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Review

A synthesis of terrestrial species extinctions in the Macaronesian Islands and their correspondence with human occupancy

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Abstract

We present the first synthesis of all known terrestrial endemic species extinctions in the biogeographical region of Macaronesia, covering all archipelagos (Azores, Madeira, Selvagens, the Canaries, and Cabo Verde) and multiple taxa (arthropods, birds, bryophytes, fungi, land molluscs, lichens, mammals, reptiles, and vascular plants). This list also includes information on the original distribution of extinct species, extinction chronologies, and likely causes of extinction, as reported by the original works' authors. Our survey identified 220 extinction records, with the highest numbers observed among land snails (111 species), arthropods (55), birds (27), and reptiles (15). The proportional impact of extinction was greatest among vertebrates: birds (50% of the original endemics lost), mammals (43%), and reptiles (28%). Very few extinctions were recorded in vascular plants or bryophytes, and none in fungi or lichens. However, these low levels of loss may partly reflect the scarcity of historical and fossil records for these taxa. Exactly half of the recorded endemic species losses (including nearly all vertebrates, as well as the arthropods and vascular plants) have extinction chronologies matching with the human occupation of the islands, providing a minimum estimate of the number of extinction events that may be directly or indirectly attributed to human activities.

Keywords: anthropogenic change, biodiversity loss, human colonization, island extinctions, Macaronesia

Introduction

Islands are renowned for their outstanding evolutionary radiations and for contributing ~20% of global terrestrial biodiversity, despite occupying only 6.7% of Earth's land area. Unfortunately, they also contribute disproportionately to the tally of endangered (~50%) and postdescription extinct species (~75%) (1). The latter are those that have vanished after having been observed alive, described, and cataloged, since the initiation of European worldwide expansion at the end of the 15th century. Within this period, the likelihood of an insular endemic species becoming extinct has been ~12 times higher than for a continental species (1). Anthropogenic extinctions before this period are less well-documented, but for those earlier-occupied islands for which good data are available, rates of extinction in their pre-European settlement typically are comparable with or surpass those of the European settlement period (2–4).

A species is considered extinct when there is no reasonable doubt that its last individual has already disappeared after exhaustive searches have been made of the known or expected habitats, in the appropriate times (e.g. day/night, seasons) and across the known historical distribution (5). Where sufficiently thorough data are lacking, it may be more appropriate to classify a species as "likely to be extinct." The eventual rediscovery of species thought to be extinct is exemplified by two species of "giant"

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lizards of the Canarian endemic genus *Gallotia*: *Gallotia simonyi* from El Hierro and *Gallotia bravoana* from La Gomera (6); such species are termed Lazarus species (7).

When species go extinct, their ecological functions are inevitably lost as well (8). If the extinct species was a keystone or engineer species (i.e. those exerting an important and distinctive role in the ecosystem), which is not directly matched by any surviving species, then the extinction event can produce trophic cascade effects affecting many other species. In an insular context, the loss of indigenous vertebrates (mainly land birds and reptiles) can have particularly large impacts on pollination and seed dispersal services, with serious knock-on implications for native plant communities (9–11). Species coextinctions occur where the extinction of one (or more) species that have close ecological relationships with another (e.g. exclusive parasites or pollinators) leaves behind "widow species" that cannot persist and so also go extinct (12, 13).

Anthropogenic extinction is generally nonrandom and arises mostly from overexploitation, habitat loss, and competition with, or predation by, anthropogenically introduced nonnative species (4). The sequence in which species are extirpated locally (e.g. from an island) or driven to global extinction (e.g. loss of the last population) is influenced by biological and geographical traits (3, 14–16). Key factors include initial rarity, small population sizes, small geographical ranges, slow population growth, large body size, flightlessness, tameness, or ecological specialization (12, 17). Where human predation of vertebrates is concerned, for example, species of larger body size, providing more effective returns for hunting efforts, may typically have been preferentially targeted. The historical record indicates that large-bodied and flightless island endemic species have been particularly prone to anthropogenic extinction (4).

As a counterpoint, it is also likely that some insular species were rare even before human arrival on the islands in question. Some such island rarities may have had limited significance for overall ecosystem functioning. While they may thus be at fairly high risk of extinction, their loss may have only marginal knock-on impacts on ecosystem functioning. The same point may apply to many species that have shrunk from a once abundant position to current rarity, i.e. they are already in effect ecologically or functionally rare. The general lack of robust baseline data can mean that, for example, when considering the members of large radiations of localized species (18), it can be difficult to determine whether the species is naturally rare or has become rare due to lengthy and extensive anthropogenic alterations of island ecosystems. Furthermore, the incompleteness of the insular fossil record, especially for less frequently preserved taxa (e.g. plants, arthropods, and fungi), makes the establishment of such baselines challenging. This constitutes part of the "Hookerian knowledge shortfall" (19).

We focus herein on the global loss of Macaronesian endemic species (hereafter "species extinction") as the data remain deficient in resolution for systematic analysis of island population losses of persisting species. We restrict our analyses to terrestrial taxa (including seabirds and seals that nest on islands) for the same reason. Our principal goal is therefore to synthesize the knowledge of terrestrial extinctions across Macaronesia, document their chronology in relation to human agency, and provide a model for comparative analyses applicable to other oceanic archipelagos.

Results

Overview of known extinctions of Macaronesian endemic species

To our knowledge, 220 endemic terrestrial species are known to have gone extinct in the Macaronesian region (Table 1, Appendix 1), which means 3.1% of the Macaronesian endemic species known to science. The highest number of recorded extinctions is from the Canaries (86 species, or 39.1% of the known Macaronesian extinctions), followed by Madeira (58 species, 26.4%), Cabo Verde (57 species, 25.9%), and, finally, Azores (19 species, 8.6%). Across taxa, mollusks account for slightly more than half of the known extinctions (50.4%), followed by arthropods (23.2%), birds (12.3%), reptiles (6.8%), vascular plants (5.0%), mammals (1.4%), and bryophytes (0.9%), with no extinctions reported so far for fungi and lichens (Table 1).

These extinction events include a mix of those apparently occurring before human arrival, posthuman arrival, and some with ambiguous timing. Its impact has been especially serious on vertebrates. Compared with the prehuman baselines, the above figures translate to a 50% loss of endemic bird species, a 42.8% loss of endemic mammals, and a 27.8% loss of endemic reptiles across the region, meaning an ~40% loss in richness of endemic vertebrates overall attributable to human action. Although invertebrates contribute with large numbers of extinct endemics, the losses amount to 18.7% of the original endemic mollusks but just 1% of the endemic arthropods. Among plants, 3.1% of endemic bryophytes and 1.1% of endemic vascular plants have been lost. Although there are a good number of endemic fungi and lichens in Macaronesia (e.g. 235 species endemic to the Canaries), no extinctions from these taxa have been recorded. Appendix 1 compiles all the information about extinct Macaronesian species, including species names, species distribution before the extinction, extinction chronologies, putative extinction causes (when known), and references.

Azorean species extinctions

Azorean extinction events have affected birds, arthropods, and vascular plants. Birds represent the highest number of extinct species, with ten species documented so far. These include six flightless rail species, three of which are described: *Rallus carvaoensis*, endemic to São Miguel; *Rallus nanus*, endemic to São Jorge (Fig. 1A); *Rallus montivagorum*, endemic to Pico; and likely three additional unnamed *Rallus* species from Graciosa, Terceira, and Santa Maria (22). Other extinct birds include the São Miguel owl, *Otus frutuosoi* (27), a large bullfinch, *Pyrrhula crassa*, endemic to Graciosa (28), and probably two undescribed endemic quail species, *Coturnix* spp., that once inhabited Santa Maria and Graciosa islands, respectively (23). More recently, an extinct endemic petrel, *Pterodroma zinorum*, which nested on various Azorean islands, has been described (29). All these species became extinct after the arrival of the Portuguese and their commensal fauna in the 15th century (22, 27, 29, 30). Neither reptiles nor nonvolant mammals managed to colonize this remote archipelago by natural means, so there were no endemic species that could become extinct. There is, however, an endemic species of bat, *Nyctalus azoreum*, which survives.

Seven endemic arthropods, including *Bembidion derelictus*, *Bradycellus chavesi*, *Calathus extensicollis*, *Calathus vicenteorum*, *Trechus torretassoi*, *Neocnemis occidentalis*, and *Nesotes azoricus* (31), as well as one vascular plant, *Vicia dennesiana* (32), have been reported as extinct. This number is fewer than might be expected, given the significant loss of native forests, but this may reflect a still unpaid "extinction debt" (33).

Madeiran species extinctions

We know of about 58 endemic species losses within the Madeiran and Selvagens archipelagos, of which 49 are terrestrial mollusks.

Table 1. Known endemic species extinctions per taxon and archipelago across Macaronesia.

Macaronesian known extinctions	Azores, *n* (%)	Madeira + Selvagens, *n* (%)	Canaries, *n* (%)	Cabo Verde, *n* (%)	Total, *n* (%)	Macaronesian extant/ extinct species	Losses within taxon, %
Birds	11 **(78.6)**	6 **(60)**	9 **(53.0)**	1 (11.0)	27 (12.3)	27/27	**50.0**
Reptiles	0	0	6 **(28.6)**	9 **(29.0)**	15 (6.8)	39/15	**27.8**
Mammals	0	0	3 **(60.0)**	0	3 (1.4)	4/3	**42.8**
Mollusks	0	49 (18.9)	60 (21.8)	2 (1.7)	111 (50.4)	483/111	18.7
Arthropods	7 (2.5)	0	0	44 (9.4)	51 (23.2)	5052/51	1.0
Bryophytes	0	2 (15.4)	0	0	2 (0.9)	62/2	3.1
Vascular plants	1 (1.3)	1 (0.7)	8 (1.3)	1 (1.5)	11 (5.0)	967/11	1.1
Total	19 (8.6)	58 (26.4)	86 (39.1)	57 (25.9)	220 (100)	6905/220	3.1

In brackets, the percentage of losses that these figures translate to as a function of the original species richness of endemic species per taxon. The percentages in the total column refer to the contribution of each archipelago and taxon to the overall Macaronesian biodiversity lost. The final two columns show the proportion of extant to extinct species and the percentage of losses within each taxon for the whole of Macaronesia. Note that (i) Macaronesia had no amphibians prior to human contact; (ii) no extinctions of endemic species have been reported for fungi, lichens, and ferns so far; (iii) in bold, taxa with 25% or more losses. For the percentage calculations, the number of endemic species per archipelago was obtained from (20), and the number of Macaronesian multiple archipelagic endemics from (21).

The timing and causes of these extinctions are poorly understood, but the majority appear to have preceded human arrival. Nevertheless, nine of them (*Amphorella grabhami*, *Actinella arcinella*, *Actinella promontoriensis*, *Caseolus bowdichianus*, *Cylichnidia cylichna*, *Geomitra delphinula*, *Leiostyla wollastoni*, *Phenacolimax crassus*, and *Truncatellina linearis*; Appendix 1) appear to have gone extinct after the colonization by the Portuguese in the 15th century (34). The extinction of the snail *C. bowdichianus* may have in part been driven by competitive exclusion following the introduction of *Theba pisana* (34).

The seven known land bird extinctions include two flightless rails: *Rallus lowei*, endemic to Madeira, and *Rallus adolfocaesaris*, endemic to Porto Santo (22); three quails: *Coturnix lignorum*, from Madeira, *Coturnix alabrevis*, from Porto Santo, and a probably still unnamed third quail, from Bugio islet (Desertas) (23). Finally, there was also at least one nocturnal raptor, the Madeiran owl (*Otus mauli*; Fig. 1B), which was also present in Porto Santo, although it is possible that the latter population belonged to a different species (26). All these extinctions seem to have occurred in response to the many changes brought about by human colonization of the Madeira Archipelago (22, 23, 26). The islands possessed no indigenous, nonvolant, terrestrial mammals (although there are three species of bats), and they have a single native lizard, the endemic *Teira dugesii*, which remains extant. Finally, *Delphinium maderense*, a Madeiran endemic vascular plant, was last seen in 1956 (35).

Canarian species extinctions

The Canary Islands have experienced the extinction of 86 endemic species, among them nine land birds, six reptiles, and three mammals, in each case a high proportion of the original tally of endemics. As many as 60 endemic land snail species have been lost, all long before human arrival and very likely due to climatic events, thus revealing past extinction dynamics not recovered for the other taxa (Table 1). Next, we consider each taxon in turn and in more detail.

The most puzzling bird extinction inferred from the Canaries is based on the discovery of fossil eggshells of large flightless birds found from the Zanclean (lower Pliocene) (4.3–3.8 Ma ago) paleontological sites in Lanzarote (36). They have been attributed either to *Struthio* and *Aepyornis* (37, 38) or to Pelagornitidae (39). These findings are difficult to interpret because the Canary Islands have never been connected with the mainland (40), and no skeletal remains have ever been found, but their extinction is most plausibly explained by climatic or environmental change (or volcanic disturbance). The rest of the extinct avian species detected so far appear to have been extant after the arrival of humans (i.e. later than the second century CE) and their losses appear most likely to have been anthropogenic in origin, arising from some combination of hunting, habitat modification and fragmentation, and the introduction of commensal species of vertebrates (41–43).

The most recent evidence of the presence of the endemic dune shearwater, *Puffinus holeae*, points to an extinction associated with the first human presence in the islands (44). Other endemic bird species, such as the flightless passerine long-legged bunting, *Emberiza alcoveri* (45), the Trias greenfinch, *Chloris triasi* (46), and the Canary Islands quail, *Coturnix gomerae* (47), may have also disappeared after the earliest human presence in the archipelago and also after the colonization of the archipelago (most probably as a commensal) by the house mouse (*Mus musculus*) (48). Anthropogenic causation also cannot be ruled out for the extinction of the Tenerife slender–billed greenfinch, *Chloris aurelioi* (Fig. 1C). While the single dated specimen (13,427–13,207 cal yr BP) (25) belongs to the prehuman period, it provides insufficient sampling of the species to provide a guide to the timing of the extinction. It also cannot be ruled out that one or more of these species survived until the time of the 15th-century Castilian conquest of the archipelago and the ensuing acceleration in habitat transformation and the introduction of exotic predators, such as cats, mice, and rats. This scenario appears to apply, for example, to the loss of the lava shearwater, *Puffinus olsoni* (49). Finally, the extinction of the black oystercatcher, *Haematopus meadewaldoi*, happened at the beginning of the 20th century, very likely due to a combination of human overharvesting of its main resource, the limpet *Patella candei*, habitat destruction, and collecting (50).

Canarian endemic reptile extinctions occurred in two distinct time frames. The first involved the demise of the giant tortoises: *Centrochelys burchardii* from Tenerife (51, 52), *Centrochelys vulcanica* from Gran Canaria (53), and two unnamed *Centrochelys* species from Lanzarote and Fuerteventura (54). These extinctions likely occurred long before human arrival, between the Miocene and Pleistocene, possibly due to catastrophic volcanic events (53–56). This group of early extinctions also includes the possible presence of snake skeletal remains on the islands of Lanzarote and Fuerteventura in fossil sites dating to the Miocene age, although these records are considered uncertain (57–59). The second wave of extinctions affected the Canarian giant lizards (*Gallotia goliath* from Tenerife and *Gallotia auaritae* from La Palma), which vanished following human arrival, probably due to a combination of hunting, habitat transformation, and the introduction of nonnative predators (56, 60–62).

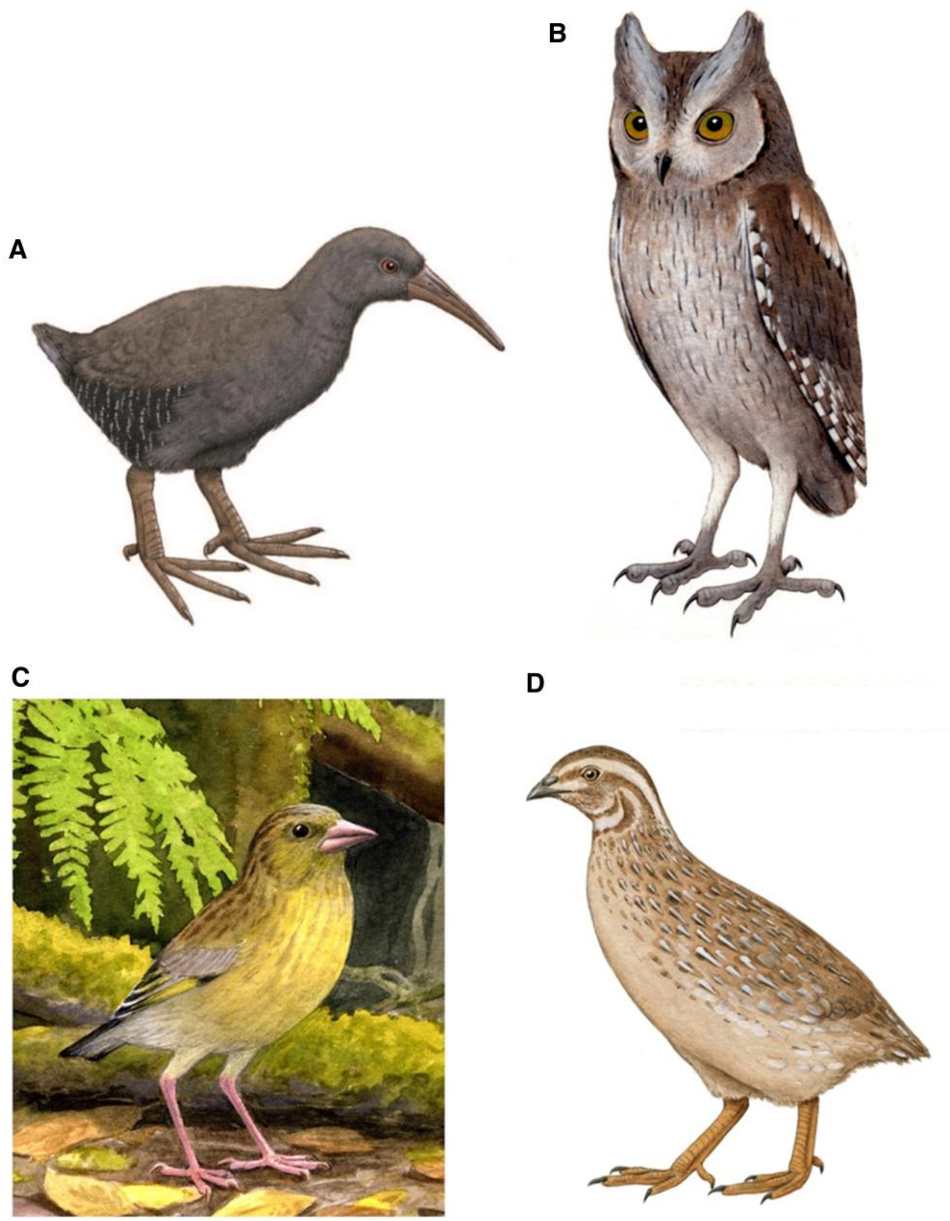

Fig. 1. Artist reconstructions of some Macaronesian extinct birds. A) São Jorge rail *(Rallus nanus)* from São Jorge Island (Azores). B): Madeiran Scops Owl (*O. mauli*) from Madeira Island. C) Slender-billed greenfinch (*Ch. aurelioi*) from Tenerife (Canary Islands). D) São Vicente Quail (*Co. centensis*) from São Vicente Island (Cape Verde). Art by Pau Oliver (A, B, and D) and Aina Bonner (C). Sources: (22–26).

Besides the extant Canarian endemic shrew (*Crocidura canariensis*), Macaronesia was home to three native, nonvolant mammal species prior to human contact, all of which were rodents endemic to the Canaries: the Tenerife giant rat, *Canariomys bravoi* (63–65), the Gran Canarian giant rat, *C. tamarani* (63, 66), and the lava mouse (*Malpaisomys insularis*) from the easternmost islands (67, 68). Radiocarbon dating shows that *C. bravoi* was still present on Tenerife at least as late as 400 cal yr BCE, which is near the time of the first human presence on the island, between 155 and 455 CE (69). Therefore, it seems likely that its extinction occurred as a consequence of the initial human colonization (65). The introduction of the non-native house mouse (*M. musculus*) by the first human settlers was hitherto considered responsible for the loss of the lava mouse (*M. insularis*) through competition or via transmission of parasites and/or diseases, although they coexisted for several centuries (67). The last record of this species (1,271–1,394 cal yr CE) indicates a late extinction, probably linked to the introduction of the black rat (*Rattus rattus*) to Lanzarote and Fuerteventura (68).

Fossil mollusks have been the subject of multiple studies in the Canaries (70–87), resulting in the identification of up to 60 extinct endemic land mollusk species, all of them with a very similar profile, i.e. showing extinction chronologies clearly before human arrival (Pliocene, Pleistocene, and Holocene), and thus, very likely attributable to either geologic or climatic events.

Although only eight endemic vascular plant species are currently known to have become extinct, it should be acknowledged that domestic herbivores introduced by humans have been grazing for nearly two millennia, with herders likely increasing fire frequency, which, in combination, may have induced cryptic extinctions (real extinctions that went undetected). This is due to the difficulty in finding well-defined fossil evidence of vascular plants on these islands (but see (88)). With the exception of the recently discovered *Ruta museocanariensis*, whose extinction can be attributed to the first Canarian settlers (89), most known vascular plant extinctions in this archipelago occurred during the 19th and 20th centuries. These extinction events were primarily driven by herbivory, urbanization, and drought episodes, among other factors. They include *Aeonium mascaense*, *Centaurea conocephala*, *Grammitis quaerenda*, *Lotus gomerythus*, *R. museocanariensis*, *Solanum nava*, *Thesium psilotocladum*, and *Viola plantaginea* (90).

Cabo Verdean species extinctions

In Cabo Verde, we know of 44 species of extinct endemic arthropods, comprising two spiders and 42 coleopterans, including species of *Apion*, *Argosomus*, *Dinas*, *Laccobius*, *Ochthebius*, and *Olibrus* (91). Almost all of them were described in the 19th century by Thomas Vernon Wollaston (92), implying that their demise is very recent and likely provoked by human activities.

Up to nine species of endemic reptiles have become extinct in Cabo Verde. Whereas one giant tortoise, *Centrochelys* sp., from Sal, went extinct in deep time, another *Centrochelys* sp., from Maio, vanished after human arrival (6, 93). The Cabo Verde giant skink, *Chioninia* [*Macroscincus*] *coctei*, which inhabited the Branco and Raso islets, was collected to extinction due to its commercial value. By 1898, no wild individuals remained, and the last captive individual died in 1940 (94). Some scholars believe that there may still be undiscovered populations of skinks on uninhabited islets (including Santa Luzia), but so far, all attempts to find them have failed. In addition to *C. coctei*, two other giant *Chioninia* skinks, *Chioninia carranzai* from Santo Antão and *Chioninia magna* from Boa Vista and Maio, were driven to extinction after the arrival of the Portuguese (6). The same fate befell four Cabo Verdean geckos, two of which belong to the genus *Tarentola*, *Tarentola gorgonica* from Santo Antão and *Tarentola pyripeternsis* from Sal. Two other species, belonging to the genus *Hemidactylus*, are considered probably extinct: *Hemidactylus cessacii* from Santiago and another yet undescribed *Hemidactylus* species from Brava (6).

The avian paleontological record is very limited, and the only extinction recorded and described was the endemic São Vicente quail, *Coturnix centensis* (Fig. 1D), which probably survived until European colonization, disappearing because of the alterations produced by human settlers (23). Finally, two species of mollusks, *Ancylus milleri* and *Leptaxis atlantaidea* (95, 96), and one vascular plant, *Habenaria petromedusa* (97), have become extinct since human colonization. Prior to human contact the islands lacked native mammals, apart from one nonendemic bat, which persists today.

Discussion

It is important to acknowledge that investment in paleontology, taxonomy, and field ecology across Macaronesia has been uneven. In general, there has been much more research effort within the Portuguese and Spanish archipelagos, particularly in recent decades, due to access to EU research funding. Thus, we postulate that the ongoing increase in research efforts, especially in Cabo Verde, will eventually alter this picture. The figures presented here should therefore be considered minimum estimates of extinction.

It should also be noted that the recoverability of the fossil record varies between taxa. For instance, the low proportion of endemic arthropods and vascular plant species that are considered extinct is likely to be a function of the low chance of finding identifiable remains (98), which is very commonly the case for oceanic islands. Vertebrate bones or mollusk shells are more readily preserved, facilitating their identification and thus the description of past extinction events in these taxa. Whereas mollusk and vertebrate fossils can be tracked back to deep time (>1 Ma), extinctions of vascular plants and arthropods identified are almost always postdescription events (35, 90, 99), most likely reflecting a sampling artifact. For the same reason, when a species is known from a single (or very few) dated fossil record, the most recent fossil available may be a misleading indicator of the timing of actual extinction and may not accurately reflect whether the extinction pre- or postdated human arrival.

Finally, the number of extinctions is necessarily related to some extent to the initial taxonomic diversity and level of endemism in a given island/archipelago, with mollusks, reptiles, and arthropods providing the highest percentage of endemism, followed by vascular plants. Whereas mollusks have radiated considerably both in Madeira and the Canaries (34, 100), this is not the case for the Azores or Cabo Verde. Nevertheless, this last archipelago contributes outstandingly with reptile diversity as a result of several well-studied radiation events (6).

Natural vs. anthropogenic changes as main drivers of extinction

Tables 2 and 3 differentiate extinctions by taxon and archipelago according to their extinction chronologies. They distinguish between those losses matching with the human occupation of the islands, which are therefore predominantly attributable, either directly or indirectly, to human activities (e.g. habitat destruction, hunting, overexploitation, introduction of predators, herbivores, or diseases), and those with extinction timelines predating human occupation, which may be linked to natural phenomena (e.g. climatic and geological events). For those species only known from fossil data, many of the radiocarbon dates for their last (and in some cases, their only) records fall long before the first human contact with the islands in question (Appendix 1). However, we follow the general consensus of the source literature in attributing those with relatively recent Holocene dates to subsequent human causation. It is possible that a few extinctions may be misattributed to human agency when they were largely caused by natural factors, and vice versa, but the general pattern is likely to remain robust. On this basis, half of the endemic species extinctions in Macaronesia (last columns of Tables 2 and 3) are attributed to natural causes and the other half to human activity. However, a large proportion of the natural extinctions inferred in this way are accounted for by land mollusks, >90% of which disappeared long before human contact.

Although half of the Macaronesian extinctions are shown to postdate human colonization, the situation varies across archipelagos. In the Canaries (78%) and Madeira (69%), a clear majority of extinctions are potentially attributable to natural causes. In contrast, Cabo Verde (95%) and Azores (100%) show the opposite trend. This is reflected in the large number of extinct mollusks recorded in the Canaries and Madeira. Mollusks are also the only taxon for which extinction events appear to predate human colonization in Cabo Verde. Mollusks have radiated spectacularly in Central Macaronesia (421 species), but not in the Azores (49 species) or Cabo Verde (10 species). Also, land mollusks represent the taxon with the earliest and most abundant fossil record, with some taxa, such as those of *Canariella* spp., dating back to the Pliocene.

We infer that natural events, either geologic or climatic causes, and also biological causes, such as species turnover (101) and/or taxon cycle dynamics (102–104), have indeed generated natural extinction of insular endemics over time across each of these

Table 2. Recorded Macaronesian endemic species extinctions (number and percentage) per taxon, differentiating between those whose chronology matched with the human occupation of the islands and are thus highly likely to be attributable to humans, and those that do not match and which might be attributable to natural (volcanic or climatic) events, although we cannot rule out that some survived to the posthuman arrival period without having yet been detected from dated fossil evidence.

Known extinctions	Birds	Reptiles	Mammals	Mollusks	Arthropods	Bryophytes	Vascular plants	Total
Prehuman contact	3 (11%)	5 (33%)	0	102 (92%)	0	0	0	110 (50.0%)
Posthuman contact	24 (89%)	10 (67%)	3 (100%)	9 (8%)	51 (100%)	2 (100%)	11 (100%)	110 (50.0%)
Total	27	15	3	111	51	2	11	220

Table 3. Recorded Macaronesian endemic species extinctions (number and percentage) per archipelago, differentiating between those whose chronology matched with the human occupation of the islands and are thus highly likely to be attributable to humans, and those that do not match and which might be attributable to natural (volcanic or climatic) events, although we cannot rule out that some survived to the posthuman arrival period without having yet been detected from dated fossil evidence.

Known extinctions	Azores	Madeira + Selvagens	Canaries	Cabo Verde	Macaronesia
Prehuman contact	0	40 (69%)	67 (78%)	3 (5)	110 (50.0%)
Posthuman contact	19 (100%)	17 (31%)	19 (22%)	55 (95%)	110 (50.0%)
Total	19	57	86	58	220

archipelagos, but it is only those archipelagos with an important land snail fauna (Madeira and the Canaries) that have provided us with a readily traceable fossil signal. Hence, the apparent dominance of prehuman period extinctions in Central Macaronesia is essentially a sampling artifact, stemming from the comparatively rich fossil record of extinct land snails on these islands, a record that extends back to the Pliocene. As a result, relying only on absolute extinction figures can be misleading when comparing the relative importance of preanthropogenic and postanthropogenic extinction events.

With the aim of making comparable extinction ratios (ERs) across different time slices (i.e. the preanthropogenic period, including the Pliocene, Pleistocene, and the Holocene until human arrival across Macaronesia, and the anthropogenic period, that is, the last ∼2,000 years), we calculated preliminary ERs for each time slice. These rates, based on the data presented in Table 2 and Appendix 1, were limited to vertebrates and mollusks. This limitation is explained because of the absence of prehuman fossil records for arthropods and vascular plants. Hence, the likelihood of some level of cryptic extinction (i.e. real but unrecorded extinctions) precludes reliable estimation of their preanthropogenic ERs. The Pliocene was included because several extinction chronologies in vertebrates and mollusks refer to this period. The anthropogenic period was defined as the last 2,000 years across the archipelagos, beginning with the initial colonization of the Canary Islands. This timeframe also accounts for the possibility of earlier, undocumented human contacts in other parts of Macaronesia prior to the formal Portuguese colonization in the XV century (see Study area).

Based on the known fossil record (which we know to be incomplete), the prehuman ER for Macaronesian vertebrates is 1 species/662 Kya, compared with 1 species/0.054 Kya for the posthuman arrival ER. Hence, the anthropogenic vertebrate ER estimated this way is ∼12.260 times (four orders of magnitude) larger than background ER. The same calculation for mollusks yields an ER of 1 species/52 Kya for the preanthropogenic period vs. 1 species/0.22 Kya for the anthropogenic period. Hence, the anthropogenic ER for mollusks is 236 times (two orders of magnitude) larger than background ER. Interestingly, Christenhusz and Govaerts (35) reported that the current global human-induced ER in vascular plants is up to 700 times higher than the background rate, a figure lying between those of the Macaronesian vertebrates and mollusks. In sum, despite 50% of the known extinctions falling before human arrival to these islands, the ERs during the anthropogenic period are estimated to be some two to four orders of magnitude (depending on the taxon considered) higher than the apparent background ER. We caution against citing these values out of context, as cryptic extinction throughout the historical and prehistorical periods is of highly uncertain magnitude, yet these crude estimates nonetheless serve to express unambiguously the dimension of human impact on islands.

A second interesting (and surprising) finding is the very low proportion of species known to have gone extinct in some taxa, such as arthropods or vascular plants, which account for merely 1% of the total endemic biodiversity (3% for bryophytes), while other taxa, such as birds (51%), reptiles (28%), mammals (43%), and mollusks (18.5%), show much higher proportions of extinction (Table 2). Although further analyses are needed, we should not assume a priori that taxa with a very low extinction fraction are better suited to withstand natural (e.g. climatic shifts or volcanic activity) or anthropogenic (i.e. hunting, gathering, or predation and herbivory by introduced species) impacts when it is entirely possible that their low ER is attributable to their low recovery rate from the fossil record. In addition, recent studies on the Azores and the Canaries predict high levels of extinction debts for arthropods and vascular plants as a legacy of anthropogenic habitat loss: these studies both support their high extinction risk in the near future while also supporting arguments for possible past cryptic losses (33, 105).

Conclusions

We have provided the first systematic compilation of endemic species extinctions reported across taxa for the Macaronesian archipelagos. The number of extinct species reaches 220, from which, in absolute terms, land snails, arthropods, and birds contribute the most. The fraction of vertebrate losses is very high, in some taxa reaching values of ∼50% (birds), 40% (mammals), 30% (reptiles), or 20% (land snails) of the original known endemic biodiversity. These fractions are, however, very low for bryophytes (3%), arthropods (1%), and vascular plants (1%), while we lack any evidence of extinct terrestrial algae, fungi, and lichens. Analyzing the extinction chronologies, we conclude that at least half of these extinctions happened after the human colonization of these archipelagos and are likely to have occurred as a result of human activities, resulting in ERs larger by several orders of magnitude in respect to the background extinction. The contrasting proportions of endemic species losses across taxa are likely to reflect various sampling artifacts, and it seems probable that, over both geological and anthropogenic timescales, a significant amount of cryptic or dark extinction remains undetected. We postulate that this cryptic extinction, particularly affecting taxa that do not produce bones or shells, will be uncovered in the future, for instance, with the analysis of paleoenvironmental DNA. The losses synthesized within the present work serve to demonstrate the devastating impact of human activity on the Macaronesian biota, adding further evidence of the importance of prioritizing conservation actions (including habitat restoration) to attenuate or reverse current extinction processes across oceanic island systems.

Study area

Macaronesia comprises 40 volcanic islands >1 km^2 and spans from 14.8°N (Brava, Cabo Verde) to 39.7°N (Corvo, Azores) and 13.4°W (Roque del Este, Canaries) to 30.9°W (Flores, Azores) (106) (Fig. 2). They are grouped into five oceanic archipelagos (in decreasing order of latitude, Azores, Madeira, Selvagens, the Canaries and Cabo Verde) (Fig. 2; Table 4), sharing floristic and faunistic affinities with the nearby parts of continental Europe and Northwestern Africa (107). Although each archipelago is biogeographically distinctive, there are sufficient shared floristic elements to sustain the case that Macaronesia constitutes a biogeographical region (109).

The Macaronesian islands are mostly associated with hotspot origins, although the Azores are linked to a triple junction between plates. These islands are geologically dynamic systems characterized by ongoing island building, eruptions of varying intensities, flank collapses that generate large tsunami waves, cycles of uplift and subsidence, and erosional processes. At the archipelago scale, only the Selvagens (with the most recent eruption in the Pleistocene) (110) and Madeira (with the most recent eruption ∼6 Kya) have been historically inactive (111). The other archipelagos have been repeatedly active during the Holocene, with their most recent eruption occurring just years ago (Tajogaite 2021, La Palma, Canaries; Caldeira de Fogo 2015, Cabo Verde) or a few decades ago (Capelinhos 1957, Faial, Azores) (108).

Unsurprisingly, given the shared floristic elements, some zonal ecosystems are found across multiple archipelagos, notably including the laurel forest (the Azores, Madeira, and the Canaries) and the thermophilous woodlands (Madeira, the Canaries and Cabo Verde). Others are exclusive, such as the Canarian pine forest and summit scrub or the Cabo Verdean *Faidherbia* savanna (112) (Table 4). For the sake of simplification in this review, based on their governance, the Selvagens archipelago will be considered part of Madeira.

Middle and late Holocene paleoecology, human colonization, and anthropogenic change in Macaronesia

Human influence on islands may sometimes predate the initiation of permanent settlement, either due to earlier failed

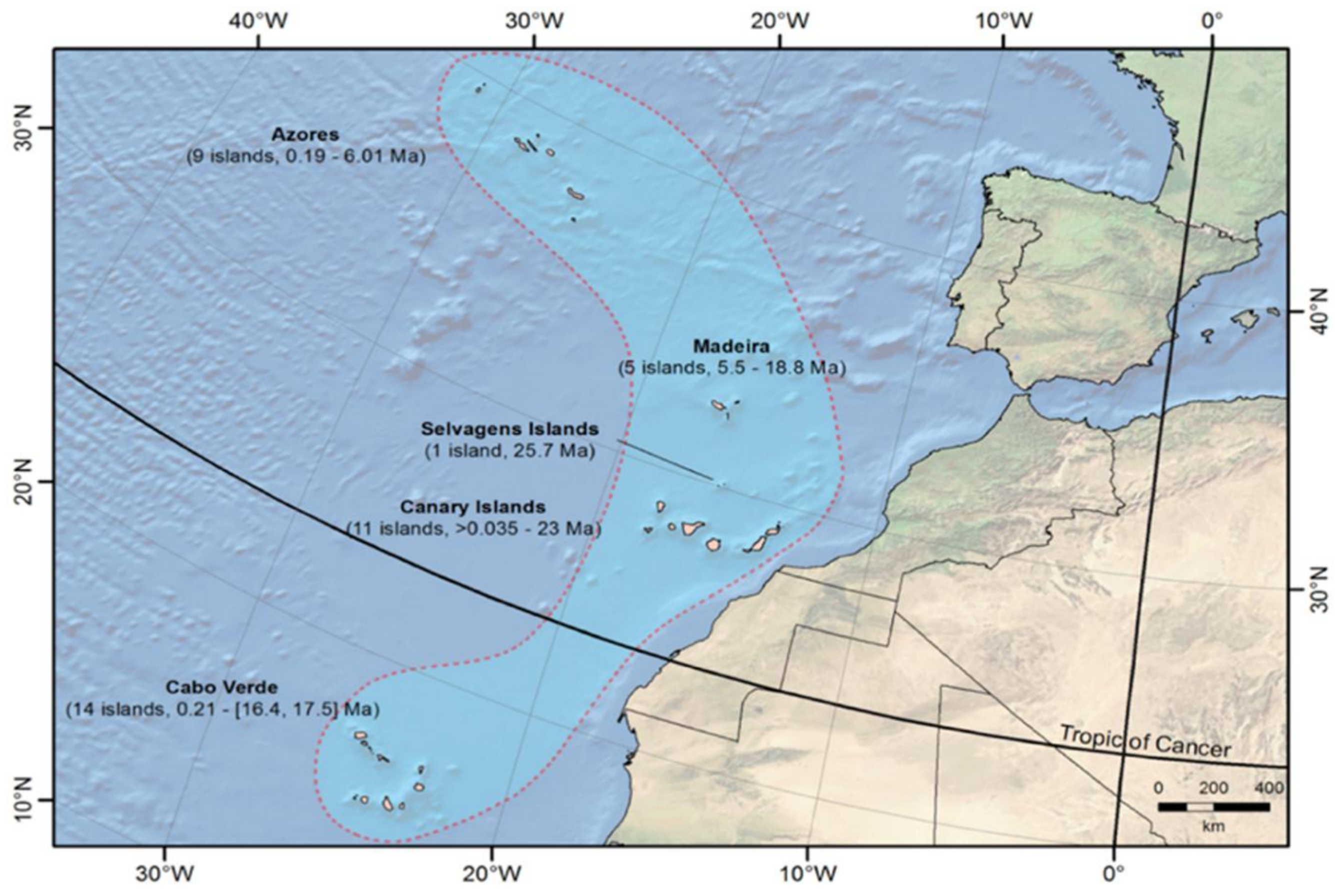

Fig. 2. Map of the Macaronesian biogeographical subregion, showing the number of larger islands and their emergent geological age range. Source: extracted with kind permission from Florencio et al. (107) (https://doi. org/10.3389/fevo.2021.718169).

Table 4. Key geographical characteristics of the Macaronesian archipelagos.

Parameter	Azores	Madeira	Selvagens	Canaries	Cabo Verde	Macaronesia
No. of Islands >1 km^2	9	5	1	11	14	40
Area (km^2)	2,764	815	4	7,447	4,033	15,061
Max. elevation (m)	2,351 (Piquinho, Pico)	1,862 (Pico Ruivo, Madeira)	136 (La Atalaya, Selvagem Grande)	3,718 (Teide, Tenerife)	2,835 (Pico de Fogo, Fogo)	3,718 (Teide, Tenerife)
Minimum distance from continent (km)	1,369 (São Miguel-Lisboa, Portugal)	630 (Porto Santo-Essauira, Morocco)	375 (Selvagem Grande-Cabo Juby, Western Sahara)	96 (Fuerteventura-Pointe Stafford, Western Sahara)	571 (Boa Vista-Dakar, Senegal)	96 (Fuerteventura-Stafford Point, Western Sahara)
Mean intra-archipelagic isolation (km)	220	32	13.3	196	141	—
Age of the oldest emerged island (Ma)	7.1 (Santa Maria) (but drowned and reemerged ~4 Ma)	14.3 (Porto Santo)	29 (Selvagem Grande) (but drowned between 24 and 13 Ma)	24 (Fuerteventura)	29 (Sal)	27 (Selvagem Grande)
Last volcanic subaerial eruption	1957 AD (Capelinhos, Faial)	6 Kya (Paul da Serra, Madeira)	Pleistocene	2021 AD (Tajogaite, La Palma)	2015 AD (Pico de Fogo, Fogo)	2021 AD (Tajogaite, La Palma)
Main zonal ecosystems	(a) *Erica* heathland (b) Laurel forest (c) Juniper woodlands (d) *Calluna* scrub	(a) Thermophilous woodlands (b) Laurel forest (c) *Erica* heathland	(a) Coastal scrub	(a) Coastal scrub (b) Thermophilous woodlands (c) Laurel forest (d) Pine forest (e) Summit scrub	(a) Faidherbia savanna (b) Thermophilous scrublands (c) Grasslands	
Current human population (M)	0.24	0.26	Only rangers	2.17	0.6	3.27

Source: Fernández-Palacios (106), modified. Archipelagic ages stem from Carracedo and Troll (108).

colonization attempts or because, in some cases, humans visited islands during voyages to rest, resupply, gather resources, or introduce commensals (e.g. goats), without the intention to settle (113, 114). As is typical of island regions (2, 115, 116), the arrival of humans has been the primary cause of alterations to, and the loss of, the original Macaronesian ecosystems and has long been linked to species extinctions (33, 105). During recent decades, paleoecological, paleontological, and archeological research has been carried out at sites distributed throughout Macaronesia (117–119), and there are undoubtedly many insights still to be gained from further research. Human colonization has diverse histories across Macaronesia, with the Canaries standing out as the most distinct archipelago.

The Canaries

The Canaries were first settled a long time ago, most likely around the second century CE, by a Berber ethnic group of pastoralists from North Africa, although the archipelago was already known to the Romans, who used Lobos Island as a land base, perhaps a century or two earlier (69). The colonists introduced goats, sheep, dogs, pigs, and house mice (119), along with cultivars such as wheat, barley, lentils, beans, peas, and figs (120). These indigenous people initiated profound ecological changes, and a number of extinction events followed their arrival.

Paleoecological research, based on the analysis of fossil pollen, charcoal, and geochemistry from sediment cores, has been undertaken in Tenerife, La Gomera, and Gran Canaria and is ongoing in Fuerteventura, La Palma, and El Hierro. A core from the now dried lakebed of La Laguna (Tenerife, 560 m asl), dating back to ∼4,700 cal yr BP, indicates a vegetation landscape comprising a mixture of laurel forest (e.g. *Morella*, *Prunus*, *Viburnum*, and Lauraceae), pine (*Pinus canariensis*), and, more surprisingly, a dominance of *Carpinus* and, to a slightly lesser extent, *Quercus*, neither of which had previously been considered native to the Canaries (121). Pine gradually declined in importance from ∼3,000 to 2,000 years ago, followed by a steep decline in *Carpinus*, starting ∼2,200 years ago, and subsequently the decline of *Quercus*, while evidence of increased fire frequency appears ∼2,000 years ago. The final disappearance of both *Carpinus* and *Quercus* roughly coincided with the final levels retrieved from the core, which also aligns with the Castilian conquest of the island at the end of the 15th century.

Analyses of a core from the Valleseco crater (Gran Canaria, 870 m asl) showed the area was occupied by a *Juniperus–Phoenix* woodland prior to human colonization (122). Evidence of increased fire frequency, along with the onset of a decline in palms and an increase in grasses, took place ∼2,300 cal yr BP. By 1,800 cal yr BP, pollen from cultivated cereals became significant, suggesting the introduction of agriculture at the site. A separate core from the Calderilla crater (Gran Canaria, 1,770 m asl) showed that, from the earliest part of the record (∼4,800 cal yr BP), the Gran Canaria highlands supported a mosaic of dry pine forest and open vegetation, which recovered spontaneously from natural forest fires (123). However, a more directional set of changes began ∼2,280 cal yr BP, with increased fire frequency, a rise in grasses and scrub vegetation, and gradual loss of pine forest cover, which ultimately disappeared. A role for animal husbandry and cultural firing was inferred as part of this process.

Finally, a different signal was detected by Nogué et al. (124) when analyzing the sediments from Laguna Grande (La Gomera, 1,250 m asl). Here, the authors detected declines in *Phoenix canariensis* and *Salix canariensis*, alongside increases in the representation of the *Morella–Erica* woody heath. These changes occurred ∼5,500 cal yr BP and have been attributed to regional climate changes coinciding with the end of the African Humid Period. Interestingly, charcoal data from this high-elevation site suggest that human arrival caused minimal changes in the catchment, with levels of burning over the last 800 years among the lowest since the onset of the Holocene. The authors attributed this to very low human densities in the island's summit region due to its cold and wet environment. This part of La Gomera continues to support extensive stands of laurel forest.

In the foregoing studies, the authors initially raised the possibility that humans may have played a role in the changes occurring ∼2,115–1,926 cal yr BP at La Laguna (Tenerife) (121), ∼2,438–2,326 cal yr BP at Laguna de Vallesco (Gran Canaria) (122), and ∼2,332–2,218 cal yr BP at La Calderilla crater (Gran Canaria) (124). Given that some published archeological data suggested human colonization of the archipelago by ∼2,400 cal yr BP or earlier (125, 126), these interpretations seemed reasonable. However, significant doubts have been raised regarding claims of human settlement prior to the second century CE (69, 119), although it is now generally agreed that certain resources were being exploited from the islands during the Roman period, potentially one to two centuries earlier, as mentioned above. This leaves three possibilities: (i) humans were indeed settled on the islands and influencing Canarian landscapes a few hundred years earlier than currently accepted; (ii) the changes in vegetation were driven by natural factors, such as subtle changes in climate; or (iii) the radiocarbon dates from the sediment cores used in the paleoecological studies may have been biased, e.g. by the incorporation of older carbon into the lake sediments. While none of these possibilities can be entirely excluded with the current data, it is clear that the full extent of the vegetation changes described in these studies can only be understood in the context of human impact throughout the pre-Castillian period.

After the Norman-Castilian conquest in the 15th century, the Canaries experienced accelerated ecological change as the predominantly farming and gathering economy of the first Canarians was replaced by an increasingly extensive and intensive agricultural model that continued to develop until the 1960s and 1970s. This postconquest model was dominated by subsistence and local market agriculture (cereals, potatoes, fruits, etc.) in the mid-elevations, leading to the destruction of the best thermophilous and laurel forest areas. At the same time, export-driven agriculture expanded across the mid-elevations and coastal areas, where different crops dominating at different times (sugar cane, wine, colorant-producing cochineal insects on *Opuntia*, tomatoes, bananas, and flowers). In the 1970s, an abrupt shift towards mass tourism began, and nowadays the archipelago is visited by more than 16 million tourists per year. Most visitors stay in coastal resorts, while agricultural abandonment has facilitated the spontaneous recovery of mid-elevation forests. These landscapes now feature large proportions of protected areas dedicated to conservation.

Azores

With the exception of the uninhabited Selvagens, the other Macaronesian archipelagos (Azores, Madeira, and Cabo Verde) were colonized by the Portuguese in the 15th century, having previously been uninhabited. Recent evidence, including cereal pollen and proxies for cattle farming, deforestation, and tree burning, suggests a failed attempt at earlier Norse colonization (∼700–850 CE) on Pico and Corvo in the Azores (127, 128). However, this early settlement proposal has been questioned due to anomalies and issues with radiocarbon dating of lacustrine materials (129).

Genetic analyses of house mice (*M. musculus*) from two Azorean islands (Santa Maria and Terceira) (130, 131) and from Madeira (132, 133) indicate a Northern Europe source population, suggesting that the mice may have been brought as stowaways on Viking voyages before Portuguese colonization. This hypothesis is supported by radiocarbon dating of mouse bones from Madeira, which yields an age of 903–1,036 cal yr CE, four centuries before the Portuguese colonization of this archipelago, coinciding with the Viking period (134).

Paleoecological research in the Azores has been carried out on four islands: Flores, Pico, São Miguel, and Corvo. Björck et al. (135) analyzed the sediments of Lake Caveiro (Pico, 903 m asl) and identified an alternation of arid and humid periods during the last 5,000 years. They attributed these variations to changes in drift ice in the North Atlantic. Increased drift ice would reduce northward heat advection, limiting the amount of warm surface water reaching the northern North Atlantic and promoting drier episodes. Conversely, during humid periods, the thermohaline circulation functioned in a "normal" way, conveying warmer surface waters northwards and increasing the evaporation and precipitation at Azorean latitudes.

Studying the oxygen isotope composition of chironomid head capsules from a ∼1,200-year sediment record from Lake Prata (São Miguel, 522 m asl), Raposeiro et al. (136) found that Azorean temperatures tend to be aligned with the prevailing past global temperatures. This pattern indicated warming during the Medieval Climate Anomaly (∼950–1,300 CE) and a subsequent cooling during the Little Ice Age (∼1,300–1,800 CE). In their analysis of sediments from the lakes of Caveiro (Pico) and Rasa (Flores, 530 m asl), Connor et al. (137) inferred that Portuguese colonization in the 15th century caused rapid, widespread, and persistent vegetation changes on an unprecedented scale over the last 2,700 years. These changes included the decline of dominant tree species, the spread of grasses and fire-tolerant species, the introduction of exotic plants, evidence for grazing and fire, and changes to soils and moisture availability. A similar conclusion was reached by Rull et al. (138) for Azul Lake (São Miguel, 235 m asl), where a landscape of dense laurisilva dominated by *Juniperus brevifolia* and *Morella faya* was replaced after Portuguese colonization by a complex of *Erica azorica/Myrsine africana* forests/shrublands and grassy meadows. Based on analyses of a core from the Caldeirão (Corvo, 400 m asl), Connor et al. (139) concluded that the island's Holocene vegetation history shows sensitivity to climate change, with shifts from open vegetation to various forest communities. Following Portuguese colonization, these forests were completely deforested due to fires, erosion, and grazing. Thus, the impact of Portuguese colonization on the Azores was abrupt and transformative. This was followed by ongoing land-use changes and species introductions that continue to the present day.

Cabo Verde

In Cabo Verde, paleoecological research based on volcanic basin sediment cores has been carried out in Santo Antão, São Nicolau, Brava, and Fogo, and is ongoing in Santiago. Evidence from Caldera de Cova (Santo Antão, 1,200 m asl) indicates that scrubland and grasslands dominated the highlands until the Portuguese settlement ∼450 cal yr BP. The Portuguese introduced commensal livestock, and their land use changes were accompanied by increased local and regional fire frequency and a still ongoing process of soil degradation (140). Castilla-Beltrán et al. (141) analyzed the sediments of Calderinha in Monte Gordo (São Nicolau, 1,000 m asl), finding that, until 400 cal yr BP, coinciding with the human colonization of the island summit, the highlands were dominated by a scrubland of native woody taxa, including *Euphorbia tuckeyana*, *Dracaena draco* subsp. *caboverdeana*, and *Ficus* spp. Increased burning, grazing, and harvesting of natural forests led to the replacement of this original vegetation largely with introduced and cultivated taxa. Castilla-Beltrán et al. (142) put forward a more complex scenario based on a core taken from Cova Galinha caldera (Brava, 810 m asl). They suggested that an influx of settlers occurred ∼1,680 CE, as people migrated from nearby Fogo Island due to volcanic activity on that island (143). This accelerated land use change and intensification on Brava, causing a reduction of the native vegetation previously dominating Brava's summit, a fern-rich woody scrubland. Finally, the analysis of the sediments of Ka Nazario caldera (Fogo, 1,010 m asl) led Castilla-Beltrán et al. (144) to conclude that in this island the vegetation changes have been mainly driven by the (still ongoing) eruptions of Fogo and of secondary volcanoes, largely masking detectable imprints of human arrival, beyond the introduction of cultivars and exotic species.

Madeira and Selvagens

Finally, the paleoecological research carried out in Madeira to date (145–148) has focused exclusively on deep-time (Miocene-Pleistocene) reconstructions. Only the research referred to above on the house mouse origins (132–134) and on the anthropogenic impact on the endemic land mollusks (34) and birds (22, 26) offers some light on the period of human contact.

In summary, across the Macaronesian archipelagos, a similar scenario emerges from the somewhat fragmentary records available. Over geological and Milankovitch-cycle timescales, evidence points to a dynamic environment shaped by regional climatic changes and in situ volcanic events (including island building and demise), which undoubtedly drove past episodes of extinction among narrowly ranged endemic species, mostly involving completely unknown species. However, within a Holocene timeframe, it is the arrival of humans that has caused the most dramatic and ongoing transformation in land and ecosystems, including agriculture, species introductions, and hunting. These changes led to the collapse of several native ecosystems and species. In an attempt to domesticate the wild nature, settlers abruptly and rapidly transformed original laurel forests (the Azores, Madeira, and the Canaries) and thermophilous woodlands (Madeira, the Canaries, and Cabo Verde) with fire, logging, and the introduction of species including domestic herbivores, rodents, and cats.

The largely agropastoral lifestyle of the first settlers of the Canary Islands was overtaken across Macaronesia following Castilian and Portuguese settlement in the 15th century by the rapid development of export agriculture (sugar cane and wine) and rangeland practices (cattle and ovicaprids). These changes were accompanied by many species' introductions and also the planting of extensive stands of exotic tree taxa such as *Acacia*, *Castanea*, *Cryptomeria*, *Eucalyptus*, and *Pinus*, to varying degrees across the region. Nowadays, perhaps with the exception of Madeira's windward slope, the natural ecology of these archipelagos is much degraded (118). Mass tourism has affected Madeira similarly to the Canaries, and in recent decades, Cabo Verde, particularly Santiago, Sal, and Boa Vista, has also begun to develop as a major tourist destination. While São Miguel and Terceira have seen emerging tourism, only the Azores, with its less favorable climate for large-scale tourism in the early 21st century, retains an economy largely based on cattle grazing, agriculture, and forestry. The resident population of Macaronesia today numbers ~3 million people, while the region receives ~18 million visitors annually (149).

Materials and methods

Information sources

We have included in our survey online digital information (in Spanish, Portuguese, English, German, and French) using the following keywords: Azores, Canary Islands, Cape/Cabo Verde, extinction, fossil, Macaronesia, Madeira, oceanic islands, paleontology, and Selvagens. We reviewed original sources of any publications recording extinctions to try to avoid data loss or misinterpretations of nonoriginal sources. After thoroughly reviewing all relevant publications, we extracted the following data:

(a) species name;
(b) pre-extinction distribution, including island and archipelago;
(c) probable causes of extinction according to the authors;
(d) extinction chronology (radiocarbon date of the fossils found for predescription extinctions or date of last report of the extant species for postdescription extinctions);
(e) reference citation details.

Supplementary Material

Supplementary material is available at *PNAS Nexus* online.

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