



# Harnessing island–ocean connections to maximize marine benefits of island conservation

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Islands support unique plants, animals, and human societies found nowhere else on the Earth. Local and global stressors threaten the persistence of island ecosystems, with invasive species being among the most damaging, yet solvable, stressors. While the threat of invasive terrestrial mammals on island flora and fauna is well recognized, recent studies have begun to illustrate their extended and destructive impacts on adjacent marine environments. Eradication of invasive mammals and restoration of native biota are promising tools to address both island and ocean management goals. The magnitude of the marine benefits of island restoration, however, is unlikely to be consistent across the globe. We propose a list of six environmental characteristics most likely to affect the strength of land–sea linkages: precipitation, elevation, vegetation cover, soil hydrology, oceanographic productivity, and wave energy. Global databases allow for the calculation of comparable metrics describing each environmental character across islands. Such metrics can be used today to evaluate relative potential for coupled land–sea conservation efforts and, with sustained investment in monitoring on land and sea, can be used in the future to refine science-based planning tools for integrated land–sea management. As conservation practitioners work to address the effects of climate change, ocean stressors, and biodiversity crises, it is essential that we maximize returns from our management investments. Linking efforts on land, including eradication of island invasive mammals, with marine restoration and protection should offer multiplied benefits to achieve concurrent global conservation goals.

land–sea linkage | invasive mammals | island management

Historically, many human societies living along the coast understood and managed terrestrial and marine natural resources interdependently. This management approach, known as a ridge-to-reef model in the tropics (1), presupposes that the workings of land ecosystems are linked inextricably with those of adjacent marine ecosystems. Patterns of resource use and management on land, the model holds, have direct connections with neighboring marine communities. As such, in traditional knowledge, resource use, and management measures are considered holistically, balancing the interacting demands on terrestrial and marine ecosystems.

In contrast, many modern institutions devoted to environmental management are siloed, building structures that separate consideration of land and sea. Management, use

policies, and conservation actions on land are largely unconnected from analogous efforts focused on nearby oceans (2, 3). Academic studies in the fields of ecology and conservation science are principally single-disciplinary, with a strong majority of general journals publishing overwhelmingly about terrestrial systems (4, 5). Funding agencies and foundations generally follow the model of separation of land and sea set up by academic, research, management, and conservation institutions, often focusing investments toward either marine or terrestrial research and management efforts. The failure to integrate perspectives from across the land–sea interface is limiting our ability to tackle the greatest problems of our time, impairing efforts to manage resources sustainably, protect biodiversity, adapt to a changing climate, and create more economically prosperous and resilient island and coastal communities (6).

An opportunity to overcome the challenges linked with modern siloing by habitat exists in science and conservation efforts focused on island ecosystems. Island ecosystems are particularly vulnerable to human-induced threats, and the ecological impacts of most of these threats are realized across each terrestrial and marine habitats. The threats

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introduced by invasive mammals offer no exception to the view that realized impacts to island ecosystems are linked from land to sea. While it is clearly known that invasive mammal management on islands can affect terrestrial landscapes, recent studies show that such management also can support coupled marine conservation efforts. In the tropical Indian Ocean, for example, a recent series of studies linked the density of seabirds on islands to the functioning of the adjacent coral reef community. Islands with high densities of seabirds were associated with faster growing reef fish populations, more foraging activity by these fishes, and increased rates of coral recovery after climate change impacts (7–9). Across the temperate Mercury Islands of New Zealand, the density of seabirds was positively related to the biodiversity of macroalgae in nearshore marine habitats (10). In each of these studies, the density of seabirds was defined largely by the current or historic presence of non-native, invasive predatory mammals. Further, the mechanism of land–sea connection is often tied to the flow of nutrients. Habitats with invasive mammals have depauperate populations of seabirds, land crabs, and other species linking land and sea, resulting in relatively low rates of nutrient input to the coupled island–marine ecosystem (11–13).

The crises of declining ocean health, biodiversity extinction, and climate change demand that we use the best available science, integrated across disciplines, to address impacts on island–ocean ecosystems (14) and to support the human communities that rely on these ecosystems. Thus, recognizing the current understanding of the mechanisms and generalities of land–sea connections and applying them to the management of island ecosystems is a priority for collaboration across the marine and terrestrial conservation and research fields. To that end, here we i) explore the historical context of integrated land–sea management on islands, ii) describe evidence of the role of invasive mammals on islands interrupting these linkages, iii) present six characteristics that principally mediate the strength of land–sea linkages, and iv) consider future research and management opportunities. Cross-disciplinary study of island–ocean ecosystems is essential to maximize the value of integrated management action toward restoring islands and oceans, benefiting both biodiversity and people.

## Building from a Legacy of Human Knowledge Linking Land and Sea

Traditional ecological knowledge of island–ocean connections and integrated management practices are well represented across numerous societies, past and present (15). Two key characteristics of this applied concept are that the unit of nature is often defined in terms of geographical boundaries (e.g., watersheds) and that abiotic components, fauna, flora, fungi, and humans within this unit are interdependent (16).

Island inhabitants often see the natural bounds of their resource limitations more readily than do those who live on continents given the more limited geographic borders of available land (17, 18). The close proximity of land and sea on islands contributed to the development of integrated forms of ecosystem-based management, with management zones corresponding to the ecology of the island landscape

and seascape (19). For example, the ancient Hawaiian watershed (*ahupua'a*) system encompassed entire valleys and stretched from the top of the mountains to the coast and shallow marine waters (19) (Fig. 1). It included a forested mountain zone, which functioned as a watershed conservation area protected by taboo (*kapu*), integrated farming zones in the upland and coastal areas, a fringe of trees along the coastline for storm and wind protection, and brackish and seawater fishponds (20). Variations of this type of integrated watershed management were present throughout the tropical Pacific, with examples including Yap (*tabinau*), Fiji (*vanua*), and the Solomon Islands (*puava*) (21–23). The common theme among integrated watershed management systems is the intimate association of a group of people with the land, lagoon, and reef, and all that grows on or within them (16). This ridge-to-reef stewardship was, and still is in some places, reflected in land tenure and management practices recognizing that upslope activities affect people and resources further down a watershed and into the ocean (24, 25).

Island ecosystems support unique biological and cultural diversity and are also highly vulnerable to natural and anthropogenic disturbances (26, 27). Because of the tight feedback between ecological and social systems on small islands, resource limitations become readily apparent, forcing people to rapidly adjust and adapt to environmental and climatic changes (18, 27). The frequency of catastrophic natural events (e.g., hurricane, tsunami, drought, flooding, lava flow) and human-induced disruptions of ecosystems (e.g., impacts triggered by invasive species) (28) resulted in the



**Fig. 1.** Example of *ahupua'a* in Hawai'i, a drawing by Marilyn Kahalewai, 1974. Reprinted with permission from Kamehameha Schools.

development of socioecological systems that anticipate environmental change (29) and plan for rapid recovery. Local-scale knowledge and observations of changes in weather, life history cycles, and ecological processes contributed to adaptive management at appropriate temporal scales among some island communities (25), with efforts targeting the relationship with the entire ecosystem, from land to sea. Indeed, considering how island communities have integrated ecological knowledge into community change serves as a catalyst for designing novel strategies for adapting to extreme challenges, such as the threats of climate change (30). Rich local knowledge and associated management practices (e.g., agroforestry, fisheries management) play key roles in building socioecological system resilience (17, 31).

**Unpacking Land–Sea Connections—The “Experiment” of Invasive Mammals on Islands.** Threats to biodiversity and human livelihoods are seen clearly on islands (14, 32), and the impacts of invasive species are among the biggest threats to achieving island management and conservation goals (33–35). Invasive species, especially mammals like rodents, cats, and goats, have devastated island ecosystems (36, 37), decimating and often eradicating untold populations of native and endemic species (38–41). The direct effects can be particularly profound on populations of seabirds, with rapid changes of seabird populations following introduction or removal of invasive mammalian predators (38, 42, 43). However, the impacts of invasive mammals extend beyond direct effects (e.g., predation, devegetation [denuding], trampling, digging) and include a broad collection of indirect effects (Fig. 2). For example, rodents directly alter plant community composition and invertebrate diversity and abundance through consumption (37, 44–49) which can be measured by their isotopic breadth in these environments (50). Following their invasion on seabird islands, rodents can transform soil chemistry indirectly by reducing populations of seabirds, which reduces the flow of labile nutrients (via seabird excretion) into the soil (51, 52). Indirect effects of invasive mammals on islands can also manifest as interaction chains, which include trophic cascades. For example, brown rats (*Rattus norvegicus*) in the Aleutian Islands impacted invertebrate communities indirectly by eliminating the birds that foraged in intertidal areas (13, 53). Related studies describe indirect impacts on communities and ecosystem properties through downstream feedback (34, 54). Invasive ungulates can drive population declines and extinctions of native animal species through changes in vegetation, such that the landscape can no longer sustain these native species (55, 56).

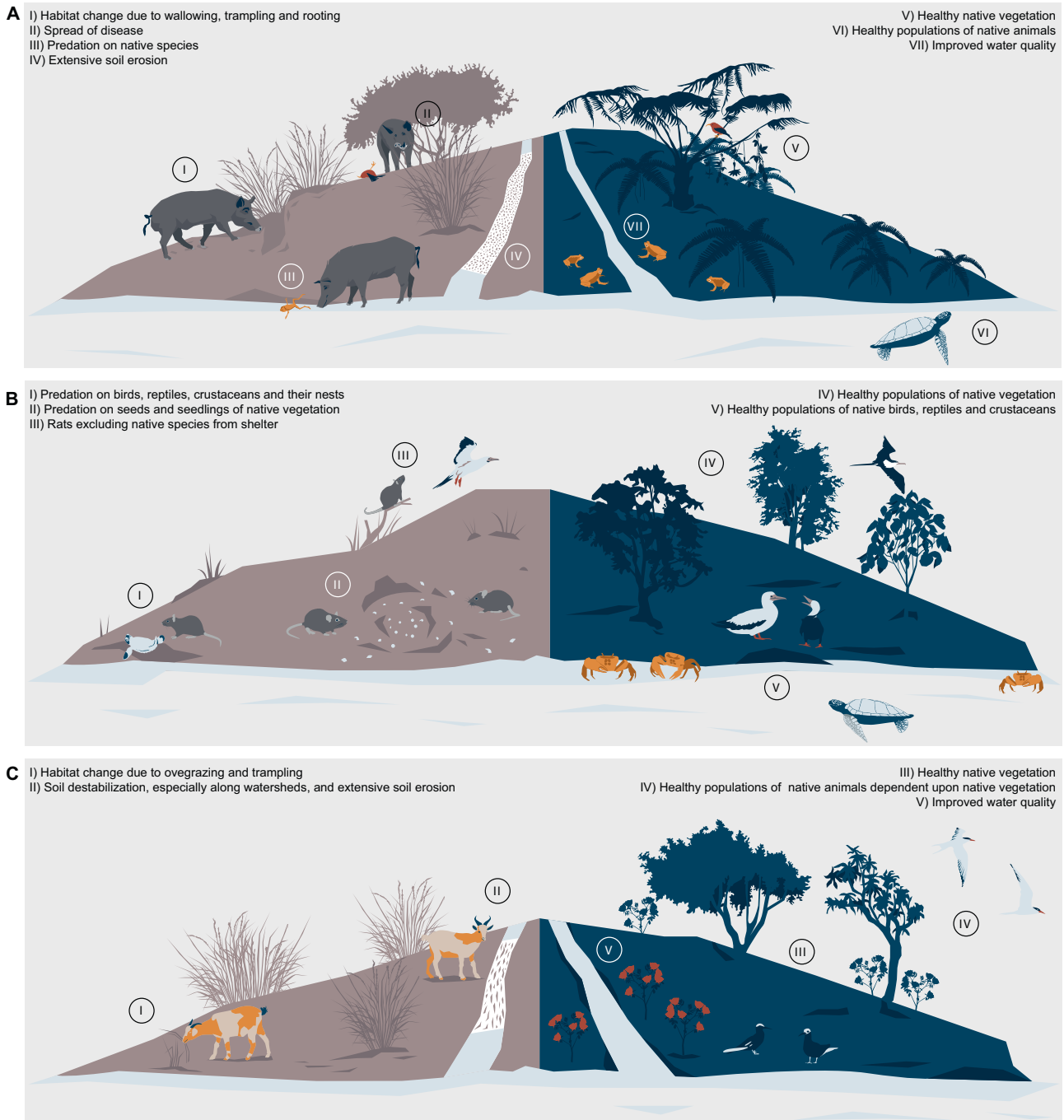
The myriad direct and indirect impacts of invasive mammals in the terrestrial island environment are increasingly well-studied. In contrast, how these impacts drive shifts in land–sea connections remains relatively understudied. Several of the indirect effects of invasive mammals involve native island fauna that have life stages spanning land and sea. Such taxa can be referred to as connector species. Seabirds, land crabs, sea turtles, sea snakes, and pinnipeds, for example, all have life cycles at the interface of marine and terrestrial systems. Many of these marine-dependent island species spend much of their lives at sea, assembling *en masse* when moving between biomes to complete circannual activities including breeding, overwintering, and molting. For

example, seabirds exhibit behavior and morphology adapted for exploiting marine resources and a reliance on islands for safe breeding and rearing habitat for their young. Island habitats are of particular importance to seabirds, as 98 of the 101 globally threatened seabird species breed on islands (57). Seabirds highlight the connectivity of islands to large oceans, serving as an ecological connection between marine and terrestrial ecosystems. At the extreme, the gray-headed albatross (*Thalassarche chrysostoma*) nests on small islands in the Southern Ocean, yet when foraging at sea, they regularly circle the globe (58).

When occupying terrestrial habitats, seabirds and other connector species transfer nutrients between land and sea. For most connector species, marine-derived nutrients are deposited on land through excrement, carcasses, eggs, and other reproductive materials, as well as feathers and molt (52, 59–63). Connector species disturb the soil via nest excavation, burrowing, and other physical activities, mixing nutrients into the soil and in some cases providing aeration (60, 64). Changes in soil nutrients and hydrogeology shape bacterial, fungal, and plant communities, promoting positive changes to invertebrate abundance and diversity, and eventually enhancing vertebrate communities (65, 66). The ecological benefits provided by connector species are not restricted to terrestrial biomes, but their activities can profoundly influence adjacent marine habitats. For example, terrestrial-derived nutrients are introduced to the sea when land crabs spawn (12). In addition, nutrient depositions on land can transfer to sea through precipitation runoff and other hydrologic connections, fertilizing the nearshore environment. A 27-fold difference in organic nitrogen in runoff waters was documented between islets with and without nesting seabirds on Palmyra Atoll in the central Pacific due to the prodigious excretion of these connector species (67).

**Generalizing the Effects of Land–Sea Connections.** The terrestrial biota of islands is just a fraction of the broader island ecosystem, and connections between land and sea are mediated by the interaction of biological processes and the island context. However, as we aim to generalize patterns of ecosystem connectivity between land and sea, we find challenges due to the wide diversity of island types. Islands vary in geology, oceanography, climate, and many other dimensions, each affecting the strength of functional connectivity between land and sea. We note that while elements of the biological system define some key elements of nutrient flow to the marine community (e.g., density of connector species like seabirds), the island context modulates the relative importance of this flow (e.g., in nutrient-poor marine ecosystems, the influx of seabird-derived nutrients will be particularly impactful).

Several studies have identified cases in which interventions on land have affected the ecological dynamics in the neighboring marine environment, yet outstanding questions remain. Can patterns of land–sea linkage be generalized across geographies? Are the observations telling of a ubiquitous ecological pattern, or are these data specific to the localities where the studies were conducted? We reviewed the literature with a goal to identify common environmental factors influencing the strength of land–sea connections. The studies spanned disciplines, including ecosystem studies,



**Fig. 2.** 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.

movement ecology, hydrology, geology, and other fields, with a subset integrating insights from multiple disciplines. Because of the singular value of insular ecosystems in simplifying process-based environmental studies (32), it was not surprising that most of these studies were conducted on islands. However, studies lacked consistency in methodology and were largely system-specific, with observations tailored to the particulars of the research system. As such, tools for meta-analysis or quantitative syntheses were impractical. Instead, we summarized here the state-of-knowledge based

upon expert-guided review and synthesis (68). Some common themes emerge from the literature, which highlight environmental conditions that disproportionately affect the strength of land-sea connections (69). We explore these within the context of potential changes in land-sea linkages likely to be associated with island conservation efforts.

The degree of benefit that the marine environment receives from invasive mammal eradications and other island restoration efforts will depend upon certain factors, both biological and physical, that mediate the strength and pattern

of the land–sea connections. The responses of wildlife populations, especially of connector species, are among the dominant change linked with eradication efforts. However, an estimate of how such population changes may propagate into significant shifts in both land and sea functioning will be based upon the geographic properties of the island. We submit that the following geographic properties most strongly mediate the strength of land–sea linkages: i) precipitation ii) elevation, iii) vegetation cover, iv) soil hydrology, v) oceanographic productivity, and vi) wave energy (Fig. 3).

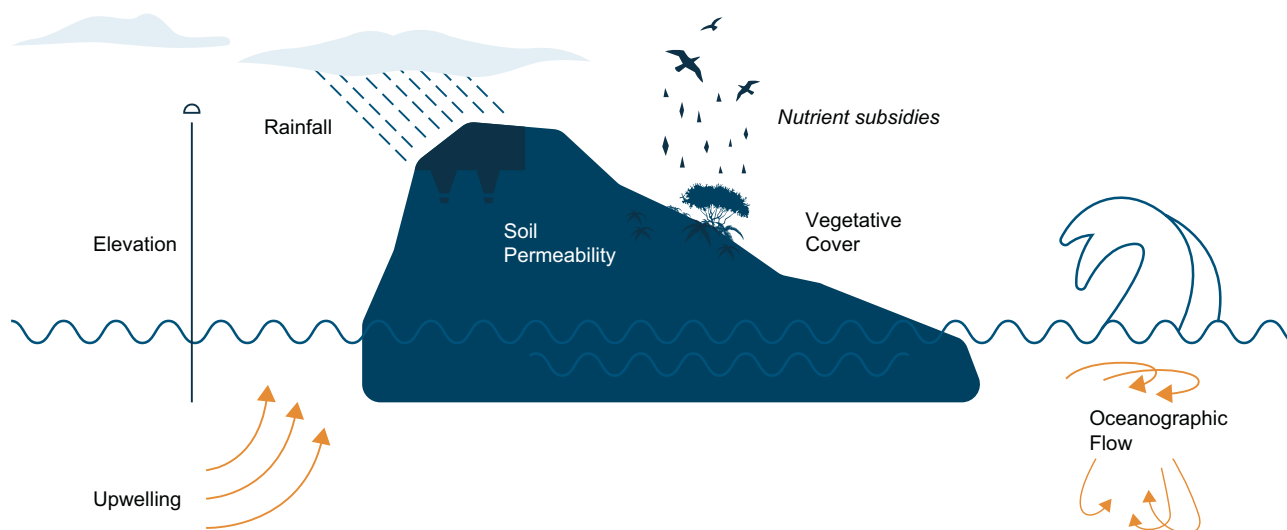
**Precipitation.** Rainfall acts as the main “flushing” mechanism for land-to-sea connections. As a result, differences in precipitation across island types will drastically change an island's connectivity with its local marine ecosystem. Given that a major form of functional connection between terrestrial and marine communities is through exchange of bioavailable nutrients that travel in surface waters, understanding watershed dynamics helps clarify expectations of land–sea linkages. All other factors held equal, increasing precipitation will increase the strength of connection between land and sea (70, 71). Further, we expect the pattern of precipitation to modulate the linkage, with more pulsed precipitation producing 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 fully capture the quantitative specifics of the hydrological system, as other island characteristics, including elevation, vegetation cover, and soil hydrology, modulate the pattern and rate of flow from land to sea (70).

**Elevation.** The flow of water from land to sea is linked to geology, including specifics of the island's elevational topography. 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 general trends we explore for the purpose of this review. Most applicable is the contrast between low-lying, high-permeability islands with a freshwater lens versus high-elevation hard rock islands

with high runoff and basal aquifers (72, 73). The distinction is especially topical as it gives a general guide delineating which island types will experience high land–sea linkage versus those with low linkage. High elevation islands can be expected to experience rapid land–sea linkage under high rainfall conditions, due to the more extensive and often steeper slopes forcing the majority of precipitation into surface runoff. Conversely, we expect low-lying islands 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 or freshwater lens.

**Vegetation cover.** Plant community composition differs dramatically across islands, ranging from sandy atolls devoid of vegetation, to shrub- and grass-dominated islands, to varied forest types of temperate and wet tropical islands worldwide. Further, the composition of vegetation along the coast can influence the flow of nutrients and sediments from land to sea (e.g., mangrove, wetlands). The structure of the plant community has multiple effects on the movement of water from land to sea. Plant community composition can impede or facilitate the population recovery of connector species to numbers sufficient to drive nutrient flows. Plants can increase net surface evaporation, and thus the latent heat flux from soils via transpiration and canopy evaporation (74, 75). 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, structurally complex plant communities such as forests access different water sources depending on the root structures of the plant community (76). Due to the higher water demand of complex plant communities, soil moisture content often is found to be higher in grasslands than woodlands (77–79). As such, one may expect an increase in groundwater and drop in surface runoff as a function of increasing vegetation cover and complexity.

**Soil hydrology.** Islands vary substantially in their soil characteristics, with diverse microbial compositions and ranging from thick, rich, and humic to thin, porous, and



**Fig. 3.** Geographic factors that have been shown to influence the strength of land–sea linkages. Factors are largely linked to the rate of water flow from land to sea as well as the nutrient context of the nearshore marine environment. Note that these factors play a particularly strong role in mediating the impact of nutrient subsidies, much introduced from allochthonous origin through connector species (e.g., seabird excretion), to members of the coastal ecosystem.

sandy. In general, thicker layers of soil with higher biological content tend to retain water for longer periods of time, thus reducing water flow from land to sea. While relative permeability of soil is a primary factor determining the magnitude of land–sea connections, the complexities of the soil ecosystem further affect the types of nutrients and other materials that can flow from land to sea. Soil permeability buffers the influence of rainfall through its effects on water retention and evapotranspiration (80, 81). Soil permeability also provides an independent vector of land–sea connectivity via submarine groundwater discharge, which introduces a distinct source of dissolved nitrogen, phosphate, and silicate to nearshore ocean waters (81–83). The soil ecosystem can modify nutrient concentrations and profiles through geological and biological mechanisms, ultimately modifying the extent of land–sea linkages.

**Oceanographic productivity.** Marine habitats experiencing significant amounts of upwelling have reliably higher nutrient concentrations and higher marine productivity. Marine environments with naturally high nutrient concentrations are more resistant to alterations in terrestrial nutrient input volume, given that these systems are already highly productive. Allochthonous input will only have strong effects if the resource being transported is scarce in the recipient ecosystem (63, 84, 85). For example, corals benefit from nutrient input with accelerated growth rates in highly oligotrophic environments, but not in eutrophic conditions (86). However, nutrient-enriched systems can still be sensitive to some alterations in nutrient stoichiometry; 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 (87).

**Wave energy.** 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 terrestrial input to the marine ecosystem, decreasing the strength of land–sea connectivity (9, 10, 88). However, features of an island's geomorphology can introduce complexities to patterns of oceanographic flow. For example, lagoonal habitats (created by barrier islands or reefs enclosing nearshore marine waters) are shallower, more enclosed areas that tend to experience lower dilution rates relative to the surrounding ocean. As such, lagoonal habitats are especially sensitive to terrestrial input of any kind, as terrestrial runoff and submarine groundwater discharge tend to pool in lagoons and remain concentrated for extended periods of time (89, 90). Features that reduce water exchange with open ocean waters tend to increase potential for strong land–sea linkages.

**Applying Ridge-to-Reef Understanding to Maximize Cobenefits of Island Interventions.** Since islands and adjacent marine habitats are connected, the removal of terrestrial invasive mammals can affect the sea. Therefore, where one or more mediating properties favor land–sea linkages, invasive mammal eradication, biosecurity to prevent reinvasion, and restoration of native flora and fauna on islands can be important nature-based tools

to benefit adjacent marine environments. Eradications remove direct threats to island–marine ecosystems and have indirect benefits via restoration of connector species that can lead to positive impacts on marine habitats, especially where mediating factors align to create strong land–sea connections. Yet not all islands offer the same opportunity for marine conservation through their land–sea linkages. Where marine conservation is among the primary drivers of management action, invasive mammal management plans may be prioritized on islands where not only the direct effects to terrestrial threatened species are high, but also where strong land–sea connections are expected to result in maximized marine cobenefits.

As we summarize our understanding of mediating properties associated with strong land–sea connections, challenges remain in operationalizing this understanding for conservation planning. To begin with, geographic comparisons of ecological expectations depend upon collection and review of geographically consistent data. The growing collection of global environmental databases provides consistent information that can be leveraged to provide quantitative estimates of informative geographic characteristics of islands across the world. While such databases provide the raw information necessary to create cross-comparable views of geographic contexts, summarizing such data to align with specific applications (such as summarizing data at the scale of an island or its nearshore waters) depends upon consistent methods of data processing. We provide information in the *SI Appendix* describing a robust approach for estimating the relative value of each mediating property for islands worldwide using globally comprehensive and publicly available databases.

Collating data on the relative values of likely properties that mediate the strength of land–sea connectivity is a critical first step, but converting such data into actionable information is not straightforward. The mechanisms of land–sea connectivity are nonindependent, yet each metric often reports distinct information (e.g., with one metric consistent with high connectivity and another consistent with low connectivity; *SI Appendix*). As such, interpreting the net effects of multiple mediating factors should be conducted with caution; whether mediating factors act independently or interactively will dramatically affect emergent patterns of land–sea connectivity for a particular set of geographic conditions. Instead, more holistic approaches of interpretation may offer insights into potential marine effects linked with island restoration efforts. Transparent presentation of geographical context, especially in comparison with other islands, provides information to complement other knowledge bases linked with decision-making that is critical to time- and cost-intensive conservation interventions like island restoration.

Our synthesis of how invasive mammal eradication efforts can influence marine conservation through land–sea connectivity is built upon an integration of disparate data sources, with only limited data available from case studies of successful island restoration efforts themselves. We thus can view our understanding as a set of hypotheses that can be tested quantitatively. Currently, when resources for monitoring efforts are available, most invasive mammal island restoration efforts are complemented with

monitoring efforts that document changes in the terrestrial island ecosystem. A unique opportunity exists to coordinate monitoring around restoration efforts, including systematic data collection from the land and the sea. As consistent collections of data describing both land and sea emerge, the importance of the mediating factors presented here can be tested. As systematic data on land and sea build further, the proposed metrics describing important factors mediating the strength of land–sea connectivity can be modified to increase predictive power, with the potential to reveal new mediating factors or perhaps novel combinations of factors that hold particular significance (e.g., through interactive effects). Presenting the state of understanding regarding factors known to maximize the strength of land–sea connectivity is in no way the terminus of scientific contribution to conservation action, but instead, given sustained investment in monitoring and coordination across restoration projects, this effort is a step in the iterative path of applied science informing critical conservation action.

Island restoration projects around the world, especially of those islands with the geographic contexts that create stronger island–marine connections, present opportunities for benefiting ecosystems above and below the waterline. Marine management today is dominated by calls for spatial management, with many advocates targeting a goal to protect 30% of the world's oceans by the year 2030. As community members, leaders, and funders invest precious financial and social capital into achieving local marine protection goals, there is pressing motivation to document realistic benefits from protection. Coupling marine protection and island restoration actions may present an additional opportunity to present more visible and immediate benefits, such as expanded ecotourism and increased resiliency to storms, that may further galvanize communities to continue to protect and restore their island–ocean ecosystems. On islands where land–sea connections are predicted to be stronger, measures to restore island ecosystems may be a notably compelling addition to a marine management and conservation portfolio. Ant Atoll in Pohnpei State of the Federated States of Micronesia, for example, sees high rainfall along with other conditions consistent with high land–sea connectivity (*SI Appendix, Table S1*). Given insights gained through this geographic contextualization, the traditional leader (*Rohsa*) and community members vested in strengthening marine conservation around the atoll may desire to further evaluate elimination of invasive mammal stressors and restoration of seabird populations as an opportunity to benefit coral reefs and other marine habitats in tandem with ocean protection efforts. The application of knowledge regarding land–sea connectivity to resource management in Pohnpei State has strong precedent, as evidenced by a campaign to migrate riverside cultivation of an important shrub (*sakau*; *Piper methysticum*) from high- to low-elevation areas to minimize sediment flow to adjacent marine habitats (24).

In any management prospectus, there will be many criteria that drive the prioritization of focal geographies, including goals of terrestrial biodiversity restoration, climate change mitigation, and local socioeconomic viability. However, in many island systems and island communities,

much value can be placed on the potential for marine cobenefits. Our review adds valuable insights to inform expectations for associated marine conservation benefits across island contexts and geographies. With consideration of these island characteristics and further assessment, conservation investments can be made with more foresight of likely benefits, and island constituents can embark on conservation efforts with informed expectations of outcomes (e.g., linked with stronger or far-reaching marine cobenefits in some cases, and more modest marine cobenefits in others). Notably, many opportunities exist to expand our knowledge of the ecological complexities of island–ocean connectivity. The frameworks of adaptive management and evidence-based conservation provide valuable guides for applying the best available knowledge as informed hypotheses to advise decision-makers to advance integrated island and ocean conservation today, while promoting research to refine management recommendations into the future (91–93).

**Pathways to Improve Application of Holistic Ecosystem Restoration of Islands.** Our understanding of land–sea connections across the globe spans multiple knowledge systems, including long-standing human knowledge from island communities through diverse perspectives from ecological and environmental sciences. However, our knowledge is limited by a lack of coordinated learning across geographies and fields. Large collections of data from both past and future restoration efforts need to be shared and integrated to explore generalities (and differences) in patterns of cross-ecosystem linkages. While conservation practitioners should use the knowledge in hand today, we also need a broader set of data covering various biogeographical and geomorphological settings of land–sea connections to better analyze the impact of invasive mammal eradications on island–marine restoration. With the growth of a coordinated and accessible set of quantitative observations, island and ocean managers will be better able to direct efforts to maximize their impacts for both terrestrial and marine conservation gains. Eradications of mammals on islands have (and will) benefit marine environments, but without standardized monitoring of the island–ocean ecosystem around these interventions, we will neither fully understand the benefits achieved nor be able to refine the management tools to maximize conservation impacts.

The urgent conservation needs of islands and oceans prompts 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 terrestrial and marine data, and conservation practitioners carrying out invasive mammal eradication projects and associated restoration actions. Through collaborative learning, we can expand the use of management and conservation tools to realize both terrestrial and marine benefits. For generations, human societies managed islands in an integrated manner. For this generation and beyond, we can apply related insights through coordinated action and learning toward the ultimate goal of effective and impactful island and marine system stewardship.

**Data, Materials, and Software Availability.** All study data are included in the article and/or SI Appendix.

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1. S. M. Fitzpatrick, C. M. Giovas, Tropical islands of the anthropocene: Deep histories of anthropogenic terrestrial-marine entanglement in the Pacific and Caribbean. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2022209118 (2021).
2. J. Waterhouse, J. Brodie, S. Lewis, D.-M. Audas, Land-sea connectivity, ecohydrology and holistic management of the Great Barrier Reef and its catchments: Time for a change. *Ecohydrol. Hydrobiol.* **16**, 45–57 (2016).
3. B. I. Ruttenberg, E. F. Granek, Bridging the marine-terrestrial disconnect to improve marine coastal zone science and management. *Mar. Ecol. Prog. Ser.* **434**, 203–212 (2011).
4. B. A. Menge *et al.*, Terrestrial ecologists ignore aquatic literature: Asymmetry in citation breadth in ecological publications and implications for generality and progress in ecology. *J. Exp. Mar. Biol. Ecol.* **377**, 93–100 (2009).
5. M. Di Marco *et al.*, Changing trends and persisting biases in three decades of conservation science. *Glob. Ecol. Conserv.* **10**, 32–42 (2017).
6. J. G. Álvarez-Romero *et al.*, Integrated land-sea conservation planning: The missing links. *Annu. Rev. Ecol. Syst.* **42**, 381–409 (2011).
7. C. E. Benkwitt, S. K. Wilson, N. A. Graham, Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. *Global Change Biol.* **25**, 2619–2632 (2019).
8. N. A. Graham *et al.*, Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* **559**, 250–253 (2018).
9. C. E. Benkwitt, B. M. Taylor, M. G. Meekan, N. A. Graham, Natural nutrient subsidies alter demographic rates in a functionally important coral-reef fish. *Sci. Rep.* **11**, 1–13 (2021).
10. L. L. Rankin, H. P. Jones, Nearshore ecosystems on seabird islands are potentially influenced by invasive predator eradications and environmental conditions: A case study at the Mercury Islands, New Zealand. *Mar. Ecol. Prog. Ser.* **661**, 83–96 (2021).
11. D. A. Croll, J. L. Maron, J. A. Estes, E. M. Danner, G. V. Byrd, Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**, 1959–1961 (2005).
12. A. Samaniego-Herrera, S. Boudjelas, G. Harper, J. Russell, "Assessing the critical role that land crabs play in tropical island rodent eradications and ecological restoration" in *Island Invasives: Scaling Up to Meet the Challenge*, C. R. Veitch, M. N. Clout, A. R. Martin, J. C. Russell, C. J. West, Eds. (IUCN, Gland, 2019), pp. 209–222.
13. C. M. Kurlle, D. A. Croll, B. R. Tershy, Introduced rats indirectly change marine rocky intertidal communities from algae-to invertebrate-dominated. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 3800–3804 (2008).
14. J. M. Fernández-Palacios *et al.*, Scientists' warning—The outstanding biodiversity of islands is in peril. *Global Ecol. Conserv.* **31**, e01847 (2021).
15. M. Gadgil, F. Berkes, Traditional resource management systems. *Resour. Manage. Optim.* **18**, 127–141 (1991).
16. F. Berkes, M. Kislalioglu, C. Folke, M. Gadgil, Minireviews: Exploring the basic ecological unit: Ecosystem-like concepts in traditional societies. *Ecosystems* **1**, 409–415 (1998).
17. S. D. Jupiter *et al.*, Opportunities and constraints for implementing integrated land-sea management on islands. *Environ. Conserv.* **44**, 254–266 (2017).
18. F. Berkes, Implementing ecosystem-based management: Evolution or revolution? *Fish Fish.* **13**, 465–476 (2012).
19. K. Y. Kaneshiro *et al.*, Hawai'i's mountain-to-sea ecosystems: Social-ecological microcosms for sustainability science and practice. *EcoHealth* **2**, 349–360 (2005).
20. B. A. Costa-Pierce, Aquaculture in ancient Hawaii. *Bioscience* **37**, 320–331 (1987).
21. S. Koshiba *et al.*, 2000 years of sustainable use of watersheds and coral reefs in Pacific Islands: A review for Palau. *Estuar. Coast. Shelf Sci.* **144**, 19–26 (2014).
22. K. Ruddle, E. Hviding, R. E. Johannes, Marine resources management in the context of customary tenure. *Mar. Resour. Econ.* **7**, 249–273 (1992).
23. J. T. Baines, "An integrated framework for interpreting sustainable development: Ecological principles and institutional arrangements for the sustainable development of natural and physical resources" in *Energy and the Ecological Economics of Sustainability*, J. Peet, Ed. (Island Press, Washington, D.C., 1989).
24. R. H. Richmond *et al.*, Watersheds and coral reefs: Conservation science, policy, and implementation. *Bioscience* **57**, 598–607 (2007).
25. H. L. McMillen *et al.*, Small islands, valuable insights: Systems of customary resource use and resilience to climate change in the Pacific. *Ecol. Soc.* **19**, 44 (2014).
26. J. Barnett, Dangerous climate change in the Pacific islands: Food production and food security. *Reg. Environ. Change* **11**, 229–237 (2011).
27. S. D. Jupiter *et al.*, Principles for integrated island management in the tropical Pacific. *Pac. Conserv. Biol.* **20**, 193–205 (2014).
28. N. J. Reo *et al.*, Invasive species, indigenous stewards, and vulnerability discourse. *Am. Indian Q.* **41**, 201–223 (2017).
29. K. B. Winter *et al.*, The *moku* system: Managing biocultural resources for abundance within social-ecological regions in Hawai'i. *Sustainability* **10**, 3554 (2018).
30. H. McMillen, T. Ticktin, H. K. Springer, The future is behind us: Traditional ecological knowledge and resilience over time on Hawai'i Island. *Reg. Environ. Change* **17**, 579–592 (2017).
31. C. Folke *et al.*, Resilience thinking: Integrating resilience, adaptability and transformability. *Ecol. Soc.* **15**, 20 (2010).
32. N. R. Graham, D. S. Gruner, J. Y. Lim, R. G. Gillespie, Island ecology and evolution: Challenges in the Anthropocene. *Environ. Conserv.* **44**, 323–335 (2017).
33. D. R. Spatz *et al.*, Globally threatened vertebrates on islands with invasive species. *Sci. Adv.* **3**, e1603080 (2017).
34. P. Pyšek *et al.*, Scientists' warning on invasive alien species. *Biol. Rev. Camb. Philos. Soc.* **95**, 1511–1534 (2020).
35. N. D. Holmes *et al.*, Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLoS One* **14**, e0212128 (2019).
36. J. C. Russell, J.-Y. Meyer, N. D. Holmes, S. Pagad, Invasive alien species on islands: Impacts, distribution, interactions and management. *Environ. Conserv.* **44**, 359–370 (2017).
37. D. R. Towns, I. A. Atkinson, C. H. Daugherty, Have the harmful effects of introduced rats on islands been exaggerated? *Biol. Invasions* **8**, 863–891 (2006).
38. P. J. Bellingham *et al.*, New Zealand island restoration: Seabirds, predators, and the importance of history. *N. Z. J. Ecol.* **34**, 115–136 (2010).
39. T. S. Doherty, A. S. Glen, D. G. Nimmo, E. G. Ritchie, C. R. Dickman, Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11261–11265 (2016).
40. E. E. McCreless *et al.*, Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nat. Commun.* **7**, 1–11 (2016).
41. H. P. Jones *et al.*, Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 4033–4038 (2016).
42. H. P. Jones, Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago. *Ecol. Appl.* **20**, 1204–1216 (2010).
43. H. P. Jones, Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.* **20**, 2075–2080 (2010).
44. C. P. Mulder *et al.*, Direct and indirect effects of rats: Does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biol. Invasions* **11**, 1671–1688 (2009).
45. J. J. St Clair, The impacts of invasive rodents on island invertebrates. *Biol. Conserv.* **144**, 68–81 (2011).
46. D. R. Towns *et al.*, Predation of seabirds by invasive rats: Multiple indirect consequences for invertebrate communities. *Oikos* **118**, 420–430 (2009).
47. G. A. Harper, N. Bunbury, Invasive rats on tropical islands: Their population biology and impacts on native species. *Glob. Ecol. Conserv.* **3**, 607–627 (2015).
48. A. B. Shiels, W. C. Pitt, R. T. Sugihara, G. W. Witmer, Biology and impacts of Pacific island invasive species. 11. *Rattus rattus*, the black rat (Rodentia: Muridae). *Pac. Sci.* **68**, 145–184 (2014).
49. F. Courchamp, J.-L. Chapuis, M. Pascal, Mammal invaders on islands: Impact, control and control impact. *Biol. Rev. Camb. Philos. Soc.* **78**, 347–383 (2003).
50. K. M. Nigro *et al.*, Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. *Restor. Ecol.* **25**, 1015–1025 (2017).
51. J. J. Thoresen *et al.*, Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecol. Appl.* **27**, 1190–1198 (2017).
52. T. Fukami *et al.*, Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* **9**, 1299–1307 (2006).
53. C. M. Kurlle *et al.*, Indirect effects of invasive rat removal result in recovery of island rocky intertidal community structure. *Sci. Rep.* **11**, 1–10 (2021).
54. J. Terborgh, J. A. Estes, Eds., *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (Island Press, Washington, DC, 2010).
55. N. H. Wehr, S. C. Hess, C. M. Litton, Biology and impacts of Pacific islands invasive species. 14. *Sus scrofa*, the feral pig (Artiodactyla: Suidae). *Pac. Sci.* **72**, 177–198 (2018).
56. M. W. Chynoweth, C. M. Litton, C. A. Lepczyk, S. C. Hess, S. Cordell, Biology and impacts of Pacific Island invasive species. 9. *Capra hircus*, the feral goat (Mammalia: Bovidae). *Pac. Sci.* **67**, 141–156 (2013).
57. D. R. Spatz *et al.*, The biogeography of globally threatened seabirds and island conservation opportunities. *Conserv. Biol.* **28**, 1282–1290 (2014).
58. J. P. Croxall, J. R. Silk, R. A. Phillips, V. Afanasyev, D. R. Briggs, Global circumnavigations: Tracking year-round ranges of nonbreeding albatrosses. *Science* **307**, 249–250 (2005).
59. C. Lowe *et al.*, Fijian sea krait behaviour relates to fine-scale environmental heterogeneity in old-growth coastal forest: The importance of integrated land-sea management for protecting amphibious animals. *Ecol. Evol.* **12**, e8817 (2022).
60. C. P. Mulder, S. N. Keall, Burrowing seabirds and reptiles: Impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia* **127**, 350–360 (2001).
61. S. S. Bouchard, K. A. Bjørndal, Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**, 2305–2313 (2000).
62. C. E. Doughty *et al.*, Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 868–873 (2016).
63. G. A. Polis, W. B. Anderson, R. D. Holt, Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* **28**, 289–316 (1997).
64. W. J. Bancroft, J. D. Roberts, M. J. Garkakis, Burrowing seabirds drive decreased diversity and structural complexity, and increased productivity in insular-vegetation communities. *Aust. J. Bot.* **53**, 231–241 (2005).
65. G. Signa, A. Mazzola, S. Vizzini, Seabird influence on ecological processes in coastal marine ecosystems: An overlooked role? A critical review. *Estuar. Coast. Shelf Sci.* **250**, 107164 (2021).
66. K. H. Orwin *et al.*, Burrowing seabird effects on invertebrate communities in soil and litter are dominated by ecosystem engineering rather than nutrient addition. *Oecologia* **180**, 217–230 (2016).
67. D. J. McCauley *et al.*, From wing to wing: The persistence of long ecological interaction chains in less-disturbed ecosystems. *Sci. Rep.* **2**, 1–5 (2012).



68. Y. Z. Foo, R. E. O'Dea, J. Koricheva, S. Nakagawa, M. Lagisz, A practical guide to question formation, systematic searching and study screening for literature reviews in ecology and evolution. *Methods Ecol. Evol.* **12**, 1705–1720 (2021).
69. P. Becker *et al.*, *Island Ocean Connections: Exploring Land-Sea Linkages in the Context of Invasive Mammal Management* (Island Conservation and Scripps Institution of Oceanography UC San Diego, 2021).
70. D. R. Stoddart, R. Walsh, Environmental variability and environmental extremes as factors in the islands ecosystem. *Atoll Res. Bull.* 1–71 (1992).
71. D. R. Stoddart, Ecology and morphology of recent coral reefs. *Biol. Rev.* **44**, 433–498 (1969).
72. N. Robins, A review of small island hydrogeology: Progress (and setbacks) during the recent past. *Q. J. Eng. Geol. Hydrogeol.* **46**, 157–165 (2013).
73. A. Falkland, Hydrology and water management on small tropical islands in *Proc. Symp. Hydrology of Warm Humid Regions*, J. S. Gladwell, Ed. (International Association of Hydrological Sciences, 1993), pp. 263–303.
74. Y. Sud *et al.*, Biogeophysical consequences of a tropical deforestation scenario: A GCM simulation study. *J. Clim.* **9**, 3225–3247 (1996).
75. T. Osborne, D. Lawrence, J. Slingo, A. Challinor, T. Wheeler, Influence of vegetation on the local climate and hydrology in the tropics: Sensitivity to soil parameters. *Clim. Dyn.* **23**, 45–61 (2004).
76. Y. Fan, G. Miguez-Macho, E. G. Jobbágy, R. B. Jackson, C. Otero-Casal, Hydrologic regulation of plant rooting depth. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 10572–10577 (2017).
77. E. Krull, D. Sachse, I. Mügler, A. Thiele, G. Gleixner, Compound-specific  $\delta^{13}C$  and  $\delta^2H$  analyses of plant and soil organic matter: A preliminary assessment of the effects of vegetation change on ecosystem hydrology. *Soil Biol. Biochem.* **38**, 3211–3221 (2006).
78. T. E. Dawson, J. R. Ehleringer, "Plants, isotopes and water use: A catchment-scale perspective" in *Isotope Tracers in Catchment Hydrology* (Elsevier, 1998), pp. 165–202.
79. A. Midwood, T. Boutton, S. R. Archer, S. Watts, Water use by woody plants on contrasting soils in a savanna parkland: Assessment with  $\delta^2H$  and  $\delta^{18}O$ . *Plant Soil* **205**, 13–24 (1998).
80. F. F. La Valle, F. I. Thomas, C. E. Nelson, Macroalgal biomass, growth rates, and diversity are influenced by submarine groundwater discharge and local hydrodynamics in tropical reefs. *Mar. Ecol. Prog. Ser.* **621**, 51–67 (2019).
81. N. J. Silbiger, M. J. Donahue, K. Lubarsky, Submarine groundwater discharge alters coral reef ecosystem metabolism. *Proc. R. Soc. B-Biol. Sci.* **287**, 20202743 (2020).
82. T. Ji *et al.*, Nutrient inputs to a Lagoon through submarine groundwater discharge: The case of Laoye Lagoon, Hainan, China. *J. Mar. Syst.* **111**, 253–262 (2013).
83. S. Santoni *et al.*, Strontium isotopes as tracers of water-rocks interactions, mixing processes and residence time indicator of groundwater within the granite-carbonate coastal aquifer of Bonifacio (Corsica, France). *Sci. Total Environ.* **573**, 233–246 (2016).
84. A. L. Subaluskay, D. M. Post, Context dependency of animal resource subsidies. *Biol. Rev. Camb. Philos. Soc.* **94**, 517–538 (2019).
85. L. B. Marczak, R. M. Thompson, J. S. Richardson, Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* **88**, 140–148 (2007).
86. M. A. Gil, Unity through nonlinearity: A unimodal coral–nutrient interaction. *Ecology* **94**, 1871–1877 (2013).
87. P. S. Kumar *et al.*, Blooming of *Gonyaulax polygramma* along the southeastern Arabian Sea: Influence of upwelling dynamics and anthropogenic activities. *Mar. Pollut. Bull.* **151**, 110817 (2020).
88. G. S. Kolb, L. Jerling, P. A. Hambäck, The impact of cormorants on plant–arthropod food webs on their nesting islands. *Ecosystems* **13**, 353–366 (2010).
89. J. Brodie, E. Wolanski, S. Lewis, Z. Bainbridge, An assessment of residence times of land-sourced contaminants in the Great Barrier Reef lagoon and the implications for management and reef recovery. *Mar. Pollut. Bull.* **65**, 267–279 (2012).
90. K. Fujita *et al.*, Distribution of large benthic foraminifers around a populated reef island: Fongafale Island, Funafuti Atoll, Tuvalu. *Mar. Micropaleontol.* **113**, 1–9 (2014).
91. L. Gillson, H. Biggs, I. P. Smit, M. Virah-Sawmy, K. Rogers, Finding common ground between adaptive management and evidence-based approaches to biodiversity conservation. *Trends Ecol. Evol.* **34**, 31–44 (2019).
92. W. J. Sutherland, A. S. Pullin, P. M. Dolman, T. M. Knight, The need for evidence-based conservation. *Trends Ecol. Evol.* **19**, 305–308 (2004).
93. M. A. McCarthy, H. P. Possingham, Active adaptive management for conservation. *Conserv. Biol.* **21**, 956–963 (2007).