Species eradication for ecosystem restoration

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Many of the world's ecosystems are under unprecedented stress as human pressures have escalated to be a dominant driver of ecosystem composition and condition. Direct impacts such as agriculture, extraction, and development are impacting vast swathes of land and ocean, while the effects of human caused climate change are felt even in the most remote parts of marine and terrestrial wilderness. These impacts are resulting in changes, ranging from ecosystem collapse or replacement, to novel mixes of species due to temperature-driven range shifts. While reducing human pressures is paramount for the future viability of vulnerable ecosystems, much attention is now also focused on whether degraded areas can be restored. Indeed, the UN has declared this the decade on ecosystem restoration, which aims to 'prevent, halt and reverse the degradation of ecosystems on every continent and in every ocean'.

Climate change and other human pressures mean the background conditions species and ecosystems now exist in have changed. As such, many researchers and practitioners recognise that restoration should restore ecosystems of the future, not the past. Therefore, restored ecosystems need to account for species that have shifted geographic ranges, and for winners and losers in response to environmental change. Restoring such ecosystem configurations should be more robust to ongoing pressures, although in many cases direct causes of degradation (e.g. extraction of trees) need to be mitigated first. Similarly, the concept of 'novel ecosystems' acknowledges that many ecosystems now exist in new configurations, often due to introduced species either through climate driven range shifts, or (often accidental) human introductions. This concept recognises that not all introduced species vastly disrupt ecosystem dynamics, and some can even replace lost functional roles. However, some introduced species can be hugely disruptive to ecosystems, causing substantial changes to populations of other species and to ecosystem processes. These species are often termed invasive species, and their eradication forms a key part of ecosystem restoration.

Invasive species eradication

By definition, an invasive species is an organism that causes ecological or economic harm in a new environment where it is not native. A diversity of species from different taxa may become invasive species outside of their normal range. For example, Japanese knotweed, which is native to east Asia but invasive in the USA and Europe, grows extremely rapidly allowing it to overgrow and smother native plants, and cause damage to buildings and roads. The brown tree snake, native to Papua New Guinea, was introduced to Guam in the 1940s where it has reached incredibly high densities and has eliminated 9 of the 11 native land bird species. Meanwhile, the Indo-Pacific lionfish was introduced in Florida in the 1980s and has since spread throughout the Caribbean and much of the tropical western Atlantic, causing substantial declines in juvenile fish populations. The rate of species introductions is increasing globally, with the economic cost of biological invasions estimated at US$1.3 trillion, and 1 in 10 of the IUCN's threatened species being adversely affected by invasives.

Although all invasive species negatively influence the invaded ecosystem, some can cause particularly widespread changes. For example, after Burmese pythons (*Python molurus bivittatus*) were introduced to the Florida Everglades via intentional release of captive pets, there were severe declines of previously abundant mammals; raccoons, bobcats, and rabbits were reduced by 80-100%. Similar impacts were reported for amphibians, reptiles, and birds. Generalist species like small mammals and opossums are resilient to python predation, shifting mammal communities from mesopredator-dominant to rodent-dominant, with implications for disease dynamics. Invasive species that exert large ecosystem-wide consequences may be priorities for eradication from an ecosystem restoration perspective.

On continental land masses, or ocean ecosystems, the diffuse nature of species presence, and connectivity of suitable habitat, means that complete eradication of invasive species is incredibly challenging. Instead functional eradication may be a target, whereby populations are reduced and maintained at a low enough level to prevent their negative consequences on native species, often at targeted sites. For example, enhancement of predators and trapping of the invasive rusty crayfish at high priority sites in North America, could reduce numbers sufficiently to benefit invertebrate prey and native fishes. Alternatively, spatial eradications, through the erection of barriers (e.g. fences) may be achieved. Many of these approaches are about controlling invasive species populations, rather than eradicating them fully. Complete eradications are more feasible in discrete isolated systems. Isolated mountain lakes are one of the few such habitats within continental land masses. After years of intentionally stocking naturally-fishless alpine lakes with game fish (e.g., trout) and live bait (e.g., minnows) to promote recreational fishing, their deleterious effects on lake food webs were recognized. Consequently, bans on stocking and fishing in alpine lakes have been enacted in several parts of Europe and North America, after which non-native trout can be fully eradicated within several years, using techniques including gill netting and electrofishing. Full recovery of native biota such as zooplankton, macroinvertebrates, and amphibians often occurs soon after fish eradication.

In contrast to most continental and ocean systems, islands are isolated and discrete ecological entities. Islands are also hotbeds for invasive species, with many islands having a very large proportion of introduced species present. For example, an estimated 49-54% of plants on Hawaii are introduced. Island ecosystems are particularly vulnerable to global change, with an estimated 61% of global extinctions being detected on islands. Small land masses and isolation meant that island flora and fauna evolved to be both unique and poorly equipped to cope to novel forms of competition and predation. Indeed, many island communities evolved in the absence of mammalian predators, and consequently they are particularly vulnerable to the introduction of predators such as rats, cats, and foxes. Unfortunately, these predators have been widely introduced by human patterns of expansion, trade and ship wrecks, with an estimated 90% of island archipelagos now harboring rats. Such introductions transform island ecology, with huge reductions and changing compositions of terrestrial flora and fauna, and reduced flows of nutrients and organic materials between island and ocean habitats.

While islands are particularly vulnerable to the negative consequences of invasive species, they are also much more practical scenarios to consider eradication efforts. Being discrete units, complete eradications become much more feasible, the likelihood of success can be relatively high, and the benefits of doing so can be dramatic. As such, conservation efforts to eradicate invasive species from islands have burgeoned. Eradication efforts have accelerated in the past 40 years, with ~1000 islands attempted, success rates remaining quite consistent at ~88%, and the most common target being invasive rats (Figure 1). While temperate islands have received most attention, eradication efforts have increased on islands across all latitudinal climate zones. Through time there has been an increase in the size of island where rodent eradications have been attempted and successful (Figure 1). A notable recent example is the eradication of mice and rats from an area over 100,000 ha on South Georgia island. With invasive species causing such substantial ecosystem change on islands, and efforts to eradicate them burgeoning, the question of how eradication dovetails into ecosystem restoration is of interest.

Role of eradication in ecosystem restoration

Definitions of ecological restoration vary, but most subscribe to the idea that restoration is the process of aiding the recovery of a damaged ecosystem. Eradicating invasive species from islands, therefore, is a form of restoration in its broadest sense. Given the time, money, and effort required to eradicate invasive species, some would consider eradication active restoration. However, others might call it passive restoration, because removing invasive species is the equivalent of ending the disturbance that disrupts ecological processes and functioning. In this strict definition, restoration then happens after the disturbance is removed and other actions, such as replanting native vegetation or reintroducing ecosystem engineers like seabirds, are initiated. Regardless of definitions, invasive species eradication serves as a powerful tool for sparking whole-ecosystem restoration, especially on island ecosystems where complete eradication of invasive mammals is most feasible. Indeed, there have been over 1,000 successful eradications of invasive mammals from islands globally, resulting in positive responses of native plant communities and the recovery, reintroduction, recolonization, or new colonization of nearly 250 animal species on over 180 islands (Figure 2).

Despite the general pattern of positive responses to invasive mammal eradication by island species and ecosystems, there have been examples of unintended negative consequences of invasive species eradication, such as explosions of weeds following the removal of herbivores. Furthermore, in cases where multiple invasive mammals are on a single island, the order of removal has important consequences because if apex predators (e.g. feral cats) are removed before invasive mesopredators (e.g. rats), that can release the mesopredator from predation and result in hyperpredation on native fauna. Even native predators can reach problematic densities following invasive mammal eradication. Following cat and rat removal on Isla Isabel island, Mexico, a native milk snake population increased 11-fold and are now responsible for depredating 40% of the booby hatchlings on the island. Such examples remain exceptions to the general rule of invasive species eradication, which typically results in significant positive gains for native flora and fauna.

Invasive species eradication can set the stage for ecological recovery as ecosystem engineers recover from population suppression. Seabirds, for example, transfer marine-derived nutrients in the form of guano, regurgitate, and carcasses to often otherwise nutrient-limited island ecosystems, and are an important component of ecological recovery on many islands (see *rat eradication for ecosystem transformation* case study below). Beyond the impacts of seabird recovery, other native species that play critical roles in ecosystems such as herpetofauna, mammals, land birds, plants, and invertebrates, have all been shown to positively benefit from invasive mammal eradication. Though island food webs are touted as more simplistic than their continental counterparts, they can still be relatively complex, yielding likewise complex responses to invasive mammal invasion and eradication. On Santa Cruz Island in the Channel Islands National Park, USA, invasive omnivorous pig (*Sus scrofa*) introduction provided a supplemental food source for native golden eagles (*Aquila chrysaetos)* such that eagle populations grew to many times beyond their historical levels. This led to hyperpredation by eagles on the native endangered island fox (*Urocyon littoralis*), which almost resulted in the extinction of the foxes from Santa Cruz Island. Once pigs were eradicated, and other conservation/restoration measures such as captive breeding, relocation of golden eagles, and the reintroduction of bald eagles (*Haliaeetus leucocephalus*) were undertaken, the island fox populations rebounded from less than 100 to over 1,000 and were removed from the U.S. Fish and Wildlife's Endangered Species list.

The recovery of the island fox illustrates a critical point - sometimes removal of invasive mammals alone is not enough to spur ecosystem restoration. Indeed, the isolated and discrete nature of islands can be a double-edged sword, as it enables full eradication of invasive species but can also hinder recovery of native species. Flightless insects, herpetofauna, and even birds that fly limited distance have all been shown to benefit from active reintroduction efforts following mammal eradication (Figure 2). The recently developed Seabird Restoration Database details the many projects dedicated to reintroducing, newly establishing, or bolstering seabird populations, often after their breeding grounds are cleared of invasive mammals. In total over 850 seabird restoration projects have occurred globally, many with the goal of sparking whole-ecosystem recovery following invasive species eradication. Another example of the need for active restoration comes from Palmyra Atoll in the Pacific. After invasive rats were removed from Palmyra in 2011, another invasive species, the coconut palm (*Cocos nucifera*), exploded in population size because the rats no longer consumed palm seedlings. These invasive trees outcompeted native trees on the island, resulting in lower habitat quality and thus lower population sizes of many native island birds. An intensive campaign sparked the removal of over one million coconut palm seedlings from Palmyra, with many seedlings of native tree species planted in their place.

Case study: rat eradication for ecosystem transformation

Rats provide an ideal illustration of how species eradications can lead to successful ecosystem restoration. Rats were introduced to the vast majority of the world's island chains as stowaways on ships. Once there, rats can transform island and nearshore marine ecosystems. Rats have now been eradicated from >500 islands, with successes expanding across latitudes and on islands of increasing size and human population (Figure 1). Despite the large number of islands from which rats have been removed, monitoring data that include both pre- and post-eradication time periods (or better yet, a true BACI-design including rat-free islands as references for restoration) are relatively rare. Although the lack of comprehensive monitoring data means the full impacts of rat eradication are unknown, there is still ample evidence that rat eradication causes widespread ecological changes. In addition, comparisons of islands that never had rats versus nearby islands with rats offer additional insights into the expected consequences of rat eradication. Here, we integrate some of these data to describe documented and likely examples of ecological restoration across island, intertidal, and marine systems caused by rat eradication.

One of the main ways that rat removal leads to ecosystem restoration is via rebounding seabird populations, which often experience large increases in breeding success, recolonization, and thus population size within decades of rat eradication (Figure 3). Seabirds - which forage at sea but roost and breed on land – act as ecosystem engineers on islands. They modify their environment by transporting large amounts of nutrients from their offshore feeding areas to their island breeding habitats and by physically disturbing soil and vegetation while creating nests. As such, an increase in seabird populations following rat eradication acts as a natural catalyst of broader ecological restoration. On islands where rat eradication leads to increased seabird populations, seabird-provided nutrient subsidies also increase, as indicated by elevated proportions of seabird-derived nutrients in soils, plants, and higher-order consumers. Thus, rat eradication not only restores populations of native seabirds, but also restores an important ecological function provided by seabirds. Island plant communities also exhibit a relatively rapid response to rat eradication, including changes in seedling abundance, plant cover, and community structure (Figure 3). These impacts are likely due to a combination of increased nitrogen and phosphorous availability from seabird-provided nutrients, disturbance by nesting seabirds, and release from direct predation by rats.

Rat eradication facilitates restoration of broader island food webs via its effects on a diverse array of higher-order consumers. For example, rat eradication precipitated re-appearances and/or population increases of insects, crabs, and reptiles on New Zealand islands without any additional restoration interventions. As for plants, the recovery of native animals is likely due to multiple direct (e.g., release from predation, competition from rats) and indirect mechanisms, with seabirds playing a role in several of these pathways (e.g., seabird burrows providing habitat, vegetation recovery providing food and habitat). Rat eradication also causes changes to the behaviour of native animals, including widening of habitat use by geckos and broader trophic niches of land crabs, providing another pathway to ecological restoration beyond increases in abundance.

The benefits of rat eradication and seabird restoration are not restricted to islands, as seabird-derived nutrients, mostly in the form of guano, run-off or leach into nearby intertidal and marine environments (Figure 3). In temperate and subpolar regions, after rat eradication nutrients from seabirds are taken up by primary producers, including marine algae, and can stimulate enhanced algal production, increase algal diversity, and alter algal community structure. However, the magnitude and timing of effects can vary based on environmental characteristics including depth and wave exposure, with the strongest effects typically occurring in shallow areas closer to shore. For example, in the Aleutian Islands, rat eradication caused a return in intertidal community structure to match rat-free reference communities, characterized by increased algal cover and decreased invertebrate abundance. These changes were primarily driven by a trophic cascade involving shorebirds, which feed on intertidal invertebrates, rather than seabirds that feed offshore. However, evidence from other systems suggests that seabirds may trigger similar trophic cascades, as seabird guano indirectly increases shorebird abundance by increasing algal cover, which provides habitat and food for invertebrates, including shorebird prey resources.

Our understanding of how rat eradication influences tropical and sub-tropical marine systems is still in its infancy. Similar to higher latitude systems, rat eradication restores flows of nutrient subsidies provided by seabirds, which are evident in coral-reef organisms including macroalgae, turf algae, and fishes and extending at least 300 m offshore. While few studies have assessed benefits to tropical marine systems following rat eradication, comparisons between rat-free and rat-infested islands demonstrate that seabirds benefit coral reefs in a variety of ways. These benefits include faster growth of corals and fishes, greater coral-reef fish biomass and ecosystem functioning, and enhanced resilience to extreme marine heatwaves. Moreover, due to their positive effects on reef organisms that play key functional roles (e.g., corals, herbivorous fishes), a return in seabirds could facilitate coral reef restoration, especially when combined with other conservation techniques (e.g., marine reserves, outplanting coral fragments). Indeed, attracting seabirds has already been harnessed in the restoration of seagrass beds, as their guano accelerates seagrass recovery.

Timescales of ecological responses

Invasive mammal removal initiates significant changes on islands - some that happen very quickly, and others that take more time (Figure 4). On islands where omnivores that target seeds (like rodents) or herbivores are removed, there is often a swift response (within 1-3 years) from plant species, with many more seedlings surviving, though sometimes burrowing activity can reduce seedling survival. Invertebrates with fast life cycles often respond quickly to eradication as well, particularly when they were previously exposed to invasive mammal predation or competition. Animals such as birds, lizards, and native mammals that served as prey and/or competitors for invasive mammals often show marked responses to invasive mammal removal, usually within five years. Seabirds in the Laridae family (gulls and terns) respond most quickly to eradication as they often don’t exhibit natal site fidelity and can take advantage of newly available high quality breeding habitat within 1-2 years following invasive mammal removal. Other seabirds, such as albatrosses, petrels, and shearwaters that exhibit philopatry and long times to reproductive maturity, can take much longer to respond; research has shown that it can take 15 years or more for increases in their nutrient subsidies to be detected in island food webs. Beyond single species recovery, it may take community composition and certain ecosystem functions much longer to recover, especially on islands reliant on philopatric seabirds to drive composition and functioning.

Future frontiers

The eradication of invasive species from larger, more complex, and often inhabited islands is becoming a real frontier. Such ambitious islands require new innovations in eradication approaches, for example to deal with complex habitats such as mangrove forests where rats can evade bait. They also require careful biosecurity planning to ensure eradicated pests are not re-introduced, especially for islands with more human transport links. Of note here is the recent announcement by New Zealand that it plans to eradicate predators from the entire country by 2050. New Zealand has been a world leader in invasive species eradication, and this ambitious goal highlights both political will in the intervention, and confidence that vastly increasing the scale and complexity of eradication efforts is possible. In continental and ocean environments, scaling up existing approaches to control invasive species populations, or fence off strategic areas, remains a key objective. Emerging technology, such as 'gene drives', a genetic modification designed to spread through a population at higher-than-normal rates of inheritance, are also a key frontier. Inserting a mutation that spreads through a population whereby offspring are infertile, could vastly scale up eradication efforts, but the approach is still laden with research, safety and ethical considerations.

The role of invasive species eradication in ecosystem restoration is an area ripe for further research. Given invasive species eradications have typically occurred in uninhabited remote places, the research to uncover their influence on the wider ecosystem is often limited. This is compounded by the timescales of ecological responses to eradications, which are typically years to decades, and thus beyond the scope of typical funding cycles. Despite this, emerging evidence points to the potential for widespread ecological changes, including across ecosystem boundaries, in response to invasive species eradications. Of course, many other factors contribute to recovery of species, communities, and functioning beyond just time since eradication. Historical and current land use, presence of other invasive species, topography, climate, and management regime all impact restoration trajectories. Given ongoing anthropogenic stressors beyond invasions, many have hypothesized that removing invasive species can create new assemblages of species and different functioning that are unlikely to return to pre-invasion configurations. Such transitions argue strongly for forward-looking restoration objectives and research that envision what healthy, functioning ecosystems of the future might look like.

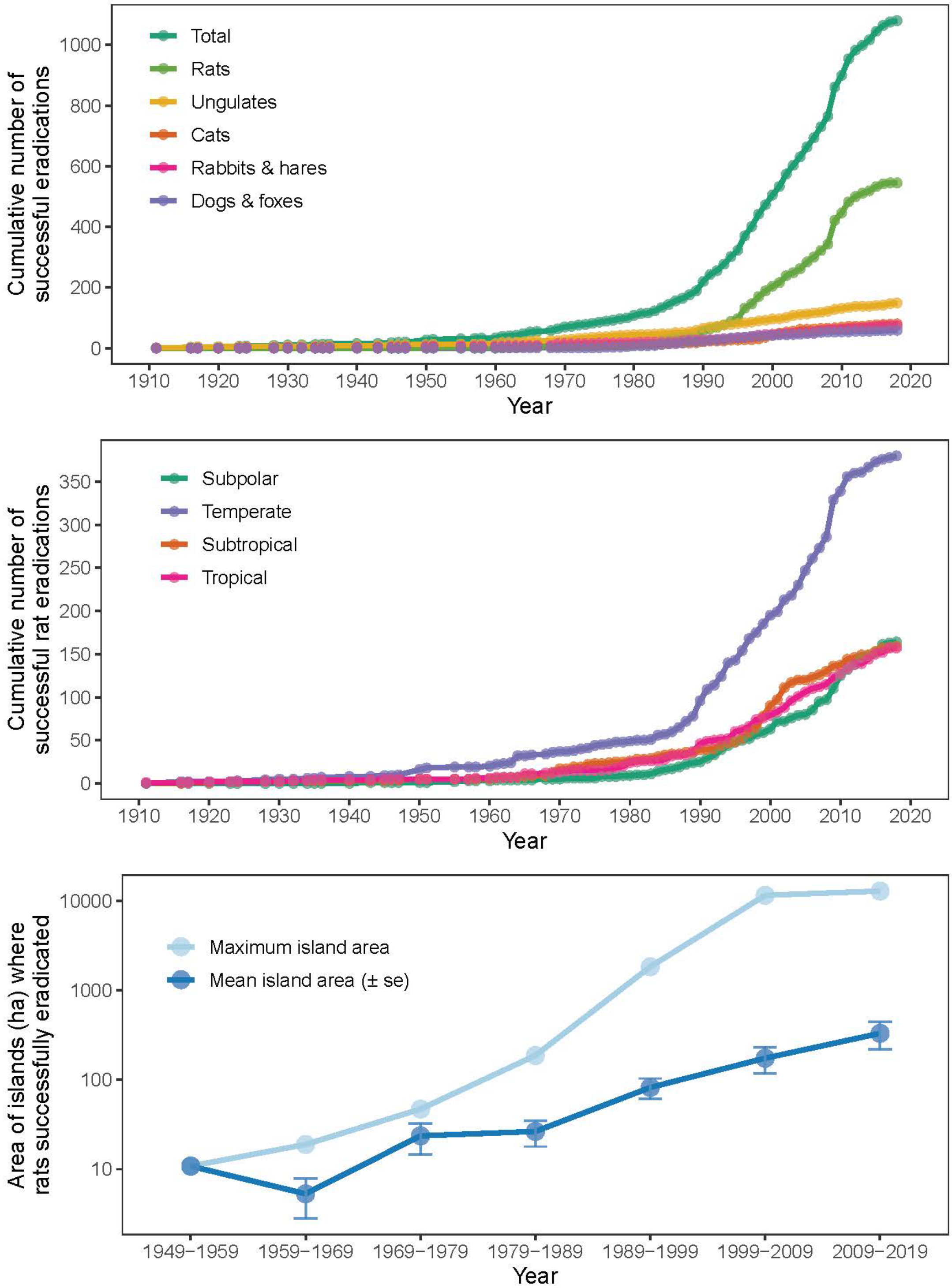

Figure 1. Temporal trends in eradication of invasive vertebrates from islands. (a) Cumulative number of successful eradications through time, including for the five groups most commonly eradicated, which collectively account for >83% of successful eradications. For rats, which account for most successful island eradications (>64%), trends vary through time by (b) geographic zone and (c) size of islands where successful eradications have occurred. Data from Database of Island Invasive Species Eradications by Island Conservation (http://diise.islandconservation.org/), accessed from Spatz et al. 2022.

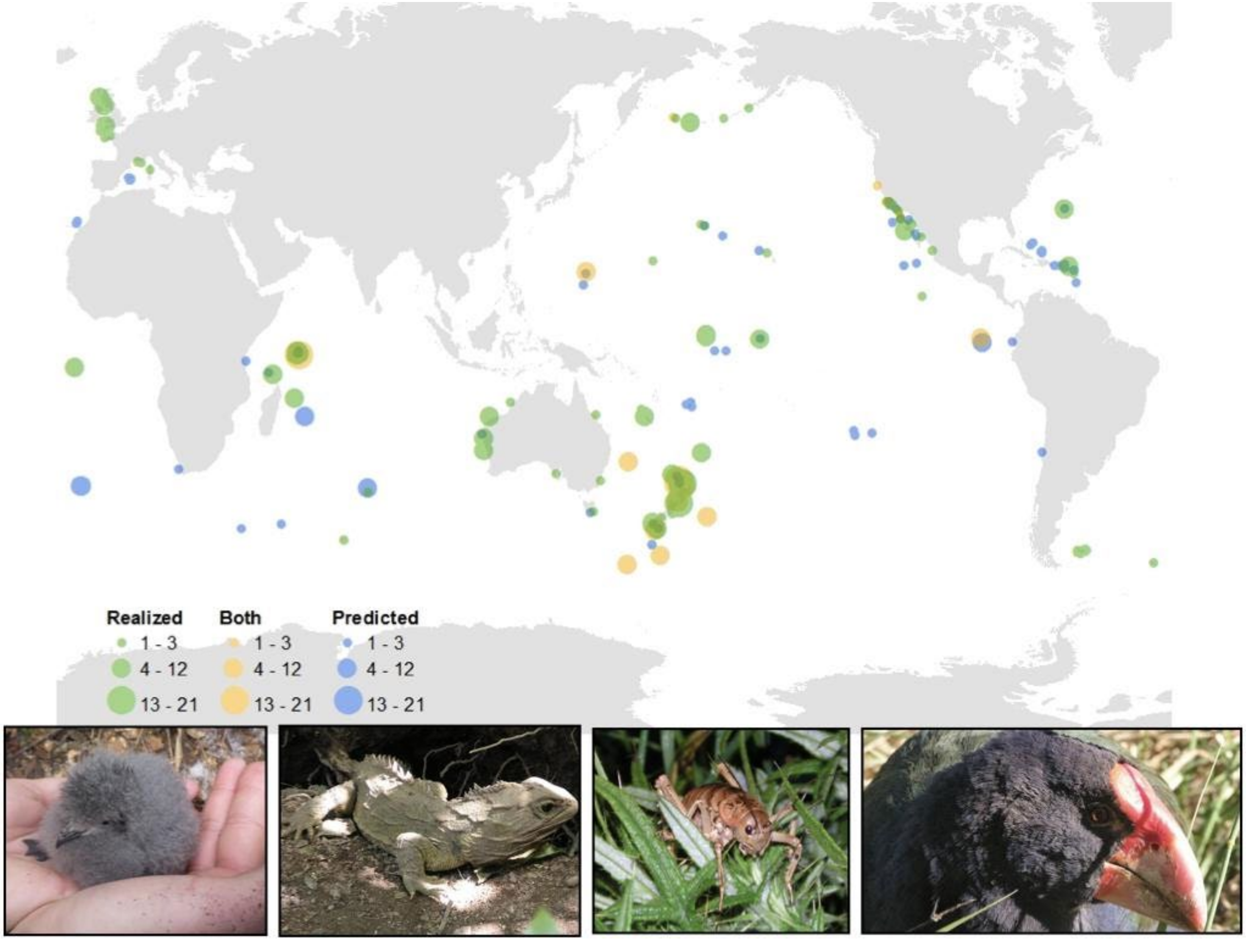

Figure 2. Islands where native fauna populations have had demonstrated and/or predicted benefits from invasive mammal eradications. Dot size indicates numbers of populations. Realized beneficiaries include vertebrates and invertebrates that have had positive outcomes measured by researchers; predicted beneficiaries are restricted to critically endangered or endangered birds, mammals, and reptiles on the IUCN Red List that experienced an eradication and thus are predicted to have benefited. Photos are some examples of beneficiaries, from left to right, a New Zealand storm-petrel chick (this species was thought extinct for over 100 years until it was rediscovered following rat and cat eradication; Photo credit: Stephanie Borrelle), tuatara (this endemic reptile increased in population and/or was reintroduced to 16 islands following mammal eradication), wētā (multiple species of these giant flightless crickets were reintroduced to 15 islands following mammal eradication), and takahē (the flightless largest rail in the world has been reintroduced to one island and introduced for conservation purposes to four other islands following mammal eradication). Top panel from Jones et al. 2016.

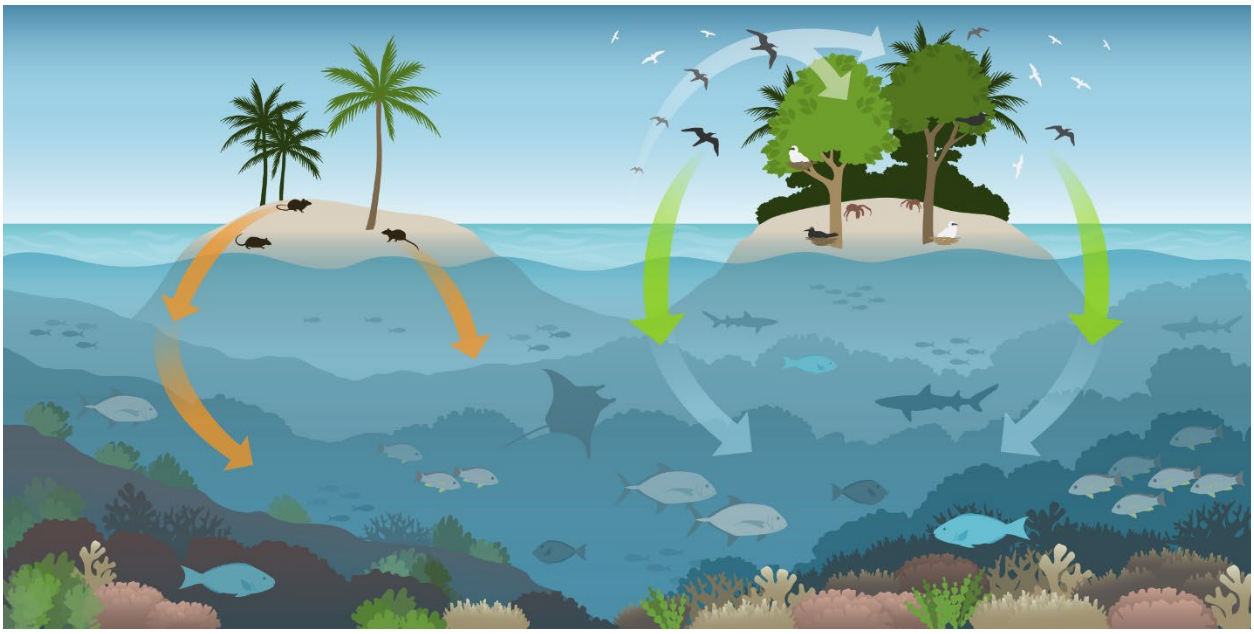

Figure 3. Conceptual illustration of the influence of invasive rat eradication on tropical islands and nearshore coral reef environments. Once rats are removed, seabirds often return to islands, sourcing nutrients from distant pelagic (open ocean) prey. Seabird nutrients boost island flora and fauna productivity, and enter the nearshore marine environment to enhance growth of organisms such as corals and fish.

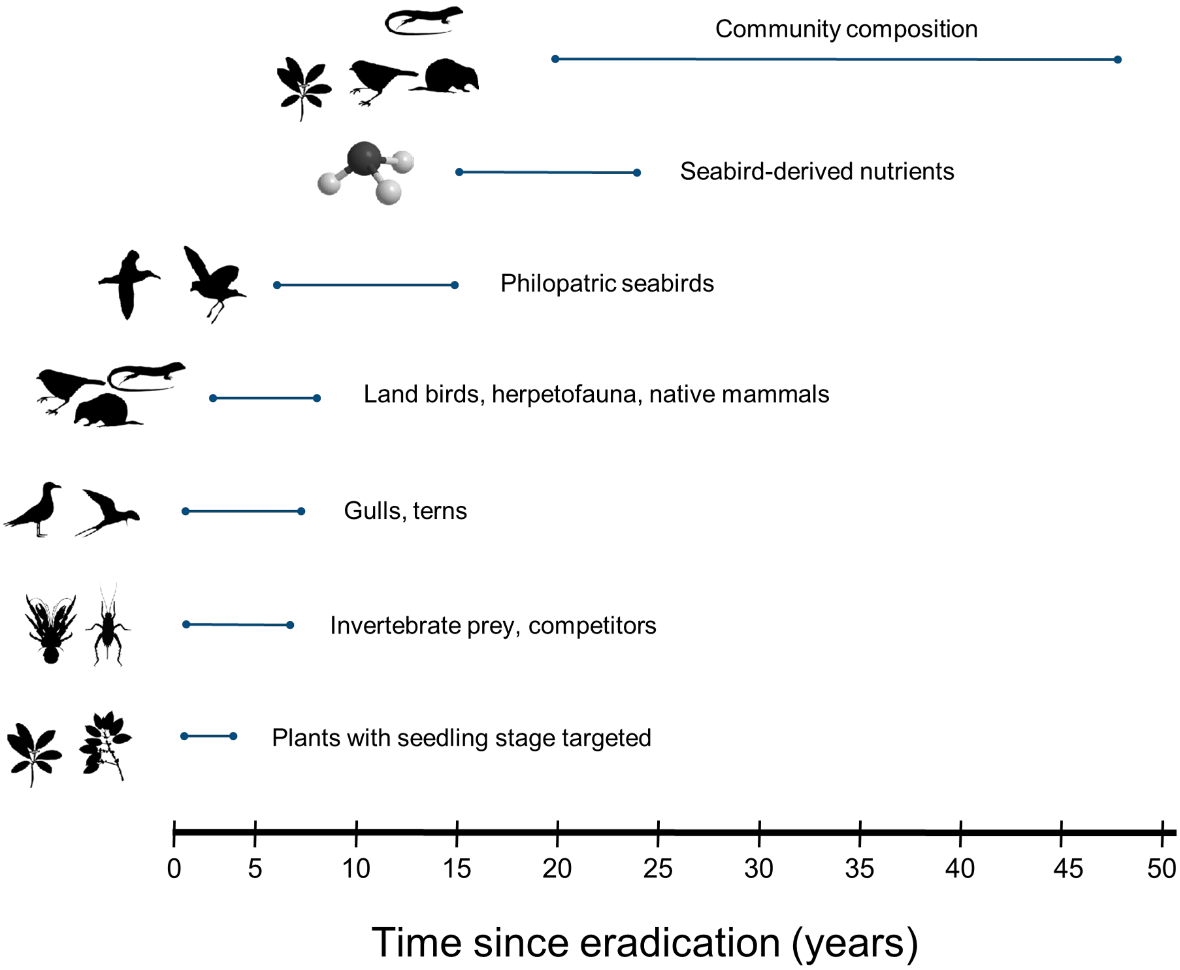

Figure 4. Approximate range of time to measurable response/recovery for a variety of insular species and functions following mammal eradication. Wētā silhouette by Melissa Broussard, accessed by creative commons license https://creativecommons.org/licenses/by/3.0/ .

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