



The paradox of anthropogenic enrichment: homogenization and downsizing of insular mammals

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Abstract

Oceanic islands are global hotspots of biodiversity – many of them harboring marvels of evolution in isolation. Unfortunately, insular biotas are also highly susceptible to extinction, especially following colonization by humans. Here, we assess the influence of humanity on the diversity and biological distinctiveness of mammals inhabiting 37 oceanic islands. We compiled lists of mammals inhabiting these islands prior to and then following colonization by hominids (including *Homo erectus* and *H. sapiens*). We then quantified the dynamics in diversity (as measured by species richness) and distinctiveness (measured as beta-diversity) among islands. We compared mammalian assemblages on islands prior to humanity, following colonization by early hominids and then following colonization by *H. sapiens* (in the latter case, separating assemblage dynamics resulting from extinctions of native species from the effects of species introductions). As expected, early hominids hardly influenced mammalian diversity or distinctiveness. In contrast, colonization by *H. sapiens* was initially followed by numerous extinctions and substantial declines in species richness, which then however rebounded to exceed pre-humanity levels. These post-humanity increases in species richness were paradoxically accompanied by substantial declines in distinctiveness among islands. This paradox of anthropogenic enrichment is readily resolved by observing that species introductions to the islands (the sources of the post-humanity surges in species richness) were comprised of a highly redundant set of small species (primarily rats and house mice), resulting in the homogenization and downsizing of island life.

Highlights

- Islands harbor a highly disproportionate number of endemic species, including mammals.
- Insular mammals often undergo remarkable evolutionary and ecological divergence from their mainland relatives, which also has made them highly susceptible to anthropogenic extinctions.
- We compiled lists of mammalian assemblages prior to and then following hominid colonization of 37 oceanic islands to determine the impacts of humanity on their diversity and distinctiveness.
- Anthropogenic activities had the paradoxical effect of increasing species richness, while demonstrably decreasing distinctiveness of mammalian assemblages among islands.
- Anthropogenic extinctions across the world's islands removed the largest and most evolutionary divergent mammals, and species introductions replaced them with a redundant set of relatively small mammals of similar morphologies and trophic functions.

Keywords: beta-diversity, biotic homogenization, endemism, extinction, islands, Mammalia, species introductions, species richness

Introduction

The Anthropocene marks a period of global change; one so powerful and pervasive that it may ultimately culminate in wholesale transformation of the most identifying and distinguishing elements of the natural world (Johnson et al. 2017, Ellis 2018, Russell and Kueffer 2019, Nogué et al. 2021). Among the last impacted and most distinctive native wildlife were those isolated across the oceans and major seas. Here, terrestrial mammals and other native wildlife that somehow reached these distant shores evolved and diverged in splendid isolation (*sensu* Simpson 1980). Their evolutionary divergence in the absence of humanity and of most mainland competitors and predators promoted the bizarre marvels of island life – dwarfed elephants and giant mice, herbaceous plants that evolved to become trees, giant flightless birds, and a myriad of other morphological, ecological and evolutionary transformations that characterized island life before humans set foot on the shores of these isolated ecosystems (Lomolino et al. 2012, 2013, Benítez-López et al. 2021, van der Geer et al. 2021).

Anthropogenic declines in biological diversity strike far deeper than simple declines in number of species, often most heavily impacting the most divergent life forms – those defining the biological distinctiveness of place (Duncan and Blackburn 2004, Whittaker and Fernández-Palacios 2007). Because of their ecological naiveté, these marvels of evolution in isolation also are those most susceptible to what Charles Darwin (1839) referred to as “the stranger’s craft of power.” Here, by ‘strangers’ Darwin was referring to colonizing populations of humans and the rats, cats, goats and shiploads of other commensals we brought with us as we expanded our domain across the globe. In a poignant parallel, Gertrude Stein’s (1937) famous quote

– “there is no there, there” —was a lament over the loss in distinctiveness of place, but in this case her hometown of Oakland, California after it had lost its distinguishing small-town sights and sounds and smells to join the rubber-stamp of urbanization of cities across the US.

The biological distinctiveness of place and how this has changed over time is, of course, central to the fields of evolutionary biology, biogeography and conservation biology (Lomolino et al. 2017). Only recently, however, has our knowledge of the fossil and sub-fossil record advanced to the point that we can now reconstruct the assemblages of species that once inhabited the world’s islands (van der Geer et al. 2017). Here we capitalize on these paleoecological reconstructions to assess the impacts of humanity on some of the most distinctive assemblages yet described – the non-volant, terrestrial mammals native to 37 islands across the Pacific and Atlantic Oceans and the Mediterranean Sea (Fig. 1). In addition to a simple measure of species diversity (richness, or number of species inhabiting each island), we also calculated measures of biological distinctiveness (endemism and beta-diversity) of these assemblages. By analyzing the dynamics in these indices of biological diversity over different stages of hominid colonization (prior to hominids, after early hominids, after *Homo sapiens*), we assessed whether anthropogenic activities most heavily impacted simple numbers of species or biological distinctiveness among islands. We then distinguished between the levels of impact wrought by natural extinctions, by extinctions associated with hominids, and the impacts following introductions of non-native mammals on richness, distinctiveness and body size distributions of native species to provide an overall assessment of the potential anthropogenic



Figure 1. World map indicating the locations of the 37 oceanic islands and island groups studied. For lists of islands studied within each of these island groups, see Materials and Methods.

homogenization (*sensu* McKinney and Lockwood 1999, Lockwood and McKinney 2001, Lomolino et al. 2001, Baiser et al. 2012, Lenzner et al. 2022) and downsizing of the world's insular assemblages of mammals.

Materials and Methods

Species data

Species list of 37 islands and Madagascar were compiled based on published datasets (van der Geer et al. 2017, Kouvari and van der Geer 2018, Michielsen et al. 2023; see Supplementary Table S1). These datasets are period-specific fauna lists, ordered by biozone or faunal unit. Chronospecies were considered as single, continuing species and not events of extinction and new arrival. Body mass data (Supplementary Table S2) were compiled from paleontological and contemporary data and region-specific review works (e.g., Sará and Morand 2002, Jungers et al. 2008, MacPhee 2009, Turvey and Fritz 2011, Lomolino et al. 2013, Verde Arregoitia et al. 2013, Moncunill-Solé et al. 2016, van den Hoek Ostende et al. 2017, Faurby et al. 2018, Kouvari and van der Geer 2018, Rozzi 2018, van der Geer et al. 2018, Athanassiou et al. 2019, Morgan et al. 2019, Ochoa et al. 2021, Besiou et al. 2022, Lyras et al. 2022) and the following online databases: Synopsis of Philippine Mammals at https://archive.fieldmuseum.org/philippine_mammals, Animal Diversity Web at <http://animaldiversity.ummz.umich.edu>, the Encyclopedia of Life at <http://eol.org>, GBIF—the Global Biodiversity Information Facility at <https://www.gbif.org/species/2438571>. References per species are given in Supplementary Table S2. This study relies on palaeontological data, supplemented with molecular data from extant species. The fossil record is inevitably incomplete due to reasons of taphonomy and population dynamics. However, due to higher population numbers of the few species on any oceanic island, the fossil record of mammal species on islands is often more complete than that on the continents. Furthermore, our estimates of changes in species numbers and endemism are globally consistent over 37 islands. If the fossil record were less complete, this would have systematically biased the estimates towards well-studied systems. Also, although fossils of small mammal species could be expected to be easier overlooked because of their size, their remains are accumulated in vast amounts by birds of prey such as owls beneath their roosting sites in caves. Thus, if a preservation bias on body size in the fossil record would have been present in our dataset, this would have been directed towards missing out on larger species rather than smaller species, so our estimate of downsizing nature remains conservative. From a methodological viewpoint, missing species irrespective their size would have lowered the total number of extinctions and should be equally distributed over the stages (pre-hominid, after early hominid, and after modern hominid arrival) keeping the distinctiveness between the stages intact.

Data analysis

Dynamics in mammalian assemblages on the focal islands were compared at the following stages: 1 - prior to humanity, 2 - after pre-hominid extinctions, 3 - after extinctions following colonization of early hominids, 4 - after extinctions following colonization of *H. sapiens*, 5 - after species introductions (considered separate from post-*H. sapiens* extinctions), and 6 – after the effects of extinctions and species introductions, combined. The stages are defined not by particular dates, but functionally based on the absence or presence of the focal hominid species, and often coincide with what is referred to as biozone or faunal unit in the palaeontological literature. Extinctions and arrivals are counted as differences between subsequent stages. The arrival of focal hominids differs per archipelago (see Rozzi et al. 2023 for details).

Comparisons in assemblage dynamics were first conducted at the levels of islands and island groups (Fig. 1), which included those of the Caribbean (Anguilla, Antigua, Barbados, Bonaire, Cuba, Curacao, Hispaniola, Jamaica, Martinique, Puerto Rico, Saint Kitts, Saint Lucia and Saint Vincent), the Wallacea Region including the Philippines (Flores, Luzon, Mindanao, Mindoro, Negros and Timor), the Mediterranean (Crete, Cyprus, Karpathos, Majorca (= Mallorca), Naxos, Sardinia, Sicily and Tilos), Macaronesia (Fuerteventura, Gran Canaria and Tenerife), and isolated islands of the Pacific (Isabella and Santa Cruz of the Galápagos; Amami, Kume, Okinawa, Tokunoshima of the Japanese islands; Santa Rosae, Channel Islands of California). Analyses were then repeated for all 37 islands, combined. Madagascar was excluded from these analyses because its high diversity in comparison to all other islands would have created high leverage and skewed the results toward that one island. We did, however, include a summary and comparison of the dynamics of Malagasy mammal assemblages to those on all other islands studied here.

Our statistical analyses of these dynamics included mixed model ANOVA in Minitab (Minitab, LLC, 2021. Minitab, available at <https://www.minitab.com>) to assess the statistical significance of differences in island level parameters (richness, number of Single Island Endemics [SIEs], and % endemism), with islands (N = 37) set as the random effects, and stages (1 – 6, as described above) set as the fixed effects. We used the Tukey Method with 95% confidence levels to compare mean values for richness, number of SIEs and % endemism among Stages 1 – 6 and identify those stages that differed significantly in these parameters. To further assess the statistical significance of changes in these parameters that were associated specifically with the arrival of *H. sapiens*, we used binomial tests based on the tallies of islands (out of the total of 37) where richness decreased between Stages 1 and 4, increased between Stages 1 and 5, and increased between Stages 1 and 6 (the latter two comparisons providing a test of anthropogenic enrichment following species introductions [Stage 5] and a test of the combined effects of introductions and post-hominid extinctions [Stage 6]).

We used two measures of beta-diversity to calculate distinctiveness among island assemblages for each of the stages of development. This included Whittaker's measure of beta-diversity (Equation 1) (Whittaker 1960) and, because the former is influenced by species richness, we also calculated Baselga's index of beta-diversity (Equation 2) (Baselga et al. 2007), which is standardized to vary between 0 (when all island assemblages are identical) to 1.0 (when no species are shared among islands). We note that although the latter measure of beta-diversity is sometimes partitioned into components of turnover and nestedness (Baselga 2010), because native insular assemblages of mammals on these islands were almost exclusively comprised of endemic species, any nestedness component would be negligible (i.e., beta-diversity we observed was almost exclusively a function of turnover in species composition among islands).

$$\text{Equation 1: } \text{Beta}_{\text{Whittaker}} = S_{\text{total}} / S_{\text{avg}}$$

$$\text{Equation 2: } \text{Beta}_{\text{std}} = U_{\text{sum}} / ((S_{\text{sum}} - S_{\text{total}}) + U_{\text{sum}})$$

where S_{total} = the total number of different species across the island group

S_{avg} = the average species richness across the islands

U_{sum} = the sum of unshared species (island endemics)

S_{sum} = the sum of species richness values for the islands considered

Because beta diversity is an assemblage (not per island) level parameter, we used randomization and resampling to assess the statistical significance of differences in beta diversity among the 6 stages of development. We used the Resampling add-on tool in Microsoft Excel (2019 Statistics, com LLC, www.resample.com; after Simon 1997). Using the data describing species occurrences during Stage 1 across all 37 islands, we first randomized (shuffled) the order of islands (maintaining the actual assemblage occurrence within each island) then selected data for the first 25 islands as our first subsample. We then calculated Baselga's beta diversity on this subsample, scored (stored) that value, then repeated the shuffle and scoring procedures for a total of 1000 runs. Whittaker's measure of beta diversity was not used in these random sampling analyses because it varies with species richness and number of islands, and therefore would have been confounded by taking a subsample of islands (25 vs. the entire 37). The statistical significance of differences in beta diversity values between the original (Stage 1) assemblages and that of each of the subsequent stages (2 – 6) were then assessed by calculating the proportion of 1000 measures generated from resampling of the original assemblages that were more extreme (lower beta diversity, indicating assemblages becoming more similar) than that observed for these stages.

In addition to these indices of beta-diversity, which estimate distinctiveness across entire group of islands, we also calculated dissimilarity based on comparisons in species composition between each pair of islands

using the Jaccard dissimilarity index (Jaccard 1912). After calculating the mean pairwise dissimilarities between all 37 islands for the initial (pre-hominid) assemblage, we then used the Mantel test (Mantel 1967) to assess whether the dissimilarities matrices differed (i.e., the assemblages became significantly more similar) during the later stages of assemblage dynamics (i.e., after pre-hominid extinctions, after extinctions following early hominids, following *H. sapiens*, and after species introductions).

To test the hypothesis of anthropogenic downsizing, i.e., that post-humanity extinctions and introductions resulted in extant assemblages that are smaller in body size than those of the original (Stage 1) assemblages, we compared the frequency distributions of body sizes among stages. We conducted chi-square tests of independence comparing the frequency distributions of body sizes for the original (Stage 1) assemblages to that of the list of species suffering extinctions following the arrival of *H. sapiens*, and to that of populations of mammal species introduced to these islands (the latter included multiple populations of some species counted as distinct introductions). We then used Fisher's Exact Test (alpha level = 0.05) to identify those cells bins (body size categories) that contributed significantly to any observed deviations from independence.

Results

Although there were some differences in dynamics of mammalian assemblages among particular islands and island groups we studied, they were relatively minor in comparison to the salient trends that emerged over the stages of anthropogenic transformation (Figs. 2 and 3). As anticipated, pre-hominid extinctions in the Pleistocene involved only a minor fraction of the native mammals. The apparent impacts of early hominids on species richness also were relatively minor, especially when viewed in comparison to those following arrival of *H. sapiens* (percent losses of mammal assemblages were 5.7%, 9.1% and 44.3% prior to hominids, after early hominids, and after arrival of *H. sapiens*, respectively). Mixed model ANOVA confirmed that species richness, number of SIEs and % endemism did not change significantly during the initial pre-hominid stages (1 – 3), with richness then declining significantly after post-*H. sapiens* extinctions (see Supplementary Table S1 for statistics). The number of SIEs declined significantly following post-*H. sapiens* extinctions (Figure 3C), while percentage endemism declined significantly following post-*H. sapiens* extinctions and species introductions, taken separately and together (Figure 3D; tests of fixed effects [i.e., influence of stages] yielded F – values of 63.57, 13.54 and 57.34 in mixed model ANOVAs for richness, SIEs and % endemism, respectively; $P < 0.001$ in all cases, and R^2 adjusted = 94%, 94% and 73%, respectively).

Inspection of Figure 2 reveals a paradox of anthropogenic enrichment, but one that is readily resolved once we look beyond simple numbers and consider the dynamics in biological distinctiveness of these assemblages. Species richness, after declining

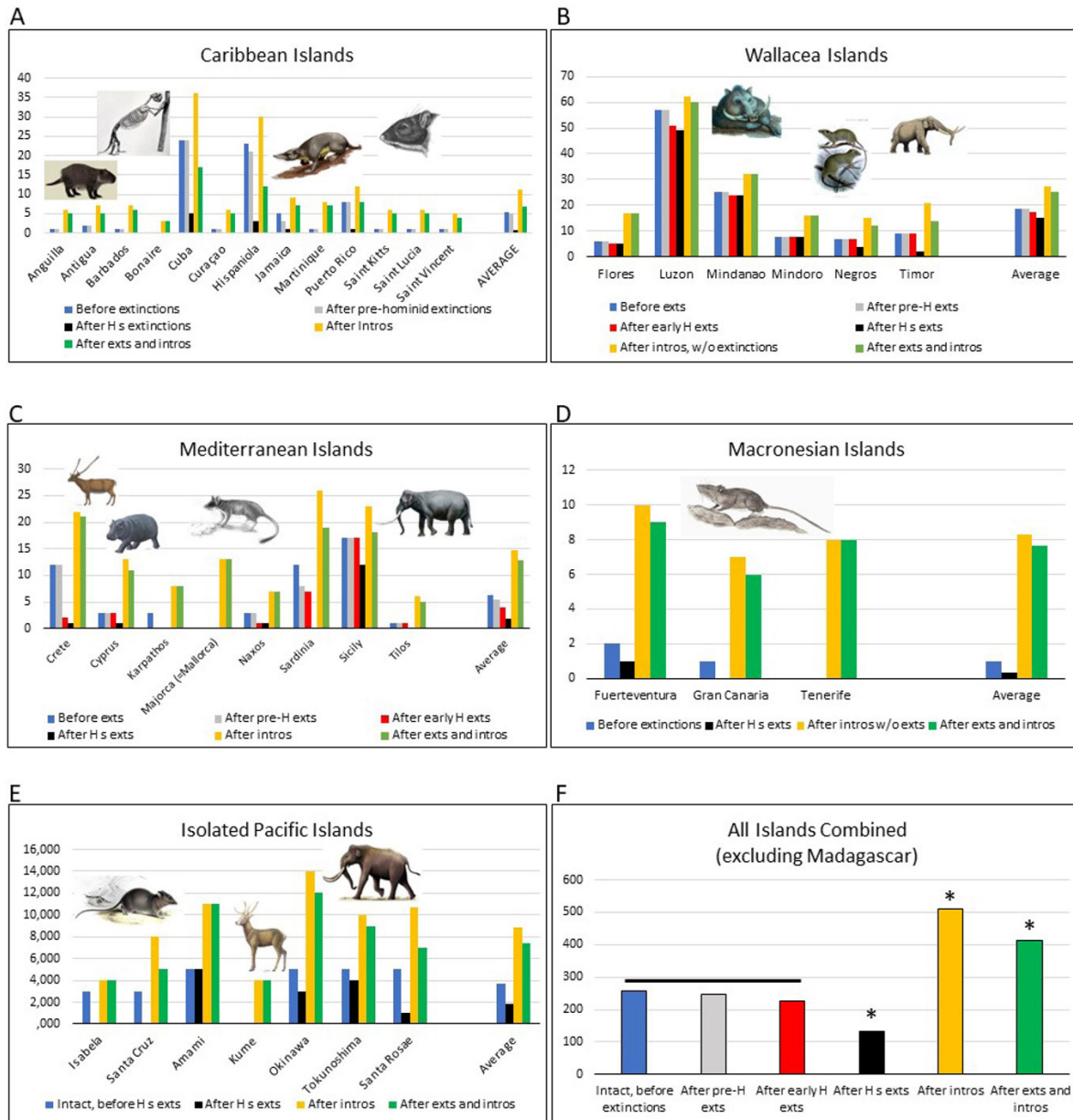


Figure 2. Variation in species richness among islands, island groups, and stages of assemblage dynamics for non-volant, terrestrial mammals on 37 oceanic islands. Stages include 1 - intact assemblages (before extinctions), 2 - after pre-hominid extinctions, 3 - after extinctions following early-hominids, 4 - after extinctions following *H. sapiens*, 5 - after species introductions, and 6 - after the combined effects of species introductions and extinctions. The number of stages experienced for each island group varies because some were not colonized by early hominids or did not experience pre-hominid extinctions. For all islands combined (Panel F), richness did not change significantly until the arrival of *Homo sapiens* on these islands, then declined significantly following post-*H. sapiens* extinctions, only to increase to levels far above those of the original assemblages following species introductions (horizontal bar in Panel F identifies those stages that did not differ significantly in richness; Tukey Method and mixed model ANOVA). The asterisks over bars in Panel F indicate that in comparison to Stage 1 assemblages, the post-*H. sapiens* extinctions (Stage 4) led to a significant number of islands declining in richness (on 31 of 37 islands), whereas species introductions taken alone (Stage 5) or together with the effects of extinctions (Stage 6) led to significant anthropogenic enrichment (with 37 of 37, and 34 of 37 islands, respectively, increasing in richness in comparison to the original, intact (Stage 1) levels ($P < 0.001$; Binomial Tests). Image sources of endemic taxa: giant hutia by Zerosvalmont (CC 0), giant sloth (CC 0), Puerto Rican nesophontes by Jennifer Montes (CC BY-SA 3.0), Martinique giant rice rat from Gervais (1855), Sulawesi pig by Hans Brinkerink, Luzon tree rats by Mintern Brothers (1883), stegodon by DiBgd (CC BY-SA 4.0), Cretan deer by Alexis Vlachos, courtesy G.A. Lyras, dwarf hippopotamus by Alexis Vlachos, courtesy G.A. Lyras, Balearic dormouse by L. Meslin in Bover et al. (2010; CC 2.5 Generic license), Sicilian dwarf elephant by George Lyras, lava mouse by Diego Ortega (CC BY-SA 4.0), Ryukyu deer by Alexandra van der Geer, Channel Islands mammoth by Egidio Viola.

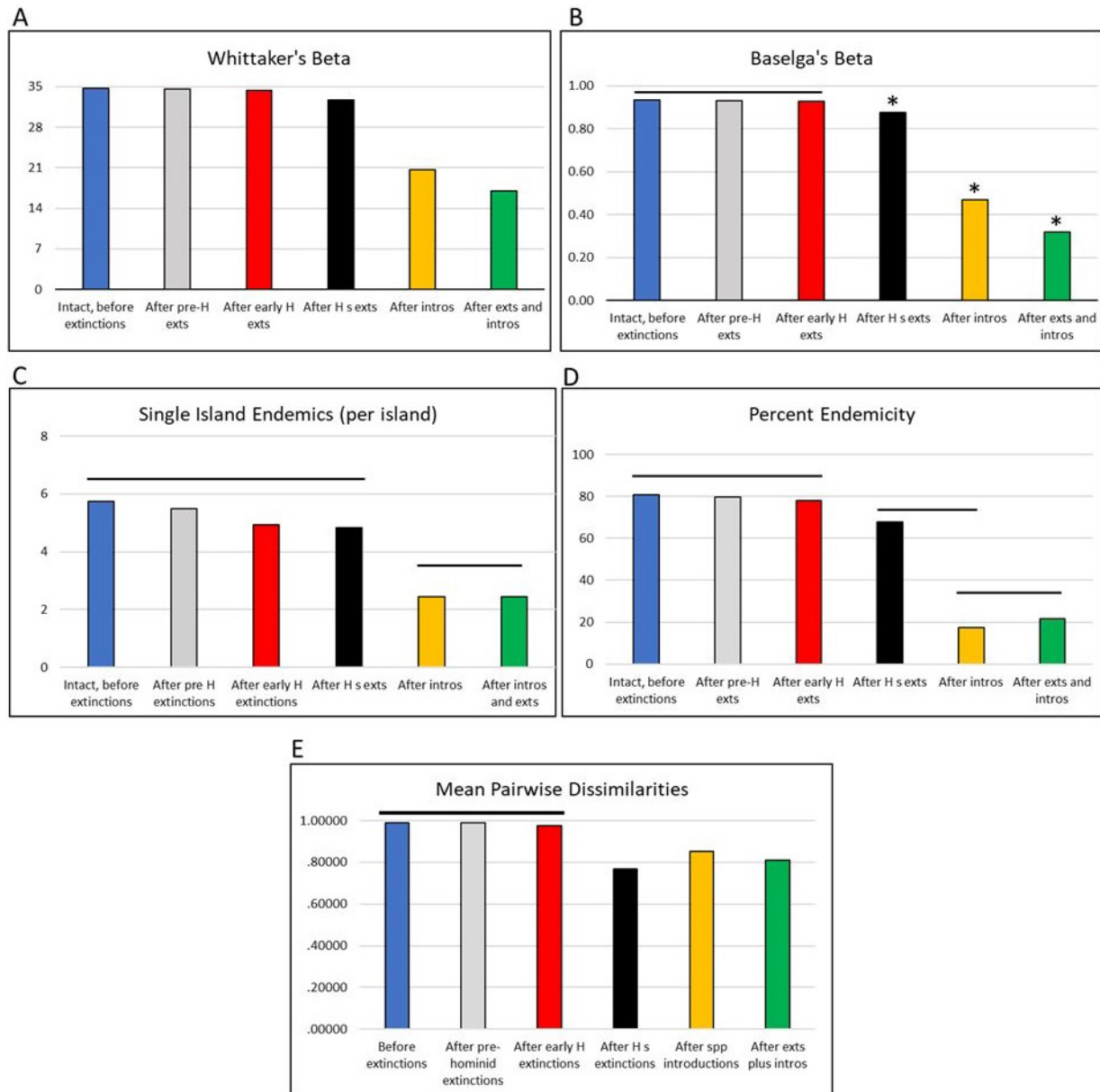


Figure 3. Dynamics in distinctiveness of insular assemblages of non-volant, terrestrial mammals following colonization by hominids. Results presented here are for comparisons of assemblages across all 37 oceanic islands studied. Horizontal line above bars in Panel B indicate that beta diversity did not change significantly prior to the arrival of *Homo sapiens*; asterisks above bars corresponding to each of the post-hominid stages indicate that beta diversity was significantly different than that of the original, intact assemblages (Stage 1; Resampling and Randomization tests; see Methods). Similarly, horizontal lines above bars in Panels C – E indicate those stages where distinctiveness among island assemblages (as measured by number of Single Island Endemics, % Endemicity, and mean Pairwise Dissimilarity) did not differ significantly from original, intact assemblages (F Tests of fixed effects from mixed model ANOVA for SIEs and % Endemicity, and Mantel Tests for Pairwise Dissimilarities).

during the initial stages of hominid colonization, actually increased on most islands, nearly doubling its initial (natural) levels when viewed across all islands, combined (Fig. 2F). The ultimate rebound in species richness was largely a function of species introductions, which more than compensated for the loss of native species.

All measures of biological distinctiveness of these island assemblages, however, declined during the

latter (post-hominid) stages (Fig. 3), and this was for two reasons. First and most obvious among the factors eroding biological distinctiveness are anthropogenic extinctions, which in nearly all cases involved SIEs, i.e., the defining elements of biological distinctiveness (Fig. 3C). These declines in mammalian assemblage distinctiveness, however, were compounded many times over by the introduction of a redundant set of species to these islands (Fig. 4). Now these islands share

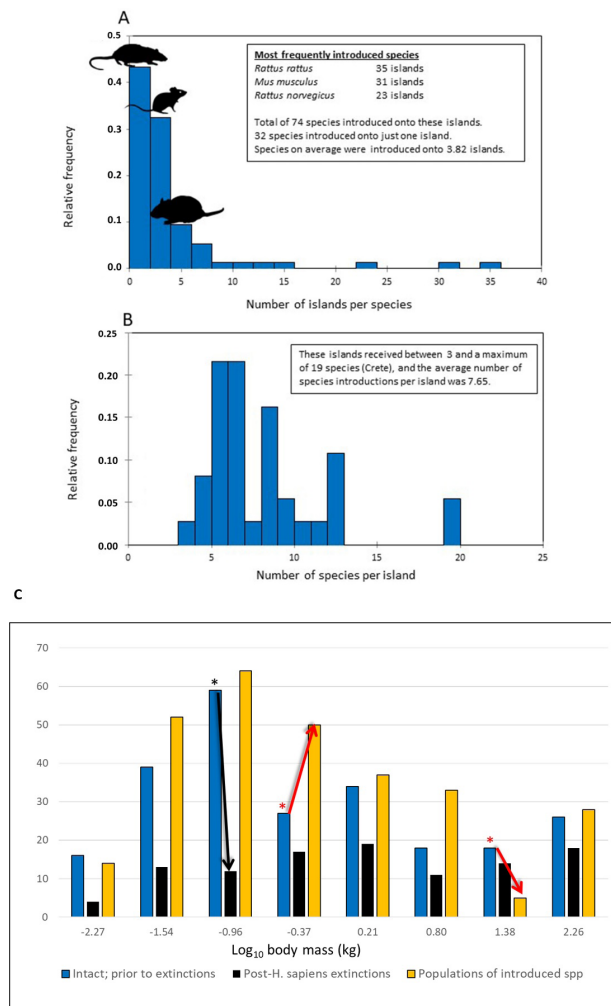


Figure 4. Relative frequencies of introductions of non-native mammals onto the 37 islands studied, including that based on (A) the number of islands each species was introduced onto, and (B) the number of introduced species received per island. (C) Differences in frequency distributions of body sizes of mammal species in the original, intact assemblages (Stage 1, blue bars) in comparison to the number of species suffering extinctions following arrival of *H. sapiens* (black bars) and to the number of populations of species introduced onto the 37 islands studied (yellow bars; values along abscissa are midpoints of the body mass bins). Arrows and asterisks indicate bins (body mass categories) that contributed significantly to the overall difference in frequency distributions of body size between the original assemblages and those suffering post-hominid extinctions (blue versus black bars; black arrow and asterisks), and between the original assemblages and populations of mammals introduced onto these islands (Fisher's Exact Test, alpha level = 0.05). Images courtesy: *R. rattus* by Ferran Sayol, *R. norvegicus* by Ryan Cupo, *M. musculus* by Daniel Jaron (CC0 1.0 Public Domain; <https://www.phylopic.org/images>)

the rats and mice and handful of other commensals repeatedly introduced to islands we colonized. Of the 74 mammalian species introduced onto these islands,

each on average was introduced onto 3.82 islands, with black rats (*Rattus rattus*), house mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*) now inhabiting 35, 31 and 23 of the 37 islands, respectively. In fact, none of these islands received just one species and each of these islands, on average, is now inhabited by 7.65 introduced species of mammals (ranging from those islands receiving a minimum of three species to the island of Crete, which is now inhabited by 31 species of introduced mammals). As a result, declines in endemism and beta diversity following species introductions far outweighed those caused by anthropogenic extinctions (Fig. 3 A-D).

Post-*H. sapiens* extinctions and introductions of populations of non-native mammals onto these islands also resulted in significant downsizing of the extant, mammalian assemblages (Figure 4C). Post-hominid extinctions, in particular those lost in Stage 4, were comprised of a set of significantly larger mammals in comparison to the original, intact (Stage 1) assemblages (Chi-square test of independence = 15.392, df = 7, $P < 0.031$). This bias was then compounded by introductions of non-native populations, which in comparison to the original assemblages were comprised of relatively small species (Chi-square = 17.089, df = 7, $P < 0.017$).

Figure 5 provides additional information on the taxonomic biases and redundant nature of extinctions and species introductions. Post-hominid extinctions were not only much more intense than those prior to colonization by hominids, but they were disproportionately high (in comparison to the composition of intact, original assemblages) in the orders Artiodactyla, Pilosa, Primates and Proboscidea (essentially even-toed ungulates; anteaters and sloths; primates; and elephants and their relatives, respectively). The taxonomic composition of introduced species included a variety of mammalian orders, but with comparatively high frequencies of rodents, small carnivores and ruminants, and notable absence of anteaters, sloths, and proboscideans. Species introductions included those from a diversity of mammalian families (Fig. 5E), but again these were biased in favor of those most closely linked to human populations – the murids (primarily mice and rats), leporids (rabbits and hares), mustelids (weasels and related species), shrews and bovids. Again, the redundancy in introductions was most intense at the species (vs. family or order) level, with between 23 and 35 islands receiving black rats, house mice and/or Norway rats.

Discussion

The demonstrable homogenization and downsizing of the world's insular mammals has important implications for the ecological transformation of these assemblages. Post-hominid extinctions removed ecosystem engineers and keystone species; most notable among these were the largest carnivores and herbivores (the latter primarily proboscideans and ungulates, the latter including Perissodactyla and Artiodactyla). These were replaced by a redundant set

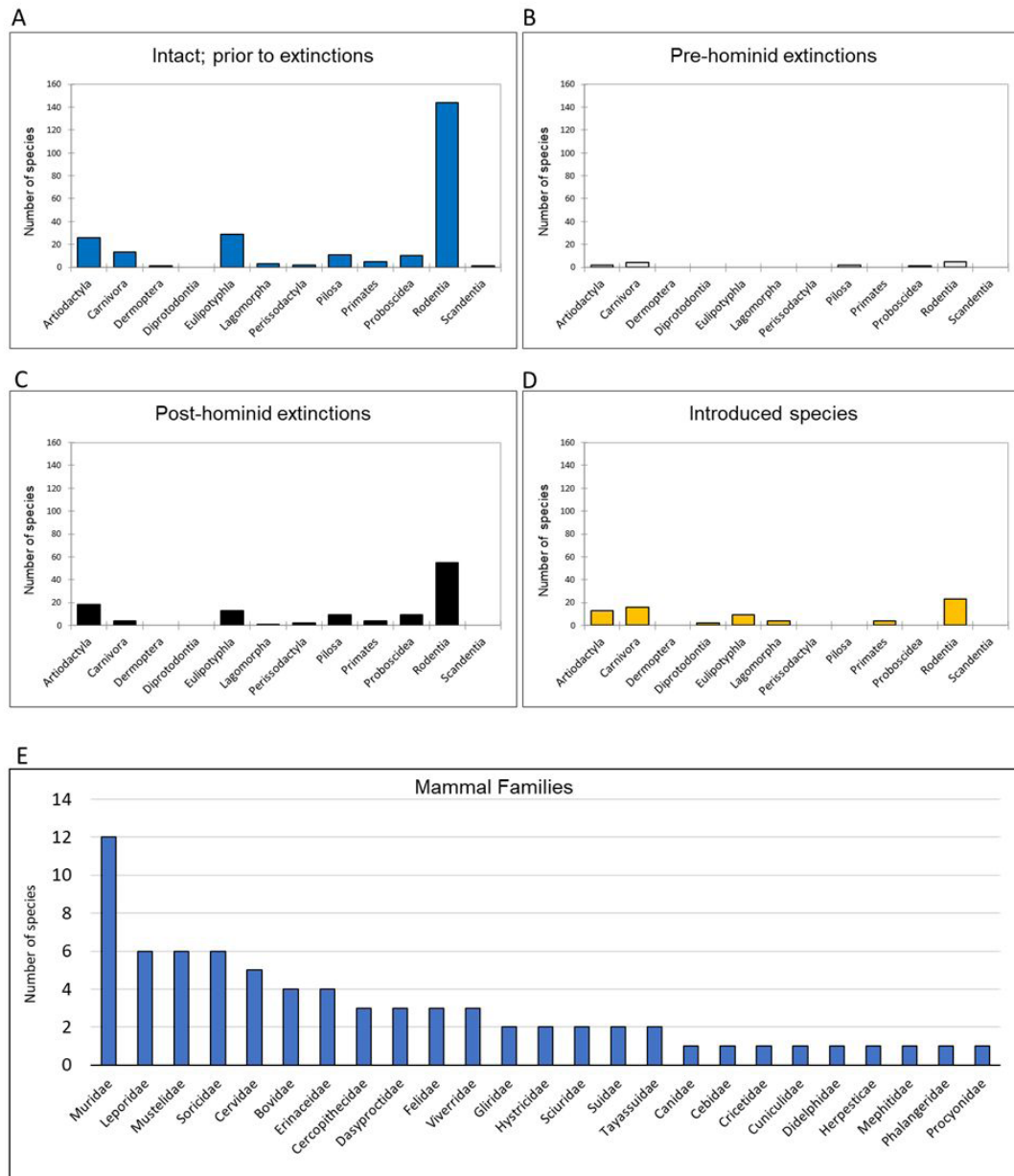


Figure 5. Taxonomic composition of species introductions onto 37 oceanic islands. (A - D) Taxonomic composition by mammalian orders during four key stages of anthropogenic transformation. (E) Frequencies of species introduced onto oceanic islands across mammalian families.

of species, replete with small generalist rodents. While it is beyond our current knowledge to reconstruct the dynamics in trophic structure and food webs of native mammals across these islands and stages of anthropogenic transformation, we did assess changes in one of the most influential morphological characteristics of mammals – their body size. Nearly all physiological and ecological characteristics of mammals are strongly influenced by their body size (Calder III 1984, Brown and Maurer 1986, Brown et al. 1993, McNab 2002, 2012). For these reasons, once isolated on islands lacking not just humans but many other mammals that otherwise tend to dominate

mainland ecosystems, the few non-volant mammals that are lucky enough to colonize these islands undergo dramatic bouts of evolutionary divergence and transformations from their mainland ancestors (van der Geer et al. 2021).

One of the most compelling of these evolutionary transformations is the island rule, which describes a graded trend from gigantism in small mammals to dwarfism in large mammals (Lomolino 1985, Lomolino et al. 2012, 2013, BÉNITEZ-LÓPEZ et al. 2021). Whereas on the mainland, ecological interactions promote evolutionary divergence in all relevant traits – body size in particular, release from those selective

pressures on species-poor islands favors convergence toward intermediate size. Thus, on islands, mice and otherwise small mammalian species often increased in size, some by 10 to over 100 times their ancestral mass on the mainland, while elephants, hippos and other 'large' mammals often dwarfed to less than 10 percent of their ancestral mass. Recent research (Rozzi et al. 2023) discovered that anthropogenic extinctions were most intense, not in the largest mammals per se, but for those mammals who experienced the most pronounced evolution of body size, whether they were dwarfs or giants. This same research also revealed that species extinctions accelerated rapidly following colonization of the islands by hominids. Thus, anthropogenic extinctions removed not just the morphologically and ecologically most distinct species, but the evolutionary most divergent mammals as well.

As indicated in the Materials and Methods, we did not include Madagascar because inclusion of this megadiverse mammalian assemblage would have disproportionately influenced and likely obfuscated insights from the results discussed above. The ecological dynamics of the Malagasy mammals (Fig. 6) are, however, qualitatively similar to that observed for the other islands we studied.

Madagascar was permanently inhabited by humans only recently (2,000 – 2,500 years ago) (Tofanelli et al. 2009, Douglass et al. 2019), followed by extinctions (i.e., post *H. sapiens*) of some 26 terrestrial mammal species, all of these endemic to the island (Kouvari and van der Geer 2018, 2019, Michielsen et al. 2023). Extinctions increased from 1.5% of the existing mammalian fauna prior to colonization to 11.7% following arrival of humanity. The latter phase of extinctions included the loss of 14 lemurs, including the ten largest species of these endemic primates at the time of colonization by humans. Even the smallest of the extinct lemurs (the giant aye-aye; *Daubentonia robusta*) was two to three times larger than its extant relative (*D. madagascariensis*). Post-*H. sapiens* Malagasy extinctions also included that of the giant fossa (*Cryptoprocta spelea*), which was roughly twice the mass of its surviving relative (*C. ferox*; 17 – 20 vs 5 – 10 kg, respectively), along with two dwarf hippos (*Hippopotamus lemerlei* and *H. madagascariensis*)

which, albeit much smaller than their mainland ancestors were still hefty mammals at over 360 kg. Malagasy extinctions also included that of three large tenrecs (*Microgale macpheeii*, *Plesiorycteropus germainepetterae* and *P. madagascariensis*) and two large rodents (*Hypogeomys australis* and *Nesomys narindaensis*), again all of these being larger than their closest living relatives.

The number of species introductions persisting on Madagascar was relatively limited in comparison to the diversity of native Malagasy species (just eight non-native species known to have established persistent populations; Supplementary Table S1). As observed above for other islands, most of the species introduced onto Madagascar were relatively small, including now broadly distributed populations of house mice, black and Norway rats, and Asian house and Etruscan shrews (*Suncus murinus* and *S. etruscus/madagascariensis*). Species introductions also included the small Indian civet (*Viverricula indica*), the wildcat (*Felis silvestris*), and the bushpig (*Potamochoerus larvatus*). With the exception of the latter species, these are all comparatively small mammals and, thus, contributed to the post-humanity homogenization as well as the downsizing of the Malagasy mammalian assemblage.

The paradox of anthropogenic enrichment may apply to other insular faunas as well. Insular birds, in particular, have experienced hundreds and perhaps over a thousand species extinctions across oceanic islands following colonization by humans (Steadman 1995, 2006, Blackburn et al. 2004, Duncan et al. 2013, Matthews et al. 2022). Again, these extinctions were highly disproportionate based on the relative land area of insular versus mainland ecosystems (Braje and Erlandson 2013, Soares et al. 2023). It remains undetermined whether species introductions have, as in mammals, compensated for or actually exceeded the numbers of native bird extinctions, but homogenization and downsizing of insular avifauna is well-documented, at least for some well-studied islands (Worthy and Holdaway 2002, Duncan and Blackburn 2004, Duncan et al. 2013, Wood 2023), as well as loss of functional richness (Soares et al. 2022, 2023).

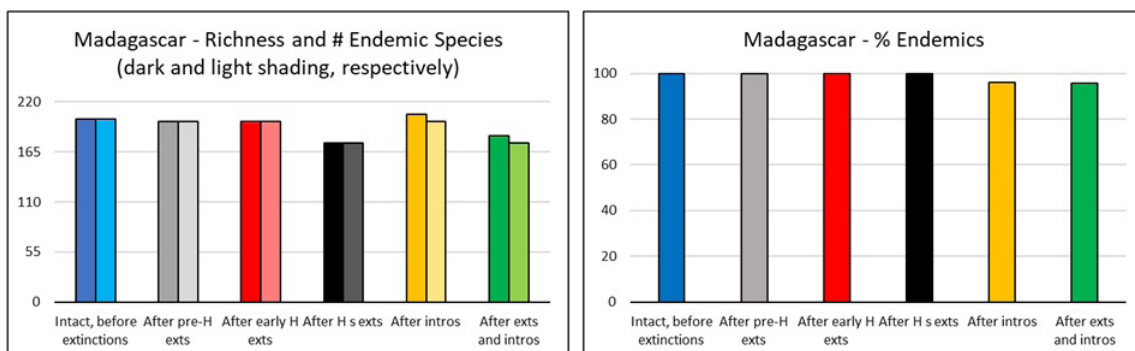


Figure 6. Dynamics in the diversity and distinctiveness of Madagascar's mammalian assemblages following colonization by hominids.

New Zealand's avifauna is a case in point, and one that appears to parallel the dynamics of Madagascar's mammalian assemblages. Prior to human colonization, New Zealand (including its offshore islands and Chatham Islands) harbored a rich avifauna that included 171 species of breeding birds (124 species of land birds inhabiting the main, offshore and Chatham Islands) (Worthy and Holdaway 2002, Duncan and Blackburn 2004, Wood 2023). Species loss rose sharply around c. 700 years ago following colonization by Polynesians and continued following permanent settlement by Europeans since c. 1800. Recent analyses estimate post-settlement extinction levels on the three largest islands (North Island/Te Ika-a-Māui, South Island/Te Waipounamu, and Stewart/Rakiura Island) at 62 of 143 breeding birds (including marine species) and 47 of 108 land birds taken separately (i.e., 43% and 44%, respectively; Wood 2023). These extinctions, and the post-Polynesian ones in particular, were highly biased against the largest species – the moa, with all of the nine species of these giant flightless birds perishing within 200 years after the arrival of Polynesians (Worthy and Holdaway 2002; Duncan and Blackburn 2004, Perry et al. 2014).

Species introductions of birds onto New Zealand may have more than compensated for the number of anthropogenic extinctions, with 131 species of non-native land birds introduced onto the islands (37 of these have established breeding populations; Robertson et al. 2013). Yet again, the anthropogenic surge in richness was accompanied by a marked decline in distinctiveness, with endemism of breeding land birds decreasing from 85% prior to, down to 49% following human settlement of New Zealand; Supplementary Table S3; see also Rosenblad and Sax 2017 and Otto et al. 2020). As observed for insular mammals, this waning of biological distinctiveness was also accompanied by a demonstrable downsizing of the New Zealand avifauna, with the moa (ranging in size from 26 to 138 kg; Latham et al. 2020) and other large native birds being 'replaced' by non-native species ranging from 0.015 kg to 10.95 kg (median mass of the 37 species of established non-natives = 0.164 kg; Supplementary Table S3).

Conclusion

Anthropogenic extinctions across the world's islands removed the largest and most evolutionary divergent species of native mammals, and introductions replaced them with a redundant set of relatively small species of similar morphologies and trophic functions. Granted, the islands we studied are now inhabited by more species of mammals than their original, pre-hominid assemblages, but they have been homogenized and downsized – their biological, ecological and evolutionary distinctiveness continues to dissolve under the ever-mounting impacts of our own species.

These appear to be the salient lessons of anthropogenic transformation of native insular assemblages, in general; species richness per se may have changed little, in some cases actually increasing, but ecological and evolutionary distinctiveness

have plummeted at regional to global scales (Nielsen et al. 2019, Ellis et al. 2021, Fraser et al. 2022, Mohammed et al. 2022, Triantis et al. 2022). Paraphrasing the lament of Gertrude Stein (1937), there indeed was a there, there, but the tragic fate of the marvels of island life was fixed once we set foot on their precious but fragile shores.

“... because I have found these islands they are lost;
Upon seal and seabird dreaming their innocent world
my shadow has fallen.”

[excerpt from the poem *Eilean Chanaidh — Shadow*,
by Kathleen Raine]

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Author Contributions

M.L. conceived the original idea, A.V. provided species data. M.L. performed the analysis with input from A.V. M.L. and A.G. discussed the results. M.L. led the writing with significant input from A.V.

Data Availability Statement

All datasets used in the study are openly available in Supplementary Tables S1-3. Statistical analyses are included in Supplementary Tables S1, S3 and S4.

Supplemental Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Table S1. Species lists of 37 oceanic islands and Madagascar with occurrence data.

Table S2. Taxonomy and body mass data for endemic and introduced mammal species of 37 oceanic islands and Madagascar.

Table S3. Bird species list of New Zealand with body mass information and calculations for changes in endemism.

Table S4. Summary of results of ANOVA mixed models.

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