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Island Ocean Connections: Exploring Land-Sea Linkages in the Context of Invasive Mammal Management

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ISLAND OCEAN CONNECTIONS

EXPLORING LAND-SEA LINKAGES IN THE CONTEXT OF
INVASIVE MAMMAL MANAGEMENT



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ABOUT THIS REPORT

Island Conservation (IC) and Scripps Institution of Oceanography (SIO), UC San Diego, co-convened a meeting of practitioners and researchers to assess the Global Links for Island Marine Restoration (GLIMR). These global experts in the diverse fields of island restoration, invasive species management, and wildlife conservation, were assembled and worked for eight months to evaluate the state of the knowledge of land-sea linkages in the context of invasive species management and island restoration. The result is this white paper synthesis of the science and research recommendations and a manuscript that will be submitted to a peer-reviewed journal. The intended audiences for this endeavor include island communities, governments, conservation and sustainable development non-governmental organizations, scientists, and funders. Throughout the report, readers will find that the key takeaways, identified by the authors, are represented in blue italics. This study was made possible by the generous support from the IC Board of Directors, the Center for Marine Biodiversity and Conservation at SIO, the Nature Conservancy California Chapter, the Leo Model Foundation, and the Archie Arnold Trust.

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EXECUTIVE SUMMARY

Human societies living along the coast have managed natural resources based upon a 'ridge-to-reef' model for generations. The management approach is based upon a common understanding that the workings of land ecosystems are inextricably linked with adjacent marine ecosystems. The importance of considering natural resources with explicit reference to land-sea linkages is perhaps most pressing on oceanic islands, especially today.

In recent decades, the number of threats to biodiversity and human livelihoods are seen at their most extreme on islands, and the impact of introduced, damaging invasive species is among the biggest threats to meeting management and conservation goals. Invasive species on islands, especially mammals like rats, cats, and goats, have devastated island ecosystems with an untold number of native and endemic species decimated by the invaders. Ecological monitoring has revealed a diverse and profound number of direct and indirect effects of invasive mammals on terrestrial flora and fauna. In only a limited number of cases have the effects of invasive mammals been studied within the context of traditional ridge-to-reef management, although, unsurprisingly the ecological impacts extend well into the marine environment.

Despite the human legacy of appreciation of land-sea linkages, modern ecological studies have only recently used such integrative perspectives to address island ecosystem management challenges. For academic research, the eradication (or the introduction) of invasive mammals from (or to) islands presents one of the most compelling experiments to describe, and ultimately predict, the specifics of land-sea ecosystem connectivity. Focused case studies have shown that invasive mammals on land can shift food web structure, alter nutrient budgets, or extirpate entire populations, affecting profound changes in the functioning of island and marine ecosystems. However, the nature and intensity of land-sea linkages is not consistent across the diversity of all island types. Understanding this variability is essential for building realistic expectations on which islands, and to what extent, we can expect meaningful marine conservation gains from invasive species management.

Despite the rarity of studies on land-sea invasive species management linkages, we found extensive scientific literature spanning multiple disciplines that helped identify factors that can influence the strength of land-sea linkages. We identify six characteristics of an island that are likely associated with the strongest links between land and sea: (i) High rainfall and (ii) high elevation islands are associated with well-linked land and sea ecosystems. Further, the strength of land-sea linkages can be influenced by the biological and geological characteristics of the island. Islands with (iii) limited vegetative cover or (iv) low soil permeability can be associated with tighter land-sea connectivity. Most evidence of strong linkages across island ecosystems are associated with nutrient subsidies from land to sea. Local oceanographic conditions, including (v) low oceanographic nutrient delivery and (vi) low oceanographic flow (e.g. currents, wave action) can maximize land-sea connectivity. When aiming for maximum marine conservation gains associated with the management of invasive mammals, these island characteristics are most promising.

As the global community expands efforts to prevent, mitigate, and eradicate the impact of invasive mammals, it is critical that we aggregate our knowledge and capacity across islands worldwide. Resource monitoring efforts that guide the application of invasive species management will be most valuable if they collect a common body of data, including observations from land to sea, and if they are shared through an open data infrastructure. Given that most resource monitoring and research professionals are trained in specialties unique to land or sea, collection of such data will depend upon collaboration across sub-disciplines and skill sets. Invasive mammal eradication is among the most important conservation interventions for islands and failing to recognize and design these projects to most benefit nearby marine environments is a huge missed opportunity. Further, missing the chance to work together to collect data from across these management efforts will be a profound failure of scientific opportunity and leave unanswered questions about how to maximize marine co-benefits. Invasive species eradication experiments are unique opportunities to expand human knowledge, building from generations of traditional learning about the fundamental importance of land-sea linkages in our coastal ecosystems.

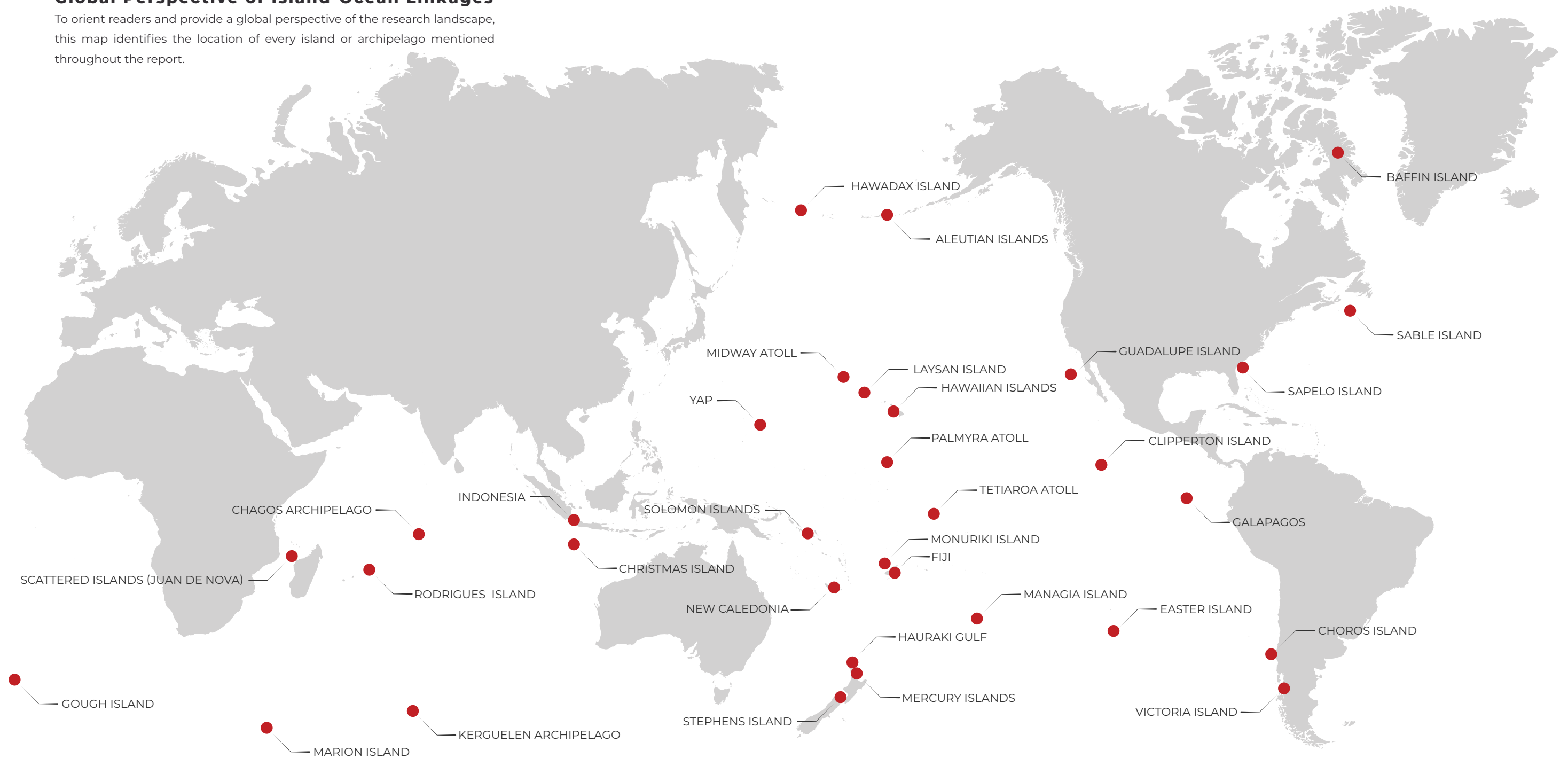
Therefore, we call for new and expanded collaborations between island communities who have been managing these systems for generations, scientists with the expertise to collect and interpret a consistent set of island and marine data, and conservation practitioners carrying out eradication projects. We advocate for integrative, interdisciplinary studies across marine, terrestrial, theoretical, and applied realms. We call for additional focus and support to carry out critical invasive species eradications on islands where land-sea linkages will facilitate the greatest marine benefits.



Credit: The Nature Conservancy

Global Perspective of Island-Ocean Linkages

To orient readers and provide a global perspective of the research landscape, this map identifies the location of every island or archipelago mentioned throughout the report.



A. MOTIVATION

Island ecosystems present a unique challenge in our study of ecology and our practice of natural resource management. Islands provide distinct geographic bounds, emphasizing the limits of the 'island' ecosystem and the connectivity with adjacent habitats. On oceanic islands, terrestrial ecosystems harbor special collections of species, including many of the planet's rarest and most threatened species. But these island species also remind us of the regular connections among ecosystems, as it is challenging to separate the ecology of island terrestrial species from the taxa and functioning of adjacent marine communities.

When considered through the lens of wildlife management and conservation, islands are viewed as a bellwether of human impacts, present and future. Island ecosystems support a myriad of endemic species, representing a disproportionate amount of terrestrial biological diversity relative to their total land area. Islands also support the livelihoods of hundreds of millions of people and island ecosystems are integral to human cultures and traditions worldwide. However, some human activities, including overexploitation, habitat changes, and, of particular focus here, non-native, invasive species, are responsible for widespread declines of island species and many global extinctions.

The impact of non-native species introductions can be particularly serious in island ecosystems. An oft-cited anecdote of the lighthouse keeper's cat (*Felis catus*) provides a profound vision of the potential impacts of species introductions to islands. As the story goes, a lighthouse keeper moved to the island Takapourewa (called Stephens island by European explorers) in Marlborough Sounds of New Zealand (Aotearoa), bringing along his pet cat, Tibbles, who was carrying a litter of kittens. The cat and its kin took to hunting the birds of the island, as the naivete to mammalian predators made these birds easy prey. Among the birds that Tibbles and her kin killed were specimens of *Traversia lyalli*, the Stephens Island wren. This flightless wren species was as yet undescribed by ornithologists and seemingly was only found on this island. Well before the lighthouse keeper's appointment on the island ended, the cats extirpated the entire population of this New Zealand endemic. The story is certainly simplified, as myriad factors contribute to species' extinctions. However, the endemic wren is extinct and cats on Takapourewa also contributed to the elimination of several other species on the island (Galbreath & Brown, 2004). The story holds power in highlighting the vulnerability of island populations to the impacts of invasive species.

The often devastating effects of invasive species on native wildlife has been recognized by management organizations and international conventions alike. For example, the United Nations Convention on Biological Diversity (CBD) established a dedicated line in the Aichi Biodiversity Targets:

Strategic Goal B: Reduce the direct pressure on biodiversity and promote sustainable use
→ Target 9: By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment.

The CBD defines 'invasive alien species' (IAS) as a non-native species whose introduction or spread threaten biological diversity. The term 'alien' refers to a taxon introduced outside of its natural range, with the introduction being mediated by humans (IUCN 2020). 'Invasive' applies to a subset of introduced,

alien species that have negative impacts within the new ecosystem (Russell & Blackburn, 2017). As the CBD definition implies, these negative impacts are primarily to native species, habitats, and ecosystems (IUCN 2020). The impacts of invasive species are also acutely felt by people on islands, slowing global efforts towards sustainable development, poverty reduction, clean water, and climate resiliency (deWit et al. 2020). In addition, some of the most widespread invasive species harm agriculture, economies, human health and culture (Russell et al., 2017; deWit et al., 2020). Notably, this definition of impact is not universal, with the government of the United States classifying invasive species as those causing harm to the environment, economy or human health (ISAC 2006).

While a broad collection of species can be designated as invasive alien species, it is notable that introduced mammals stand out with disproportionate impacts on island ecosystems. Management actions that have targeted the eradication of invasive mammals from islands have produced a multitude of success stories, likely preventing continued declines of over 250 island-native terrestrial species (Jones et al., 2016). Further, in looking into future conservation opportunities, Holmes and colleagues (2019) identified a collection of over 150 islands where the control of invasive mammals could stave off the probable extinction of highly threatened native vertebrates. Employing our most powerful tools of invasive mammal abatement -- biosecurity, control, and eradication -- is a priority for the conservation of threatened species living on islands. However, our understanding of island ecosystems suggests that the benefits of invasive mammal abatement extend well beyond the preservation of target terrestrial species. Recent ecological studies have suggested that the eradication of invasive mammals on some islands can lead to cascading ecological effects spanning the workings of both land and adjacent marine ecosystems (Graham et al., 2018, Rankin & Jones, 2021). ***In this report, we seek to establish the state of knowledge regarding the linkages between terrestrial and marine ecosystems, with a particular lens on the role of invasive mammals in altering these linkages.*** Importantly, only a small number of well-documented studies track changes in both terrestrial and marine ecosystems through an invasive mammal eradication (or an invasion) event. As such, we depend upon complementary sources of knowledge to build this state of the science. We review data from geological and ecological sciences, along with insights from historical sources and Indigenous island groups.

Our intention and desire is for this land-sea linkage information to be applied, where most advantageous, so that invasive mammal eradications address the critical conservation needs of our islands and oceans. The international community is building consensus around the use of nature-based solutions as we work toward natural resource management, conservation, and sustainable development goals. While the value of invasive mammal eradication in support of protecting and restoring species populations on islands is well established, the cascading ecological co-benefits linked to invasive management is less recognized. ***As such, communities, governments, non-governmental organizations (NGOs), scientists, and funders may be underinvested in island restorations as a marine conservation and resiliency strategy.*** Building from the state-of-the-science report here, we highlight the potential of invasive mammal eradication to serve as an important tool for 'ridge-to-reef' ecosystem management on islands, expanding our portfolio of impactful nature-based solutions as we push toward global conservation and sustainable development goals.

B. NATURAL PROCESSES ON ISLANDS CONNECT TO THE MARINE ENVIRONMENT

Islands Play a Critical Role in Healthy Marine Ecosystems

Oceanic islands have been studied extensively in ecology because of the discrete nature of the terrestrial landscape and the allure of their unique natural history. The widely referenced works of MacArthur and Wilson (1963, 1967), for example, provide a quantitative conceptual framework for predicting the species richness of islands based upon the processes of colonization and extinction. This theory of island biogeography predicts that more species can persist in equilibrium on larger islands, while remote islands will receive fewer colonizations and hence support lower richness. Importantly, this perspective of equilibrium dynamics has no comment on the identity or function of island taxa, which are often narrowly endemic to a single island or archipelago (Simberloff, 1974). However, adaptations to island life, the lack of an evolutionary history with mammalian invaders, and restricted geographic ranges predispose island populations to be particularly sensitive to anthropogenic change (Graham et al., 2017). While the costs of population loss from islands may be particularly impactful in our effort to preserve species and global biodiversity, the ecosystem changes associated with dramatic alterations of population sizes and community structure on islands have cascading effects that extend widely.

The terrestrial biota of oceanic islands is just one fraction of the broader island ecosystem. The terrestrial wildlife lives in intimate association with the surrounding ocean ecosystems. Animals on land may forage within intertidal communities, dive into coastal waters for prey, or fly or swim many kilometers to find prey across the open ocean. The water and nutrient budgets of island plants are affected by both physical and biological linkages to the surrounding ocean. In complement, the marine species living adjacent to islands have myriad functional linkages with the terrestrial ecosystem. Wind and precipitation will force high concentrations of organic and inorganic materials into the waters for marine species to exploit. The island's geological structure can alter oceanographic patterns, in many cases introducing unusually high concentrations of limiting food or nutrients to marine species. And the movements of terrestrial species may transport materials actively from land to sea, further enriching the marine community. As the terrestrial biota of islands changes, however, the linkage pattern to the adjacent marine community likewise changes. The ecology on land and the ecology of the sea are especially linked on islands, given their intimate coupling in close proximity. As such, on islands the multidimensional 'health' of terrestrial ecosystems is de facto linked to the 'health' of marine ecosystems.

The tight linkage between land and sea can be considered through the prominent example of seabird ecology. Seabirds feed in the ocean and most are obligate land breeders, nesting and roosting regularly on islands. In so doing, seabirds connect land and sea, defining nutrient cycling globally (Doughty et al., 2016). Feeding on fish in the open ocean, many seabirds transport substantial quantities of nutrients from the ocean to islands through their droppings, feathers, eggs, chicks, and ultimately their carcasses (Polis et al., 1997). Seabirds often nest in dense colonies on islands, transporting such high levels of nutrients that movement of nitrogen and phosphorus through seabird colonies occurs at a magnitude comparable to other major global N and P flows (e.g., inputs to ocean via groundwater and rivers, sea-to-land transfer via commercial fisheries; Otero et al. 2018). Because of these strong influences on the terrestrial habitats in which they breed, seabirds are often termed ecosystem engineers and these breeding islands are called 'seabird islands' (Mulder et al., 2011). Yet this substantial, natural role of seabirds as regional nutrient pumps is often impacted directly or indirectly through the activities of humans (Polis et al., 1997; Graham

et al., 2018). Seabirds are the most threatened of all bird groups and their numbers have been decimated globally due to invasive species introduced to their breeding colonies, fisheries bycatch, pollution, and other threats (Paleczny et al., 2015, Dias et al., 2019).



Figure 1. The hydrological and oceanographic flow of water helps to define the quantitative specifics of land-sea flow of nutrients in island ecosystems.

Linkages between land and sea are not wholly mediated by biology. Islands vary widely in geology, geography, oceanography, and many other dimensions, each affecting the strength of functional connectivity between land and sea. Extending the example of seabird effects, we must contextualize the magnitude of biotic influence on nutrient cycling with other factors. The presence of islands in the ocean shifts marine nutrient cycling itself. For example, islands can shift deep ocean currents creating localized regions of upwelling, creating hotspots of nutrients and associated high productivity of phytoplankton, termed the island mass effect (Doty & Oguri, 1956). Other physical and oceanographic drivers can influence nearshore nutrient availability, including internal waves, oceanic mixing, surface currents, and wave climatology (Gove et al., 2016). And the hydrological and geological patterns on land can affect the magnitude of nutrient flow from land to sea, including elements of rainfall, soil type, island size and aspect, and coastal morphology (e.g., presence of lagoon; Fig. 1). Taken together, it is clear that while elements of the biological system define some key elements of nutrient flow to the marine community (e.g., density of seabirds), the island context will modulate the relative importance of this flow (e.g., in nutrient-poor marine ecosystems, the influx of seabird derived nutrients will be particularly impactful to marine ecosystems).

We argue that the biota of islands should not be viewed as distinct ‘terrestrial’ and ‘marine’ communities, but instead considered as an island-marine ecosystem whole. The patterns of land-sea linkages, however, will vary across geographies due to the specifics of the biotic and abiotic context. In this report we search for generalizations to help us to set expectations regarding land-sea linkages, with a particular lens to patterns affected by invasive mammals.

C. TRADITIONAL MANAGEMENT PRACTICES EMBRACE A RIDGE-TO-REEF MODEL

The western (modern) scientific understanding of land-sea linkages is in its infancy, but Indigenous islanders understand this linkage intrinsically. The ecosystem concept of resource

management existed in numerous ancient societies in various parts of the world and continues to exist in some cultures today (Gadgil & Berkes, 1991). Two key characteristics of this concept are that: (a) the unit of nature is often defined in terms of geographical boundaries (e.g., watersheds), and (b) abiotic components, fauna, flora, and humans within this unit are all considered to be interlinked (Berkes et al., 1998). As a functional part of the ecosystem, people contributed to the maintenance of natural processes through practices that replenished resources and enhanced their productivity by developing systems of integrated agriculture, aquaculture, and water and riparian management (Johannes et al., 1983; Smith & Pai, 1992; Williams & Hunn, 2019). For example, the New Zealand Māori form of introduction, *Pepeha*, references identity and heritage, including a personal statement of the mountain and body of water that shapes oneself (Murton 2012). This holistic world view that people are connected to the entire ecosystem recognizes the limitations of focusing solely on specific natural settings (a common practice in Western science), which are place-specific and limited in context.

The native population of Pohnpei developed a complex system of resource management, with the island and its surroundings classed into several concentric domains (Raynor and Kostka 2003). This included an inner core - the upland rainforest (*nanwel*) - and the outer rings in marine space - mangrove forest (*naniak*), lagoon (*nansed*), and ocean (*nan-madau*). The middle concentric ring in the Pohnpei "world" was made up of settled coastal areas (*nansapw*). Ranked titles reflected the political structure, and amongst these, titles connoting a resource regulation function are common, e.g., *Sou Madau*, 'master of the ocean', *Souwel Lapalap*, 'Great master of the forest' (Raynor and Kostka 2003).

Island ecosystems, particularly on small islands, pose a unique situation in that the land and sea resources are tightly coupled owing to the relatively small sizes of the watersheds. Island people often see their resource limitations more readily than do those who live on continents (Berkes 2012; Jupiter et al., 2017). Many island communities share a similar knowledge of basic resource conservation principles that are the result of centuries of continuing experimentation and innovation. Members of some island cultures learned that their terrestrial and marine resources were limited and introduced appropriate conservation measures. Communities that exceeded those limits and the carrying capacity of island environments ultimately met their demise (Johannes 2002a, Tainter 2006). On islands, areas for cultivation are spatially constrained compared to continents, such that agricultural land use had to become more sophisticated than the traditional slash and burn practice of many initial colonizers (Mueller-Dombois 2007). The specifics of island geographies has led to the development of highly complex and integrated forms of ecosystem-based management with numerous management zones, corresponding to the ecology of the island landscape (and seascape) used to guide production and stewardship practices (Kaneshiro et al., 2005).

The tambak management system in Indonesia established mixed freshwater and seawater fishponds in delta ecosystems and associated lagoons (Costa-Pierce 1988). The paddy rice fields produced both rice and fish during the flooded period of rice production. The nutrient rich wastes of the paddy rice—fish production system was allowed to flow downstream into polyculture ponds (*tambak*) where shrimps, crabs, fish, vegetables, and tree crops could be produced (Davidson-Hunt and Berkes 2001). The water waste then flooded mangrove forests, enriching the coastal fisheries.

The ancient Hawaiian watershed (*ahupua'a*) system encompassed entire valleys and stretched from the top of the mountains to the coast and shallow waters (Kaneshiro et al., 2005; Fig. 2). It included a forested mountain zone, which functioned as a watershed conservation area protected by taboo, integrated farming zones in the upland and coastal areas, a fringe of coconut palms (*Cocos nucifera*) along the coastline for storm and wind protection,

and brackish and seawater fishponds (Costa-Pierce 1987). Variations of this type of integrated watershed management can be found throughout the region, with examples including Yap (*tabinau*), Fiji (*vanua*), and the Solomon Islands (*puava*) (Baines 1989, Ruddle et al., 1992). The common theme among these integrated watershed management systems is the intimate association of a group of people with the land, reef, and lagoon, and all that grows on or within them (Berkes et al., 1998).

Island ecosystems support unique biological and cultural diversity but are also highly vulnerable to natural and anthropogenic disturbances (Barnett 2011, Jupiter et al., 2014). Because of the tight feedback loops between ecological and social systems on small islands, resource limitations become readily apparent, forcing people to rapidly adjust and adapt to environmental and climate change (Berkes 2012, Jupiter et al., 2014). The frequency of catastrophic natural events (e.g., hurricane, tsunami, drought, flooding, lava flow, etc.) resulted in the development of social-ecological systems that include the anticipation of and rapid recovery from environmental change (Winter et al., 2018). Indigenous communities have a long history of responding and adapting to environmental change, particularly the introduction of invasive species (Reo et al., 2017). Local-scale knowledge and observations of changes regarding weather, life-history cycles, and ecological processes contributed to adaptive management at appropriate temporal scales among some island communities (McMillen et al., 2014). This knowledge was formed through historical resource-use practices and long-term, qualitative observations over a restricted geographical area (Delevaux et al., 2018). Such rich local knowledge and associated management practices (e.g., agroforestry, fisheries management) played a key role in building social-ecological system resilience (Folke et al., 2010, Jupiter et al., 2017).

In Fiji, the concept of *vanua* encompasses all land-water area and its inhabitants, including the human occupants along with their traditions, customs, beliefs, values, and institutions, and have been established from the time of a founding ancestor (Ravuvu 1983, Baines 1989).

There is a rich history of traditional knowledge and management systems from throughout the Asia Pacific region, particularly in the islands of Oceania (Johannes 1978, 1982, Friedlander et al. 2018). Over several thousand years, Pacific Islanders developed knowledge systems that enabled extensive voyaging, the initial settlement, and continuous habitation of islands across a range of climatic and biogeographic variables (McMillen et al. 2014). In many Pacific islands, the same village or clan owned both the upland areas and the coastal reefs and treated the land-sea interface as a continuum rather than a boundary (Richmond et al. 2007). This “ridge-to-reef” stewardship is reflected in land tenure and management practices recognizing that upslope activities affect people and resources further down a watershed and into the ocean (Richmond et al. 2007, McMillen et al. 2014). The extension of the bounded unit to the outer edge of the reef acknowledges the ecological insight that the ecosystem does not end at the limit of dry land but includes the coastal marine ecosystems (Berkes et al. 1998).

Inuit people in the Arctic regions of Canada, Greenland, Alaska, and Russia recognize the linkages between land and sea, and the dynamic landscape of sea ice that connects them. They recognize how these connections are influenced by astronomical phenomena (e.g., the phases of the moon), environmental factors (e.g., wind direction), tides and tidal currents, geographical features (e.g., the shape of a bay and of the features underwater), the actions of animals (e.g., the way in which a seal swims), and the behavior of the ice (e.g., whether the ice will break or stay; Aporta 2017). Such knowledge permits Inuit to anticipate change, minimize risk, predict where and when animal food resources will be (Aporta 2017).

Natural-resource management systems of Indigenous communities based on communal property concepts continue to function in the face of changes in the circumstances in which they operate (Baines 1998). All have been weakened by changes accompanying cultural and economic shifts associated with colonization and globalization, yet some have adapted and persist today in various forms.

D. PERSPECTIVES OF INVASIVE SPECIES ACROSS CULTURES

A common feature of human migration is the introduction of new species to the local environment. The patterns and rates of species introductions have shifted radically, linked with histories of socio-cultural colonization. An important distinction exists in the human relationship with invasive species, contrasting patterns of shared migration among people and species versus the pattern of species introductions that were not linked with movement of peoples. Across the patterns of species introductions, the variety of social and cultural reactions offers valuable insights. We provide a brief introduction to this variety of reactions, comparing examples from shared versus unshared migrations of people and other species.

The movement of people across landscapes and across seascapes has very often been coupled with the transport of species. The value of the transported species includes provision of food, medicine, or cultural importance. For example, voyaging Polynesians left rats on some islands to ensure a food supply upon return. And early people in the Caribbean islands came from South America and brought domestic dogs (*Canis lupus familiaris*), agoutis (*Dasyprocta leporina*), armadillos (*Dasybus cf. novemcinctus*) and opossums (*Didelphys marsupialis*; Giovas 2017). Kerry-Anne Mairs (2007) tracked such a pattern of species migration in parallel to the movement of people across Pacific islands, and she synthesizes the pattern with the terminology of “transported landscapes”, as follows:

Although expansion into the near Pacific began around 40,000 years ago (Kirch 2000), further development of voyaging and the expansion into Remote Oceania did not begin until after 1500 BC. On settling a new island, early island colonizers would have sought to transform their new environment into a familiar and manageable landscape by creating “transported landscapes”, also referred to as a “portmanteau biota” (Crosby 1986) or “cultural capital” (Diamond 2005) that echoed the environment of their homelands and promoted ecological homogenisation. A transported landscape consisted of a combination of specific plants, animals and subsistence methods as well as knowledge, beliefs, and social organisation that were introduced and implemented from the homeland to each newly colonised island. Colonisers of Remote Oceania brought with them a cultural capital of pigs, dogs, chickens and rats and edible plants such as the taro, yam, sweet potato, banana, coconut and breadfruit. The Norse introduced a cultural capital to the islands of the North Atlantic of cows, pigs, sheep, goats, horses, ducks, geese, dogs and barley.

In some cases, individual species from this “transported landscape” have established populations in the new location, fitting ecological definitions of invasive species. In cases where the Indigenous population of the island has maintained cultural continuity since arrival, these new species to the island landscape remain within this shared landscape and the species continue to be valued and used as cultural and social resources.



Figure 2. Example of ahupua'a in Hawai'i, a drawing by Marilyn Kahalewai, 1974. Reprinted with permission from Kamehameha Schools.

A more complex situation emerges when species are introduced to landscapes through human activities exogenous to those of a human community. In island ecosystems of the past 500 years, the Indigenous populations have witnessed the arrival of countless new species associated with patterns of European and other colonization. In fact, the vast majority of all species introductions explored in canonical ecological treatments of biological invasions are the result of modern exploration and colonization (Elton 1958, Vitousek et al. 1996, Trigger 2008). In such cases, the Indigenous peoples are met with a novel species, or set of species, which perhaps challenges existing relationships with the ecological landscape. In a recent study of Indigenous peoples in the United States and Canada, Reo and colleagues (2017) states:

Indigenous nations' invasive species work is generally underreported in the literature but includes communication and education initiatives, scientific research that tests new stewardship strategies, ecosystem restoration through Indigenous knowledge, and adaptation of cultural practices to account for changing conditions, including incorporating introduced species into Indigenous food systems.

We believe that this pattern of underreporting is common across most Indigenous communities. However, a collection of case studies offer insights into the perspectives of some Indigenous communities to the exogenous introduction of species to the local environment (e.g., Robinson et al. 2005, Pfeiffer and Voets 2008, Reo and Ogden 2018).

Indigenous cultural values about introduced species do not always align with dominant contemporary conservation paradigms, and these cultural values should be understood as an aspect of the broader knowledge systems and ethical commitments that have proven beneficial to conserving environments and species (Reo et al. 2017). Invasive species are included into Indigenous cultures in a wide variety of ways. In a broad ethnoscientific review, Pfeiffer and Voets (2008) propose three categories to describe the breadth of impacts of invasive species on human cultures. Invasive species may be viewed as culturally impoverishing -- in these cases, the arriving species may replace culturally important native species. In most cases, the ecological sciences focus upon similar impacts (Elton 1958, Vitousek et al. 1996, Holmes et al. 2019). Alternatively, invasive species may be viewed as culturally enriching -- in these cases, the arriving species may ultimately augment cultural traditions of food, medicine, language, etc. For example, Trigger (2008) reviews a narrative regarding the perceptions of house cats to some Aboriginal communities in Australia, in which the species (which is ecologically defined as an invasive species) has been 'naturalized' into traditions and cultures. Finally, an invasive species may be culturally facilitating -- in the words of the authors, the species may provide "continuity and reformulation of traditional ethnobiological practices", species "whose presence in alien landscapes allow diaspora communities to perpetuate their ethnobiological interactions with nature, enabling post-migration cultural continuity" (Pfeiffer and Voets 2008). This last category applies most commonly to the relationship between displaced persons and the species in their new environment. In sum, the common narrative from the ecological sciences that invasive species have a uniform and negative impact on ecosystems and local cultures is not a ubiquitously shared perspective among all societies.

Finally, there is value in considering the approaches that Indigenous groups have employed in the management of invasive species; one common approach has been the use of selective harvest. Among Indigenous peoples of the United States and Canada, the management of invasive plants is often integrated into the management of more traditional foods (Reo et al. 2018). To mitigate perceived risks to culturally important plants, people will harvest more or less of competing plant species including

invasive species (Reo et al. 2018). Selective harvest is not unique to plants, but is realized in the systemic take of invasive animals, as evidenced in some Aboriginal groups of Australia in the relationship with invasive cats, rabbits (*Oryctolagus cuniculus*), and other mammals (Robinson et al. 2005, Trigger 2008). Management of both historically present and recently introduced species through patterned harvest is noted across multiple cultures, including both 'island' and 'mainland' communities (Geary et al. 2019). Importantly, such patterns of population management are often linked to broader perspectives of landscape management on islands including explicit recognition of land-sea linkages

E. INVASIVE ALIEN MAMMALS ARE A GLOBAL CONCERN, ESPECIALLY ON ISLANDS

Exploration and Colonization Introduced Invasive Species and Diminished Integrated Ridge to Reef Management

The age of European exploration of the world's islands began in the late 15th and early 16th century and left few islands untouched across the Pacific, Caribbean, North Atlantic, and elsewhere. These exploratory voyages led to the rise of global trade and the creation of European colonial empires on islands in many places across the world. Missionaries soon arrived in most regions, with the exception of the interiors of the largest islands, such as those in Melanesia, and some small and remote islands. By the late 19th century entrepreneurial traders from Europe and the US were present across many of the world's islands. For many islands, contact with western people led to population declines of the native peoples. Where integrated agriculture had relied on terraces or irrigation, as in Hawai'i, labor shortages brought these to ruin, promoting soil erosion. While the human impacts on remote Pacific islands after colonization are most well documented, accounts of detrimental impacts are also recorded following the colonization of North Atlantic islands, particularly with regards to the exploitation of forest resources, exploitation of wild food resources, and soil erosion related to the introduction of grazing animals (Mairs 2007).

The impact of human colonizers on island environments not only caused environmental degradation, but in some cases, the unsustainable demands put on island environments by colonizers instigated episodes of cultural stress. In extreme cases, such as on Rapa Nui (Easter Island; Chile) and Mangaia (Cook Islands), environmental consequences of colonization concluded with a sharp decline in population (Diamond 2005, Kirch 1997a; 1997b). More commonly, the establishment of cash economies and the arrival of foreigners led to the development of commercial activities to feed and resupply merchant ships and the ever-growing non-native populations. Traditional local authority mostly disintegrated due to colonization, commercialization, and economic development (Johannes 1978, Ruddle and Hickey 2008).

Colonization, the import of invasive species to the islands, and the impacts on native island flora and fauna varied across the globe, with some of the most thoroughly documented cases in the Pacific. Transcontinental movement paired with the ecological vacuum created by drastic human depopulation helped goats (*Capra hircus*), cattle (*Bos taurus*), and pigs (*Sus scrofa*) to colonize widely. Whalers often stranded goats on Pacific islands so as to ensure a ready food supply when they were in need (McNeil 1994). Cattle were introduced to Hawai'i in 1793, and by 1845 they had become a pest, eating and trampling crops. This created opportunities for alien weeds to coexist with grazing animals. New rodents, particularly

the black or ship rat (*Rattus rattus*), brown or Norway rat (*R. norvegicus*), and Pacific rat (*R. exulans*), upset island ecology. Collectively, these three species of rats may have been the most consequential alien intruders. Deer (*Dama dama*, *Odocoileus hemionus*, *Cervus elaphus*, *C. timorensis*, *C. unicolor*), rabbits, and opossums had a notorious effect on native trees and grasses, many of which have been widely replaced by alien species more compatible with these creatures. In New Zealand the introduction of cats, stoats (*Mustela erminea*), weasels (*M. nivalis*), and ferrets (*M. furo*), intended to control the rat population, led to further decreases in the number of native birds (King 1984). The mongoose (*Herpestes auropunctatus*) was introduced to Fiji in 1873 (and to other islands around the globe around this time) to control rats in the cane fields, but instead it extinguished seven native species of birds.

Contemporary Understanding of Invasive Species

There is ample modern scientific evidence showing that invasive species are a global threat, particularly on islands. IAS threaten ecosystems and human well-being globally (Millennium Ecosystem Assessment 2005). Invasive species are a major driver of the global extinction crisis (Bellard et al., 2016; Butchart et al., 2010; Doherty et al., 2016) threatening biodiversity values via species loss, extirpations, habitat loss, competition and disease (Russell et al., 2017).

Invasive species can compromise ecosystem services for people and can be a direct threat to human health and livelihoods, with many invasive species serving as life-threatening disease vectors and harming agricultural productivity (Reaser et al. 2007). The economic impact of invasive species is vast and rising, with US\$1.288 trillion (2017 USD) estimated between 1970–2017, reaching US\$162.7 billion in 2017 alone (Diagne et al. 2021).

While human exploration and colonization in past centuries brought invasive species broadly across the world, globalization and international trade in the late 20th century are major drivers of trends in global invasive species spread. Invasive rodents have been common hitchhikers on vessels, estimated to now occur on ~80% of the world's island groups (Jones et al. 2008, Towns et al., 2006). Other mammalian commensals including goats, pigs, rabbits, and cats are widespread across the globe since they were regularly deliberately introduced (Doherty et al., 2016; Medina et al., 2011). Notably, many taxonomic groups show no signs of saturation, with the rate of new invasive species introductions not slowing (Seebens et al., 2017) and projected to increase through 2050 (Seebens et al., 2021). Climate change will affect invasion dynamics by altering pathways of introduction, distribution, impacts and management effectiveness (Hellmann et al., 2008), and compounding threats from invasive species (Mainka & Howard 2010).

Invasive mammals have proven to be particularly harmful to island biodiversity and environments (Hilton & Cuthbert 2010). Evolution on islands led to unique ecological outcomes (Whittaker & Fernández-Palacios, 2007), including high rates of endemism with plant and vertebrate richness 9.5 and 8.1 times greater than continental areas, respectively (Kier et al. 2009). Many insular species evolved in the absence of mammalian competition, predation, and herbivory, with the absence of such traits leading to high vulnerability upon first contact with humans and novel introductions of other species. Outcomes can be surprisingly large regardless of the size of the introduced animal. One of the smallest invasive mammals, the house mouse (*Mus musculus*), preys upon and kills the largest of seabirds, the albatrosses on Gough Island in the Atlantic Ocean, Marion Island in the Indian Ocean, and Pihemanu / Kuaihelani (Midway Atoll National Wildlife Refuge) in the Pacific (Holthuijzen et al. 2021).

Although islands represent only 5% of terrestrial land area, since 1500, 75% of amphibian, reptile, bird, and mammal extinctions have been on islands (Tershy et al. 2015), and nearly 40% of globally threatened vertebrates are island species. On oceanic islands worldwide, more extinctions

of native species are attributable to invasive species impacts than to habitat loss or degradation (Brooks et al., 2002; Bellard et al., 2017). Island extinctions are not limited to the past, with recent losses including the Christmas Island pipistrelle bat (*Pipistrellus murrayi*), the Round Island burrowing boa (*Bolyeria multocarinata*), and the po’ouli (*Melamprosops phaeosoma*) a honeycreeper species from Hawai’i.

The impacts that invasive mammals have on island terrestrial biodiversity have cascading harmful effects on terrestrial ecosystem functions such as pollination, seed transfer and germination, and can create domino effects in food webs and nutrient cycles (Aslan et al., 2012).

Invasive mammals on islands can restructure the terrestrial ecosystems both directly and indirectly via multiple downstream feedback mechanisms. For the purposes of this review, we define direct effects as invader impacts on species populations through species interactions, such as predation, competition, or disease transmission. These direct impacts on key terrestrial species may reduce population sizes by eliminating individuals or by degrading habitat quality, causing local extirpations or global extinctions. Invasive mammalian predators may consume or kill all life stages of native species, or they may target a single life stage, such as the eggs or nestlings of birds, or seeds of plants, causing population declines without directly impacting adults. Invasive mammals targeting a single life stage may prolong the collapse of the native species population, which may be reversed if the invasive species is removed in time. A well-known example of this concerns the long-lived tortoises of the Galapagos, where adults of the species might persist for 100+ years in the presence of invasive rats (Clark 1981), but the population cannot grow until rats are removed and tortoise recruitment rebounds (Rueda et al., 2019). Although some species interactions can be mediated by a third party – for example, disease transmission may occur through a shared vector, and competitors may interact only through a shared, limited resource – for our purpose, we consider species interactions as direct mechanisms.



Figure 3 (A,B,C). Diversity of terrestrial ecosystem changes that have been documented to follow island introduction of invasive mammals. The ecosystem changes are linked to the ecology of the invasive mammal, and some of the stereotyped shifts are captured. (A) Pigs are a common invader across islands, often introduced deliberately by humans for food. (B) Rats and other rodents are often introduced accidentally, traveling aboard ships and colonizing islands worldwide. (C) Goats can be introduced to islands for their perceived value as livestock, but without management can lead to dramatic shifts to island ecosystems. Note that the effects of invasive mammals will vary based upon the natural history of the island and the exact species of invader.

The considerable global impacts of invasive mammals on islands are reviewed in detail elsewhere (Courchamp et al., 2003; Medina et al., 2011; Harper & Bunbury 2015; Bellard et al. 2017; Graham et al., 2017); however, it is valuable to highlight some of the more significant introduced mammals, in terms of both number of introductions and impact (Courchamp et al. 2003). Here, we focus briefly on these important species (i.e., cats, goats, pigs, rabbits, rats and mice) and illustrate a generalized comparison of impacts on the terrestrial environment from pigs, rats and goats (Figure 3).

Carnivores, such as feral cats, can decimate native populations that evolved in the absence of predators. Seabirds are a particularly easy prey; just 25 years after five cats were introduced to Marion Island and 30 years after 4 cats were introduced to the Kerguelen Archipelago, cat populations had grown to the thousands and impacts were estimated at 0.5 million burrowing petrels and 1.2 million birds killed per year (van Aarde & Skinner 1981; Pascal 1980). Herbivores, such as goats and rabbits, are notorious for overgrazing and trampling, reducing plant cover and available food for native inhabitants and increasing erosion (Chynoweth et al., 2013; Figure 3a). One example of these extreme impacts occurred on Guadalupe Island, Mexico, where it was believed invasive goats caused multiple plant species to become extinct or extirpated. It was not until after goat removal that the species were later rediscovered due to reestablishment from the seed bank (Keitt et al., 2005; Luna-Mendoza et al., 2019). Similarly, invasive European rabbits heavily impact native vegetation, such as on Laysan Island in the Northwest Hawaiian Island Chain, where their introduction caused the loss of 22 plant species in just 20 years (Watson 1961). Unfortunately, their impact on vegetation likely had cascading impacts to the insect community and ultimately caused the extinction of three bird species and a severe decline in the critically endangered Laysan duck (*Anas laysanensis*) population. In addition, rabbits' use of burrows can accelerate erosion and lead to declines in burrowing seabird species populations as they directly compete for their burrows (e.g., Cleeland et al., 2020). Finally, effects of invasive omnivores, such as the feral pig, three invasive rat species, and house mouse, are wide-ranging, as they include many of the combined impacts of herbivores and carnivores via activities such as browsing, seed and seedling predation, predation on native wildlife, and competition for food resources (e.g., Caut et al., 2008; Nigro et al. 2017; Wolf et al., 2018; Fig. 3b and 3c). These species are opportunistic foragers and have been documented depredating all levels of the food web, including seeds, insects, crabs, sea turtle eggs, and seabirds. Furthermore, in the case of pigs, their contribution to erosion is likely greater than just the denuding of landscapes as their rooting behavior (i.e., turning over the soil) causes soil disturbance, furthering sedimentation within streambeds (Dunkell et al., 2011; Fig. 3c).

- I) Predation on birds, reptiles, arthropods, and their nests.
- II) Predation on seeds and seedlings of native vegetation.
- III) Rats excluding native species from shelter.

- IV) Healthy populations of native vegetation.
- V) Healthy populations of native birds, reptiles and arthropods.

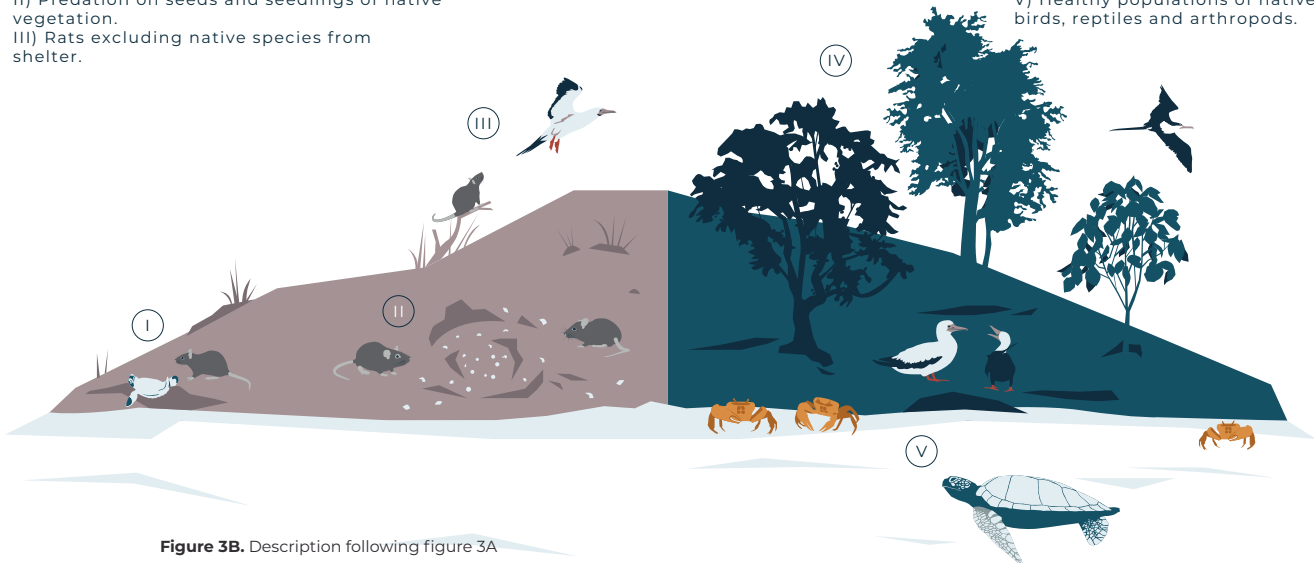


Figure 3B. Description following figure 3A

Management of Invasive Mammals on Islands

The severe consequences of invasive mammals on islands drove the development of today's abatement strategies and techniques (Veitch et al., 2011). Biosecurity, control and eradication are the three primary strategies for invasive mammal threat management on islands (Russell et al., 2017).

- **Biosecurity** represents the actions of prevention, detection, and rapid response to new incursions, and represents the most cost-effective approach with the highest likelihood of success (Broome 2007).
- **Control** is to reduce the size of the invasive mammal population below a key management threshold (akin to harvesting) but requires continual investment to maintain benefits (Bomford & O'Brien 1995).
- **Eradication** attempts to remove the invasive mammal population entirely, either during the initial stages of invasion (as a biosecurity rapid response), or for established populations where technical and socio-political feasibility can be met (Cromarty et al., 2002).

Additional management responses include the creation of 'islands within islands', as seen with predator-proof fencing in New Zealand and Hawai'i (Young et al., 2013), and asset protection where the management is not of the invasive population but of the affected resource (IUCN 2018). In the extreme, asset protection can include conservation translocations to create insurance populations of extremely threatened species (IUCN/SSC 2013).

I) Habitat change due to overgrazing and trampling,
II) Soil destabilization, especially along watersheds, and extensive soil erosion.

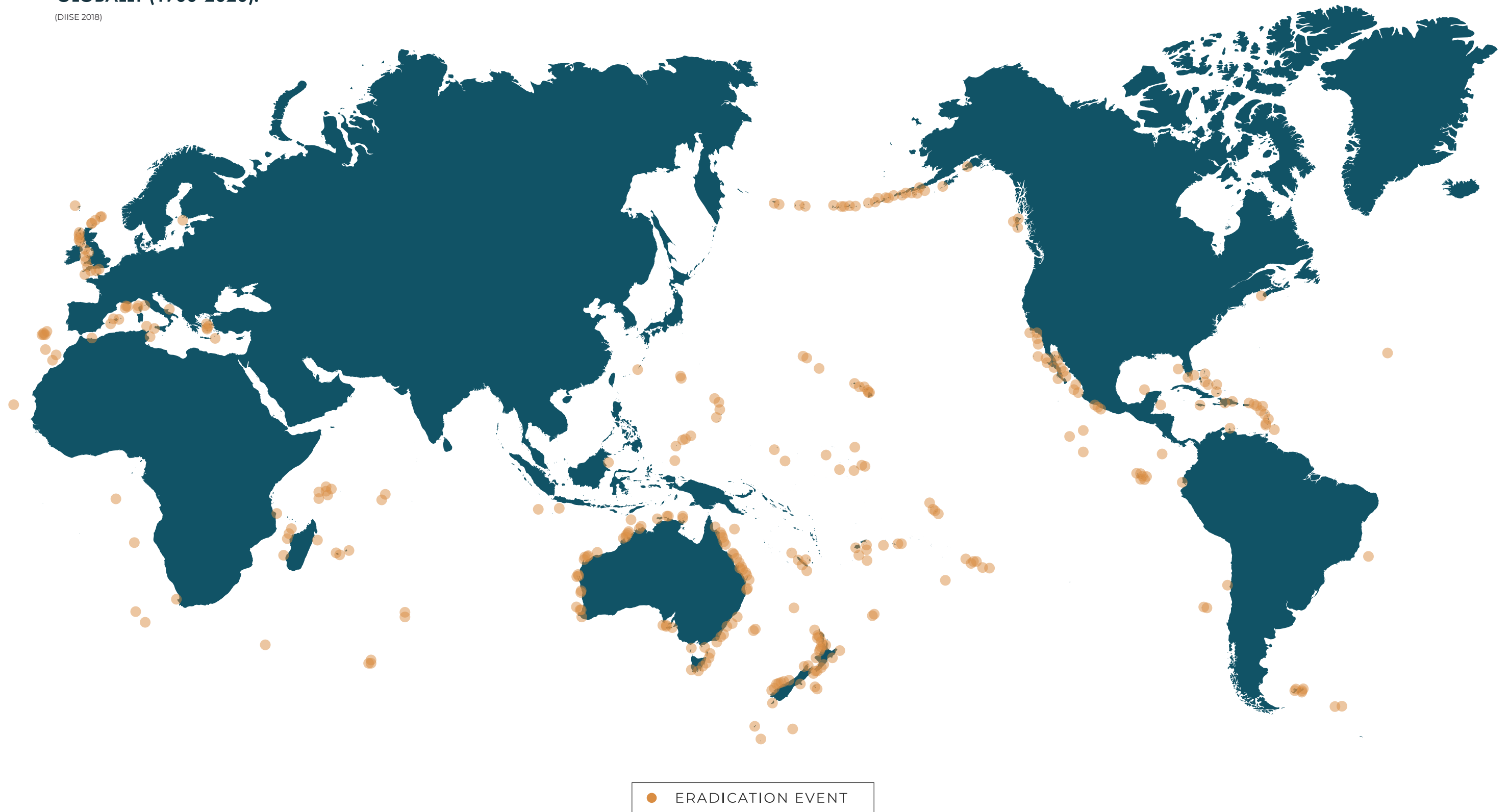
III) Healthy native vegetation,
IV) Healthy populations of native animals dependent upon native vegetation,
V) Improved water quality.



Figure 3C. Description following figure 3A

FIGURE 4.
INVASIVE MAMMAL ERADICATION
INTERVENTIONS CONDUCTED
GLOBALLY (1900-2020).

(DIISE 2018)



Due to the devastating impacts of invasive mammals, eradication techniques to completely eliminate invasive mammals from islands have been developed and paired with long-term biosecurity to prevent future invasions (Veitch et al., 2011). **For many islands around the world, eradication has proven to be an effective nature-based conservation tool with clear evidence of recovery of terrestrial native species and island ecosystems (Brooke et al., 2017; Jones et al., 2016).** To date, more than 1,500 invasive mammal eradications have been attempted on islands worldwide, with an average success rate of 88%. The greatest rate of attempts occurred between 2010 and 2020, and has since slowed, concurrent with an increase in the size and complexity of islands where projects are being implemented (DIISE 2021). Geographically nearly 80% of these efforts have taken place in eight countries (New Zealand, Australia, United States, United Kingdom, France, Ecuador, Mexico and Seychelles) and their territories, with lower rates in Small Island Developing States (Russell et al., 2017; Fig. 4). **The accelerated pace of biodiversity loss and terrestrial ecosystem degradation necessitates a dramatic increase in the scale, scope, and pace of invasive mammal eradications on islands worldwide.**

In complex landscapes there may be unexpected or secondary responses to eradications tied to ecological release of other invasive species following the invasive species removal (Zavaleta et al., 2001). Thus, multiple eradication outcomes and phased plans are important to consider. For example, the removal of rats and goats from Monuriki Island in Fiji led to the spread of invasive grasses and invasive strawberry guava vine tangles that captured several wedge-tailed shearwater (*Ardenna pacifica*) adults and juveniles. But these vines also helped to stabilize the exposed soils, which rapidly allowed dry forest tree shoots to anchor and establish (Fisher et al., 2019). To mitigate some of these negative impacts, *Pisonia* tree sticks were spread across the beach to provide shade to inhibit invasive grass growth. Despite the care required in planning these projects, eradication of invasive mammals remains a prerequisite management action for restoration of many island ecosystems.

Because we know that ecological inter-dependencies exist between oceans and islands, we can expect that invasive mammals on islands also impact the marine environment. While less attention has been placed on understanding these types of indirect effects on marine systems, this knowledge is essential to ascertain where invasive mammal eradications around the globe may most benefit the entire island-marine ecosystem.

F. THE INFLUENCE OF TERRESTRIAL INVASIVE SPECIES ON ISLAND-MARINE ECOSYSTEMS

Considering Direct and Indirect Effects of Invasive Mammals

Invasive mammals on islands can impact native species, their ecological functions, and terrestrial and marine ecosystem properties through direct effects (e.g., consumption, trampling), and also through indirect effects. Indirect effects may manifest in various ways, but the key difference is that the outcomes arise at least one step removed from direct effects. For example, rats directly alter plant community composition and invertebrate diversity and abundance through consumption (Courchamp et al., 2003; Shiels et al., 2014; Harper & Bunbury 2015). Following their invasion on seabird islands they also transform soil chemistry indirectly by reducing populations of seabirds, which reduces flow of labile nutrients (via seabird excretion) into the soil (Fukami et al. 2006; Thoresen et al., 2017).

Two major classes of indirect effects are commonly observed with invasive mammals on island systems. The first is via interaction modifications, whereby the direct effects of invasive species are modified through the interaction of one or more additional invasive species. The simplest case of interaction modifications occurs where two invading species interact with each other. The interaction can result in a neutral or weakened impact of one or both species on native species and ecosystems, if the two species interfere or compete for shared resource needs, or if one species consumes the other. For example, in cases where both mice and rats are invasive on islands, rats as the dominant competitor suppress the density and shift the diets of the mice (Caut et al., 2007). A corollary relevant for management is that removal of the rats alone can lead to ecological surprises, for example, population irruptions of mice from competitive release (Caut et al., 2009) or unconstrained recruitment of coconuts previously controlled by rat predation on apical meristems (Wolf et al., 2018).

In many cases, however, the impact of multiple invasive species can cause profound impacts due to their capacity to interact positively with other non-native species. For example, rooting and wallowing by feral pigs degrade soils directly, and by facilitating invasive earthworms, contributes to a positive feedback loop further degrading soils and releasing N-enriched effluents from watersheds (Wehr et al., 2018). On Isla Victoria, Argentina, numerous species of pines (*Pinus spp.*) have been introduced but were limited in their distribution by the absence of mutualistic ectomycorrhizal fungi in soils (Nunez et al., 2013). Feral boars in this system disperse exotic fungi that promote further invasion by *Pinus* species. This interaction, where the positive interplay between two or more invasive species (here, exotic pigs and fungi) facilitate the secondary invasion of a third species or functional group (here, pines), is termed an 'invasional meltdown' (Simberloff & Von Holle 1999).

The second major type of indirect effects of invasive mammals on islands are interaction chains, which include cascading interactions and downstream feedback loops. Cascading population effects, or trophic cascades, occur where the invasive mammal impacts the abundance or distribution of lower trophic level species indirectly, by consuming species at intermediate trophic levels. For example in the Aleutian Islands, brown rats impacted intertidal invertebrate communities indirectly by eliminating the seabirds that foraged in intertidal areas (Kurle et al., 2008; Kurle et al., 2021). More generally, many studies describe indirect impacts on communities and ecosystem properties through downstream feedback (Terborgh & Estes 2010; Pysek et al., 2020). Invasive ungulates can drive population declines and extinctions of native animal species through changes in vegetation, such that the landscape is no longer suitable for these native species (Chynoweth et al., 2013; Wehr et al., 2018). Feedback loops can also include hydrological changes tied to vegetation changes or direct disturbance of slopes that fill into aquatic habitats needed for native aquatic species on islands.

'Champion Species' that Help Link Land and Sea are Impacted by Invasive Mammals

Understanding many direct and indirect effects in the terrestrial environment is relatively straightforward and well-studied, but there are several relatively understudied avenues by which these changes can drive shifts in the land-sea connections. Some of the less understood indirect effects of invasive mammals involve island fauna that have life stages spanning land and sea. These 'champion species', such as seabirds, land crabs, sea turtles, and pinnipeds, have life cycles at the interface of marine and terrestrial systems. Many of these species spend much of their lives at sea, assembling en masse when moving between biomes to complete circannual activities including breeding, over-wintering, and molting; seabirds are a good example. Of the 346 species of seabird, most use islands to nest and roost. Indeed, ninety-eight of 101 threatened seabird species breed on islands (Spatz et al., 2014). Seabirds

are ambassadors of the marine and terrestrial worlds; their behavior and morphology are adapted for exploiting marine resources, and islands provide the safe habitat needed to breed and raise young. As such, seabirds highlight the connectivity of small islands to large oceans. Species such as grey-headed albatross (*Thalassarche chrysostoma*) nest on small islands in the Southern Ocean, yet when at sea, they regularly circle the globe.

When occupying terrestrial habitats, champion species transfer nutrients between the marine and terrestrial environments. For the majority of champion species, marine-derived nutrients are moved to land through excrement, carcasses, eggs and other reproductive materials, and feathers and molt. Champion species disturb the soil via nest excavation, burrowing, and other physical activities, mixing nutrients into the soil and in some cases providing aeration. Changes in soil nutrients and hydrogeography shape bacterial, fungal, and plant communities, promoting positive changes to invertebrate abundance and diversity, and eventually enhancing vertebrate communities. The ecological benefits provided by champion species are not restricted to terrestrial biomes. In the case of land crabs, terrestrial-derived nutrients are introduced to the sea when they spawn via larvae. In addition, nutrient depositions on land can transfer to sea through precipitation runoff and other hydrologic connections, fertilizing the nearshore environment.

Mammal introductions, especially when the introduced species behaves as a novel predator on islands, are one of the most damaging threats to champion species that link marine and terrestrial habitats. Native island communities have evolved in the absence of mammalian predation and competition and as a result, native species often lack the protective mechanisms necessary to enable coexistence with introduced mammals. Mammal introductions have caused extinctions and localized extirpations of champion species, leading to a loss of land-sea linkages that promote ecosystem function, resulting in myriad direct and indirect consequences to island biodiversity. A brief review of the natural history of four groups of champion species follows.

SEABIRDS

Seabirds are one of the best studied species linking terrestrial and marine environments. Seabirds are the prototypical island ecosystem engineer, and the islands on which they breed support high diversity of terrestrial invertebrates (Polis & Hurd 1995; Zmudczyńska et al., 2012) which can enhance diversity amongst higher trophic levels (Jakubas et al., 2008; Hentati-Sundberg et al., 2020). Seabird impacts are variable across taxa, as their species-specific life histories dictate their ecosystem impacts. Burrow-nesting seabirds (*Alcidae*, *Procellariidae*, *Hydrobatidae*, *Oceanitidae*, and *Spheniscidae*) make some of the most extreme modifications to island habitats (relative to surface-, crevice-, and tree-nesting species). Some of the most iconic studies demonstrating the direct and indirect effects of mammalian disruptions come from New Zealand, where suppressed seabird nesting activity on rat invaded islands had reduced soil fertility relative to uninvaded islands (Fukami et al., 2006), leading to a reduction in seedling germination (Grant-Hoffman et al., 2010) and eventually a loss in ecosystem functioning. In extreme cases, the loss of allochthonous input has entirely transformed islands, as occurred in the Aleutian Islands of Alaska where Arctic foxes (*Alopex lagopus*) caused the transition of maritime grassland to tundra (Croll et al. 2005, Maron et al. 2006) and intertidal communities lost algal complexity after the invasion of brown rats (Kurle et al., 2008).

LAND CRABS

Land crabs are variable in the frequency and duration of their movements between terrestrial and marine biomes; species belonging to the family Gecarcinidae may only spend 4 – 5 weeks of their lives at sea during their larval phase (Wolcott & Wolcott 1982) while other species undertake daily migrations to the ocean or burrow into a wet ground layer to retain moisture. Large populations of land crabs can be a significant source of zooplankton to the marine environment when they spawn, in some cases synchronizing egg laying, releasing millions of larvae into the ocean (e.g., Hartnoll et al., 2007). Land crabs also provide ecosystem services through soil bioturbation and aeration, influence seed dispersal, control litter decomposition, facilitate nutrient cycling, and act as predators in island communities. The semi-terrestrial squareback marsh crab (*Armases cinereum*) at Sapelo Island is such an integral vector for nutrient flow between saltmarsh and adjacent forest that changes in their population structure would fundamentally change ecosystem function (Hübner et al., 2015). Indeed, changes in crab populations elsewhere, particularly in response to invasive species, have resulted in profound ecological consequences. At Clipperton Island, the orange land crab (*Gecarcoidea planatus*) was severely suppressed by introduced pig and black rat, causing the encroachment of weedy vegetation across the historically sparsely vegetated atoll (O'Dowd et al., 2003). Following black rat eradication at Palmyra Atoll and its islets, the crab species composition changed, two new crab species were detected on the island, and the diet of most crabs changed (Nigro et al., 2017). Relative to the other island fauna discussed here, the contribution of land crabs to terrestrial-marine linkages is understudied and is in need of further examination.

SEA TURTLES

Sea turtles provide significant marine-derived nutrient and energy subsidies when nesting. Coastal beach and dune environments in which sea turtles nest are often nutrient limited, and stability of these ecotones is facilitated through vegetation structure that relies on their inputs (Hannan et al., 2007; Vander Zanden et al., 2012). Although sea turtles have evolved with native predators that consume eggs and juveniles, nest depredation by non-native species exacerbates predation pressures and threatens local populations. Across south Atlantic US states, for example, feral pig predation is a primary threat to incubating nests (Engeman et al., 2019; Butler et al., 2020). At Teti'aroa in the tropical south Pacific, black and Polynesian rats have been observed attacking hatchling green sea turtles (*Chelonia mydas*) as they emerge from the nest (Gronwald et al., 2019).

PINNIPEDS

Pinnipeds are also key vectors for nutrient transfer from land to sea, particularly through large quantities of carcass biomass (predominantly deceased pups and placentae; Quaggiotto et al., 2018). Especially in polar regions where decomposition is slow, mammal subsidies may persist long after the mortality or birthing event. For example, at Baffin Island, butchered seal and marine mammal remains from ancient Indigenous hunting still influence freshwater eutrophication (Michelutti et al., 2013). Within their coastal rookeries, seal pupping activities can promote plant succession (Magnússon et al., 2020) and diversity (Norton et al., 1997).

Pinnipeds, such as Hawaiian monk seals (*Īlio-holo-i-ka-uaua* or *Monachus schauinslandi*) are impacted by invasive species through localized lethal outbreaks of toxoplasmosis, a cat-borne disease. The parasite, *Toxoplasma gondii*, is present in rodents on small Pacific Atolls that support feral cat populations (Wallace et al., 1972), and monk seals can be infected through contact with dead rodents containing tissue cysts or through runoff contaminated by cat feces (Aguirre et al., 2007). Alternately, pinnipeds may also create

conditions favorable for invasive species. At Sable Island, Nova Scotia, gray seals (*Halichoerus grypus*) enhance the nutrition of marram grass (*Ammophila breviligulata*), an important dietary item of feral horses (*Equus ferus caballus*; McLoughlin et al., 2016).

CASE STUDIES OF INVASIVE SPECIES ERADICATIONS AND LAND-SEA LINKAGES

The impacts of invasive mammals on land-sea linkages, and in some instances, the recovery of those islands after invasive species removal, has been documented in tropical and temperate environments. While these case studies are rare and focused primarily on examining interactions between invasive rat eradication, seabird populations, and marine nutrient inputs, they have measured a diversity of impacts and linkage components with consistent results: invasive species impacts on land-sea linkages appear similar across temperate environments and similar across tropical environments. Figures 5 and 6 depict the generalized temperate and tropical island-marine ecosystems with and without the presence of invasive mammals, based upon information gathered from the following case studies.

TROPICAL INDIAN OCEAN

Contrasting islands with and without black rats – A natural experiment in the Chagos Archipelago, central Indian Ocean, helps underscore the role of invasive rats and seabird nutrients on adjacent coral reefs. Black rats were introduced to some islands of the archipelago in the 1700s. Other islands within the same atolls, of similar size and geomorphology, have never had rats present. Graham et al. (2018) studied six islands with rats present, and six islands with no rats. They found the islands with no rats had 750 times more seabirds, which resulted in ~250 times more nitrogen deposition on the islands through guano. Using nitrogen stable isotopes, they showed that this nutrient signal was apparent in soils and new leaf growth of coastal shrubs, and while the effect size became smaller in the marine environment, the higher nitrogen signature was detectable in sponges, algae, and herbivorous damselfish on coral reefs an average of 230m from shore. Using fish otoliths to determine age, these damselfish and one species of parrotfish (bullethead parrotfish, *Chlorurus sordidus*) were shown to grow faster adjacent to islands with seabird colonies, and biomass of the entire fish assemblage was ~50% greater (Graham et al., 2018; Benkwitt et al., 2021a). The rates of two key ecosystem processes performed by fish on coral reefs, grazing of algae and bioerosion of dead reef substrates, were 3-4 times faster on reefs adjacent to the rat-free islands. Similar patterns of land-sea linkage have been documented from islands where rats have been recently eradicated. Considering islands in Chagos and the Scattered Islands of Madagascar where rats were eradicated within the past 10-15 years, Benkwitt et al. (2021b) revealed elevated levels of bio-available nitrogen in the adjacent marine environment (extending at least 300m from shore) relative to rat-infested islands.

Interactions with climatic disturbance – The initial work in the Chagos Archipelago was conducted in 2015. Shortly thereafter, a major El Niño event caused coral bleaching and mortality across much of the tropics (Hughes et al., 2018), including the Chagos Archipelago (Head et al., 2019). In 2018, the interaction between this climate disturbance and the invasive species status of islands was investigated by repeating coral reef surveys adjacent to 12 study islands (Benkwitt et al., 2019). Coral cover was lost on reefs regardless of whether they were adjacent to islands with rats or seabirds. However, on reefs adjacent to islands with seabirds, the open space became dominated by crustose coralline algae, which binds dead reef together and is a favorable settlement substrate for coral larvae, and *Halimeda*, a calcifying green macroalgae. Further, while small and specialized fish species, such as those that feed on live coral, declined on all reefs, larger functionally important species of fish, such as herbivores and piscivores, remained at higher

FIGURE 5 (A, B.) Example of ecosystem shifts caused by the introduction of invasive mammals to low-latitude (tropical) islands. (A) z (B) With the introduction of invasive mammals, seabirds and native flora and fauna are reduced significantly. Cascading effects of native population reductions limit the flow of nutrients to nearshore habitats. In some cases, pathogens that become endemic in the population of invasive mammals move to marine species (e.g., toxoplasmosis in invasive cats moving to monk seals in Hawai'i).



biomass adjacent to islands with seabirds. Collectively, these early results suggest coral reefs adjacent to islands with seabirds may recover faster and more effectively between increasingly frequent coral bleaching events. Another study used this dataset to assess how biodiversity-ecosystem function (BEF) relationships respond to the combined impacts of climate change and invasive species (Benkwitt et al., 2020). Strong positive BEF relationships were retained regardless of the disturbance, but invasive rats directly lowered functions through their disruption of biomass enhancing seabird nutrients, while climate change reduced functions by negatively impacting biodiversity levels on reefs.

TROPICAL PACIFIC OCEAN

Seabird nutrients are incorporated into corals and enhance growth rates – A study from Fiji showed that nitrogen of symbiotic algae (*zooxanthellae*) in corals was greater adjacent to an island with no rats and abundant seabirds, compared to an island with invasive rats present (Savage 2019). Using a coral reciprocal transplant experiment, corals grew four times faster in lagoons adjacent to the island with no rats and abundant seabirds, compared to the island with rats and few seabirds. In New Caledonia, corals assimilated seabird derived nitrogen into their tissues and into their symbiotic zooxanthellae algae (Lorrain et al., 2017), further suggesting corals may benefit from seabird nutrient subsidies.

Seabird nutrients enhance plankton and plankton feeding megafauna – Palmyra atoll is dominated by two primary forest types – native forest and coconut palm, with native forest providing preferred nesting habitat for seabirds (Young et al., 2010). Prior to the successful rat eradication program, native forest recruitment was limited in part due to rat predation (Wolf et al., 2018). Using biochemical measurements and stable isotopes of nitrogen from areas of island dominated by native vegetation and high seabird densities, and palm dominated areas with few birds, seabird nutrient effects were traced from islands out to the marine environment (McCauley et al., 2012). Nutrients were greater in soil and leaves on the islands and in water runoff from islands adjacent to the areas where seabirds were in higher numbers. This translated to a higher abundance of zooplankton and more manta rays feeding in these areas, suggesting that the expansion of native forest and associated seabird nesting (both released from rat predation pressure) will benefit the marine food web.

TEMPERATE PACIFIC OCEAN

Eradicating rats and cats enhances macroalgal diversity on temperate reefs – Working in the Mercury islands of New Zealand, Rankin & Jones (2021), assessed nutrient subsidies from seabirds to nearshore macroalgal communities among islands never invaded by mammalian predators (rats and cats), an island where predators were eradicated 30 years before, and an island where predators were eradicated two years prior to the study. Macroalgal diversity was greatest in nearshore waters of the never-invaded island treatment, followed by the 30-yr eradication, and lowest on the island eradicated two years previously. Isotope signatures of nitrogen were greatest for the never invaded island, but among the eradicated islands, were greater adjacent to the island eradicated 2 years previous, with indications that other factors such as island size and island geomorphology (i.e., factors linked with patterns of hydrological run-off) influence these patterns.

Seabird nutrients affect intertidal algal and invertebrate dynamics – Studying the Aleutian islands, where some islands have invasive brown rats, and some are rat-free, Kurle et al. (2008) showed that invasive rats control a cross-ecosystem trophic cascade in intertidal rocky reef habitats. Where rats had decimated seabird populations, they reduced the role of seabirds in feeding on intertidal invertebrate species, leading to abundant invertebrate populations overgrazing fleshy algal cover. The predation upon native seabirds by introduced arctic foxes in the Aleutian islands also led to broad consequences for the

island-marine ecosystem. The reduced transport of nutrients from land to sea by the seabirds decreases soil fertility, transforming grasslands into dwarf shrub- and forb-dominated vegetation (Croll et al., 2005; Maron et al., 2006). Eradication of foxes and rats from one of these islands (formerly called Rat Island, now Hawadax Island) returned the trophic cascade to one controlled by seabirds within 11 years (Kurle et al., 2021). Increasing seabird numbers reduced intertidal invertebrate populations, leading to an increase in fleshy algae.



FIGURE 6 (A, B.) Example of ecosystem shifts caused by the introduction of invasive mammals to high-latitude (temperate) islands. (A) An island, free of invasive mammals, supports abundant populations of seabirds. These birds search for food resources in intertidal habitats and oceanic waters. Through local consumption of invertebrates, seabirds contribute to the structuring of intertidal habitats. (B) With the introduction of invasive mammals, seabird populations are reduced significantly. Because of reductions in predation of invertebrates, the intertidal community sees a boom in herbivore populations and a shift to algal barrens.

G. MEDIATING FACTORS AFFECT THE STRENGTH OF LAND-SEA CONNECTIONS

The case studies in the previous section demonstrate the possible outcomes of interventions to eradicate invasive mammals to restore land-sea linkage. ***The degree of benefit that the marine environment receives from terrestrial invasive species eradication will depend upon certain factors -- biological and physical -- that mediate the strength and pattern of land-sea linkage, with those island-marine ecosystems that offer the best potential for strong linkages benefiting most from such interventions. We propose that the following properties and processes most strongly mediate the strength of land-sea linkages: (i) precipitation (ii) elevation, (iii) vegetation cover, (iv) soil characteristics, (v) oceanographic nutrient availability, and (vi) oceanographic flow.***

PRECIPITATION

Rainfall acts as the main “flushing” mechanism for land-sea interactions. As a result, differences in precipitation across island types will drastically change an island’s connectivity with its local marine ecosystem. Given that a major form of functional linkage between terrestrial and marine communities is through exchange of bioavailable nutrients, understanding watershed rates helps clarify expectations of land-sea linkages. All other factors being equal, increasing precipitation will increase an island’s land-sea linkage. Further, the pattern of precipitation will modulate the linkage, with more pulsed precipitation oftentimes leading to more direct linkages (e.g., with less percolation through the soil and more surface flow during intense rainfall events). However, precipitation patterns alone fail to capture the quantitative specifics of the hydrological system, as the geomorphology of the island modulates the pattern and rate of flow from land to sea. Important island characteristics include elevation, vegetation cover, and soil characteristics.

ELEVATION

The flow of water from land to sea is linked to the basic geology, including specifics of the island’s maximum and average elevations. Island hydrogeology is variable due to the complexities introduced by unique geomorphologies across and within island types globally. While there is some inconsistency in how best to categorize island types in the current literature, there are some general trends that can be agreed upon and explored for the purpose of this review. Most applicable is the distinction between low-lying, high permeability islands with a freshwater lens versus high elevation hard rock islands generally displaying high runoff and basal aquifers (Falkland 1993; N.S. Robbins 2013). The distinction is especially topical as it gives a general guide delineating which island types will experience high land-sea linkage in time and space versus those with low connectivity as precipitation increases. High elevation islands can be expected to experience high and rapid land-sea linkage under high rainfall conditions, due to the high elevation forcing the majority of precipitation into surface runoff. Conversely, low lying islands can be expected to experience less of an immediate increase in connectivity with increased precipitation due to a greater percentage of the precipitation being held in the aquifer / freshwater lens. Basal aquifers exist on most islands making them globally relevant to island hydrology. However, low-lying limestone islands tend to have aquifers in the form of “freshwater” lenses while volcanic islands have basal and/or perched aquifers.

VEGETATION COVER

Plant community composition differs dramatically across islands, ranging from sandy atolls devoid of vegetation, to barren shrub and grass-dominated islands, to varied forest types of tropical high islands worldwide. This diverse array of communities has distinct effects on the movement of water from land to sea. In general, terrestrial vegetation influences land-sea linkages in two distinct ways. First, more complex plant communities with more developed root systems will reduce flow of water from land to sea. However, in many cases when vegetation is removed (as by overgrazing and burrowing by some invasive mammals), the loss of vegetative cover can liberate soil and increase flow of damaging sediments from land to sea.

Vegetation cover holds a primary role in defining hydrological flows from land to sea. Plant communities can increase surface evaporation, and thus the latent heat flux from soils via transpiration and canopy evaporation (Osbourne et al., 2004; Sud et al., 1996). Independent of the effects on moisture convergence flux and its influence on precipitation, an increase in evapotranspiration (i.e., evaporation from the land plus transpiration from plants) translates to a decrease in the total water moving from land to sea. Additionally, more complex plant communities, such as forests, have been shown to access different water sources depending on the root structure of the plant community. Several studies have found that due to the higher water demand of complex plant communities, soil moisture content is often much higher in grasslands than woodlands (Midwood et al., 1998; Dawson & Ehleringer 1998; Krull et al. 2006). As such, one may expect an increase in groundwater and drop in surface runoff as a function of vegetation cover and complexity. Tree canopies intercept rainfall, thus, with greater leaf area, less precipitation reaches the soil surface to accumulate and runoff. Additionally, the presence of more significant root structures, such as those present in trees as opposed to grasses, increases the infiltration of rainfall into the soil profile (Osbourne et al., 2006). However, the small topographic gradient and high permeability of low-lying atolls makes surface runoff irrelevant. Thus increasing vegetation simply decreases groundwater recharge on many low-lying atolls and transpiration dominates total evapotranspiration.

Sedimentation to the marine environment can have significant impacts on ecosystem functioning and resilience in the long term across island types (Aumack et al. 2007; Dunkell et al. 2011). Sedimentation occurs through a number of mechanisms, all of which involve destabilization of surface sediments and lead to increased suspended sediments in surface runoff. While many species of vertebrates and invertebrates contribute to destabilization of surface sediments, most notable are the impacts of burrowing, sharp hooves, and overgrazing of riparian (streambank) vegetation. Invasive ungulates have been known for decades to overgraze native vegetation, particularly riparian vegetation (Roper & Saunders 2020), causing shifts in community structure that generally decrease streambank stability (Gaston 2015; Allen & Lee 2006). Less stable streambanks contribute to increased suspended sediments in stream water, and consequently in nearshore marine habitats such as coral reefs and kelp forests (Beschta & Ripple 2009/2011; Golbuu et al., 2011; Dunkell et al., 2011). Therefore, we can expect islands with more cover of vegetation and specifically more complex riparian vegetation to exhibit less sedimentation to the nearshore marine environment.

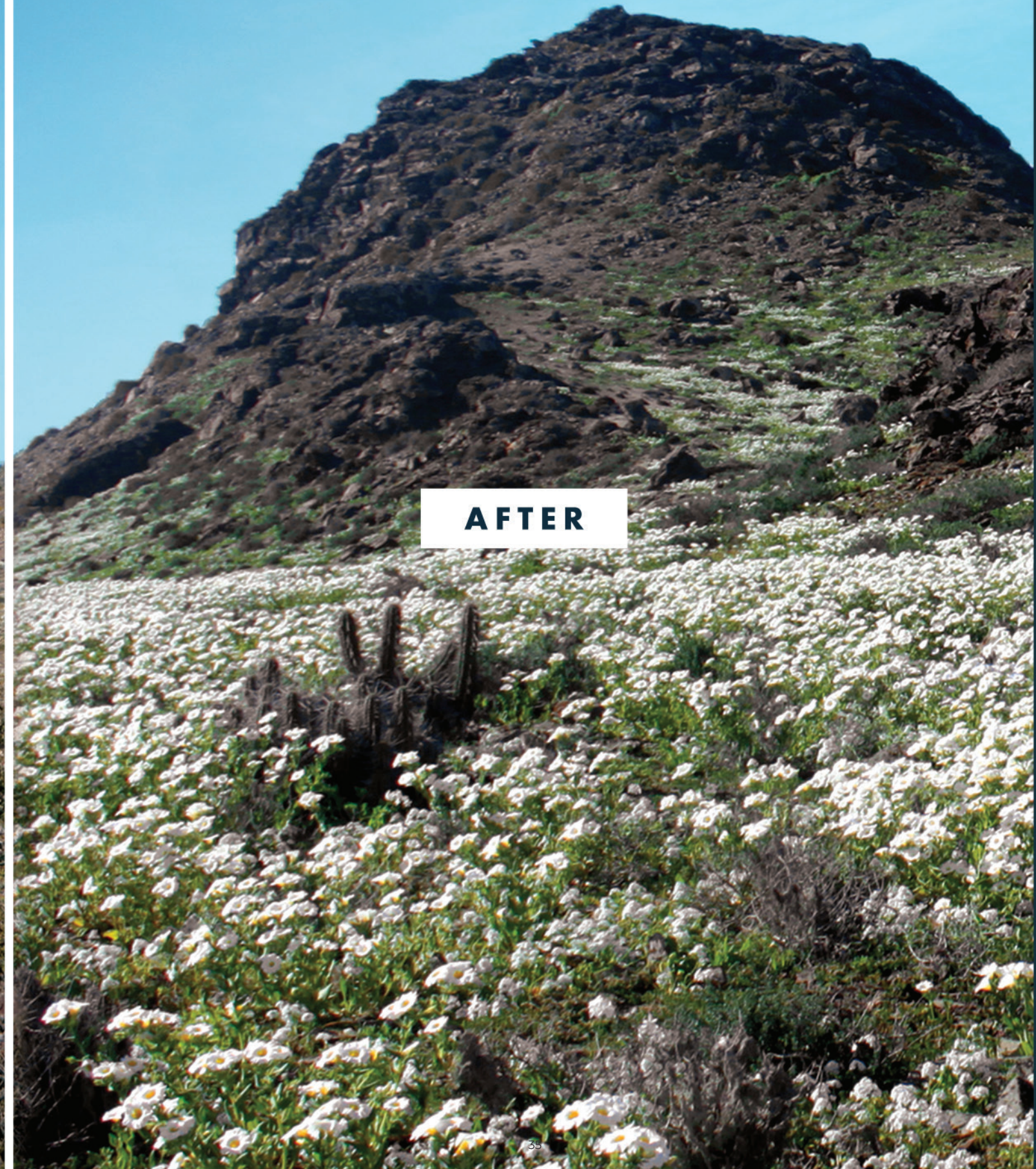
BEFORE AND AFTER THE REMOVAL OF INVASIVE RABBITS

Humboldt Penguin National Reserve
Choros Island, Chile (2013 - 2015)

BEFORE



AFTER



SOIL CHARACTERISTICS

Islands vary dramatically in their soil characteristics, ranging from thick, rich, and humic to thin, porous, and sandy. In general, thicker layers of soil with higher biological content tend to retain water for longer periods of time, thus reducing water flow out of the system (e.g., from land to sea). While relative permeability of soil is a primary factor determining the magnitude of land-sea linkages, the complexities of the soil ecosystem further affect the types of nutrients and other materials that can flow from land to sea. The soil ecosystem can modify nutrient concentrations and profiles through geological and biological mechanisms, ultimately modifying the extent of land-sea linkages.

Soil permeability is not only a buffer on the effect of rainfall through its effects on water retention and evapotranspiration, but also exists as an independent vector of land-sea connectivity via submarine groundwater discharge (Silberger et al, 2021; La Valle et al, 2019). Submarine groundwater discharge has been shown to influence the temperature, pH, nutrient concentrations, and total alkalinity of nearshore marine environments, and can be traced using Ra isotope activity (Bishop et al., 2017; Paytan et al., 2006; Blanco et al., 2011; Silberger et al., 2021; La Valle et al., 2019). The increased residence time of submarine groundwater allows for more water-rock interactions to occur, distinguishing it from surface runoff. Studies show submarine groundwater discharge to be a significant source of dissolved nitrogen in the form of ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-) and a source of phosphate (PO_4^{3-}) and silicate (Silberger & Lubarsky 2020; Santoni 2016; Ji et al., 2013). Relative to surface runoff, submarine groundwater discharge may be more concentrated in dissolved inorganic nitrogen and silicate with lower concentrations of phosphate. In addition to nutrients, submarine groundwater discharge can have significant effects on pH, total alkalinity/dissolved inorganic carbon and net ecosystem calcification/net ecosystem productivity therein.

Soil nutrient profiles largely determine the nutrient profiles passed on to the nearshore marine environment. Plants can mediate the composition and concentration of nutrient profiles entering the nearshore marine environment through their modification of soil nutrient profiles via plant cycling, nutrient leaching, and nitrification in the rooting zone (Jobaggy & Jackson 2001). Studies on horizontal nutrient patterns in soils have revealed that plant cycling can lead to “fertility islands” in systems where nutrients in soils may be scarce on average, such as under trees in the savannah or shrubs in deserts (Zinke 1962; Belsky et al., 1989; Jackson & Caldwell 1993; Schlesinger et al., 1996; Burke et al., 1998). However, soil nutrient profiles *de facto* are dependent on a combination of these processes as well as their mediation by the soil microbiome and climate.

Detritivores in the soil ecosystem play a crucial role in nutrient mineralisation, and studies have shown that different detritivore communities can have a variety of impacts on soil nutrient profiles. In a study of soil macroinvertebrates on sub-antarctic Marion Island, Smith (2007) found that native caterpillars stimulated nitrogen, calcium, magnesium, and potassium mineralisation between two to five times more than the introduced slugs, while the two species stimulated carbon and phosphorus to the same degree. These results are particularly crucial for islands with invasive species, as Marion island also has an introduced population of house mice which prey only on the native macroinvertebrates, avoiding the introduced slug. In addition to differing nutrient profiles, detritivores are known to consume litter at different rates. The introduced chironomid midge *Limnophyes minimus* has been shown to consume up to an order of magnitude more litter than the endemic *Pringleophaga marioni* annually (Hanel and Chown 1998). Thus, without intervention, the impacts of these two invasive species alone are likely to completely alter soil nutrient profiles, ecosystem functioning, and consequently the nutrient profiles

transported to the nearshore marine habitat. These two introduced species on Marion island illustrate the drastic yet often overlooked impacts of invertebrates, particularly detritivores, on ecosystem functioning as a whole. These impacts are especially relevant when nutrient delivery across systems is the main focus, as is often the case when studying land-sea linkage.

OCEANOGRAPHIC NUTRIENT AVAILABILITY

Marine habitats experiencing significant amounts of upwelling have reliably higher nutrient concentrations and higher marine productivity as a result of the delivery of cool, nutrient-rich water. Environments with naturally high nutrient concentrations are more resilient to alterations in terrestrial nutrient input volume as these systems are already highly productive. Due to the context dependency of resource subsidies, allochthonous input will only have strong effects if the resource being transported is scarce in the recipient ecosystem (Polis et al. 1997; Marczak et al., 2007; Subalusky et al. 2018). Thus, upwelling can reduce the influence of land-sea linkages by increasing the productivity of the adjacent near shore marine system until terrestrial input is comparatively negligible. In a study on coral growth, Gill et al. (2017) found that corals are likely to benefit from nutrient input in highly oligotrophic environments, with no such benefit of nutrient addition for corals in more eutrophic (higher nutrient) conditions. This illustrates the contextual importance of the marine environment. However, nutrient enriched systems are still sensitive to alterations in nutrient composition, and it is also possible for high upwelling to be triggered by a particular limiting nutrient. For example, phosphate from terrestrial runoff shifted nutrient ratios in the already nutrient-rich marine communities off the southwest coast of India in 2016, leading to an algal bloom (Kumar et al., 2020). Determining whether nutrients introduced through shifted land-sea linkages associated with invasive mammal eradication could shift nutrient profiles (e.g., ratios of limiting nutrients) significantly in areas of high upwelling remains an area of research opportunity.

OCEANOGRAPHIC FLOW

Just as local oceanography influences nutrient availability in nearshore marine ecosystems, nearshore bathymetry and oceanographic flow govern the residence times of nutrients in nearshore marine habitats. High wave impact and strong currents can dilute any terrestrial input to the marine ecosystem, decreasing local land-sea linkage (Kolb et al., 2010; Benkwitt et al. 2021; Rankin & Jones 2021). However, features of an island's geomorphology can introduce complexities to patterns of oceanographic flow. For example, lagoonal habitats (created by barrier islands or barrier reefs enclosing nearshore marine waters) are shallower, more enclosed areas that tend to experience altered water flow and lower dilution rates relative to the surrounding ocean. As such, lagoonal habitats are especially susceptible to terrestrial input of any kind, as terrestrial runoff tends to pool in lagoons and remain concentrated for extended periods of time. Lagoonal habitats may positively impact connectivity by facilitating pooling of terrestrial runoff and submarine groundwater discharge (Fujita et al., 2014; Brodie et al.; 2012). Using isotope analysis of macroalgal nitrogen on a low-lying pacific atoll, Fujita and colleagues (2014) found that oceanic algae likely received most of their nutrients from upwelling while algae in the lagoon close to populated areas received most of their nutrients from terrestrial sources. Certainly lagoons vary widely based upon size and shape, with water residence times ranging from a few days to months. Features that reduce water exchange with open ocean waters tend to increase potential for strong land-sea linkages.

Integrating the Effects of Mediating Factors on Land-Sea Linkages

The strength of connectivity of island-marine ecosystems varies across a gradient, depending upon these mediating factors. **Evidence suggests that the most important geological and oceanographic factors are the elevation of the island, precipitation, local oceanography, and the cover and complexity of vegetation on the island. Of the mediating factors we list here, precipitation is likely of primary influence in defining the strength of land-sea linkages, regardless of the island type, with higher rainfall associated with tighter land-sea connections. The oceanographic context of high land-sea connectivity consists of generally low nutrient concentrations in ocean waters and low rates of flow or exchange with open-ocean waters. Each of these mediating factors can influence patterns of nutrient delivery and sedimentation into marine habitats, thus affecting marine community structure and function.** Importantly, these mediating factors are not all of equal importance and hold potential to interact with one another in affecting the strength of land-sea linkages.

H. ERADICATIONS OF INVASIVE MAMMALS FROM ISLANDS BENEFIT BOTH LAND AND SEA ECOSYSTEMS

Since islands and adjacent marine habitats are inextricably connected, the removal of invasive mammals will inevitably affect both land and sea. Therefore, invasive mammal eradication can be an important nature-based tool to benefit the adjacent marine environment. Eradications and their ability to remove direct threats to island-marine ecosystems, as well as their indirect benefits via champion species restoration, can have positive impacts on marine habitats, especially where mediating factors align to create strong land-sea linkages. Invasive mammal eradication offers a new, under-recognized means to manage from ridge to reef.

Complementary land-sea management not only increases the spatial scope of conservation interventions but also has the potential to accelerate the recovery of ecosystems following eradications. And since the management of invasive mammals results in such a broad range of potential impacts, they are not only a valuable conservation tool for ecosystem health and biodiversity, but also for land and sea ecosystem functions people rely upon. More than 3 billion people depend on oceans for their livelihoods (United Nations 2021) and more than 730 million people, or approximately 11% of the world's total population, depend upon island resources. Removing the threat of invasive species will protect island-marine ecosystems and promote their resilience for island communities, providing human livelihoods, food security, tourism revenue, agriculture, and protection from extreme climatic events (deWit et al., 2020; Plazas-Jimenez 2020; Beck et al., 2020).

Ecosystem-level Management Increases the Efficacy of Restoration Efforts for Land and Sea

While many island-marine ecosystems may passively recover after terrestrial invasive mammals are removed, the speed and extent of the changes on land and at sea can be facilitated with active, ecosystem-level management (Jones 2010a). **For example, given that the presence of native champion species plays a large role in connecting islands and oceans, helping these species and their habitats rebound can recover island ecosystems and strengthen links with surrounding marine communities.** Many seabird populations respond quickly to invasive species eradications alone (Keitt & Tershy 2003; Cooper et

al., 1995; Buxton et al., 2014), while others do not recover passively following mammal eradications, resulting in still-broken land-sea linkages (Jones & Kress 2012). Actively restoring seabirds through reintroduction, chick translocation, or decoys and vocalization playbacks can increase the pace of recolonization to post-eradication islands and reinstate nutrient cycling to enhance island recovery. Analogous efforts of species-level restoration for other champion species, like sea turtles and pinnipeds, hold promise to accelerate land-sea conservation gains following eradication efforts. This 'rewilding' approach offers not only faster responses to restoration on land and in the water, but also enduring, sustainable benefits.

Humans are the most significant modulating factors of any environment in which they are present, thus they have a significant impact on the level of land-sea connectivity on islands. The intervention of invasive species removal, thus, should not be considered as a stand-alone effort to restore entire island-marine ecosystems. Instead, complementary efforts of effective resource management can provide amplification of land-sea conservation benefits following eradication of invasive mammals. When terrestrial species are provided strong management protections, we may expect more rapid recovery of native flora and fauna (with associated indirect benefits) following an eradication effort than in cases where the terrestrial system is deforested or otherwise disturbed. ***Similarly, well-managed marine protected areas (MPAs) in nearshore waters can provide the enabling conditions to swiftly realize ecosystem gains when land-sea connectivity is strengthened. Further, through the benefits afforded by strengthened land-sea connections, invasive mammal eradications can greatly improve the conservation status of MPAs.***

Invasive mammal eradication on islands should be approached through the local lens of land-sea linkage to achieve maximal conservation gains. Protection and restoration efforts solely focusing on islands or oceans, without regard for land-sea linkages and the tool of invasive mammal eradications, may be overlooking a critical opportunity to maximize outcomes.

Strengthening Land-Sea Linkages to Support Resiliency in a Changing Climate

Since island systems are among the most vulnerable to climate change, taking advantage of the opportunity to integrate land-sea linkages into climate resiliency efforts is critical. The effects of climate change on island terrestrial and marine ecosystems vary across the globe, including shifts in temperature, rainfall, sea levels, storm severity and intensity (IPCC 2021). For example, the effects of climate change typically manifest on tropical coral reefs as warm-water anomalies that trigger more frequent and severe coral bleaching events (Hughes et al., 2018). Increased precipitation can lead to increased sediment erosion and runoff into nearshore marine ecosystems. This, along with sea level rise that erodes coastlines, results in impacts to water quality, with particular impacts on coral reefs and mangroves (USGRP 2009). The cumulative impacts of invasive species and climate change, and the interaction between these two factors, compounds the threat to island-marine ecosystems (Mainka & Howard 2010). Further, since invasive species reduce ecosystem functioning, resilience to climate impacts is likely diminished.

Invasive species eradications can help rebuild island-marine ecosystem resiliency by restoring linkages and buffering climate impacts. For example, increased seabird nutrients may promote recovery of reefs after bleaching events through their positive influence on crustose coralline algae and herbivorous fishes (Benkwitt et al., 2019). In addition, reefs with adjacent seabird nutrient subsidies may exhibit coral growth rates up to four times of those without seabirds (Savage 2019), and therefore result in larger reefs to buffer islands from extreme storm surge and flooding events. Increases in plant productivity that occur on islands after an invasive mammal eradication can contribute to carbon sequestration and the recovered vegetation may help to stabilize soils and reduce erosion due to storm events. The results

A Double-header Wrasse (*Coris bulbifrons*) swims in coral gardens below Mount Gower and Mount Lidgbird, Lord Howe Island, Australia
Credit: Jordan Robins / The Nature Conservancy



are less loss of land for island inhabitants and terrestrial biodiversity and a reduction of sediment that can negatively impact surrounding marine ecosystems such as coral reefs, seagrass beds, and kelp forests. By and large, where invasive mammal eradications help restore land-sea linkages, we expect the resulting better functioning, intact ecosystems can enhance climate change resilience for island inhabitants and species at land and sea (Spatz et al., 2017), but there are few focused studies on this topic.

Implementing Eradication Projects for Marine Conservation

Not all islands offer the same opportunity for marine conservation through their land-sea linkages. ***Given our current understanding of the value of land-sea linkages for increasing the efficacy of conservation interventions, we must prioritize islands for invasive species management where linkages can be utilized to maximize marine co-benefits.*** Where marine conservation is among the primary drivers of management action, our understanding of the patterns and expectations of land-sea linkages can guide where communities, marine funders, and conservationists should focus their invasive species eradication efforts.

While some important projects have and are taking place that take this ridge to reef approach, these should be built upon and scaled up to regional and global levels to have the conservation impact needed to address the dire needs of islands and oceans. Since we expect strong linkages where we know the mediating factors align, and many islands where invasive mammal eradications have already taken place match these conditions, the marine environment has likely benefited in these places, but these impacts were not recorded. Therefore, our current understanding of land-sea linkages on islands across the globe is still premature due to a lack of proper analysis of cross ecosystem effects. In order to refine our expectations of land-sea linkages, we need a broader set of data covering various biogeographical and geomorphological settings so that we can analyze the impact of eradications on island restoration as a whole. Once this analysis is further along, island restoration practitioners will be able to better direct efforts to maximize their impacts for both terrestrial and marine conservation gains. Past and future eradications of mammals on islands have and will benefit the marine environment, but without standardized monitoring of the full island-marine ecosystem around these interventions, we will not understand the extent of the benefits achieved, nor will we be able to refine the use of this tool for more effective marine conservation.

I. BUILDING OUR KNOWLEDGE ON INVASIVE MAMMAL ERADICATION AND LAND-SEA LINKAGES

Investigations of land-sea linkages are disappointingly rare, but incredibly necessary to build the knowledge base that will help us properly manage and conserve marine and terrestrial resources into the future. Many of the best studies available rely on collating information across islands of different invasion histories to correlate changes at sea with differing management histories on land rather than directly testing for land-sea linkages. The few studies that have investigated land-sea linkages are often heavily focused toward land or sea, and rarely integrate both perspectives. In addition, land-sea linkage studies have largely focused on impacts of rat eradication, leaving gaps in our understanding about the impacts of eradication of other invasive mammals on island-marine ecosystems.

We carried out a literature search to synthesize the current state of the knowledge regarding forms of land-sea connectivity on islands, with a specific emphasis on mechanisms likely to be influenced by the introduction and eradication of invasive mammals. [The literature database is available here.](#) Appendix 1 provides an expansive summary of topical studies, with a focus on the variables that have been measured in descriptions of effects of invasive mammals; many of these response variables have value in our consideration of patterns of land-sea linkages. The variables span a wide range of ecosystem components (Appendix 1). Among the most frequently quantified is the abundance of terrestrial taxa including both invasive species and native species. Densities and demographic characteristics of seabirds are common response variables, with more targeted assessments of plant, invertebrate, and microfaunal communities conducted inconsistently across studies. In a minority of case studies, researchers have quantified intertidal and nearshore marine ecosystems, considering the composition of flora and fauna with reference to composition of the adjacent terrestrial ecosystem. Beyond community composition, a large number of studies track the pools and flux of organic nutrients within the community. These studies include samples of the terrestrial biota as well as soil and watershed composition. As with the biota, a minority of studies sample comparable nutrient descriptors in the marine environment. Further, some studies consider functional characteristics of the ecosystem in the form of biological rates (e.g., grazing, bioerosion) as potential contributors to impacts of land-sea connectivity. A collection of environmental variables have been sampled to contextualize structural elements of the ecosystem, for example including temperature, sunlight, environmental chemistry, and physical flow (e.g., wind, waves). In balance, the scientific literature offers a broad spectrum of potential descriptors and contributors to patterns of land-sea connectivity

Since no one research group could reasonably be expected to measure all the variables listed in Appendix 1, it is important to prioritize which variables may be considered 'consensus' baseline descriptors topical to our understanding of land-sea connections. ***There have been no previous attempts to recommend a standardized set of priority variables that researchers and practitioners should measure to understand land-sea linkages. Our team has collated those variables describing the island ecosystem (marine and terrestrial) that, based on our expert opinion, are the most important and relevant to measure (Tables 1 and 2).*** We characterize these according to the types of changes we expect to see in various categories of biota, function, and structure, with an emphasis on being able to document island-wide responses to invasive mammal eradications. We separate out the specific types of response variables that we recommend be collected in the terrestrial (Table 1) and marine (Table 2) environments, together with references of examples of those research methodologies. Measuring these priority variables will help us fill knowledge gaps that exist on land-sea linkages and their responses to invasive mammal removal. Note that we separate the metrics by habitat type -- terrestrial and marine -- as we find that field scientists and practitioners are commonly trained in methodologies that have habitat specificity (and oftentimes unique jargon or expertise)..

The consensus variables identified in Tables 1 and 2 represent a synopsis of the general ecosystem structure and core dynamics most likely to be affected by introduction or eradication of invasive mammals. The priority response variables can be linked to what are believed to be the highest-order changes to the ecosystem in response to invasive mammals. The consensus metrics include estimation of the abundance of key taxa, including the animals and plants that define major elements of the island ecosystem. Further, the variables include estimation of major pools of organic nutrients, using dominant primary producers as an indicator of potential major changes in nutrient flow. A final set of variables is introduced to describe the structure of the ecosystem, considering the erosion patterns of terrestrial soil and shifts in structural complexity in the sea. It is critical to note that these variables will not describe

all changes in land-sea patterning associated with introduction or eradication of invasive mammals. However, we find that almost all published studies and reports about the ecological consequences of such invasives include at least this baseline assessment of ecosystem patterning. And without at least some common ecosystem metrics being collected from across island case studies, the broader research community will have no means to investigate generalities and anomalies in patterns of land-sea linkages from across global examples. For the global community to learn from the growing collection of eradication case studies, it is essential that a core set of common data types from each terrestrial and marine ecosystems be collected and shared.

We emphasize that the proposed ecological variables introduced in Tables 1 and 2 describe metrics that can assist in the tracking of patterns of ecosystem change within one island and provide a common base of information for comparing across islands. The implementation of a monitoring protocol that includes the estimation of these variables should be realized with consideration of each island's geography and

human context. We designed these tables to provide entry into the definition of consensus response variables, yet provide no prescriptive methodology; the design of a sampling protocol must be tailored to the specifics of the geography (e.g., area, field conditions, accessibility, safety) and thus we recommend building specific sampling protocols in consultation with trained professionals. Further, the tables provide consensus opinion about the ecological information that holds value for consideration within and across islands. The collection of ecological data always occurs within a cultural context, highlighting the importance of employing biocultural approaches for survey design (Sterling et al., 2017). An island's history and biological diversity will often be linked closely to cultural values from local communities. Especially when these ecological data are being collected in support of island management proposals or projects, it becomes critically important that the data generated are locally accepted and collected with respect to local cultural norms and knowledge bases. Working in concert with local expertise, both technical and cultural, will maximize the impact of ecosystem data collected.

POTENTIAL IMPACTS OF MAMMAL ERADICATION	PRIORITY RESPONSE VARIABLE	JUSTIFICATION	FIELD METHODOLOGY	UNITS	REFERENCES
CHANGE IN BIOTA	Abundance -- dominant plant species/ vegetation types	The density and composition of the plant assemblage can reflect characteristics of the bottom-up (e.g., nutrient delivery) and top-down (e.g., herbivore community) ecosystem conditions.	Remote sensing, Line-point intercept surveys, Plot survey, Fixed point photographs	Percent cover (by species / vegetation type), Number of plants/ trees per unit area	Hill et al. 2005; Croll et al. 2005
	Abundance -- dominant invertebrates (Include land crabs in tropical environments) Abundance -- dominant vertebrates (Include seabirds, plus others appropriate to local context (e.g., shorebirds, reptiles, sea turtles))	Invertebrates are a key part of the food web and/or serve key ecological roles. Crabs in particular help to break down and recycle nutrients, can be ecosystem engineers, and are at the top of the food chain in many ecosystems. Seabirds and some other vertebrates directly transfer nutrients from marine environments to the terrestrial community, while others forage in the nearshore intertidal environment and impact the food web.	Land crabs: Strip transects; Other invertebrates: Pitfall traps, Sweep nets, Soil collection, Malaise traps Seabirds: Burrow or nest counts within plots, Island/colony-wide survey via drone imagery, Acoustic surveys, Shoreline surveys; Other vertebrates: Beach or habitat-specific surveys or counts	Number of individuals per unit area or sample (by species / taxon) Number of individuals, nests, or tracks per unit area stratified by vegetation or habitat across island (by species / taxon) or Total count	Yi et al. 2012; Fisher et al. in prep; Soil invertebrates: Towns et al 2009; Ground-dwelling invertebrates: Holthuijzen et al 2021. in press; Land crabs: Samaniego et al. 2019 Seabirds: VanderWerf and Young 2018; Shorebirds: PRISM 2018; Sea turtles: TCOT 2002; Borke et al. 2014; Kurle et al. 2021; Croll et al. 2016
CHANGE IN FUNCTION	Vegetation nutrients	The concentration of signature nutrients in plants will allow tracing of marine-derived nutrients throughout the terrestrial and marine food web.	Stable isotope analysis of new leaf growth from three individuals of same plant species	$\delta^{15}N$ (ratio of concentrations of stable isotopes of N)	Post 2002; Jones 2010a; Jones 2010b
CHANGE IN STRUCTURE	Erosion rates (in cases of invasive herbivore eradication)	The marine environment is impacted by the influxes of soil, which is affected by invasive herbivores and is mediated by the terrestrial plant and animal community.	Erosion pins	Absolute value of pin height change (extent of pin height change whether erosion or deposition)	Kearney et al. 2018

Table 1.

Priority response variables describing status and trends in the terrestrial environment. Note that methods are intended to represent methods that are commonly applied (increasing comparability across data streams), represent changes of notable interest for most management priorities, and do not require extreme methodological specialization (i.e., are broadly available across user groups). Further, many geographical case studies will require the addition of surveys for 'champion species' or other taxa of particular ecological, economic, or cultural importance. The response variables provided here are intended to represent the foundation of ecological context for coastal marine ecosystems that can be compared broadly across geographies. Sampling should consider spatial variability across the island.

POTENTIAL IMPACTS OF MAMMAL ERADICATION	PRIORITY RESPONSE VARIABLE	JUSTIFICATION	FIELD METHODOLOGY	UNITS	REFERENCES
CHANGE IN BIOTA	Abundance -- dominant benthic algae	The composition of the macroalgal assemblage can reflect characteristics of the bottom-up (e.g., nutrient delivery) and top-down (e.g., herbivore community) ecosystem conditions	Photoquadrat or line-point intercept surveys	Percent / proportion of benthic habitat (by species / taxon)	English et al., 1997; Hill and Wilkinson, 2004; Preskitt et al., 2004; Eleftheriou, 2013; GCRMN, 2016; UCSC website
	Abundance -- dominant macroinvertebrates	Macroinvertebrates are important contributors to coastal marine communities, serving both key ecological roles and often high fisheries value	Belt transect survey	Number per unit area (by species / taxon)	English et al., 1997; Bortone et al., 2000; GCRMN, 2016; PISCO website
	Abundance -- dominant vertebrates (diurnal, non-cryptic fishes)	Fish are important contributors to coastal marine communities, serving both key ecological roles and often high fisheries value. Surveys including size estimates provide insights into functional roles of fishes, as consumption and productivity scale with individual size	Belt transect survey	Number per unit area (by species / taxon)	Brock 1954; Bortone et al., 2000; Samoilyls et al., 2000; PISCO website
	Abundance -- dominant 'champion' megafauna (as appropriate, e.g., pinnipeds)	Large vertebrates like pinnipeds can be dominant predators altering community structure; further, such taxa often carry strong legal and cultural value	Distance sampling, transects, or mark-recapture	Number per unit area (by species / taxon)	Buckland et al., 2018
CHANGE IN FUNCTION	Nutrient concentration (estimated within dominant benthic algae)	Capturing an estimate of the bio-available nutrient environment is important, though nutrient flux in coastal marine environments is highly variable. The tissue of sessile primary producers (e.g., algae) have been shown to provide reliable estimates of time-averaged nutrient availability		$\delta^{15}N$ (ratio of concentrations of stable isotopes of N)	Umezawa et al., 2002

Table 2.

Priority response variables describing status and trends in marine community structure. Note that methods are intended to represent methods that are commonly applied (increasing comparability across data streams), represent changes of notable interest for most management priorities, and do not require extreme methodological specialization (i.e., are broadly available across user groups). Further, many geographical case studies will require addition of surveys for 'champion species' or other taxa of particular ecological, economic, or cultural importance. The response variables provided here are intended to represent the foundation of ecological context for coastal marine ecosystems that can be compared broadly across geographies. Sampling should consider spatial variability across the marine environment adjacent to the terrestrial environment.

J. KNOWLEDGE GAPS AND FUTURE RESEARCH TO STRENGTHEN ISLAND-MARINE CONSERVATION

Need for Additional Studies Across Geographies and Contexts

Our review has shown that there are strong datasets for tropical ecosystems such as the Chagos archipelago and others, growing information in the Hauraki Gulf of New Zealand, and to a lesser extent, the Aleutian Islands. But we are still lacking the in-depth globally-reaching datasets necessary to fill knowledge gaps. We call for more research in temperate systems, sub-antarctic and polar regions, and longer time series in more well-studied locales. We also emphasize that improving access to existing data sets and collecting standardized data across islands and geographies will be critical to extract comparable information. Just as having local and Indigenous community ownership or support is an essential part of conducting successful conservation actions like invasive species eradications, it is equally important that stakeholders come together with conservation practitioners and scientists to outline area-specific knowledge gaps and design how to fill them. As conservation interventions expand globally, we recommend that funding for eradication programs be increased so that measurement of terrestrial and marine variables can be built into the programs going forward. With such consistent data available, eradication practitioners can partner with local communities and scientists to collect, analyze, and interpret such data (sensu Kappes & Jones 2014).

It is important to recognize that some response variables will be more compelling than others to different stakeholders, project funders, and supporters. For example, some stakeholders may be more inclined to support projects that quantify and demonstrably improve ecosystem services like surrounding fishery productivity, carbon sequestration, or coastal community livelihoods. Most ecosystem services are a derivative of the priority variables we list, so these could be converted to ecosystem services, depending on the circumstances. We offer the priority variables listed here as the potential starting point of any land-sea linkage study, and also encourage researchers to use their insight to add variables, measuring for the given context. Ideally, studies of land-sea linkages could take a before-after control-impact study design, such that data are collected before and after mammal eradication on islands as well as on islands with mammals still present (impact) and those without mammals (control). Finally, images can be incredibly compelling for storytelling and garnering support and funding, so we urge researchers and practitioners to collect high quality imagery in addition to the scientific variables we suggest as high priority.

In summary, as we consider the roles of invasive mammals in land-sea linkages in additional geographies, we encourage the collection of data using shared, standardized metrics to address the following priority research questions:

- ***Which champion species, nesting ecology or phenology, or community assemblages result in the strongest land-sea linkages?***
- ***Is there a threshold population size that must be reached before champion species can facilitate meaningful land-sea linkages?***
- ***What will climate change mean for the strength of island-marine linkages and how might it affect our ability to predict outcomes of conservation interventions?***
- ***Can we predict community composition or ecosystem processes at sea by measuring variables on land?***
- ***To date, our knowledge of land-sea linkages associated with invasive mammal eradication has focused solely on rat eradications; how does the eradication of non-rat invasive mammals affect adjacent marine ecosystems?***

Leveraging Advanced Technologies for Land-Sea Linkage Studies

Our ability to quantify and contextualize the effects of invasive species eradications on land-sea linkages is at least partially limited by the amount and resolution of observational data sufficient to do so. This is particularly true given that ecosystem responses to removal efforts may yield slow, incremental change to both terrestrial and marine systems. Fortunately, emerging methods of environmental and biological observation, coupled with methods for data synthesis, hold promise for rapidly improving the resolution and extent of island ecosystem monitoring. The field methodologies for measuring priority response variables are primarily survey-based observational data. As such, priority island ecosystem monitoring technology should focus on scaling cost-effective methods for collecting, retrieving, and analyzing landscape scale observational data. Future work prioritizing the highest value measurement technologies by response variable and ecosystem would benefit future monitoring programs.

Quantifying biological responses of species and communities

Traditional methods of biological assessment rely on visual, organismal observations. However, biological responses to restoration may well occur outside the community of organisms that scientists can easily enumerate. For instance, sublethal impacts to species may manifest as stress responses that impact reproduction or growth. In addition, the biological components of the ecosystem beyond visual detection (microbiome, pathogens, etc.) may well have a strong response to restoration. To assess these types of responses, next generation 'omics methods hold promise in assessing sub-organismal and microbiological responses to management action (Zhang et al., 2010). In addition, environmental DNA may also prove effective in providing increased accuracy in the detection and enumeration of cryptic and rare species (Ota et al., 2020). The collection and long-term storage of environmental DNA to support such efforts is relatively easy, and may well prove valuable even if immediate sample workup is impossible or unaffordable in the near term.

Passive acoustic observations, made possible by the ongoing development of long-term hydrophone/microphone monitoring stations, also hold promise for detecting biological responses to management (Borker et al., 2015, Buston et al., 2018). In addition to capturing acoustic signatures of organisms as a proxy for presence/abundance, such recordings can also capture changes in animal behaviors (e.g., reproductive behaviors, aggression). Finally, changes in the acoustic soundscape of marine and terrestrial systems can provide a synthetic index of ecosystem change.

Quantifying spatio-temporal abundance of species and communities

Emerging, inexpensive methods of capturing high resolution spatio-temporal data offer the potential to generate observations that are highly sensitive to ecosystem change. On the terrestrial side, camera-equipped aerial drones or satellites can provide targeted, high-resolution imagery needed to construct detailed habitat maps across entire island landscapes (Chabot & Bird 2015). In general, satellites offer better temporal resolution for long term trend analysis (Lohr et al., 2014) while aerial imagery offers better spatial resolution. In the marine environment, recent efforts mesh diver-generated benthic imagery into synthetic, large-scale (10-10,000m²) 3-dimensional benthic habitat maps. At larger scales, airborne multi-spectral and LIDAR surveys afford the potential for rapid and very large scale (100s-1000s km²) benthic habitat classifications and 3D structural composition of nearshore habitats (Hedley et al., 2016). In concert with the evolution of these spatial data collection methods, innovations in spatial data analysis have grown rapidly, with tools such as Vector Autoregressive Spatio-Temporal (VAST) package affording powerful inference from spatio-temporal analysis of univariate or multivariate data (Thorson 2019).

Emerging methods to assessing flux between terrestrial and marine systems

Understanding connections between marine and terrestrial ecosystems that are responsive to invasive species eradication efforts requires observations that can quantify flux. Evolving molecular tracer methods, such as compound-specific stable isotope analysis, offer the potential to link basal sources of primary production to upper trophic levels, within and between terrestrial and marine ecosystems (McClelland & Montoya, 2002; Whiteman et al., 2019). Similarly, trace element analysis can provide tracer signatures in soils and sediments that can inform probabilistic estimates of sources and fates of sediment flux to marine ecosystems resulting from changes in terrestrial ecosystems (Blake et al., 2018). As the affordability and sensitivity of these tracer analyses improve, we anticipate that they will prove hugely valuable in characterizing the flux of energy, nutrients and sediments across ecosystems.

Data archiving and mining methods

The ongoing evolution of information-rich observational methods demands infrastructure capable of sustaining the ingestion, processing, and storage of such observations. Long-term, repeated photographic mapping surveys of benthic ecosystems, for instance, can rapidly generate petabytes of digital files. Fortunately, cloud storage and computing platforms have made such scalable data storage and analysis tools available and affordable to the general public. At the same time, new platforms for analytic tool version control, archiving and sharing (e.g., GitHub), have democratized the use of advanced software tools capable of capitalizing on evolving, high resolution observations. Artificial intelligence tools are both rapidly evolving and are increasingly incorporated into the data analysis process for large observational data sets (e.g., imagery, acoustics) to supplement the human processing of monitoring data (Gonzalez-Rivero et al., 2020). The continued evolution and adoption of these data management and analysis tools is a critical part of efforts to leverage advanced technologies in assessment efforts.

Traditional Knowledge and Historical Data Illuminate Land-Sea Linkages

Traditional ecological knowledge (TEK) can provide invaluable information to better understand land-sea linkages. TEK is an alternative to modern science as it provides insight into how ecosystems function and human-environment relationships that modern science cannot (Hunn 1993). The information about how local communities have adapted to changes in the environment offers alternative knowledge and perspectives based on locally developed practices of resource use (Berkes, Colding & Folke 2000). TEK provides local intimate knowledge learned over the course of more than 100 human generations on the animals, plants, soil, weather, and detailed maps of local topography (Hunn 1993).

Understanding how people responded to their environment in the past can suggest relevant and culturally appropriate methods as starting points for addressing ecosystem disruptions and framing adaptation planning (Hunn 1993; McMillen, Ticktin and Springer 2017). The palaeoecological records for restoring ecological resilience requires understanding long-term trends which, in conjunction with TEK, can enhance the understanding of resource and ecosystem conditions by characterizing the complex ways that societies have mediated environmental outcomes in the past (Kittinger et al., 2011). These tools can be used to understand the ecosystems prior to invasions on islands and learn about land-sea linkages. TEK of particular regions and areas can help to reconstruct islands or localities prior to invasion of non-native species by understanding the knowledge of the natural environment – the species it contains and how it functions, as well as the evolution of local traditions of the communities whose livelihoods depend directly on these local resources (Hunn, 1993; Berkes, Colding & Folke, 2000; Teixeira et al., 2013). The study of TEK applications to track land-sea linkages can help managers in the generation, accumulation, and transmission of knowledge to guide the direction of resource management (Berkes, Colding & Folke, 2000), while the reconstruction of the historical information through paleoecology can reveal what

ecosystems were like in the past (Kittinger et al., 2011). Utilizing this information to reconstruct terrestrial and marine ecosystems on islands can benefit the datasets on ecological conditions to get long-term trajectories of environmental decline and create more sound eradication and monitoring programs.

It is important to integrate both TEK and modern science to serve as tools to conserve the world's resources when monitoring, responding to and managing ecosystem processes and functions (Hunn 1993; Berkes, Colding & Folke 2000). Integrative efforts have proven to be relatively cost effective and accurate in the planning of conservation efforts while also increasing community engagement in the implementation of the conservation actions (Teixeira et al., 2013).

However, there is no single optimum approach for integrating local, traditional and scientific knowledge (Raymond et al., 2010). The key is to consider multiple views and multiple methods when integrating different types of knowledge for environmental management of land-sea connectivity.



Aerial drones can advance island-marine restorations and data collection efforts by decreasing the cost and time required and increasing precision.

K. A CALL TO ACTION- REVISIT 'RIDGE TO REEF' LEARNING AND CONSERVATION

There is an incredibly important opportunity to treat islands and their marine ecosystems as linked, integrated entities for both conservation and research. Ecological interdependencies between oceans and islands are clear and substantiated, although there has been a history of treating marine, nearshore, and terrestrial ecosystems independently. Humans have recognized this for centuries and modern science is beginning to catch up with case studies that confirm these land-sea linkages. In a time when the conservation of both islands and our oceans has never been more important, terrestrial invasive mammal eradication on islands offers a critical nature-based tool to advance both. Doubling down on a 'ridge to reef' philosophy that includes the removal of island invasives and long-term biosecurity will pay disproportionate dividends for the entire linked ecosystem. Furthering our basic scientific understanding of land-sea linkages in the context of invasive mammal eradication will allow us to apply this tool where and how it can maximize conservation gains. Creating a future where we better understand these systems and we are optimizing our outcomes requires us to overcome the systemic, societal, philosophical, and financial barriers to an integrated approach to learning and managing our islands and oceans.

Shared Learning for Islands and Oceans

There are many prospects for removing barriers to better island-marine ecosystem conservation, and they all begin with a better understanding of the linkages from ridge to reef. While some recent case studies have highlighted geographies and island contexts where land-sea linkages benefit from invasive mammal removal, these studies are scant and leave gaps in our knowledge around the biological, geological, and oceanographic factors mediating the linkages.

Science across silos

It is perhaps unsurprising that scientific investigations of land-sea linkages are sparse. After all, academic institutions are paragons of silos - each department usually has its own buildings, faculty, staff, classes, and majors. Students tend to take classes mostly from their major and work closely only with professors and peers in their major, resulting in a loss of common principles, shared learning, and shared understanding between students across majors and sub-disciplines. Such siloing is especially true of marine versus terrestrial ecologists - marine ecologists often major in Marine Biology while terrestrial ecologists typically major in Ecology and Evolutionary Biology. From undergraduate studies through to the rest of their careers, terrestrial and marine scientists rarely overlap or interact - a fissure that comes at the peril of deeper understandings about how marine and terrestrial ecosystems are influenced by, and influence, each other. As academia and science look toward more interdisciplinary approaches to tackle the greatest problems of our time and of the future, collaborations among scientists from different disciplines will become increasingly needed. ***We call for collaborations among marine and terrestrial ecologists to help fill the knowledge gaps we have around land-sea linkages with modern and indigenous knowledge.*** And this knowledge should be driven by an overall goal of applying best practices across island conservation efforts like invasive species management.

In many cases, new and expanded collaborations between scientists with the expertise to interpret island and marine data, and managers and conservation practitioners carrying out eradication projects are key to furthering our understanding around land-sea linkages and invasive mammal interventions. However, in other parts of the globe such as small island nations, the roles of eradicator, manager and scientist fall to the same government department or non-profit, or even to the same individuals. ***We call for increased training, funding and material support to local managers and conservation practitioners on small island developing states to encourage and enable them to conduct long***

term monitoring of ecosystems before, during and after eradications. International scientists, including those working with NGOs, can play a useful role in training and mentoring local managers and practitioners to design suitable and sustainable monitoring programmes for their needs and the local context. Increasing capacity for local partners, including those with limited formal scientific training, can help to bring more cost-effective methods for research and monitoring that can be applied to island-marine ecosystem restoration.

Ideally, financing for these collaborations should be integrated into the price of mammal eradications (Kappes & Jones 2014). The funding practitioners receive is often solely for removing invasive species, with very little to none allotted to the post-eradication conservation impact monitoring that could help us better understand impacts of eradications on land-sea linkages. In most cases, this is because the eradication programs can themselves cost millions of dollars (Donlan & Wilcox 2007; Martins et al., 2006) and practitioners and managers struggle to fund the baseline projects. In other cases, managers may not seek additional funding for long term monitoring associated with eradications as a priority because they do not understand how valuable the information could be to future conservation. To truly realize the goal of restoring island ecosystems, more funding for monitoring and post-eradication management at both the regional and local island level, and closer collaboration between scientists and restoration practitioners is necessary. Integrating the in-depth knowledge collected on land and at sea to build a deeper understanding of these linkages will require strategic partnerships that bring together scientists working in each ecosystem, along with key stakeholders such as managers, governmental institutions and Indigenous communities.

Resourcing land-sea linkage investigations

Another reason so few studies have addressed land-sea linkage knowledge gaps is a lack of funding for restoration, monitoring, and research. Funding agencies themselves are often siloed and the removal of invasive species and restoration of islands (one of the least funded segments in conservation philanthropy today) have been largely the domain of terrestrial biodiversity conservation funders, even where marine conservation co-benefits are to be gained. Most of the funding for scientific exploration is not available for the type of applied science that is necessary to better understand land-sea linkages and how they are impacted by species invasions and eradication. Monitoring on one or a few islands, and long-term monitoring in general, is typically not of sufficient interest to attract large dollar government funders that expect cutting edge and carefully controlled experimentation. Of course, mammal eradications could be construed as treatments in a natural experiment, and we encourage more scientists to take this approach. Some applied funding sources exist but are often focused on specific problems in specific geographies, which makes putting together the consortium of funding and resources needed to properly understand land-sea linkages and how they operate globally exceedingly difficult.

Furthermore, only a handful of philanthropic foundations and major donors who focus on ocean conservation are supporting ridge to reef restoration and research projects. Together, these financial barriers prevent communities, scientists, NGOs, governments, and funders from knowing where, how, and to what extent we can apply island restorations (and invasive species eradications in particular) to maximize the co-benefits to marine habitat and wildlife. ***We advocate for support for integrative, interdisciplinary studies across marine, terrestrial, theoretical, and applied realms, and for prestigious funders like US National Science Foundation and traditional marine and terrestrial private foundations to lead the way.*** With increases in effort and funding, the resulting larger dataset could better be tracked locally, compared globally, and lead to great advances in utilizing invasive mammal eradications for whole island-marine ecosystem restoration.

Collecting insights from the past and working together in the future

A critically important component of expanded partnerships for land-sea knowledge and conservation should be the people who have for generations understood the unique connections between land and sea and have relied on these interactions for their livelihoods. While there is a lot to be learned from inclusive studies using modern scientific methods, traditional knowledge can also make significant contributions. After all, many of the world's islands that are affected by invasive species are inhabited or used by Indigenous and local people. It is only recently, mainly in the 2010's, that the integrated marine-terrestrial philosophy that characterizes traditional ecological knowledge began to be appreciated more widely, and there are still few efforts that make full use of this knowledge to manage invasives on islands. Funding and organizational infrastructure still represent a challenge to developing research collaborations and co-production between Indigenous and non-Indigenous researchers, particularly due to a lack of an inadequate timeline for researchers to develop trust and meaningful partnerships with communities. ***We call for the funding and research communities to work together to support the capacity of Indigenous peoples, local communities, and local agencies to lead or participate in the development of research proposals, timelines, budgets and implementation around land-sea research and monitoring.***

Opportunities for Land-Sea Connectivity in Contemporary Island and Ocean Conservation

Just as research efforts are siloed, the current governance and management of island ecosystems often includes an artificial division of terrestrial and marine environments. These siloes are maintained among government agencies, communities, NGOs, and the donor community, and extend to most conservation endeavors across the globe. Enormous potential lies in revisiting and recommitting to a ridge to reef conservation philosophy at the global and local levels that recognizes land-sea linkages to improve our knowledge, policies and management of island and ocean ecosystems. ***We call on island and marine managers to evaluate where invasive mammal eradication can have the greatest benefit for marine systems, and urgently build collaborative projects to realize these outcomes.***

International agreements and efforts can drive integrated land-sea conservation

Revisiting a 'ridge-to-reef' approach means we need to ensure that global organizations, partnerships and programs are aligned to think about the goals, planning, funding and implementation in an integrated way. The challenge of resourcing and mobilizing momentum around huge global initiatives, such as the United Nations Sustainable Development Goals (SDGs) is immense. To hit the targets needed to achieve the Life Below Water SDG (14), it is estimated that the world must spend US\$175 billion per year, while accomplishing just one of the 12 targets aimed at the Life on Land SDG (15), sustainable forest management, would cost US\$70-160 billion per year (Castrén 2014). These costs pale in comparison to the cost of inaction for life on land and below water, which stands at the loss of US\$125-140 trillion per year due to loss and degradation of our terrestrial and marine ecosystems and their services (OECD 2019). The costs of invasive species impacts on land alone are estimated at more than US\$162.7 billion (Diagne et al., 2021) annually, but we know that if we were to add the cost of the degradation and loss of land-sea linkages attributed to invasive species, it would drive this number significantly higher.

The recent focus on climate change and its impacts is encouraging and essential since it can undermine and compromise our islands and oceans. However, the recent focus on climate change means that some island and ocean restoration initiatives are receiving less funding and support since restoration is not yet

well recognized as essential to combating climate change and promoting resilience to climate impacts. Our outcomes argue for fully utilizing the power of the links from islands to oceans —eradication of invasive mammals can help serve as a nature-based solution to meet the United Nations SDGs around Life on Land (SDG 15), and should be considered as a valuable tool for accomplishing the Life Below Water (SDG 14) and Climate Action (SDG 13) goals.

Because oceans and island ecosystems support billions of people across the world, the restoration of island-marine systems through invasive mammal eradication can also boost efforts around poverty and hunger reduction (SDGs 1 and 2), clean water and sanitation (SDG 6), and sustainable communities (SDG 11; deWit et al., 2020). Especially with the rise of COVID-19 and its devastating impacts to human health and economies, it is more important than ever to put our global effort and finances into work that benefits our natural world and people. ***Governments, managers, and marine and development funders can now recognize whole island-marine ecosystem restoration, including invasive mammal eradication and biosecurity, as a multi-tool of conservation and sustainable development, where benefits can accrue across the board.***

Global ecosystem restoration initiatives offer an ideal place to underscore the ability and importance of conservation actions that cross the terrestrial-marine boundaries. For example, 2021 starts the UN Decade on Ecosystem Restoration, a ten year movement aimed at preventing, halting and reversing the degradation of ecosystems worldwide. While the initiative calls out the importance of restoration of 8 different ecosystem types, including coasts and oceans and forests, it also can highlight ecosystem restoration tools such as invasive species management and island restoration, that could help address all the targeted ecosystems in a truly whole-ecosystem approach.

Uniting regional and local levels in island-marine management and governance

Islands and their marine ecosystems often have unclear management authority or nearby marine areas are governed separately from terrestrial areas. This disconnect needs to be addressed through better collaboration across management entities or the readjustment of management authority altogether to meet the interconnected needs of island-marine ecosystems. Working across management authorities and expertise and bringing disciplines together could leverage policy options and opportunities that can come only from a collaborative and transdisciplinary approach. ***With community leadership or support, we encourage management authorities to work with practitioners and scientists not only on invasive mammal eradication, but also on long-term biosecurity, protection and/or management of islands and their marine habitats.***

On a regional scale, island-marine restoration could use the sea as a uniting factor in regions where archipelagos are currently siloed. The integration of Indigenous peoples and traditional knowledge into these regional and local goals, governance and management of island-marine ecosystems presents a huge opportunity to be more successful in our restoration endeavors. International agreements, such as the Convention on Biological Diversity, now recognize traditional ecological knowledge. And some countries, like New Zealand, provide better examples of acknowledging Indigenous peoples' rights and integrating their perspectives into policy and management (Lyver et al., 2018). While some international partnerships are making strides, highlighting the importance of Indigenous peoples and local communities in the conservation of territories and areas around the world (ICCA Consortium 2021), much is still required to fully integrate local and indigenous people into the conservation of island-marine ecosystems.

We can do this. We are poised to identify and overcome the challenges of our siloed governance structures, capacity and knowledge. We envision a future where we can work together: terrestrial and marine, modern science and Indigenous knowledge, researchers and practitioners, funders and managers, all for more connected and thriving island-marine ecosystems. A whole ecosystem research and restoration approach to island-marine conservation that includes invasive mammal management offers a promising nature-based solution that is supported by modern science and is rooted in the human legacy. Not only can we not afford to delay or fail in the conservation of our connected islands and oceans, but everyone and every sector can benefit from our collective effort. The conservation community can see habitat and species gains on islands and their nearshore environments, with these outcomes often more tangible and rapid than for almost any other intervention. For policy makers, the costs of inaction are greater than the costs of these tested, effective nature-based solutions, paying dividends for the economy. The collaborative, interdisciplinary approach we outline supports the rights and knowledge of Indigenous communities, and the restoration results can lead to better management and natural resources. Finally, funders have an opportunity to have a massive impact supporting high-priority, multi-benefit work in this under-recognized tool for ocean and island conservation.

**WE CALL ON STRONG,
CROSS-CUTTING COLLABORATIONS
TO ACT FOR OUR ISLANDS AND OUR
OCEANS AND FOR ALL OF US THAT
RELY UPON THESE INTERCONNECTED
ISLAND-MARINE ECOSYSTEMS.**



Kaho'olawe Island, Hawai'i is the smallest of the eight main Hawai'ian Islands, at 28,800 acres (11,520 hectares). Located near Maui, Kaho'olawe is the largest unpopulated and wholly protected island in the archipelago, offering an unprecedented opportunity to protect Hawai'ian species and culture.

Appendix 1

Comprehensive list of ecosystem components that have been described when considering land-sea linkages on islands. The components have each been described with a number of specific variables, quantifying distinct elements of the component (e.g., abundance, concentration). Relevant citations are included for each variable.

ECOSYSTEM COMPONENT	SPECIFIC VARIABLES	REFERENCES
TERRESTRIAL INVASIVE SPECIES	presence/absence, abundance, time present or eradicated, pressure (qualitative or quantitative), diet of invasive species slated for eradication, stomach analysis, fecal analysis, feeding trials, direct observation of feeding / examining pellets, feces	Benkwitt et al. 2019, Brattstrom 2015, Favero-Longo et al. 2010, Gizicki et al. 2018, Grant-Hoffman et al. 2010, Houghton et al. 2019, McLoughlin et al. 2016, Pisanu et al. 2010
TERRESTRIAL VERTEBRATES -- SEABIRDS	species identity, nesting type (burrow, ground, tree, etc.), nesting density (quantitative or qualitative), abundance, phenology, colony age, number of breeding pairs, guano deposition, diversity, reproductive activity/reproductive success (including egg depredation), biomass, body condition, location, distance to colony, age, presence/absence, diet or foraging behavior, movement, pellet or bolus deposition, metal or metalloids exposure, trace elements	Anchundia et al. 2014, De La Pena-Lastra et al. 2019, De La Pena-Lastra et al. 2020, De La Pena-Lastra et al. 2021, del Moral and Magnusson 2014, Duda et al. 2020, Gagnon et al. 2015, Gauthier et al. 2011, Gizicki et al. 2018, Grant et al. 2021, Grant-Hoffman et al. 2010, Harrington et al. 2020, Hata et al. 2014, Honig and Mahoney 2016, Jones 2010b, Lamb et al. 2014, Major et al. 2017, McFadden et al. 2016, Michelutti et al. 2009, Molina-Montenegro et al. 2013, Natusch et al. 2017, Ndu et al. 2020, Orwin et al. 2016, Springer and van Vliet 2014, Thomsen and Green 2016, VanderWerf et al. 2014, Young et al. 2009, Zhong et al. 2017, Zmudczyńska et al. 2012, Zwolicki et al. 2012
TERRESTRIAL VERTEBRATES -- NATIVE VERTEBRATES (NOT SEABIRDS)	presence/absence, abundance, dens or other breeding areas, movement (satellite tracking), body mass and other morphometric measurements, fecal analysis	Gauthier et al. 2011, Balčiauskas et al. 2018, Thomsen and Green 2016, Barrett et al. 2005, Richardson et al. 2019, Pisanu et al. 2010
TERRESTRIAL INVERTEBRATES	species identity, community composition, abundance, presence/absence/occupation, biomass, body mass, body length, diversity (alpha, beta, gamma), density, functional traits, non-native/invasive and their presence/absence species identity, community composition, community structure, abundance, cover, presence/absence, diversity (alpha, beta, gamma, functional, taxonomic, etc.), annual production (live aboveground plant biomass), density, litter decomposition rate, aboveground net primary productivity (ANPP), seedling germination/growth, litter thickness or other characteristics, diameter at breast height, basal area, herbivory, palatability, peat core, microscopic pollen and identification, charcoal analysis, radiocarbon dating, habitat, tree ring/dendrochronological analysis, physiological performance, growth/height, functional traits, $\delta^{18}O$ stem water, tree canopy height, non-native/invasive species presence/absence, trace elements, basal area, below-ground root	Adriuzzi et al. 2013, Forey et al. 2021, Gizicki et al. 2018, Harrington et al. 2020, Houghton et al. 2019, Jones 2010b, Kolb et al. 2010, Nigro et al. 2017, Orwin et al. 2016, Pisanu et al. 2010, Thorensen et al. 2017, Zhong et al. 2017, Zmudczyńska et al., 2012 Adriuzzi et al. 2013, Cipro et al. 2018, De La Pena-Lastra et al. 2019, De La Pena-Lastra et al. 2021, del Moral and Magnusson 2014, Duda et al. 2020b, Dudley et al. 2020, Favero-Longo et al. 2010, Forey et al. 2021, Gauthier et al. 2011, Gizicki et al. 2018, Grant-Hoffman et al. 2010, Hata et al. 2014, Houghton et al. 2019, Jones 2010b, Kirch et al. 2015, Krull et al. 2012, Lamb et al. 2014, McFadden et al. 2016, McLoughlin et al. 2016, Molina-Montenegro et al. 2013, Natusch et al. 2017 Orwin et al. 2016, Peay et al. 2012, Pisanu et al. 2010, Wardle et al. 2012, Wilmshurst et al. 2015, Wright et al. 2010, Young et al. 2009, Zhong et al. 2017, Zmudczyńska et al. 2012
TERRESTRIAL BACTERIA AND FUNGI	microbial biomass, including C, N, and P, community composition, diversity, basal respiration, chlorophyll fluorescence	Wright et al. 2010, Zhong et al. 2017, Peay et al. 2012, Wardle et al. 2012, Ramírez-Fernández et al. 2019, Durrett et al. 2014, Molina-Montenegro et al. 2013

MARINE FAUNA	species identity, community composition, community structure, abundance, diet, coral characteristics (skeletal density, extension rate, calcification rate, skeletal macrobioerosion rate), reef structural complexity, body condition, recruitment, density, biomass, approximate mass, coral cover, % live coral, nesting colony sizes, clutch sizes, timing of nesting, predation on eggs and hatchlings, predator exclosure experiments	Baum et al. 2016, Benkwitt et al. 2019, Carreiro-Silva et al. 2012, Duda et al. 2020a, Flores La Valle et al. 2020, Fujita et al. 2014, Gagnon et al. 2013, Gagnon et al. 2015, Gagnon et al. 2016, Lapointe et al. 2011, Lisi et al. 2018, Olson et al. 2019, Papacostas and Freestone 2016, Rizzari et al. 2014, Saha et al. 2018, Sims et al. 2020, Springer and van Vliet 2014
MARINE FLORA	abundance, macroalgal growth or growth rate, size/size structure, photosynthesis, diversity (alpha, beta, gamma), non-native macroalgae, virus, heterotrophic bacteria, and phytoplankton abundance, viral turnover, rate, viral-induced mortality of bacteria, percentage of bacterial standing stock removed, photosynthetic yield, ETS activity, herbivory	Baum et al. 2016, Gagnon et al. 2015, Lisi et al. 2018, Payet et al. 2014, Rankin and Jones 2021, Reef et al. 2012, Reymond et al. 2011, Rizzari et al. 2014, Wedding et al. 2018
FLORA AND FAUNA NUTRIENTS	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, %C, %N; nucleic acid composition, %P, trace metals	Cox et al. 2013, Fujita et al. 2014, Gagnon et al. 2013, Honigh and Mahoney 2016, Lisi et al. 2018, Olson et al. 2019, Rankin and Jones 2021, Reef et al. 2012, Shatova et al. 2016, Shatova et al. 2016, Sims et al. 2020, Wisshak et al. 2010
TERRESTRIAL NUTRIENTS	$\delta^{15}\text{N}$, $\delta^{13}\text{C}$, %N, %P, guano deposition, C:N:P, C/N or C:N ratio, total P (TP) and bioavailable P (P-bio)	Balčiauskas et al. 2018, Barrett et al. 2005, Caut et al. 2012, Cipro et al. 2018, De La Pena-Lastra et al. 2020, Durrett et al. 2014, Favero-Longo et al. 2010, Hata et al. 2014, Hawke and Blark 2009, Hawke and Miskelly 2009, Jones 2010a, Jones 2010b, Kirch et al. 2015, Kolb et al. 2010, Lapointe et al. 2011, McFadden et al. 2016, McLoughlin et al. 2016, Michelutti et al. 2009, Michelutti et al. 2013, Mizota 2009, Nigro et al. 2017, Pisanu et al. 2010, Richardson et al. 2019, Thorensen et al. 2017, VanderWerf et al. 2014, Wardle et al. 2012, Wright et al. 2010, Young et al. 2009, Zhong et al. 2017, Zmudczyńska et al. 2012
WATER/SEAWATER NUTRIENTS	NO _x (nitrate + nitrite), urea, ammonia, dissolved inorganic nitrogen, PO ₄ ³⁻ (phosphate), stormwater nutrient pollution, chlorophyll-a concentration, ²¹⁰ Pb and ¹³⁷ Cs, polychlorinated biphenyls, $\delta^{18}\text{O}$, total alkalinity (TA), dissolved inorganic carbon (DIC), soluble reactive phosphorus, dissolved organic carbon released, bioactive metals, macronutrients, particulate organic matter, lateral nutrient distribution capacity, diffusion capacity, vertical movement of nutrients, nutrient flux	Cox et al. 2013, Doughty et al. 2015, Duda et al. 2020a, Honig and Fujita et al. 2014, Lapointe et al. 2011, Mahoney 2016, Morimoto et al. 2010, Michelutti et al. 2009, Michelutti et al. 2013, Payet et al. 2014, Rankin and Jones 2021, Reef et al. 2012, Shatova et al. 2017, Shatova et al. 2016, Shatova et al. 2017, Sims et al. 2020, Wisshak et al. 2010
ECOSYSTEM PROCESSES	microbioerosion, bioerosion, accretion, macroboring, grazing	Carreiro-Silva et al. 2012, Chazottes et al. 2017, Wisshak et al. 2010
WATER CHARACTERISTICS	water depth, light intensity / photosynthetically active radiation / (PAR) / surface irradiance, water quality (total dissolved oxygen, total dissolved phosphorus, dissolved organic carbon, particulate nitrogen, particulate phosphorus, particulate organic carbon, chl a, and TSS), salinity, water temperature or sea surface temperature (SST), runoff, electrical conductivity, pH/alkalinity, wave movement (wave exposure), wave impact, wave action, wave power	Baum et al. 2016, Blanco et al. 2010, Dale et al. 2017, Duda et al. 2020a, Flores La Valle et al. 2020, Fujita et al. 2014, Gagnon et al. 2015, Kolb et al. 2010, Lisi et al. 2018, McFadden et al. 2016, Morimoto et al. 2010, Rankin and Jones 2021, Reymond et al. 2011, Saha et al. 2018, Sims et al. 2020, Wisshak et al. 2010, Wedding et al. 2018

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