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The Mediating Factors of land Sea Connectivity on Islands

Author
Becker, Ceiba Belenos

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The Mediating Factors of Land-Sea Connectivity on Islands

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by

Ceiba Becker

Committee in charge:

Professor Stuart Sandin, Chair

Professor Andrew Barton

Professor Jennifer Smith

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Table of Contents

List of Figures

List of Tables

ABSTRACT OF THE THESIS

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Ceiba Becker

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Abstract

Are island ecosystems connected to their nearshore marine environment? Islands are global biodiversity hotspots and the management of their natural resources is vital to the maintenance of global biodiversity and the survival of Earth's life support systems. However, both research and management have been slow to incorporate the importance of land-sea connections into their practice. Terrestrial and marine habitats are inextricably connected; incorporating the connections between the two to any

research or management of these systems will improve efficacy by improving the resolution of our understanding of ecosystem drivers. If we are to incorporate land-sea connectivity into research and management, we first need to clarify our understanding of the patterns and variability of connectivity across geographic and biological contexts. The focus of this paper is to identify the factors mediating the ecological connection between land and sea on islands, which can be interpreted to determine the local importance of land-sea connectivity and identify candidate mechanisms defining the connectivity. With more detailed understanding of land-sea linkages, there is opportunity to apply this knowledge toward applied issues of island resource management and restoration. Using a practical case study of island restoration, we operationalize our proposed factors mediating the strength of land-sea connectivity to compare a set of islands targeted for restoration efforts, creating a prioritization based upon the island-specific estimated potential for improved land-sea connectivity and associated marine co-benefit of terrestrial management.

Introduction

Land-sea connectivity on islands is defined by multiple ecosystem factors, including the biology and ecology of species living on islands and the specifics of the physical environment of the land and sea. For example, erosion is a driving force behind land-sea connectivity on islands, forcing both organic and inorganic materials into nearshore environments. Furthermore, an island's geological structure, as well as its location, alters the local oceanographic patterns that can either concentrate or dilute any terrestrially derived materials. The diversity of factors influencing land-sea connections creates a complex perspective of cross-ecosystem connectivity, challenging the current philosophical isolation of terrestrial and marine habitats on islands.

While land-sea connectivity is largely driven by environmental factors, the most immediately relevant source of cross ecosystem connectivity comes from "connector species" which are fauna generally living in one ecosystem but using a neighboring ecosystem to hunt or to forage. These species are connectors in that they actively transport materials from one ecosystem to another, oftentimes in very large quantities. In the last few years, studies have started focusing on a perspective that links land and sea ecosystems; such studies have focused largely on seabirds, and their marine impacts on near-shore environments such as littoral zones and coral reefs (Kolb 2010, Graham & Benkwitt 2021, McCauley et al. 2012). For example, Kolb et al. 2010 found that seabirds were a significant source of nutrients to nearshore littoral communities in the Baltic Sea. Gagnon (2013, 2015) continued to explore land-sea connection while adding ecological context and finding that cormorants could in fact have both bottom-up and top-down effects on benthic communities through nutrient subsidy and selective predation. Further, in several geographically distinct locations across the tropics, studies on marine islands have found similarly significant impacts of seabirds with coral reefs. These pioneering land-sea studies have found that seabirds cannot only increase the resilience of the reef by increasing the biomass of functionally important coral reef fish, particularly herbivorous parrotfish, and calcifying algae, but the excretion of these seabirds can provide nutrients for the corals themselves to assimilate, increasing coral growth rates therein (Graham et al. 2021, Savage 2019).

While a handful of studies continue to investigate mechanisms of land-sea connectivity *in situ*, they serve to highlight the conceptual divide between land and sea studies in the ecological sciences. Researchers and managers working on land or sea ecosystems often conduct their work in 'silos', focusing principally on their single ecosystem. Such professional 'siloing' serves to compartmentalize the way we approach natural resources, thus simplifying our management of each. However, the potential ecological implications of land-sea connectivity are not functionally independent, and our understanding of integrated island ecosystems requires integrated investigation. Here we suggest that there is unique value in incorporating land-sea connectivity in our consideration as a means to improve efficacy and efficiency of natural resource management and research on islands. Land-sea connectivity is complicated, and to truly understand the extent to which islands impact their nearshore environments we need more focused attention on the state of knowledge of integrated land-sea linkages. Here we review the currently available literature to flesh out those factors most relevant to determining the level of land-sea connectivity on a given island. We hope this thesis may serve as an initial steppingstone encouraging further studies as well as the incorporation of land-sea linkage into management practices on islands where connectivity is clearly strong. Efficiently conserving island ecosystems is key to preserving global biodiversity as well as reaching humanity's goals for a sustainable future (De Wit et al. 2020).

The goal of this thesis is to lay the groundwork for mitigating the philosophical divide in the current paradigm of marine and terrestrial science with a hypothesis on the main globally relevant environmental factors mediating the strength of the land-sea connection on a given island. This thesis is organized into two core processes: an expert guided literature review of the currently available literature to determine themes of connectivity and operationalizing these themes into actionable metrics to be used in a global analysis land-sea connectivity on a suite of marine islands. The islands used in this analysis were suggested by our NGO partner Island Conservation as potential targets for terrestrial eradication. This provided us with an additional opportunity: to use the mediating factors to establish the strength of the land-sea connection on each island, allowing us to prioritize these conservation targets by their potential for the nearshore marine ecosystem to co-benefit from terrestrial eradication.

I. Exploring the State of Knowledge for Land-Sea Connectivity

To bridge the gap between land and sea, we conducted a coordinated review of the disparate literature on all the potential mechanisms connecting the two. In total, we reviewed and added roughly 500 peer reviewed papers to our final select literature database. The results of this study are the product of a collaborative effort between academic institutions, the Center for Marine Biodiversity and Conservation, and the NGO Island Conservation to establish the state of the science on the potential for terrestrial eradications to impact an island's nearshore marine environment. While biological aspects of land-sea linkages were explored as part of the greater literature review, here we focus on the physical and environmental aspects of these connections, as they are key globally relevant mediators of land-sea connectivity on islands.

Once all the relevant literature had been reviewed a draft describing the findings for each focused section was prepared, which were then compiled before undergoing a lengthy consultation period. During this period, our findings were reviewed by all those involved in the project. The process of this coordinated review followed the advised expert guided review outlined in Foo et al. (2021). While many relevant studies were conducted on islands, we also included mechanism-specific studies conducted on continents.

In recent years several studies have linked the impacts of eradications to the resilience of their nearshore environments and have begun exploring the mechanisms of these cross-system linkages *in situ*. However, no study has reviewed all possible linkages from land to sea on islands across island types to date. Here we reviewed the currently available literature describing the potential mechanisms connecting the terrestrial environment to its nearshore marine habitat. Based on this review, we identified four main themes determining land-sea connectivity on islands: island hydrology, terrestrial vegetation, oceanographic context, and anthropogenic impacts as being the main themes.

I. Island Hydrology

Precipitation 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 influence on its local marine ecosystem. Increasing precipitation will inevitably increase an island's land-sea connectivity, however, the relative increase in connectivity will be dependent on a variety of physical factors. Here, we parse out what determines the difference in the impact of increased precipitation between islands. We suggest that as average precipitation increases, its direct and indirect impact on the local marine environment can be summarized as a function of the island’s geomorphology and thus, its hydrology. Specifically, the island’s perimeter:area ratio, spatial distribution of soil permeability, presence of an aquifer or lens, and the island’s total evapotranspiration. Given the published literature indicating the key typology of island hydrology to be dependent on elevation and geology, we will focus on these main guiding factors in our breakdown of the impact of island hydrology on land-sea connectivity.

(i) Perimeter: Area Ratios

The perimeter:area ratio of islands is a measurement with several applications due to its nature as a ratio independent of island size (Feder 1988). Polis & Hurd 1995 & 1996 found it to be an effective proxy for the relationship between terrestrial productivity and marine input on an island. This is due to the mathematical scaling of coastlines being linear while island area scales as a squared function, leading small islands to have more coastline per unit area and thus more marine input per unit area via beach wrack. The perimeter:area (P:A) ratio of an island describes the sea-land flux of that island as the terrestrial productive capacity of the island (area) in relation to the size of the channel through which it interacts with the ocean (perimeter) (Polis & Hurd 1995, Polis & Hurd 1996). According to the P:A ratio as a proxy for terrestrial productivity to marine input, land-sea connectivity should scale up proportionally with island size. However, cross-system linkage species such as seabirds may disrupt the scaling of this relationship by increasing connectivity regardless of coastline restrictions. Additionally, Polis & Hurd studied islands in the Gulf of California which are among the driest ecosystems in North America in terms of annual rainfall (Polis & Hurd 1995, Polis & Hurd 1996). This may have contributed to unusually low lower bounds for land-sea connectivity.

(ii) Soil Permeability

Soil permeability across islands is largely dependent on the basic geology of the island in addition to the island's maximum and average elevations; however, as a general rule, less permeable soils result in a greater percentage of precipitation becoming runoff and thus increasing land-sea connectivity (Falkland 1993, Robins 2013). Island hydrogeology is highly 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 purposes of this paper. Most applicable here 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, Robbins 2013). This distinction is especially applicable for this paper as it gives a general guide delineating which island types will experience high land-sea connectivity in time and space versus those with low connectivity as precipitation is increased. High elevation, low permeability islands can be expected to experience increases in land-sea connectivity under high rainfall conditions, due to the low permeability rock and high elevation forcing most of the precipitation into surface runoff. Conversely, low-lying, high permeability islands are generally expected to experience less of an increase in connectivity with increased precipitation due to a greater percentage of the precipitation being held in the aquifer/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 or perched aquifers. Additionally, the perimeter: area ratio is a measure of the hydrological flux of an island, as precipitation is a function of area but can only cross into the sea via the perimeter of an island. Smaller, shorter islands such as low-lying atolls are expected to have a less significant increase in land-sea connectivity following increases in precipitation when compared to larger, taller islands with all other factors held constant.

(iii) Subterranean Groundwater

The spatial distribution of soil permeability is not only a buffer on the effect of rainfall through its effects on water retention and evapotranspiration (Falkland 1993, Robins 2013), but also exists as an independent vector of land-sea connectivity via submarine groundwater discharge (SGD) (Silbiger et al. 2020, La Valle et al. 2019). SGD has been shown to influence the temperature, pH, nutrient concentrations, and total alkalinity (TA) of nearshore marine environments and can be traced using Ra isotope activity (Bishop et al. 2017, Paytan et al. 2006, Blanco et al. 2011, Silbiger et al. 2021, La Valle et al. 2019). The increased residence time of subterranean groundwater (SG) allows for more water-rock interactions to occur, distinguishing it from surface runoff. Phosphate is relatively highly reactive and thus tends to sorb to aquifer materials, causing SGD to have decreased concentrations of phosphate (Bishop et al. 2017). The hydrolysis of silicate materials is directly linked to the intensity of water-rock interactions. While it is a slow process, concentrations of both SiO_3 and 13C are known to increase gradually with groundwater residence time (Santoni 2016).

Both nitrification, the conversion of ammonia to nitrate by bacteria, as well as denitrification, the conversion of nitrate to nitrogen gas by bacteria, occur in SG. Ultimately, studies show SGD to be a significant source of dissolved nitrogen in the form of NH_4, NO_3, and NO_2- as well as PO_4^{3-} and SiO_3^- (Silbiger et al. 2020, Santoni 2016, Ji et al. 2013). In a study on Hainan Island, Ji et al. 2013 found the average concentrations of dissolved inorganic nitrogen (DIN), PO_4^{3-} and SiO_3^- for surface runoff to be 15.6, 5.7, and 8.1, respectively, finding contrarily the average concentrations of DIN, PO_4^{3-} and SiO_3^- for groundwater to be 218, 12, and 171, respectively. Relative to surface runoff, SGD may be more concentrated in DIN and silicate with lower concentrations of phosphate.

In addition to nutrients, SGD can have significant effects on pH, TA/DIC, and net ecosystem calcification and productivity (NEC/NEP) therein. Many studies have found SGD to contribute to increases in pCO_2 and decreases in pH (Wang et al. 2014); however, Silbiger et al. 2020 point out the importance of the context of the near-shore marine environment when considering effects on pH. Depending on the maximum values and range of net ecosystem productivity, inputs of low pH and high CO_2 may actually feed productivity and bring an increase in pH. Most important to consider when considering the effects of SGD on DIC, pH, and TA is the relative TA of the nearshore environment to that of the SGD. Total alkalinity represents the buffering capacity of seawater, and thus the greater the TA of the nearshore environment, the more resilient it is to perturbations of pH by high CO_2 SGD. Cyronak et al. 2013 found SGD to be a significant source of TA into Muri lagoon in the Cook Islands and claimed SGD had the potential to be 6 times higher than oceanic TA. Impacts of SGD on TA are highly variable by island type and depend mainly on the geology of the island as well as the TA and ecosystem conditions of the local nearshore environment.

II. Terrestrial Vegetation

We know the terrestrial biome not only impacts the nearshore marine ecosystem directly but also acts as a mediating factor on the significance of land-sea connectivity. We hypothesize this effect to be primarily dependent on island vegetation cover and complexity. The main pathways of mediation on land-sea connectivity by terrestrial biology include stabilization of sediments, translation of surface runoff to groundwater, diversification of terrestrial nutrient input, increased evapotranspiration and latent heat fraction therein, in addition to decreased total water contribution.

(i) Impacts of Terrestrial Vegetation on Hydrology

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 surface sediment destabilization and lead to increased suspended sediments in surface runoff. While many species of vertebrates contribute to the 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 (Dunkell et al. 2011). Less stable streambanks contribute to increased suspended sediments in stream water, and consequently in nearshore marine habitats such as coral reefs and kelp forests (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.

Plant community composition differs drastically across islands, ranging from a sandy atoll void of any vegetation, to the barren shrub and grass-dominated Tristan de Cunha, to the jungle of tropical high islands worldwide. This diverse array of communities has distinguishable effects on the movement of water from land to sea. Plant communities have been shown to increase surface evaporation, and thus the latent heat flux from soils via transpiration and canopy evaporation (Osbourne et al. 2004, Sud et al. 1996). This helps cool the surface temperature while increasing moisture convergence. Independent of the potential effects on moisture convergence and its influence on precipitation, this increase in evapotranspiration translates to a decrease in the total flux of water from land to sea. Additionally, more complex plant communities, such as forests, have been shown to preferentially access different water sources depending on the root structure of the plant community. Several studies have found that due to the higher demand of these more 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). We predict that an increase in groundwater and drop in surface runoff can be expected as a function of vegetation cover and complexity, for islands where surface runoff is relevant. 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). Both of the previous mechanisms increase as a function of vegetation cover and complexity. However, the small topographic gradient and high permeability of many low-lying atolls make surface runoff irrelevant, thus increasing vegetation simply decreases groundwater recharge (Werner et al. 2017, White et al. 2002, White et al. 2010). In fact, transpiration dominates total evapotranspiration on many low-lying atolls (White et al. 2002, White et al. 2010). Essentially, low-lying atolls may have soils with high runoff potential, but they also often have a high percentage of their area covered by vegetation which sucks up the groundwater, forcing the fresh groundwater lens into a state of constant recharge and leaving little extra water for runoff.

(ii) Impacts of Terrestrial Vegetation on Nutrient Profiles

While plant communities may differ greatly between islands, the presence of even the most basic plant community can be expected to diversify nutrient profiles entering the nearshore marine environment in the form of direct litterfall, dissolved organic matter (DOM), and particulate organic matter (POM) (Delong & Brusven 1994, Peterson et al. 2003). Litterfall is the direct effect of weathering on vegetation resulting in dead plant mass, such as leaves reaching the ground. Litterfall increases with plant community complexity: herbaceous habitats have very low litterfall, while deciduous tree habitats are amongst the highest (Delong & Brusven 1994). On the other end of the size spectrum are contributions of dissolved organic matter. DOM consists of organic forms of carbon, nitrogen, sulfur, and phosphorus, generally smaller than 0.7μm.

Plants may also 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). Plant cycling and nutrient leaching work in opposite directions and are dependent on local environmental parameters (i.e. local limiting or abundant nutrients). Plant cycling is the process of nutrients being brought above ground into vegetation before being recycled as litter, creating shallower nutrient pools with concentrations decreasing with soil depth. Contrarily, leaching creates the opposite nutrient profile with nutrients gradually being removed from soil by root systems above the maximum rooting depth, below which nutrients are concentrated due to their positioning outside the reach of plant roots. 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. In a global analysis of soil nitrogen patterns, Post et al. 1985 concluded that nitrogen and C:N ratios were mainly dependent on Holdridge life zone. Holdridge life zones are defined by biotemperature, precipitation, and the potential evapotranspiration/precipitation ratio (Post et al. 1982). To summarize, there are three main zones of distinct nutrient cycling processes. The first, wet tropical, can be classified by large amounts of soil nitrogen associated with recalcitrant humic materials in an advanced state of decay, and low C:N ratios. The second, temperate, can be classified by moderate carbon & nitrogen storage and variable C:N ratios. Lastly, wet tundra is characterized by high carbon & nitrogen storage with high C:N ratios. Holdridge life zones are still applicable and in use today

(Jungkunst et al. 2021), thus, we suggest their application in contextualizing the impact of different island plant communities on the diversification of terrestrial input to the marine environment. The diverse array of plant communities between islands globally can be expected to diversify and increase the terrestrial nutrient input to the nearshore environment via DOM and litterfall as a function of vegetation cover, complexity, and Holdridge life zone.

(iii) Oceanographic Context

(i) Oceanography

The oceanographic conditions of an island can have a significant impact on the level of land-sea linkage experienced by the local marine environment. Coastal oceanography defines the abiotic parameters of the marine environment and thus the local ecosystem existing within it. This can also influence the level of land-sea connectivity present on an island either positively or negatively. High wave impact can dilute any terrestrial input to the marine ecosystem, decreasing local land-sea connectivity (Kolb et al. 2010, Benkwitt et al. 2021). Although indirectly, upwelling can have a similarly negative effect on the land-sea connectivity by increasing the productivity of the marine system to the point of terrestrial influence becoming comparatively negligible. Contrarily, lagoonal habitats may have the opposite effect on connectivity by facilitating the pooling of terrestrial runoff and subterranean groundwater, leading to increased nutrient concentrations and a positive effect on land-sea connectivity (Fujita et al. 2014). Therefore, oceanography has the potential for diverse effects on land-sea connectivity, all of which are modulated by bathymetry.

Several attempts have been made to model the hydrological relationship between terrestrial runoff and local oceanography that ultimately determines the degree to which coastal marine ecosystems are impacted by watershed discharge (Cogle et al. 2006, Paris-Cherubin 2008, Mckergow et al. 2005). In the following section we synthesize the findings of current literature for the purpose of hypothesizing oceanographic conditions under which strong land-sea connectivity may be expected.

In marine habitats that favor upwelling, we see reliably higher nutrient concentrations and higher marine productivity as a result of the upwelling nutrient-dense 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). In a study on coral growth, Gill et al. 2017 found that corals are likely to benefit from nutrient input in highly oligotrophic environments, while the opposite is true for corals in high 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 creates the perfect storm by perfecting nutrient ratios for algal blooms as seen off the southwest coast of India in 2016 (Kumar et al. 2020). Due to the eutrophic nature of upwelling regions, they are expected to be more resilient to input from terrestrial runoff on average. However, should the right limiting nutrients be introduced into the system, upwelling regions areas are also at higher risk of algal bloom.

Lagoonal habitats are shallower, more enclosed areas that tend to experience less water flow, higher temperatures, and higher temperature variability under normal conditions. For these reasons, 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. Using isotope analysis of macroalgal nitrogen on the low-lying Pacific Fongafale atoll, Fujita et al. 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. While development on Fongafale Island is concentrated on the lagoonal side of the atoll, these results point to the increased effects of terrestrial pollution in the lagoonal habitat, as opposed to the decreasing effects in the oceanic habitat. Water residence times of lagoons vary considerably with lagoon size but can be anywhere from a couple of days to months.

(ii) Nearshore Marine Ecosystems

There are several near-shore marine ecosystems that are highly linked to the terrestrial environment and thus deserve special attention when considering land-sea connectivity. In this section, we highlight key nearshore ecosystems particularly vulnerable to terrestrial impact, including coral reefs, mangroves, kelp forests, and seagrass beds.

Several studies have shown the positive impacts of terrestrial vertebrate eradications on coral reefs in populations of fish as well as sessile benthic organisms. However, these effects are dependent on the island's degree of land-sea connectivity as well as the local biomass of marine herbivore populations and cannot be assumed to hold true for all island types. For coral reefs with low herbivore populations, increased nutrient concentrations are likely to lead to macroalgal dominance and potential phase shifts as has been seen on many Caribbean coral reefs (Hughes 1994). However, Savage 2019 conducted a transplant experiment between highly similar reef sites inside MPAs to show the positive effect of seabird nutrient subsidies on coral growth rates. This study found some coral fragments of the species *Acropora formosa* to grow at rates of 15 cm/y when transplanted to seabird islands, amongst the highest recorded in the current literature. This demonstrates how significantly nutrient input can positively affect coral under the right environmental circumstances. Graham et al. 2018 studied 12 islands in the Chagos archipelago and found that seabird nutrient enrichment increased biomass of all functionally important coral reef fish with the greatest effect being on the most important functional group - herbivores. Thus, nutrient input has the potential not only to benefit keystone habitat-forming coral but can also help to facilitate an environment conducive to reef growth. In fact, one study found that seabird nutrient subsidies lead to higher cover of crustose coralline algae (CCA) and *Halimeda* following a bleaching event, two calcifying algae species that could contribute to increased reef resilience to bleaching (Benkwitt et al. 2019).

While each of the previous studies represent positive effects of nutrient subsidies from seabird colonies on coral reefs, it is important to note that each of these studies was conducted in highly pristine reef environments with high fish (particularly herbivore) biomass. On the other hand, Fabricius 2005 emphasizes the complexity of the relationship between terrestrial runoff and coral reef health, pointing to the potential for DIN to reduce calcification, reproduction, and increase the competitive dominance of algae (Fabricius 2005). Fabricius 2005 also points out that while corals have a capacity for heterotrophy, some can rely entirely on heterotrophy for short periods; high concentrations of POM favor true heterotrophs and alter the oligotrophic conditions in which corals are competitively dominant (Fabricius 2005). Overall, coral reefs are globally important nearshore ecosystems that need to be considered when planning terrestrial management as well as vice versa.

Mangroves represent key land-sea ecosystems that provide a number of ecosystem services, including some particularly applicable to land-sea connectivity, such as filtration of terrestrial pollutants, erosion control, and habitat for land-sea linkage species such as seabirds (Nagelkerken et al. 2008, McFadden et al. 2016, Mumby et al. 2004). The opposite effect is equally important, in that key land-sea linkage species can have strong positive effects on mangroves and their ecosystem services. McFadden et al. (2016) showed that seabirds nesting in mangroves contributed to significantly higher biologically important nutrients in mangrove soils as well as vegetation. This is a clear example of how nutrient enrichment from seabirds has the potential to increase mangrove growth rates, carbon sequestration, and mangrove ecosystem services. Mangroves provide habitat for both seabirds and fish communities, hence in some cases mangrove restoration also has the potential to effectively revive populations of both these cross-ecosystem species. In the Gujarat region of India, mangrove restoration has contributed roughly 500 million USD to the commercial fishing industry by providing nursery habitats for commercially relevant fish (Das 2017). Keller et al. (2017) analyzed the importance of mangrove ecosystems as buffers of anthropogenic pollution of a nearby landfill to the marine environment, specifically to a marine protected area. In their field survey, all samples containing high heavy metal concentrations representing pollution were found on the side neighboring the landfill, while none were found on the marine region of the mangroves. This indicates that the mangroves appeared to effectively filter out the anthropogenic pollutants, preventing them from degrading the local MPA. Mangroves provide a number of cross-ecosystem services, all of which may benefit from healthy seabird populations.

Seagrass beds are a unique form of land-sea connectivity, as they represent the only true marine plant. However, they are also unique in their provision of ecosystem services, including carbon sequestration, nutrient retention and recycling, ecosystem engineering, and support of coral reef productivity and biodiversity (Campagne et al., 2015, Cullen-Unsworth et al., 2014, Nordlund et al., 2016). Seagrass beds also provide food sources to the terrestrial environment in the form of living tissue to some coastal vertebrates, sea wrack, as well as by supporting terrestrial invertebrate biomass (Heck Jr. et al. 2008). Thus, where present in nearshore habitats, seagrass beds are an important consideration for terrestrial and marine management. Seagrass beds can be particularly susceptible to terrestrial input, with numerous studies showing the negative effects of increased siltation, sediment runoff, and organic matter concentrations to be amongst the greatest threats to seagrass habitats globally (Quiros, 2017, Bach et al., 1998, Mascaró et al., 2009, Orth et al. 2006). Quiros et al. (2017) identifies the importance of considering land use when setting up marine reserves by analyzing the covariance of seagrass bed variables with those of the MPA versus those of nearby land use. They found that the MPA had no effect on seagrass condition, while terrestrial protection had significant positive effects, and area of farmland and human development had the strongest negative effects.

Kelp forests represent vital nearshore biodiversity hotspots, as kelp are ecosystem engineers that provide habitat and a food source not only for commercially relevant fish species but for a wide array of fish and invertebrate species along temperate coasts globally. Since kelp must attach to the benthos via a holdfast while existing in the shallow photic zone, they are restricted to habitats directly adjacent to shorelines and are highly susceptible to terrestrial input via any mechanism. Several studies have shown the negative impacts of sedimentation on kelp communities, primarily due to increased light scattering by suspended sediments and decreased photosynthetically active radiation as a result (Aumack et al. 2007).

(iv) Anthropogenic Context

Humans are one of 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 presence of humans on an island generally translates to deforestation, urban development, agriculture, as well as pollution of many forms such as sewage, plastics, agricultural runoff, and heavy metals. As discussed earlier in this section, decreases in vegetation cover and complexity as well as in soil permeability all lead to increased surface runoff. While the presence of humans on islands has rarely translated to a positive impact on nearshore marine ecosystems, it can certainly be said that the presence of humans on islands increases land-sea connectivity. Thus, as we not only increase land-sea connectivity but create additional polluting forms of land-sea connectivity, it's only logical that we take land-sea connectivity into account as we study and manage our own natural resources. However, for the purposes of this study, we've excluded the anthropogenic mediation of land-sea connectivity due to its complexity and its ties to local culture and national development.

Operationalizing the Mediating Factors of Land-Sea Connectivity

After reviewing the current literature relevant to land-sea connectivity on islands, a few general themes emerged as globally important factors mediating land-sea connectivity on islands. Based on these themes, we suggest total precipitation, soil permeability, terrestrial vegetation cover and complexity, elevation, nearshore wave energy, and nearshore nutrient concentrations to be the most critical globally relevant mediating factors of connectivity. When these mediating factors align, they create the perfect physical and environmental conditions for strong land-sea linkage and thus healthy marine ecosystems. To further investigate the validity of our mediating factors of connectivity, we conducted a prioritization exercise to determine which island environments currently house strong land-sea connections and thus potential for marine co-benefit. In our attempt to qualitatively analyze these mediating factors of connectivity to predict the level of land-sea connectivity across a range of island types, we simplified each of our mediating factors of connectivity into a single metric. This involved not only determining the most relevant and quantifiable metric for each factor, but also ensuring that there was minimal overlap between metrics. All of these mediating factors of connectivity are interconnected and related in some form, and in order to qualitatively analyze their associations, it’s key that each metric contains maximal distinct information.

To complete this task, we gathered the best data available for each of the factors. Most of the data used for this analysis is satellite data and thus is simply extracted from the relevant database. Once we acquired the data, we organized data for each mediating factor into 7 categorical ordinal groups. This grouping style allowed us to more readily compare the land-sea linkage on each island, using these linkage values to create a final land-sea linkage score by summing the categorical ordinal value in each mediating factor for each island. The ordinal nature of each mediating factor is dependent on its impact on land-sea connectivity. More precipitation means more linkage between the two ecosystems, and thus islands with greater precipitation receive a higher linkage value for their precipitation cell. This process follows for each mediating factor and is explained in greater detail below.

I. Metrics Defining the Strength of Land-Sea Connectivity

(i) Precipitation

Total annual precipitation is the most important first order metric for defining the impact of precipitation on an island's land-sea linkage. Given our assumption of precipitation acting as a flushing mechanism, the total annual precipitation gives us an idea of exactly how much flushing is happening. While incorporating the annual number of rainy days or the maximum versus average precipitation may have fine-tuned our metric to better capture the amount of runoff caused by precipitation, we chose to stick with the total precipitation to better capture the flushing effect in its totality. Additionally, total precipitation has been used in several other ecological studies as a climate metric (Weigelt & Kreft 2013). For the purposes of this qualitative analysis, we used a 30year average annual total precipitation value for each island.

The precipitation data were collected from Worldclim version 2.1 (Fick and Hijmans 2017), a global database of historical climate data. The data from Worldclim are derived from the MODIS satellite system with a spatial interpolation for missing data. Data used here were the 30 s interval precipitation per pixel averaged by year, and we calculated a mean annual precipitation value for each pixel from 1970-2000. Then, for each island, all pixels that created the least convex polygon of the coastline were selected, and a mean of pixels was reported in units of mm y^{-1}. To determine ordinal linkage values for our precipitation data, we created seven categories evenly distributed across the range of precipitation values observed. The highest values of precipitation were given the highest category score.

(ii) Soil Hydrology

To define the impact of soil types on land-sea connectivity we focused on the impact of distinct soil types on island hydrology. Due to our assumption that precipitation acts as the main flushing mechanism connecting land and sea, the relative importance of soil types is in their potential to saturate and create surface runoff. For the purpose of this analysis, the soil hydrology dataset from Ross et al. 2018 is a perfect fit. Their dataset includes globally consistent data for runoff potential based on soil texture, bedrock depth, and groundwater at 250m spatial resolution.

Soil hydrology data was accessed manually from the Global Hydrologic Soil Groups (HYSOGs250m) for Curve Number-Based Runoff Modeling on NASA's EarthData site, via the Spatial data access tool (SDAT). This is a global map including pixels for all land masses corresponding to the hydrologic soil groupings distinguished in Ross et al. 2018. In their study of the soils of the world, they grouped the world's soils into four hydrologic groupings to simplify determining runoff potential. However, they also included an additional 3 groupings that are relevant only to wet soils with relatively full water tables. These additional 3 groupings are defined with a "/" to signify the moisture level dependence of these soils. Essentially, for an "A/D" soil, the soil hydrology will represent group A when it is well drained but will be more representative of group D when the water table is full. Soils with less infiltration and high runoff are expected to have a positive impact on land sea linkage, thus from strongest to weakest linkage value, the soils were ranked as follows: Group D, Group D/A, Group C, Group C/A, Group B, Group B/A, and Group A.

(iii) Vegetation Cover

For the purposes of this project, we used a simple single ecosystem approach for estimating the impacts of ecosystem type on land-sea connectivity. Given the overlap between Holdridge life zone and our precipitation metric, we simplified the metric for the impact of the terrestrial biome to the spatially dominant ecosystem type on each island. Data describing vegetation cover were collected from the Esri Global Ecosystem Explorer layer (Hall 2020). The Global Ecosystem Explorer provides a range of ecosystem information and is unique among ecosystem data layers in providing consistent data across land features of all sizes (including small islands, which are often omitted in other data layers). Vegetation data for an island are reported as the most common cover type across the island area. While many islands have heterogeneous vegetation landscapes, the most common vegetation type serves as a parsimonious description of the integrated island area without introducing unfounded assumptions that would be required to average effects across multiple vegetation types.

Vegetation cover differs from the other 5 mediating factors in that defining and ordering the impact of each ecosystem is less dependent on the variation within our dataset, and more dependent on the current understanding of the influences of vegetation on hydrology and nutrient fluxes. In essence, the denser the vegetation the greater its complication of land-sea connectivity. We know from our meta-analysis of the mediating factors that grasslands hold more water than woodlands, forests with greater leaf area decrease the percentage of precipitation reaching the ground, and that tree roots allow more water into the soil allowing for less runoff (Midwood et al. 1998, Dawson and Ehleringer (1998), Krull et al. 2006, Osbourne et al. 2006, Werner et al. 2017, White et al. 2002). Thus, we ordered the ecosystems in order of greatest to least connectivity: desert, temperate grassland, savanna, Mediterranean scrub, tropical dry forest, temperate deciduous forest, and tropical moist forest.

(iv) Elevation

For the purpose of this study, we've selected maximum elevation as our metric for the impact of elevation on land-sea connectivity. The impact of elevation on land-sea connectivity is dependent on many other geomorphologic variables unique to the island such as the distribution of impermeable soils, island area and thus its slope, as well as orographic effects and heterogeneity of island topography. However, given the positive correlation between elevation, precipitation, and runoff, we assumed that maximum elevation would capture the impact of elevation on land-sea linkage without being too complex or overlapping with our other metrics for the mediating factors (Garcia-Martino et al. 1996).

Elevation data were collected from Esri elevation layers. Esri elevation data are a synthesis of multiple elevation datasets that are optimized to create a consistent elevation profile across the globe (Wilson 2018). The elevation layer was standardized with a resolution of 24 m in the digital elevation model, given that this was the finest resolution available across all 44 restoration target islands. The maximum elevation of the land within the island's coastline was reported here in units of meters. Several studies have found logarithmic functions to describe the relationship between precipitation and elevation, which would support the use of log-transformed bins in defining the impacts of elevation on runoff and thus land-sea linkage (Vicuna et al. 2011). Given the non-linear effects of elevation on island hydrology, ordinal linkage values were based upon a logarithmic spacing of values, distributed across the range of maximum elevation values observed. The highest values of elevation were given the highest category score.

(v) Chlorophyll Data

For the purposes of this study, chlorophyll-a is used as a proxy for the impact of oceanographic productivity on land-sea connectivity. Nearshore nutrient concentrations provide the context for the relative importance of any nutrient input from an island to its nearshore environment (Subalusky et al. 2018). The impact of allochthonous input to the local marine ecosystem will be relative to the local nutrient concentrations. Islands with higher average nearshore nutrient concentrations will need more allochthonous nutrients for a measurable ecological effect to occur. Chlorophyll acts as a proxy for phytoplankton biomass in nearshore waters, which we assume to be dependent on local nutrient levels and fluxes. While this is a complicated relationship, and nutrient pulses resulting from runoff often force phytoplankton communities from nitrogen limitation to phosphorus limitation, its generally assumed to be true that increased nutrient concentrations will result in some level of increased algal biomass (Hoyer et al. 2002, Meng et al. 2022, Ringuet & Mackenzie 2005, Zheng et al. 2007). Given that nutrient concentrations are the main drivers for variance in chlorophyll-a concentrations, we utilized satellite data on nearshore chlorophyll-a concentrations as a proxy for nearshore nutrient concentrations.

Oceanographic productivity was estimated using a common proxy of concentration of chlorophyll *a* pigments in the shallow, nearshore waters, reported in the units of mg m^{-3}. Chlorophyll *a* concentration is estimated from spectral data from the MODIS-AQUA satellite, covering the global oceans. Because of challenges associated with reflectance from terrestrial and benthic habitats, spectral data were used only within a buffer area seaward of, but not including, pixels covering the 60-m isobath or shallower, following published methods (Gove et al. 2013). Given the non-linear effects of nutrient availability on marine processes, ordinal linkage values were based upon a logarithmic spacing of values, distributed across the range of oceanographic productivity values observed. The lowest values of oceanographic productivity were given the highest category score.

(vi) Wave Data

The oceanographic context of any given island is likely to be a complex combination of surface currents, coastal waves, tidal effects, wind speed and direction, and finally oceanographic current flows. However, if theoretically, a natural resource manager had to decide which island to put a sewage pipe on, it might be said that between the local oceanography of, for example, Escudo de Veraguas in the Western Caribbean and Gough Island in the South Atlantic, the decision would be obvious. The ocean around Gough simply has more energy than Isla Escudo de Veraguas, and thus provides an example of an island on which we'd expect nearshore nutrient input of any kind to have a short residence time in the nearshore environment. While it may be an oversimplification, we included wave energy as a metric to account for differences in the signal from a calm lagoonal habitat to an open ocean island such as Gough. Additionally, wave energy has been used as an ecological metric for dispersal of allochthonous nutrients in similar studies of land-sea connectivity (Kolb et al. 2010, Brocke et al. 2015). The most important driver of connectivity here is the allochthonous nutrients' residence time in the nearshore environment, and as such would be the ideal metric of the oceanographic context for land-sea connectivity on a given island. However, given the array of *in situ* measurements as well as the potential for complications created by the heterogeneities of island coastlines, we've simplified the metric to the islands total wave energy.

Wave energy was estimated based upon a synthesis of products from NOAA's WaveWatch 3 global wave model. Island-specific products were extracted from a 0.5 degree grid cell that contained the island's areal centroid. Information on estimated wave height, period, and direction were combined to create an integrated estimate of annual mean wave energy following published methods (Gove et al., 2013) reported in the units of kW m^{-1}. To determine ordinal linkage values for our wave energy, we created seven categories evenly distributed across the range of values observed. The lowest values of wave energy were given the highest category score.

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II. Global Comparison of the Mediating Factors across Islands

(i) Target Island Table

The table below is a result of our efforts and in its totality displays summary data on the mediating factors of connectivity for 45 islands. The initial purpose of this table was to use the mediating factors to establish the strength of the land-sea connection on each island. Once the strength of the connection between terrestrial and marine ecosystems has been established on each island, we can share this information with our partners to contribute to the prioritization of limited resources for maximal conservation benefit.

In order to simplify conceptualizing land-sea linkage on islands, we created a "linkage score" for each island. Visible in the last column, the score is simply a sum of each island's respective score for each of the mediating factors of connectivity. Thus, each island's value for a given factor can be grouped into one of 7 ordinal categories, where 7 is the highest land-sea linkage and 1 is the lowest.

Table 1: Metrics describing the values of defined factors mediating the strength of land-sea connectivity. Data are collected for 45 islands that are targets for eradication and terrestrial restoration efforts from management colleagues. Columns are the mediating factors and rows are individual islands. The color shading indicates ordinal binning based on hypothesized impact on land-sea connectivity, defined the in table key at the bottom.

Site	Precipitation ($mm\ yr^{-1}$)	Hydrologic Group	Vegetation	Elevation (m)	Oceanographic Chl-a (mg m-3)	Wave Energy ($kW\ m^{-1}$)	Linkage Value
Floreana	455	D	G	568	0.04	16.6	33
Rock Islands	3575	D	A	210	0.02	7.8	32
Marquesas	1650	D	A	1252	0.01	16.7	31
Kaho'olawe	1092	C	E	452	0.02	14.6	31
Gough	3207	C	F	908	0.06	81.8	31
Ulong	3424	D	A	82	0.06	7.8	30
Ant	4443	C	A	26	0.02	13.5	29
Chagos	2570	D	A	33	0.01	22.1	29
Coiba	2746	C	A	423	0.04	13.7	29
Aldabra	984	C	G	17	0.02	15.5	29
Aleipata	3207	C	A	209	0.02	20.8	29
Sonsorol	2957	D	A	18	0.02	10.1	29
Ulithi	2536	D	C	20	0.02	16.6	29
Late	2142	C	A	489	0.02	22.2	28
Ailinginae	1962	D	A	20	0.01	18.1	28
Rongerik	1936	D	A	20	0.01	20.7	28
Apolima	3155	C	A	143	0.02	15.8	28
Jemo	1969	D	A	18	0.01	20.1	28
Maria	731	D	B	708	0.16	20.9	28
Niulakita	3081	D	A	23	0.02	22.0	28
Erikub	2673	D	A	25	0.02	19.3	28
Mercury Islands	1580	C	B	235	0.15	11.9	27
Ata	1899	C	A	279	0.01	25.0	27
Naamonuito	3089	C	A	24	0.00	17.7	27
Mona	1028	C	C	90	0.01	7.5	27
Tahanea	1574	D	A	18	0.02	14.6	27
Alejandro Selkirk	1011	C	B	1355	0.02	58.1	26
Isla Escudo de Veraqua	2801	C	A	50	0.12	7.4	26
Pitcairn	1466	C	A	334	0.01	48.0	26
Reitoru	1565	D	A	15	0.01	27.1	26
Savana	1046	C	C	81	0.04	6.5	26
Bokak	1439	D	A	7	0.01	26.3	26
Tetiaroa	1845	D	A	24	0.02	20.0	26
Kamaka	1669	D	A	170	0.05	41.7	26
Lobos de Afuera	24	C	G	42	0.79	22.2	25
Enderbury	968	D	A	9	0.00	17.0	25
Lobos de Tierra	16	C	G	73	0.90	19.9	25
Socorro	355	A	C	1040	0.01	25.3	24
San Jose	908	C	E	9	0.51	4.5	24
Niau	1620	C	A	19	0.02	15.1	24
Chincha Norte	23	C	G	34	1.88	24.6	24
Henderson	1400	C	A	40	0.01	46.2	24
Malden	706	D	A	10	0.02	24.5	24
Kanton	655	D	A	7	0.02	17.2	24
San Felix	216	C	B	180	0.03	46.5	23
Amsterdam	1269	A	F	998	0.04	98.4	22

Relative_strength_	Precipitation ($mm\ yr^{-1}$)	Hydrologic Group	Vegetation	Elevation (m)	Nearshore Nutrients ($\mu mol\ L^{-1}$)	Wave Energy ($kW\ m^{-1}$)	Linkage Value
7	>3814	Group D	G- Desert	>525	0- 0.011	0.0 - 15.0	15-16
6	3181-3814	Group C/D	F - Temperate Grass	220 - 525	0.012- 0.031	15.1 - 30.0	17-18
5	2548-3181	Group C	E - Savannas	92 - 220	0.032- 0.087	30.1 - 45.0	19-20
4	1915-2548	Group B/D	D - Mediterannean S	39 - 92	0.088 - 0.242	45.1 - 60.0	21-22
3	1282-1915	Group B	C - Tropical Dry For	16 - 39	0.243 - 0.674	60.1 - 75.0	23-24
2	649-1282	Group A/D	B - Temperate Decic	7 - 16	0.675 - 1.880	75.1 - 90.0	25-26
1	0-649	Group A	A - Tropical Moist F	<7	>1.881	>90.1	≥27

The table consists of a high range of island types, with a significant representative diversity present for each mediating factor. What stands out immediately is the lack of a consistent source of strong linkage across the islands and their factors. Islands with the highest linkage scores are all a mix of factors with some, but not all, indicating high connectivity. Surprisingly, not all of the mediating factors have to align with strong linkage values in order for an islands terrestrial-marine connection to be significant.

In the islands with the highest connectivity scores, each island has an exceptionally strong linkage outlier for at least one column. For example, The Marquesas Islets have relatively high precipitation, high runoff potential soil, relatively low nutrient concentrations and wave energy, high elevation, but they have the most complex terrestrial vegetation. The Marquesas Islets remain amongst the highest connectivity islands despite the complex vegetation bringing down the linkage score.

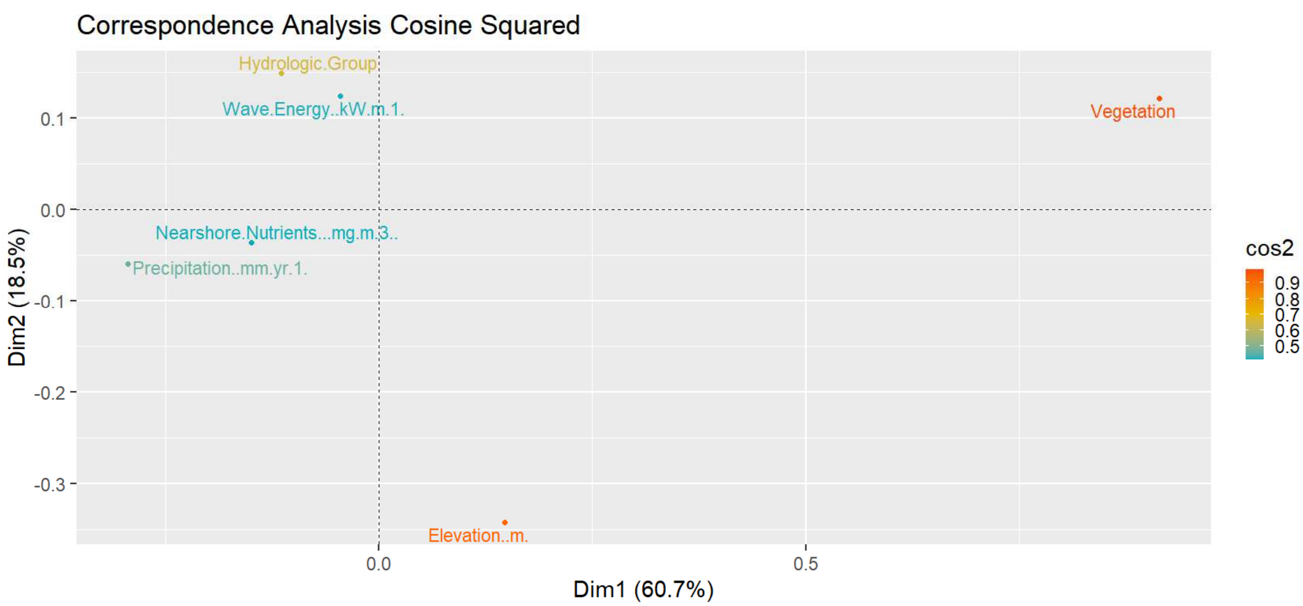
Gough island stands out with a linkage score hindered mainly by its oceanographic conditions. Gough is just south of the 40-degree latitude in the Atlantic Ocean and thus has strong wave energy around its coasts and is, relative to the other islands, small. Gough is an example of an island with linkage scores that were impacted by the log transformation, however the final linkage score of Gough remained the same. This is because the ordinal value for Gough's elevation went up because of the transformation, but its value for chl-a went down. This fluctuation of values balancing out resulting from the log transformation occurred for Gough as well as the other top 8 islands.

Socorro stands out as having a series of strong linkage values but has group A soils and very low levels of annual precipitation. Group A soils are well-drained and gravelly, allowing for high infiltration and low runoff even during high pulse precipitation events. The impact of Socorro's well-drained soils is likely exacerbated by its high elevation, relative to atolls with similar soil as atolls will have a small depth to the water table.

Although the table covers an extensive range of island types, these analyses are not representative of all islands but simply the ones focused on for eradication and conservation action today. For example, there are significantly more atolls than other island types, and as a result more tropical islands than temperate. While it's impossible to know the underlying impacts of this, we can certainly say that the results of our correspondence analysis of island-ocean linkage will be disproportionately driven by, and thus applicable to, tropical atolls. The table we created is full of valuable data and likely has more in-depth trends than we can interpret by strictly observing it.

(ii) Patterns of Covariance of the Mediating Factors of Connectivity

In order to conceptualize the data provided by the table and discuss trends and relationships present therein, we ran a correspondence analysis on the linkage table itself. Correspondence analysis is a convenient tool for investigating the association between islands, mediating factors, and between the mediating factors themselves. Correspondence analysis uses a similar formula to a Chi-square contingency test by creating residuals from expected values based on the data itself. These Chi square distances help us better understand the relative associations that exist within our dataset.



<u>Figure 1:</u> Correspondence Analysis biplot with mediating factors color-coded based on their cosine squared value. X and Y axes are the first, and thus greatest variance, dimensions from the correspondence analysis. Higher cosine squared value corresponds to greater strength of association between a mediating factor and the island datasets variance.

Figure 1 is a simple biplot based on the correspondence analysis of our island-marine linkage table with only the mediating factors themselves depicted. Each mediating factor is colored based on their respective cosine squared value. This value is an indicator of the level of association between the mediating factors and the variance amongst islands. The higher the cosine square of a mediating factor, the more of the dataset's variance is represented by that factor. This is interesting to consider, as according to this analysis, vegetation cover represents more variance than any of the other mediating factors, followed by elevation.

While we expected precipitation to have the strongest influence, vegetation cover and elevation certainly fit the bill. Vegetation cover and complexity influence not only the quantity and diversity of nutrients reaching the nearshore habitat, but also influence soil hydrology itself with potential for long-term implications. Additionally, the cover and complexity of terrestrial vegetation inherently contain information on the other terrestrial mediating factors of connectivity given that terrestrial biomes directly depend on the local climate. Elevation has the second highest cosine squared value. Given that island hydrology has been historically classified into two main functional types, either “high-rise” or “low-lying” islands, it follows logically that elevation would describe a great deal of variance between islands (Falkland 1993, N.S. Robbins 2013). It’s important to consider the relative importance of the mediating factors not only for understanding land-sea connectivity but also for prioritizing metrics for research, management, or conservation action should resources be scarce for a particular project.

Moving into more theoretical space, we can analyze the following biplot in Figure 2, with red labeled triangles representing islands and blue arrows pointing out the strength and direction of association of the mediating factors.

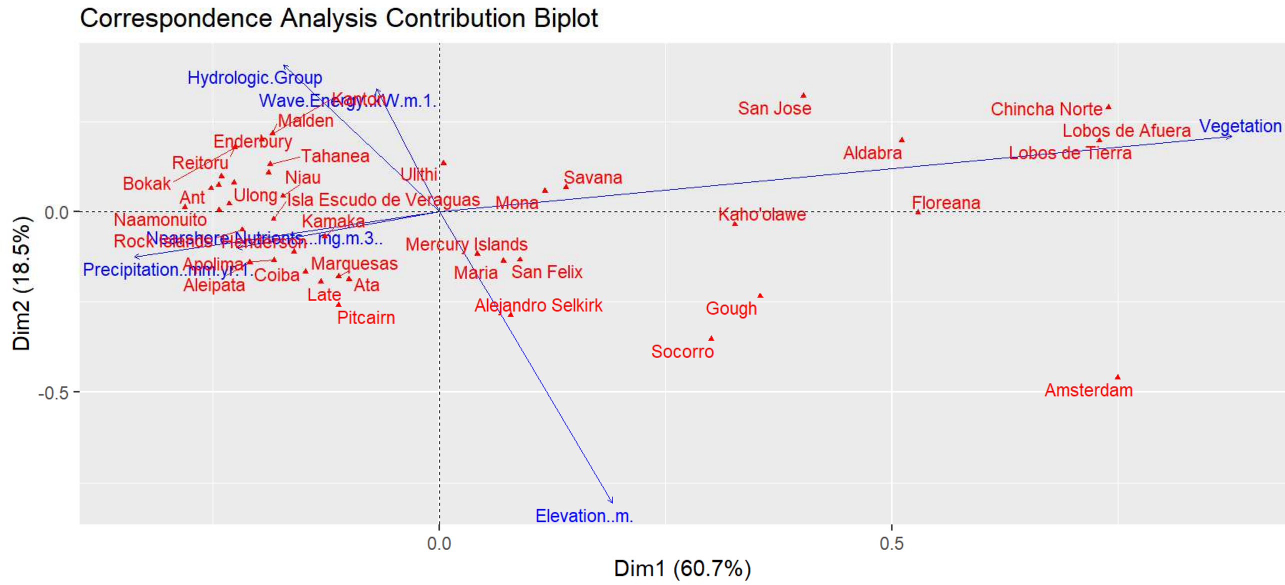


Figure 2: Symmetrical biplot of the correspondence analysis on land-sea linkage table. Blue arrows depict the direction of association between the mediating factors and axes while red triangles are the islands plotted onto the first two dimensions of the CA as axes. X and Y axes are the first, and thus greatest variance, dimensions from the correspondence analysis.

From figure 2 we can see two obviously tightly packed pairs of arrows, the first are nearshore nutrients and precipitation while the second is soil hydrology and wave energy. While it has been established that chlorophyll and precipitation are not only correlated, but that increases in precipitation are likely to increase nearshore nutrient concentrations due to runoff and the successive effects of eutrophication (Guo et al. 2022), this isn't consistent with our analysis. Given that our input to this analysis is based entirely on our hypothesized impact of each factor on land-sea connectivity, namely that more precipitation results in an increase in connectivity while less nearshore nutrient concentrations are expected to increase the impact of connectivity, our results show the converse: more precipitation appears to be associated with lower nearshore nutrient concentrations.

While this result is unexpected, it is likely being driven by the large amount of equatorial pacific atolls in our dataset, which often exhibit this relationship due to the impacts of the Indo-Pacific warm pool (IPWP). This relatively warm region of water exists under ‘normal’ conditions, or anytime other than during an El Niño event, and is caused by the pacific trade winds driving surface waters west causing them to pile up. The warm pool is lower in salinity and nutrients overall due to the increased stratification caused by the thermocline. The increased sea surface temperature also causes surface evaporation and increased rainfall (Ganachaud et al. 2011, Deckker 2016). Given that a disproportionate amount of the islands in our dataset, particularly those with high precipitation such as Anhd atoll, exist in the IPWP, it's likely that this “steam engine of the globe” is driving the relationship between precipitation and nearshore nutrient concentrations that is clear in our correspondence analysis.

Regional level drivers such as the Indo-Pacific warm pool can overpower island specific effects. We hypothesized that more precipitation would be linked with increases in nearshore nutrients from runoff. While our correspondence analysis presented the opposite, this result is likely due to the global nature of our analysis and thus the regional effects of the Indo-Pacific warm pool. In our dataset, islands with the most precipitation were inside the region where precipitation and nutrient depth profiles are controlled largely by the IPWP.

Soil hydrology and elevation appear to affect linkage in opposing directions, which is intuitively illogical as we’d expect higher elevation islands to have less permeable volcanic soils translating to more runoff and increased linkage. However according to Ross et al. 2018, “High runoff potential soils occur predominantly within tropical and sub-tropical regions" and thus this result may reflect our dataset, largely due to the high proportion of low-lying atolls that also have low permeability soils. While this result is in stark contrast to our hypothesis on the relationship between soil hydrology and elevation, it makes more sense after taking a closer look at the methods defining the soil hydrology dataset. Ross et al. 2018 classified each soil group by the least transmissive soil layer, with clays allowing for little water transfer and coarse sandy soils with large pore spacing allowing for maximal water transfer. The other main input to soil classification is depth to impermeable soil layer or depth to water table. When considering these two inputs it follows logically that low lying atolls will have a range of soil types but often a very small depth to the water table.

However, high vegetation cover causes significant evapotranspiration on these low-lying atolls, competing with groundwater recharge and thus often leads to little or no percentage of precipitation resulting in runoff, even though their soils have high runoff potential (Werner et al. 2017, White et al. 2002, White et al. 2010). This water-hungry vegetation likely contributed to significantly less groundwater recharge and thus a much lower proportion of precipitation resulting in runoff. In fact, when compared with the grassland covered half of Roi-Namur island, Gingerich 1992 found that the half-covered in dense vegetation including coconut trees had 84% lower groundwater recharge. This level of evapotranspiration is likely occurring on low-lying atolls globally, and while we currently have no way to be certain it would follow logically that a significant proportion of precipitation is being lost to evapotranspiration on any low-lying atoll with significant proportion of its area covered by complex vegetation. Although these low-lying atolls may have high runoff potential soils, it’s possible that they often still have very little runoff.

Our analysis included both the Chagos archipelago in the Indian Ocean and Mercury islands in New Zealand, both islands with recently published evidence suggesting strong land-sea connectivity. The Chagos archipelago is the study location of a significant proportion of the land-sea linkage specific studies to date, largely focused on the return of seabirds and their impacts on coral reef ecosystems (Benkwitt & Graham 2021). As these studies have shown strong linkages between land and sea in these environments, we expected our review of the local mediating factors of connectivity would result in a high linkage score for these island chains. Supporting our hypotheses for land sea connectivity, Chagos has quite a high linkage score of 29 and is the 8th highest linkage island.

The Mercury Islands have a similarly high linkage score of 27, which is logically slightly lower than Chagos given the nature of our analysis and the land-sea linkage studies that took place there. Most mediating factors suggest potential for strong land-sea linkage on the Mercury Islands, with the main exception being their complex terrestrial vegetation and seemingly high nearshore nutrient concentrations. The temperate deciduous forests on the Mercury Islands likely decrease the total flux from land to sea, which is a common trend amongst temperate islands in our analysis. However, the higher chlorophyll-a concentrations in the nearshore environment are expected given the macroalgae dominant rocky reefs found there. These macroalgal communities are likely increasing the chlorophyll-a values, thus inflating our nearshore nutrient proxy. However, these communities are more likely affected by land-sea linkage than actually impacting it themselves. Rankin and Jones 2021 found the macroalgal communities on the Mercury islands to be impacted by nutrient input from seabirds, so while the Mercury islands have a lower linkage score in our analysis, it's likely that the *in situ* land-sea connectivity on these islands is comparable to that of the Chagos archipelago. The juxtaposition of these two island chains is a perfect example of the importance of understanding the local dynamics of a given island as well as its nearshore environment when considering management action.

(III). Application of Insights for Maximizing Conservation Gains

Factors presumed to mediate the strength of land-sea connectivity have been identified with the ultimate goal of contributing to increased efficacy of management and conservation of island ecosystems. Importantly, this work contributes to efforts to bridge the philosophical divide that has led to operational ‘siloing’ or separation of marine and terrestrial science. In fact, the collaboration between academic institutions and the NGO Island Conservation to which this thesis belongs has laid the groundwork for resolving the lack of land-sea integration across research and management. We have begun to shift the paradigm with two steps in the direction of incorporating land-sea connectivity: 1.) a white paper describing the state of the science as well as a strategy for improving and standardizing monitoring on land and sea, and 2.) The Island Ocean Connection Challenge (IOCC). The IOCC is a global call to action with the goal of launching a new era of island restoration- one which incorporates land-sea connectivity to optimally restore both marine and terrestrial environments. The ultimate goal of this challenge is to maximize preservation of biodiversity in whole island ecosystems, through invasive species eradication and restoration of native ecosystems.

Our land-sea linkage table provides an estimate of the strength of the land-sea connection, and thus potential for marine co-benefit, for a suite of islands around the world. Island Conservation is using this information as an initial blueprint for incorporating land-sea connectivity into management actions to maximize conservation gains on island ecosystems with limited resources in a changing world. Our top land-sea connectivity island, Floreana, is a top target for Island Conservation given its unique flora and fauna- particularly in the nearshore marine environment- as well as it's potential for a strong land-sea connection and thus for marine co-benefit following terrestrial restoration.

These six mediating factors of connectivity can be used to consider the local impact of the land on the nearshore marine environment when conducting research, management, or conservation action at the interface of land and sea on a marine island. This is particularly true when considering the placement of a marine protected area (MPA) along an islands coastline. Several studies have shown the importance of considering the influence of the terrestrial environment on its nearshore neighbor when conducting integrated land-sea connectivity planning for biodiversity conservation (Makine et al. 2013, Alvarez-Romero et al. 2011). While this analysis is focused on the island-wide scale, the same mediating factors of connectivity could be applied on the single-island scale when prioritizing a variety of nearshore marine habitats around an islands coastline for protection. The quality of the nearshore marine habitat would remain the top priority, however considering the relative influence of the adjacent terrestrial environment might help to prioritize similar nearshore marine habitats.

Conclusion

This review of both the literature and the currently available satellite data has suggested environmental factors mediating land-sea connectivity on marine islands. Given that land-sea connectivity research is in its infancy, this study focused on singling out the distinct first-order effects of an island's physical and environmental factors to distinguish factors globally relevant to mediating this often crucial cross-ecosystem connectivity. These mediating factors of land-sea connectivity are suggested for science, natural resource management, and environmental policy conducted at the land-sea interface zone. While this study focused on whole island land-sea connectivity, the mediating factors described here can be extrapolated to determine the strength of local land-sea connection at a variety of scales as it applies to conceptualizing potential cross-ecosystem impacts of a given conservation goal on land or sea. Completion of more land-sea linkage specific studies will help to create a more explicit picture of the heterogeneity of land-sea linkage across island types. Use of each of the mediating factors should be goal dependent, with local flora, fauna, and environmental conditions creating the context for deciding which in situ measurements and following actions are necessary.

References:

Álvarez-Romero, J. G., Pressey, R. L., Ban, N. C., Vance-Borland, K., Willer, C., Klein, C. J., & Gaines, S. D. (2011). Integrated land-sea conservation planning: the missing links. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 381–409. https://doi.org/doi:10.1146/annurev-ecolsys-102209-144702

Aumack, C. F., Dunton, K. H., Burd, A. B., Funk, D. W., & Maffione, R. A. (2007). Linking light attenuation and suspended sediment loading to benthic productivity within an arctic kelp-bed community. *Journal of Phycology*, *43*(5), 853–863. https://doi.org/10.1111/J.1529-8817.2007.00383.X

Bach, S. S., Borum, J., Fortes, M. D., & Duarte, C. M. (1998). Species composition and plant performance of mixed seagrass beds along a siltation gradient at Cape Bolinao, The Philippines. *Marine Ecology Progress Series*, *174*, 247–256. https://doi.org/10.3354/MEPS174247

Barnosky, A. D., Brown, J. H., Daily, G. C., Dirzo, R., Ehrlich, A. H., Ehrlich, P. R., Eronen, J. T., Fortelius, M., Hadly, E. A., Leopold, E. B., Mooney, H. A., Myers, J. P., Naylor, R. L., Palumbi, S., Stenseth, N. C., & Wake, M. H. (2014). Introducing the Scientific Consensus on Maintaining Humanity's Life Support Systems in the 21st Century: Information for Policy Makers. *The Anthropocene Review,* 1(1). https://doi.org/10.1177/2053019613516290

Bellard, C., Rysman, JF., Leroy, B. (2017). A global picture of biological invasion threat on islands. *Nature Ecology & Evolution 1***,** 1862–1869 https://doi.org/10.1038/s41559-017-0365-6.

Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R., & Mwonga, S. M. (1989). The Effects of Trees on Their Physical, Chemical and Biological Environments in a Semi-Arid Savanna in Kenya. *The Journal of Applied Ecology*, *26*(3), 1005. https://doi.org/10.2307/2403708

Benkwitt, C. E., Gunn, R. L., Le Corre, M., Carr, P., & Graham, N. A. J. (2021). Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. *Current Biology*, *31*(12), 2704-2711.e4. https://doi.org/10.1016/J.CUB.2021.03.104

Benkwitt, C. E., Taylor, B. M., Meekan, M. G., & Graham, N. A. J. (2021). Natural nutrient subsidies alter demographic rates in a functionally important coral-reef fish. *Scientific Reports*, *11*(1), 1–13. https://doi.org/10.1038/s41598-021-91884-y

Benkwitt, C. E., Wilson, S. K., J Graham, N. A. (2019). Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. *Wiley Online Library*, *25*(8), 2619–2632. https://doi.org/10.1111/gcb.14643

Benkwitt, C., Gunn, R., Corre, M. L., Biology, P. C.-C. (2021). Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. *Elsevier*. https://doi.org/10.1016/j.cub.2021.03.104

Bishop, J. M., Glenn, C. R., Amato, D. W., & Dulai, H. (2017). Effect of land use and groundwater flow path on submarine groundwater discharge nutrient flux. *Journal of Hydrology: Regional Studies*, *11*, 194–218. https://doi.org/10.1016/J.EJRH.2015.10.008

Blanco, A. C., Watanabe, A., Nadaoka, K., Motooka, S., Herrera, E. C., & Yamamoto, T. (2011). Estimation of nearshore groundwater discharge and its potential effects on a fringing coral reef. *Marine Pollution Bulletin*, *62*(4), 770–785. https://doi.org/10.1016/J.MARPOLBUL.2011.01.005

Brocke, H. J., Polerecky, L., De Beer, D., Weber, M., Claudet, J., & Nugues, M. M. (2015). Organic Matter Degradation Drives Benthic Cyanobacterial Mat Abundance on Caribbean Coral Reefs. *PLOS ONE*, *10*(5), e0125445. https://doi.org/10.1371/JOURNAL.PONE.0125445

Burke, I. C., Lauenroth, W. K., Vinton, M. A., Hook, P. B., Kelly, R. H., Epstein, H. E., Aguiar, M. R., Robles, M. D., Aguilera, M. O., Murphy, K. L., & Gill, R. A. (1998). Plant-soil interactions in temperate grasslands. *Biogeochemistry*, *42*(1–2), 121–143. https://doi.org/10.1007/978-94-017-2691-7_7

Carr, M. H., Robinson, S. P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E. J., & Williams, M. (2017). The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 6–29. https://doi.org/10.1002/AQC.2800

Cyronak, T., Santos, I. R., Erler, D. V., & Eyre, B. D. (2013). Climate of the Past Geoscientific Instrumentation Methods and Data Systems Groundwater and porewater as major sources of alkalinity to a fringing coral reef lagoon (Muri Lagoon, Cook Islands). *Biogeosciences*, *10*, 2467–2480. https://doi.org/10.5194/bg-10-2467-2013

Das, S. (2017). Ecological Restoration and Livelihood: Contribution of Planted Mangroves as Nursery and Habitat for Artisanal and Commercial Fishery. *World Development*, *94*, 492–502. https://doi.org/10.1016/J.WORLDDEV.2017.02.010

Dawson, T.E., Ehleringer, J. R. (1998). Plants, isotopes and water use: A catchment-scale perspective. Isotope tracers in Catchment Hydrology, *Elsevier*. https://doi.org/10.1016/B978-0-444-81546-0.50013-6

De Deckker, P. (2016). The Indo-Pacific Warm Pool: Critical to world oceanography and world climate. *Geoscience Letters*, *3*(1), 1–12. https://doi.org/10.1186/S40562-016-0054-3/FIGURES/6

Delong, M. D., & Brusven, M. A. (1994a). Allochthonous input of organic matter from different riparian habitats of an agriculturally impacted stream. *Environmental Management*, *18*(1), 59–71. https://doi.org/10.1007/BF02393750

Dunkell, D. O., Bruland, G. L., Evensen, C. I., & Litton, C. M. (2011). Runoff, Sediment Transport, and Effects of Feral Pig (Sus scrofa) Exclusion in a Forested Hawaiian Watershed. *Pacific Science ,65*(2), 175–194. https://doi.org/10.2984/65.2.175

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/J.MARPOLBUL.2004.11.028

Fairbanks, R. G., Evans, M. N., Rubenstone, J. L., Mortlock, R. A., Broad, K., Moore, M. D., & Charles, C. D. (1997). Evaluating climate indices and their geochemical proxies measured in corals. *Coral Reefs*, *16*, 93–100.

Falkland, À. C. (1993). Hydrology and water management on small tropical islands. *IAHS PUBLICATION,* 263-263.

Feder, J. (1988). The Fractal Dimension. *Fractals*, 6–30. https://doi.org/10.1007/978-1-4899-2124-6_2

Fick, S.E. and R.J. Hijmans (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology,* 37:4302-4315.

Fitzpatrick, S., Giovas, C.M. (2021). Tropical islands of the Anthropocene: Deep histories of anthropogenic terrestrial–marine entanglement in the Pacific and Caribbean. *National Academy Sciences*, *118*. https://doi.org/10.1073/pnas.2022209118/-/DCSupplemental

Fujita, M., Ide, Y., Sato, D., Kench, P., Chemosphere, Y. K. (2014). Heavy metal contamination of coastal lagoon sediments: Fongafale Islet, Funafuti Atoll, Tuvalu. *Elsevier*. https://doi.org/10.1016/j.chemosphere.2013.10.023

Gagnon K, Yli-Rosti J, Jormalainen V (2015) Cormorant-induced shifts in littoral communities. *Marine Ecology Progress Series.* 541:15-30. https://doi.org/10.3354/meps11548

Gagnon, K., Rothäusler, E., Syrjänen, A., Yli-Renko, M., & Jormalainen, V. (2013). Seabird Guano Fertilizes Baltic Sea Littoral Food Webs. *PLOS ONE*, *8*(4), e61284. https://doi.org/10.1371/JOURNAL.PONE.0061284

Ganachaud, A. S., Sen Gupta, A., Orr, J. C., Wijffels, S. E., Ridgway, K. R., Hemer, M. A., & Kruger, J. C. (2011). Observed and expected changes to the tropical Pacific

Ocean. *Vulnerability of tropical Pacific fisheries and aquaculture to climate change. Secretariat of the Pacific Community, Noumea, New Caledonia*, 101-187.

Garcia-Martino, A. R., Warner, G. S., Scatena, F. N., & Civco, D. L. (1996). Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. *Sas.Upenn.Edu*, *32*(4), 41–65.

Gil, M. A. (2013). Unity through nonlinearity: A unimodal coral-nutrient interaction. *Ecology*, *94*(8), 1871–1877. https://doi.org/10.1890/12-1697.1

Gingerich, S. (1992). *Numerical Simulation of the Freshwater Lens on Roi-Namur Island, Kwajalein Atoll Republic of the Marshall Islands*. University of Hawaii. https://search.proquest.com/openview/bac90035918046bea9751a7e0821de3b/1?pq-origsite=gscholar&cbl=18750&diss=y

Gove JM, Williams GJ, McManus MA, Heron SF, Sandin SA, Vetter OJ, et al. (2013) Quantifying Climatological Ranges and Anomalies for Pacific Coral Reef Ecosystems. PLoS ONE 8(4): e61974. https://doi.org/10.1371/journal.pone.0061974.

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., & MacNeil, M. A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature*, *559*(7713), 250–253. https://doi.org/10.1038/s41586-018-0202-3

Hall, K. 2020. *Global Ecosystem Explorer Explore bioclimates, landforms, geology and land cover on planet Earth*, viewed 23rd May 2022, https://teach-with-gis-uk-esriukeducation.hub.arcgis.com/pages/lesson-ecosystem-explorer

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/SCIENCE.265.5178.1547

Jackson, R.B., Caldwell, M. M. (1993). Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology, 81(4), 683-692*. https://doi.org/10.2307/2261666

Ji, T., Du, J., Moore, W. S., Zhang, G., Su, N., & Zhang, J. (2013). Nutrient inputs to a Lagoon through submarine groundwater discharge: The case of Laoye Lagoon, Hainan, China. *Journal of Marine Systems*, *111–112*, 253–262. https://doi.org/10.1016/J.JMARSYS.2012.11.007

Jobbágy, E. G., & Jackson, R. B. (2001). The distribution of soil nutrients with depth: Global patterns and the imprint of plants. *Biogeochemistry*, *53*(1), 51–77. https://doi.org/10.1023/A:1010760720215

Jobbágy, E. G., & Jackson, R. B. (2004). The uplift of soil nutrients by plants: Biogeochemical consequences across scales. *Ecology*, *85*(9), 2380–2389. https://doi.org/10.1890/03-0245

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology*, *22*(1), 16–26. https://doi.org/10.1111/J.1523-1739.2007.00859.X

Jungkunst, H. F., Goepel, J., Horvath, T., Ott, S., & Brunn, M. (2021). New uses for old tools: Reviving Holdridge Life Zones in soil carbon persistence research. *Journal of Plant Nutrition and Soil Science*, *184*(1), 5–11. https://doi.org/10.1002/JPLN.202100008

Kappes, P. J., Benkwitt, C. E., Spatz, D. R., Wolf, C. A., Will, D. J., & Holmes, N. D. (2021). Do Invasive Mammal Eradications from Islands Support Climate Change Adaptation and Mitigation? *Climate, 9*(12), 172. https://doi.org/10.3390/CLI9120172

Keller, J. A., Wilson Grimes, K., Reeve, A. S., & Platenberg, R. (2017). Mangroves buffer marine protected area from impacts of Bovoni Landfill, St. Thomas, United States Virgin Islands. *Wetlands Ecology and Management*, *25*(5), 563–582. https://doi.org/10.1007/S11273-017-9536-0/TABLES/6

Kolb, G. S., Ekholm, J., & Hambäck, P. A. (2010). Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters. *Marine Ecology Progress Series*, *417*, 287–300. https://doi.org/10.3354/MEPS08791

Krull, E., Sachse, D., Mügler, I., Thiele, A., & Gleixner, G. (2006). Compound-specific δ13C and δ2H analyses of plant and soil organic matter: A preliminary assessment of the effects of vegetation change on ecosystem hydrology. *Soil Biology and Biochemistry*, *38*(11), 3211–3221. https://doi.org/10.1016/J.SOILBIO.2006.04.008

La Valle, F. F., Thomas, F. I., & Nelson, C. E. (2019). Macroalgal biomass, growth rates, and diversity are influenced by submarine groundwater discharge and local hydrodynamics in tropical reefs. *Marine Ecology Progress Series*, *621*, 51–67. https://doi.org/10.3354/MEPS12992

Leyshon, C. (2018). Finding the coast: Environmental governance and the characterisation of land and sea. *Area*, *50*(2), 150–158. https://doi.org/10.1111/AREA.12436

Lubarsky, K. A., Silbiger, N. J., & Donahue, M. J. (2018). Effects of submarine groundwater discharge on coral accretion and bioerosion on two shallow reef flats. *Limnology and Oceanography*, *63*(4), 1660–1676. https://doi.org/10.1002/LNO.10799

Makino, A., Beger, M., Klein, C. J., Jupiter, S. D., & Possingham, H. P. (2013). Integrated planning for land–sea ecosystem connectivity to protect coral reefs. *Biological Conservation*, *165*, 35–42. https://doi.org/doi:10.1016/j.biocon.2013.05.027

Mascaró, O., Oliva, S., Pérez, M., & Romero, J. (2009). Spatial variability in ecological attributes of the seagrass Cymodocea nodosa. *Botanica Marina*, *52*(5), 429–438. https://doi.org/10.1515/BOT.2009.055/MACHINEREADABLECITATION/RIS

McFadden, T. N., Kauffman, J. B., & Bhomia, R. K. (2016). Effects of nesting waterbirds on nutrient levels in mangroves, Gulf of Fonseca, Honduras. *Wetlands Ecology and Management*, *24*(2), 217–229. https://doi.org/10.1007/S11273-016-9480-4/FIGURES/6

Midwood, A. J., Boutton, T. W., Archer, S. R., & Watts, S. E. (1998). Water use by woody plants on contrasting soils in a savanna parkland: Assessment with δ2H and δ18O. *Plant and Soil*, *205*(1), 13–24. https://doi.org/10.1023/A:1004355423241

Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., Wabnitz, C. C. C., & Llewenyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature, 427*(6974), 533–536. https://doi.org/10.1038/nature02286

Nagelkerken, I., Blaber, S. J. M., Bouillon, S., Green, P., Haywood, M., Kirton, L. G., Meynecke, J. O., Pawlik, J., Penrose, H. M., Sasekumar, A., & Somerfield, P. J. (2008). The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany*, *89*(2), 155–185. https://doi.org/10.1016/J.AQUABOT.2007.12.007

Orth, R.J., Carruthers, T.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. (2006). A Global Crisis for Seagrass Ecosystems, *BioScience*, Volume 56, Issue 12, Pages 987–996, https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Osborne, T. M., Lawrence, D. M., Slingo, J. M., Challinor, A. J., & Wheeler, T. R. (2004). Influence of vegetation on the local climate and hydrology in the tropics: Sensitivity to soil parameters. *Climate Dynamics*, *23*(1), 45–61. https://doi.org/10.1007/S00382-004-0421-1/FIGURES/14

Paytan, A., Shellenbarger, G. G., Street, J. H., Gonneea, M. E., Davis, K., Young, M. B., & Moore, W. S. (2006a). Submarine groundwater discharge: An important source of new inorganic nitrogen to coral reef ecosystems. *Limnology and Oceanography*, *51*(1 I), 343–348. https://doi.org/10.4319/LO.2006.51.1.0343

Polis, G. A., & Hurd, S. D. (1995). Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the United States of America*, *92*(10), 4382–4386. https://doi.org/10.1073/PNAS.92.10.4382

Polis, G. A., & Hurd, S. D. (1996). Linking Marine and Terrestrial Food Webs: Allochthonous Input from the Ocean Supports High Secondary Productivity on Small Islands and Coastal Land Communities. *147*(3), 396–423. https://doi.org/10.1086/285858

Post, W. M., Emanuel, W. R., Zinke, P. J., & Stangenberger, A. G. (1982). Soil carbon pools and world life zones. *Nature, 298*(5870), 156–159. https://doi.org/10.1038/298156a0

Post, W. M., Pastor, J., Zinke, P. J., & Stangenberger, A. G. (1985). Global patterns of soil nitrogen storage. *Nature, 317*(6038), 613–616. https://doi.org/10.1038/317613a0

Quiros, T. E. A. L., Croll, D., Tershy, B., Fortes, M. D., & Raimondi, P. (2017). Land use is a better predictor of tropical seagrass condition than marine protection. *Biological Conservation*, *209*, 454–463. https://doi.org/10.1016/J.BIOCON.2017.03.011

Raymond, P. A., Mcclelland, J. W., Holmes, R. M., Zhulidov, A. V., Mull, K., Peterson, B. J., Striegl, R. G., Aiken, G. R., Gurtovaya, T. Y., & Raymond, P. A. (2007). Dissolved organic carbon and dissolved organic nitrogen export from forested watersheds in Nova Scotia: Identifying controlling factors. *Global Biogeochemical Cycles*, *21*(4). https://doi.org/10.1029/2007GB002934

Roberts, C. M., McClean, C. J., Veron, J. E. N., Hawkins, J. P., Allen, G. R., McAllister, D. E., Mittermeier, C. G., Schueler, F. W., Spalding, M., Wells, F., Vynne, C., & Werner, T. B. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, *295*(5558), 1280–1284. https://doi.org/10.1126/science.1067728

Robins, N. S. (2013). A review of small island hydrogeology: Progress (and setbacks) during the recent past. *Quarterly Journal of Engineering Geology and Hydrogeology*, *46*(2), 157–165. https://doi.org/10.1144/QJEGH2012-063

Roper, B. B., & Saunders, W. C. (2021). How Cattle and Wild Ungulate Use of Riparian Areas Effects Measures of Streambank Disturbance. *Rangeland Ecology & Management*, *74*, 32–42. https://doi.org/10.1016/J.RAMA.2020.08.009

Santoni, S., Huneau, F., Garel, E., Aquilina, L., Vergnaud-Ayraud, V., Labasque, T., & Celle-Jeanton, H. (2016). Strontium isotopes as tracers of water-rocks interactions, mixing processes and residence time indicator of groundwater within the granitecarbonate coastal aquifer of Bonifacio (Corsica, France). *Science of The Total Environment*, *573*, 233–246. https://doi.org/10.1016/J.SCITOTENV.2016.08.087

Sathish Kumar, P., Kumaraswami, M., Ezhilarasan, P., Durga Rao, G., Sivasankar, R., Ranga Rao, V., & Ramu, K. (2020). Blooming of Gonyaulax polygramma along the southeastern Arabian Sea: Influence of upwelling dynamics and anthropogenic activities. *Marine Pollution Bulletin*, *151*, 110817. https://doi.org/10.1016/J.MARPOLBUL.2019.110817

Schlesinger, W. H., Raikks, J. A., Hartley, A. E., & Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, *77*(2), 364–374. https://doi.org/10.2307/2265615

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M., & Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, *21*(11), 4128–4140. https://doi.org/10.1111/GCB.13021

Silbiger, N. J., Donahue, M. J., & Lubarsky, K. (2020). Submarine groundwater discharge alters coral reef ecosystem metabolism. *Proceedings of the Royal Society B*, *287*(1941). https://doi.org/10.1098/RSPB.2020.2743

Subalusky, A. L., & Post, D. M. (2019). Context dependency of animal resource subsidies. *Biological Reviews*, *94*(2), 517–538. https://doi.org/10.1111/BRV.12465

Sud, Y.C., Lau, W. K-M., Walker, G.K., Kim, J-H., Liston, G.E., Sellers, P.J. (1996). Biogeophysical consequences of a tropical deforestation scenario: A GCM simulation study. *Journal of Climate, 9(12) 3225-3247.* https://doi.org/10.1175/1520-0442(1996)009<3225:BCOATD>2.0.CO;2

Vicuña, S., Garreaud, R.D. & McPhee, J. (2011). Climate change impacts on the hydrology of a snowmelt driven basin in semiarid Chile. *Climatic Change* **105,** 469–488. https://doi.org/10.1007/s10584-010-9888-4

Wang, G., Jing, W., Wang, S., Xu, Y., Wang, Z., Zhang, Z., Li, Q., & Dai, M. (2014). Coastal acidification induced by tidal-driven submarine groundwater discharge in a coastal coral reef system. *Environmental Science and Technology*, *48*(22), 13069–13075. https://doi.org/10.1021/ES5026867

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world’s islands. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(38), 15307–15312. https://doi.org/10.1073/PNAS.1306309110

Werner, A. D., Sharp, H. K., Galvis, S. C., Post, V. E. A., & Sinclair, P. (2017). Hydrogeology and management of freshwater lenses on atoll islands: Review of current knowledge and research needs. *Journal of Hydrology*, *551*, 819–844. https://doi.org/10.1016/J.JHYDROL.2017.02.047

Wilson, J.P. (2018). Environmental applications of digital terrain modeling. John Wiley & Sons.

White, I., & Falkland, T. (2010). Gestion des lentilles d'eau douce dans de petites îles du Pacifique. *Hydrogeology Journal*, *18*(1), 227–246. https://doi.org/10.1007/S10040-009-0525-0/FIGURES/16

White, I.M., Falkland, A., Crennan, L., Metutera, T., Etuati, B., Eita, M., Pascal, P., Anne, D. (2002). Hydrology of conflicts over shallow groundwater use and management in low coral islands. *International Symposium on Low-lying Coastal Areas. Hydrology and Integrated Coastal Zone Management.*

Young, O. R., & Steffen, W. (2009). The earth system: Sustaining planetary life-support systems. *Principles of Ecosystem Stewardship: Resilience-Based Natural Resource Management in a Changing World*, 295–315. https://doi.org/10.1007/978-0-387-73033-2_14/TABLES/1

Zinke, P. J. (1962). The pattern of influence of individual forest trees on soil properties. *Ecology,* 43 (2), 130-133. https://doi.org/10.2307/1932049