans, as well as widespread habitat destruction, including termite mound razing and invasion by pricklypear, *Opuntia* spp. [51].

In other cases, the impact of humans might have been indirect, through habitat alteration. The weevil *Trigonoscuta rossi* Pierce, 1975 was apparently limited to the sand dunes at Fort Ross in northern California. It was last found in 1975; an unregistered rise in sea level has been held responsible. However, in that coastal vegetation cattle grazing prevents invasive plants to overgrow native ones [52]. Thus, the beetle's demise may have paradoxically been caused by inclusion of its habitat in Fort Ross State Park in 1973, when intensive ranching stopped. The perennial herb *Eriocaulon inundatum* Moldenke, 1951 is known only from two specimens collected in 1943 in the estuary of the Saloum river in Senegal; after failure to locate any living individuals, increasing droughts were listed as a threat, when in fact the area has been thoroughly destroyed by extensive salt mining. The shrub *Faramea chiapensis* Borhidi, 2006 lived only in a small area of cloud forest in Chiapas [53]; although its taxonomic status is unclear [54], the whole area appears to have been destroyed for cultivation [55].

As on islands, there is no evidence for climate change playing any role in these continental extinctions.

3.1.3. Freshwater extinctions

Freshwater ecosystems share their isolated nature with true islands, and their biodiversity is severely threatened. Yet, five freshwater species are listed by IUCN as extinct due to climate change, three of which are fishes. The Utah Lake sculpin, *Cottus echinatus* Bailey & Bond, 1963 was last seen in the 1920s, victim of pollution and introduced predators [56,57]. The cichlid *Tristramella magdelainae* (Lortet, 1883) was described from specimens collected in the mid-19th century in Damascus, Syria, but its whole habitat has long been destroyed. Nevertheless, its taxonomic distinctness is questionable, so it is likely to be extant [58]. In a similar way, the cyprinid *Telestes ukliwa* (Heckel, 1843) was listed as extinct since 1988, when exotic fishes thrived in the only river it inhabited in Croatia; it is still extant [59].

The other two freshwater species listed are springsnails. *Pseudamnicola desertorum* (Bourguignat, 1862) is known only from its original description from a thermal spring in Algeria that no longer exists. It is likely a synonym of *P. letourneuxiana* (Bourguignat, 1862), described from the same locality and still extant elsewhere [60]. Its disappearance from the type locality cannot be attributed to atmospheric events. *Graecoanatolica macedonica* Radoman & Stanovic, 1978 was endemic to shallow habitats in Lake Doiran,

on the Macedonian-Greek border. Water extraction from this lake caused a fatal drop in water level in the 1970's and 1980's [61].

These cases highlight the fact that abuse of water resources and the spread of exotic species are caused by human stupidity, not climate change. They support the general finding that direct human impacts on rivers are extinction triggers much stronger than those derived from predicted climate change [62].

3.1.4. The first mammalian casualty?

The murine rodent *Melomys rubicola* was restricted to Bramble Cay, a tiny flat island isolated in the Torres Strait between Australia and Papua New Guinea. It is now surely extinct [63]. It was concluded that climate change had a paramount role in its demise, with increasing storm surge destroying its dwindling habitat. Thus it was widely announced as the first mammal species to become extinct due to climate change [64]. The story, however, is a bit more complex.

The Erubam Le people have long visited the key to harvest fish, turtles and birds; at least in the 1970s, they were actively catching melomys by beating them with sticks. Killing for fun, European crews extensively hunted the species in the late 19th and early 20th centuries. Just as wastefully, Australian fishing boat crews released dogs on the island to chase the rodents, at least until around 2000. Native title rights were granted over most of the island in 2004 [65], likely increasing hunting pressure on a critically small population. Clearly, all human groups hunted the naive rodent beyond any sustainable catch.

Thanks to protection, nesting seabird populations have increased sharply. In 2014 most of the remaining, severely degraded vegetated area was occupied by seabirds, numbering some 18 000 pairs. Green turtles nest at high densities and trample the whole island. In nearby Raine Island, nesting females increased between 1975 and 2005, from some 1 000 to nearly 14 000 [66]. The melomys were known to avoid areas occupied by roosting seabirds. In 2011 all traps set in Bramble Cay were damaged, moved or buried by turtles. In 2014 no suitable terrestrial habitat remained. The comeback of breeding fauna had an unforeseen impact because the island itself has changed. The phosphate rocks that make the island's core were heavily mined; now they stand just 3 m above high tide. Thus, susceptibility to unusual storms and trampling did not derive from a rising sea level, but from a human-made lowering of the island.

Under these threats, it is not surprising that the melomys population crashed, from several hundred in 1978 to an estimated 92 in 1998; in 2002 only 10 remained, and the last lonely sighting occurred in 2009, before any survival plan was devised. Invoking climate change for this decline lacks any evidence whatsoever. Besides, this media-oriented, unscientific stand only fostered a fatalist attitude that effectively prevented urgent conservation action [67]. The cause of the Bramble Cay melomys extinction was sadly all too usual –human encroachment in the form of unlimited hunting, thorough ecological disturbance and the impact of alien predators.

3.1.5. Two pseudo-extinctions in remote islands

After discarding spurious claims for most cases of extinctions caused by climate change, two remain where some climatic factor may have been involved in a plausible, mechanistic way. These involve land snails belonging to the family Cerastidae, a taxon of puzzling biogeographic origins living in Africa, south-western Arabia, central and southern India, Sri Lanka, Nepal, Thailand, New Guinea and Australia, as well as on islands of the western Indian Ocean [68–72]. The two species discussed below live in single islands of the Republic of Seychelles.

The land snail *Pachnodus velutinus* (Pfeiffer, 1841) is known only from the permanently moist forest at the summits of northwestern Mahé. In contrast to most other congeners its shell is exceedingly thin, given that it is never exposed to desiccation. At lower elevations, in considerably less humid forests, *P. niger* (Dufo, 1840) is found. In the rather wide belt in between, a third taxon occurs (Figure 1). This has been considered a hybrid between the other two species, because its external morphology appears somewhat intermediate, individual variation does not follow a geographical cline, and all three taxa will mate and produce offspring in captivity; the putative hybrid expanded uphill and *P. velutinus* apparently disappeared in 1993, so this was interpreted as a documented case of genetic swamping [14]. It was later on reassessed as caused by climate change, in the form of reduced rainfall [73]. Either scenario is highly problematic.

The last candidate for extinction through climate change is the reported disappearance of the land snail *Rhachistia aldabrae*, endemic to the remote Aldabra Atoll in the tropical Indian Ocean (Fig. 4). It was not observed alive for several years and was thus proposed to have been an early victim of global climate change [15]. This species has recently been observed alive [74], stirring considerable debate over such premature claim [75]. This rediscovery highlights two problematic issues: in terms of methodology, it casts doubts on the tools available to assess species extinction; for the credibility of climate change science, it is relevant to revise this case.

3.2. A stronghold at the summit

In 1993, which was a mildly dry year, I observed the putative hybrid *Pachnodus* successfully colonizing the altered habitat along the western slope of Mount Copolia (Figure 1). Between 430 and 495 meters altitude, the invasive cinnamon tree (*Cinnamomum verum*) and the vanilla vine (*Vanilla planifolia*) had largely displaced native vegetation. However, this snail was not rare on the trunks and branches, from 0.4 to 2.0 meters above the ground. All specimens were active, apparently feeding on small lichens growing over the cinnamon's bark. Its range ended abruptly where the very moist cloud forest remains near the summit.



Live specimen of the *Pachnodus* species living on invasive cinnamon in the disturbed vegetation on the western slope of Mt. Copolia (Mahé, Seychelles; 20 October 1993; CRA-4473).

This native habitat formed a narrow belt between 502 and 511 meters altitude on the southern (wettest) slope, below the bare granite extending to the summit (529 m). Here the thin-shelled upland specialist *P. velutinus* was quite common (Figure 2). Live specimens, both adult and juvenile, were crawling on the wide leaves of the native palm Latanyen Lat (*Verschaffeltia splendida*), about 1 m above ground; there were also specimens on the wet litter on the thin soil.

All specimens of *P. velutinus* were fairly uniform in shape and coloration, and none could be deemed hybrid. On the ground there were some broken shells, most likely resulting from predation by the alien tailless tenrec, *Tenrec ecaudatus*. Obviously, the species was alive and not rare the year it was supposed to have gone extinct.

3.2.1 No genetic swamping

It has repeatedly been postulated that range shifts triggered by climate change may drive rare taxa to extinction through genetic (or just demographic) swamping. Although the idea is compelling, there is little evidence to back this prediction; the outcome of hybridization may vary widely, and extinction risk from it seems to depend on the ecological context [76, 77]. In the case of *P. velutinus*, this scenario is highly problematic.

There is no reason whatsoever to support the idea that the *Pachnodus* taxon living at intermediate elevation could be a hybrid, nor did I find any specimen that could indicate introgression into the species living in the mist forest. Mating between closely related land snail species (as reported by [14]) is not uncommon, although the viability and fitness of the F1 is unknown; no morphological feature in the observed *P. velutinus* could indicate past hybridization. The only pattern that can be extracted from my field observations is an expansion of the species living at intermediate elevation, as invasive vegetation displaces the native forest.



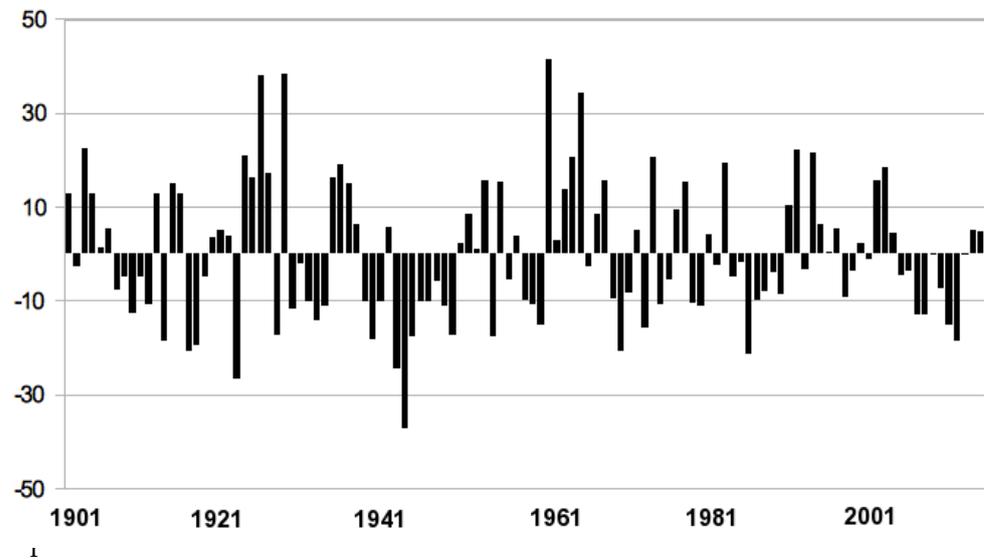
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of the mist forest endemic *Pachnodus velutinus* near the summit on the southern slope of Mt. Copolia (Mahé, Seychelles; 20 October 1993; CRA-4475). The specimen at left was live collected; shell length (along coiling axis) is 17.1 mm. The other two shells are remains of predation, likely by the invasive afrosericid *Tenrec ecaudatus*.

3.2.2. Dry and spicy, not sexy

There was no unusual climatic variation in Mahé when *P. velutinus* became scarce: between 1972 and 1993, rainfall fluctuated as usual, and only moderately so around the long-term average (Figure 3). Thus, the purported relationship between reduced rainfall and the apparent extinction of this species must be discarded.

A more likely alternative is that *P. velutinus* is disappearing as the highest forests in Mahé are altered by invasive species. The spread of cinnamon has been taking place there for decades, with pervasive consequences on native ecosystems [78,79]. The spread of this small tree substitutes a monospecific stand with no understory for the once lush rainforest, rendering a much drier habitat. From a snail's perspective, changes in temperature and water regime must stay within its ability to cope with it through physiological response [80]. Thus, areas invaded by alien vegetation become unsuitable habitat for the narrow-range summit's endemic. Thus, the decline in snail abundance in the native forest cannot be attributed to any climatic factor.



cent departure of annual rainfall from long-term (1901-2015) average (1692.615 mm) in Mahé, Seychelles. This time series shows no trend distinguishable from the x-axis ($y = -0.013x + 0.719$, $R^2 < 0.0001$); the same applies for the segment between 1972 and 1983 ($y = -0.018x - 0.273$, $R^2 < 0.0001$).

Predation by the tailless tenrec is an additional serious threat. This is a highly adaptable afrosericid native to Madagascar that was introduced into several Indian Ocean islands. It is a voracious omnivore, and is exceedingly prolific. It appears to be responsible for stark declines of native land snails on the Seychelles [32,81,82]. Thus, the culprit of the declining demography of *Pachnodus velutinus* is not climate change, being instead the impact of exotic invasive species.

At any rate, declaring this moist forest specialist extinct seems premature on the basis of the few data available and the small proportion of its range actually explored.

3.3. The first claim was unwarranted

3.3.1. Snail hunting in the scrub

Live specimens of *Rhachistia aldabrae* are quite conspicuous, at least at a short distance (Fig. 4). Perhaps surprisingly, the data on collections (Fig. 5a) are very scanty [15,83], and the few specimens collected in the 20th century were the outcome of fortuitous encounters and casual collecting [84]. In the first place, only a tiny fraction of the island's area was explored in any of the visits that yielded some specimens, as well as in the last two that were planned to look for this species. Finding arboreal snails in a thicket is not easy and potential habitat in Aldabra extends over some 110 Km² of very rough terrain. In fact, exploration of this atoll is still yielding the discovery of new

species, including a mammal [85]. Yet, the question is whether the U-shaped distribution of encounters with this species can tell anything.

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dabrae on bushes in the thicket of Aldabra (Seychelles). (Photograph by Martin van Rooyen, courtesy of the Seychelles Islands Foundation).

The link between number of snails found (dead or alive) and climate change was proposed on the basis of a linear regression on annual rainfall [15]. Although rainfall (both annual and wet-season) has been steadily diminishing in Aldabra over the last four decades [22,86], the yearly drop is just about 0.5% of the mean. Moreover, there is extreme variation, up to nearly four-fold differences among consecutive years [22]. Even so, a positive relationship between snail abundance and rainfall was reported. However, the reported analysis contains inexplicable errors: data from 1996, 1989, and 2000 were missing; rainfall in 2006 was 1788 mm, not 1000 mm; and number of snails for 1975, 1976, 1977, 1998 and 2006 must be corrected to 12 (not 1), 10 (not 5), 1 (not 23), 0 (not 7) and 0 (not 1), respectively.

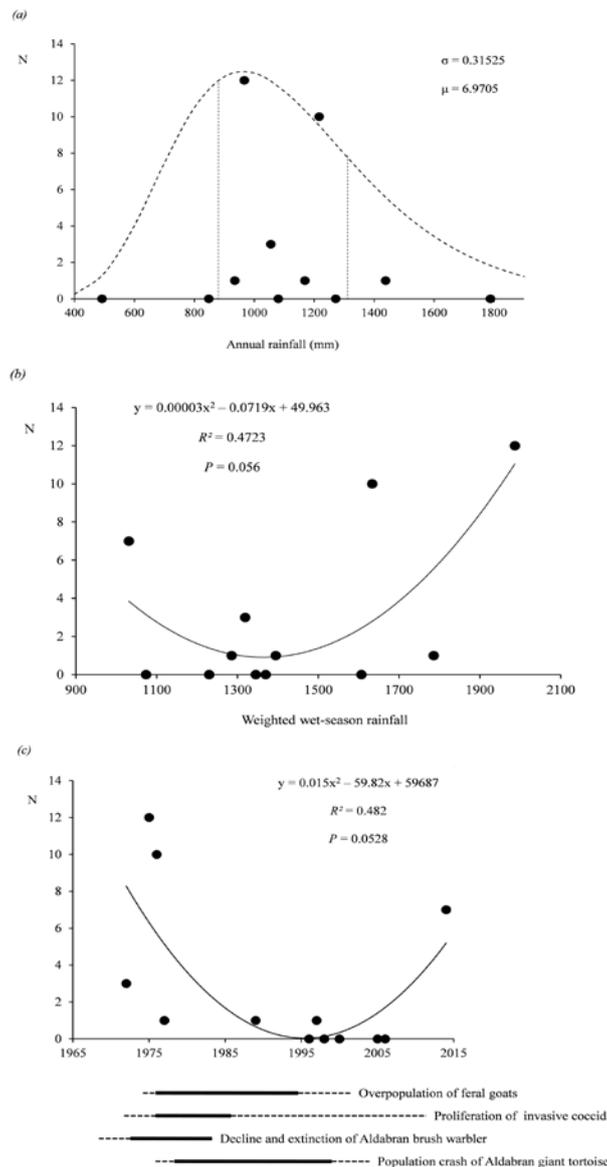
Taking the raw snail counts and annual rainfall data (exact values from [22,86]), the graph looks very different indeed (Figure 5a). These two variables show no relationship at all ($R^2 = -0.003$; adding the data point for 2014 does not improve this result). The only pattern is that all snails were found in years with medium-range rainfall. Thus, the only thing one can say is that if you are going snail hunting in a tropical dry scrub, you should rather choose a good year. It is wise to avoid very dry years, because there will be few snails and these will be well hidden. And it is advisable to avoid very wet years as well, because field work will be miserable and snails too hard to spot in lush vegetation.

Now, taking rainfall data from a few years in a row prior to each collecting event does make sense. Mathematically, this is so because climate data are autocorrelated. This means that the search for climate change trends taking data points in a time series as independent is grossly inadequate [87,88]. In biological terms, it's because the impact of good or bad years is cumulative: finding a snail in a seasonally dry biome implies that there have been reasonable conditions during the last wet seasons, most importantly the most recent ones. Thus, a weighted measure can be devised as the sum of last wet season's rainfall plus half that of the preceding plus a fourth of the one before. Doing this reanalysis, a U-shaped relationship appears between number of snails found and weighted wet-season rainfall (Figure 5b). Although this relationship does not reach standard significance, high cumulative values mean finding more snails under favorable conditions than during dry spells, as expected. However, weather alone cannot explain why snail abundance drops at intermediate values.

3.3.2. An alternative explanation

A top-down control of the snail's population dynamics by introduced rats may occur on Aldabra. These are likely the major predators of *R. aldabrae* (at least one rat-predated shell was found [89]). Rat populations are largely bottom-up controlled by rainfall in seasonally dry environments [90], peaking at intermediate values of cumulative rainfall [91]; in the Aldabran mixed-scrub, rats breed only during the wet season [92]. Thus, the snail population is likely controlled by the fluctuating abundance of invasive rats. Its survival under such intense predation may be attributed to isolated evolution under the perennial presence of abundant native predators such as land crabs. This is likely the case among island birds [93]. Indeed, the native flightless rail, *Dryolimnas (cuvieri) aldabranus* is apparently resistant to rats, although it survives only where feral cats are absent [94]. For at least some island endemics, coexistence with invasive predators may be possible if their behavior and life history turn out to be exaptations.

The snail's decline might have been caused by the combined effects of several exotic invasive species (Figure 5c). Non-native species have deep effects on island ecosystems [20,46]; remote and inhospitable Aldabra is no exception. The atoll's vegetation suffered heavily from prevalent damage by goats, whose population exploded between the setting of a research station by the Royal Society in 1971 and culling of some 1 800 individuals between 1987 and 1997 [95–101]. Native woody plants were also strongly affected by the invasive coccid *Icerya seychellarum*, first noticed in 1968, peaking in 1975 and subject to biological control since the late 1980's [102]. Habitat degradation and direct predation by introduced rats are deemed responsible for the extinction of the endemic Aldabran brush-warbler, *Nesillas aldabrana*, discovered in 1968. There were just five individuals in 1975, only one of which remained in 1977, to be last seen in 1983 [95–103]. Likewise, the endemic Aldabra giant tortoise, *Aldabrachelys gigantea*, experienced a population decline of 22 % in total and up to 93 % locally between 1974 and 1997, directly attributable to browsing and shade removal by goats [100]. This downward trend continued until a further overall reduction to half the original count between 1999 and 2002; in 2003 the tortoise population started to recover [104].



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early recorded abundance of *Rhachistia aldabrae* (N, live snails and recent shells) with rainfall over time. (a) Annual rainfall is unrelated to snails recorded ($R^2 = 0.003$, $P = 0.881$; datum for 2014 not included, but has no effect). A log-normal distribution is fitted to discriminate records from favorable years (50% central range). (b) Snails recorded tend to a U-shaped plot against weighted rainfall during successive wet seasons. (c) Snail records crashed and recovered during the study period, coinciding with demographic changes in other species.

The apparent extinction of *R. aldabrae* coincided with these other declines and the highest intensity of the causal impacts, thus it might have been a real population downfall. However, instead of climate change, it's the ecological changes triggered by

exotic invasive species that look wrought havoc on that remote island. The snail's rediscovery might be a symptom of that fragile ecosystem's recovery under sound management in recent years.

3.3.3. The sighting record is key

Even if many extinctions are predicted as a consequence of human-induced climate change, no island snail species appears to have fallen yet to this global threat. Yet, many island-endemic snails are barely known, very poorly sampled and increasing a largely undocumented extinction wave [27,105]. There is a need to evaluate the status of ill-known species with scant data under multiple, synergistic threats. The challenge is thus to use robust statistical methods aimed at narrowing uncertainty about species survival.

Often only a sparse sighting record is available, but from this evidence it is possible to calculate the probability of a species being extinct over time [106,107]. Bayesian methods that give the probability that a species is extant given the sighting data have the advantage of incorporating prior information that allows using different types of information in a transparent, repeatable way [108,109]. All of these should perform well provided that they are selected in accordance with the most limiting factor – the data [25,109]. Indeed, a sighting record contains much information [110] that must be understood along with the underlying processes [111–115].

Using Solow's original Bayesian method it was concluded that the probability of *R. aldabrae* being extinct reached significance in 2006 [15]. However, that analysis started with a non-informative prior. In fact, a reasonable prior is needed for a successful Bayesian model [26,109,116,117] given that it will increase accuracy [26] and especially prevent the sighting data from dominating the calculation of the posterior probability [109,118]. Thus the data can be reanalyzed with adequate methods.

Early collections cannot be considered comparable to more recent ones, so it seems sensible to consider only data obtained after the research station was established. Entering these data into the simple, freely-available spreadsheet provided by Rivadeneira and colleagues [25,119], under a constant sampling effort, the upper boundary of a 95 % confidence interval calculated with Solow's frequentist method [106] is 2017. This method tends to underestimate time to extinction, so a better option is the optimal linear estimation [120], which is unbiased, accurate with more than ten sightings and robust against false extinctions [25,109,121]. Using the same spreadsheet, this improved method yields a revised upper boundary in 2023. This may be suspect, because variations in survey effort in Aldabra have been prominent, due to different goals during the widely spaced collecting trips, as well as to the snail's progressive restriction to undisturbed habitats.

Indeed, when the probability of sighting a species decreases over time, either due to a lower sampling effort or a real demographic decline, or a synergistic combination of these two factors, the basic assumption that the sighting series should be produced by a random stationary process is violated, and thus many of the methods perform poorly [25,117]. Likewise, the kind of survey affects the sighting rate, and this in turn affects the performance and accuracy of various methods [121]. The analysis can thus be repeated

considering three sampling efforts: 1 for very dry and very wet years, 2 for intermediate years, and 3 for the last two surveys specifically designed to locate the species. The outcome is again 2023.

Survey information additional to the sighting record [122] and uncertainty in the prior belief that the species is extant are explicitly included in the user-friendly, freely available spreadsheet by Lee [26]. First, detectability bounds must be stated as the probability of seeing a specimen: 0–0.5 is generous (Table 1). Next, survey quality bounds have to be entered as the probability of seeing the species given that it is extant. This can be conceived as the product of encounter rate (probability of hitting occupied habitat along a transect) and species detectability (probability of detecting at least one specimen). Thicket patches large enough (above the percolation point as defined in [123]) are uncommon and scattered, mostly on the southern half of the atoll. It seems safe to assume an encounter rate between 0.02 in the south and 0.2 in the north. Three different survey types can be recognized, with optimistic bounds: 0.05–0.4 for survey 1 (unfavorable years), 0.1–0.8 for survey 2 (favorable years), and 0.8–0.9 for survey 3 (last two surveys, aimed at this species). Finally, a prior of survival is 0.84–0.96. This is the probability that the species is extant in at least one patch of scrub not overgrazed by goats on the atoll's southern half and/or in at least one growth not razed by rats on the north, each of these set as 0.6–0.8. With these inputs, $P(e)$ for 2006 is 0.529 (variance 0.079). However, $P(e)$ decreases over time in the absence of sightings (Figure 6). This underestimation artifact stems from assuming a uniform rate of sightings; it underscores the need of well-planned surveys [26,117,121,124,125].

Table 1. Settings for Bayesian calculation of $P(X | s)$ for *Rachistia aldabrae*.

Detectability bounds (P of seeing a living specimen): $D = 0-0.5$

Survey quality bounds (P of seeing the species in survey x given that it is extant): $d_x = e h_x$

encounter rate (P of hitting occupied habitat along a transect): $e = 0.02-0.2$

detectability in habitat (P of detecting there at least one specimen, h):

$$h_1 = 0.05-0.4 \qquad d_1 = 0.001-0.08$$

$$h_2 = 0.1-0.8 \qquad d_2 = 0.02 - 0.16$$

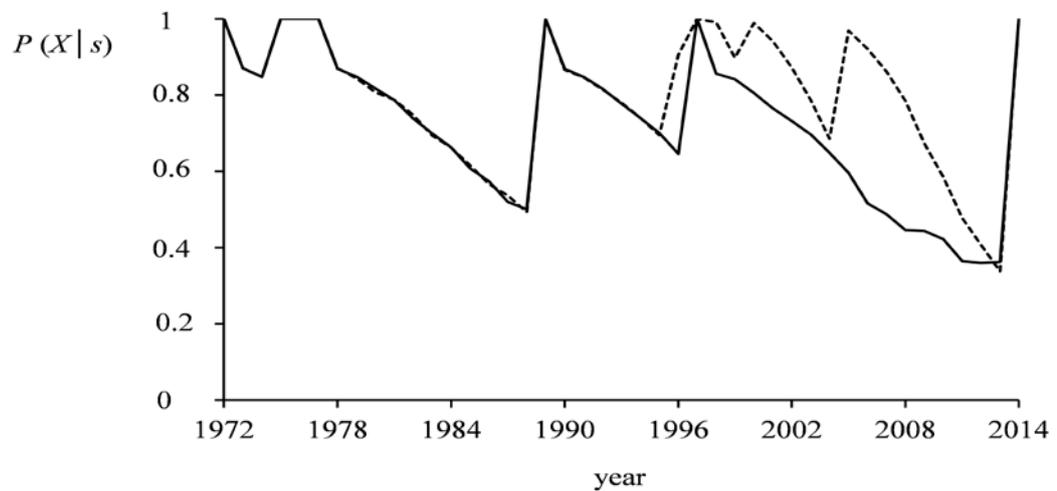
$$h_3 = 0.8-0.9 \qquad d_3 = 0.016-0.18$$

Prior belief that the species is extant: $P(X) = 1-(1-P_S) \cdot (1-P_N) = 0.84-0.96$

P_S (P that it survives in at least one suitable patch on southern half): $P_S = 0.6-0.8$

P_N (P that it survives in at least one suitable growth on northern half): $P_N = 0.6-0.8$

False detectability bounds (probability of seeing an old shell if extinct): $f = 0-0.01$



bility of *Rachistia aldabrae* being extant over time, given the sighting record. The solid line stands for certain sightings (live snails and recent shells); the dashed line shows values when including uncertain (old shells).

Old shells (found in 1996, 1998, 2000 and 2005) are a likely signal that the species is extant. This kind of data should not be discarded, but treated instead as uncertain sightings [26,112,122,126–128]. Shell decay varies with species, habitat and climate [129,130]; the fairly thin shells of *R. aldabrae* should degrade in about three or four years. False detectability bounds (probability of seeing an uncertain given the species is extinct) may optimistically be set at 0–0.01. $P(e)$ in 2006 then raises to 0.922 (variance just 0.009). Extending the analysis to every year in record, a tighter, shallower jigsaw graph reflects this increase (Fig. 6). From the sighting record alone, it is clear that there were no grounds to declare the species extinct.

Eventually, evidence points at exotic invasive species as the cause of a strong population bottleneck in the case of *R. aldabrae*. This snail appears to be sensitive to variations in rainfall, and lives only in a low-lying island. Thus it is indeed at high risk from climate change. The good news is that its rediscovery is a symptom of recovery of Aldabra's fragile ecosystems under sound management in recent years. For other species endemic to islands it's simply too late, and many are severely threatened by even a moderate rise in sea level.

3.4. Dangerous shortcuts

Perhaps not surprisingly, methods aimed at circumventing the previous considerations have been devised. One shortcut consists in using non-informative priors to analyze a sighting record[131,132]. Unfortunately, such priors happen to be strongly

informative and depending on human uncertainty; a prior that explicitly takes into account factors involved in the extinction process will yield a more reliable estimate [118].

A more radical shortcut involves a discrete probabilistic model that pools data from many species in order to estimate extinction parameters [133]. In principle, this has the advantage of allowing to consider sighting records that contain very few data points, often only one. Thus it was applied to a large set of worldwide, randomly chosen land snail species, with the aim of assessing specific and overall extinction rates [133,134]. However, this method suffers from serious shortcomings. On statistical grounds, it has flaws: a uniform prior to start with, considering different species as independent replicates, assuming a constant probability of being collected, and aiming at a common parameter in timing. In the real world, species vary widely in detectability, threats often affect in parallel several species, the historical vagaries of biological exploration have left a strong imprint on data available, and species differ enormously in their susceptibility to extinction.

Besides, the data used to test the model suffers from serious shortcomings. It includes several ill-assessed species, such as *Papillifera papillaris* (Müller, 1774) which is invasive outside of its native range in Sicily and southernmost Italy [135,136]. In addition, the "random" selection of 200 species involved a random picking of genera and then repeating the selection including all species in each chosen genus. This procedure is effectively biased to select island species, for two reasons: island dwellers often have unusual morphologies and thus have often been placed in separate genera, at the expense of rendering related continental genera paraphyletic; and island genera often include unusually large numbers of species (and subspecies). Thus, the outcome that extinctions are concentrated on island-rich regions is partly an artifact.

As shown above, many species are known from single records, but just some of these have been declared extinct. Assessing whether they are extant cannot be reliably solved through models, needing instead field work, or at least updated evaluations of habitat suitability [137–139]. Eventually, attempts to assess conservation status and extinction rates for poorly known taxa are just as good as the evidence available.

4. Conclusions

Although no recorded extinction can be attributed to climate change, this is a paramount threat to biodiversity. The cases examined support the general rule that invasive species and habitat destruction are the two major causes of biodiversity loss, especially on islands [8,16,140,141]. In the case of biological invasions, denying their impact on extinction rates [142] seems untenable; it is probably more productive to search for common patterns that may yield predictive power [20,46,143]. How these factors will interact with climate change is the key question; it has not been comprehensively assessed [9], but the role of human activities appears to be the ruling factor [144]. The point is that ecosystems are complex, simple explanations seldom, direct human impacts prevalent, and indirect effects varied and intense.

Something is clear about the impact of global climate change on biodiversity—it will have a profound impact on species distributions, and those unable to follow will likely become extinct. However, the time lag predicted until extinction actually occurs varies widely across taxa. In low-dispersal, short-lived, restricted-range species, the lag will be shorter [145]; for many plants, in contrast, it may be quite extended [28]. In addition, predicting range shifts is far from straightforward, because it must take into account critical factors such as life cycles involving ecologically distinct areas [146], human-induced modifications in species distributions [147], survival in marginal refugia as disturbance relicts [46,148–150], physiological and behavioral plasticity [6,151], and their interactions [2,121,152,153]. There is thus much scope for ambitious, proactive programs centered on prevention of impacts on island ecosystems [154]. This can only be achieved through careful monitoring and analyses.

In all the cases analyzed herein, climate change is not (still) an issue. In exchange, a pattern appears where exotic invasive species have played a critical role in many (perhaps most) recorded extinctions. Indeed, the impacts of aliens (surely always reinforced by direct human impacts) may actually be the main cause of species extinctions in the Anthropocene. Yet, a troubling combination of factors seems to be growing, as climate change promotes biological invasions [16–20,155]. Disentangling the contributions of different causes becomes increasingly critical.

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