DATA AND TOOLS TO OPERATIONALIZE RIDGE-TO-REEF MANAGEMENT AND BUILD ISLAND RESILIENCE IN OCEANIC ISLAND ENVIRONMENTS

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By

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DEDICATION

To my teachers, partner, friends and family whose guidance, support and love has empowered me to reach beyond the realms of possibility.

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ABSTRACT

Around the Pacific, a cultural renaissance rooted in the concern over declining natural resources seeks to revive traditional ridge-to-reef management approaches to promote social and ecological resilience in a changing climate. However, the effectiveness of ridge-to-reef management remains unclear due to a poor understanding of the cumulative effects of human and natural disturbances. In high Pacific islands, land and sea are tightly connected through social and ecological processes as a result of their small size and steep elevation gradients. Therefore, new tools are needed to inform resilience management over spatial scales relevant to Pacific Islanders. This research focused on three ridge-to-reef systems under community-based-management in Hawaiʻi (Hāʻena and Kaʻūpūlehu) and Fiji (Kubulau), which capture a wide spectrum of natural disturbances governing high Pacific islands.

Based on local data from Hāʻena and Kaʻūpūlehu, I developed a novel predictive modeling framework linking land and sea drivers to coral reef benthic and fish indicators, at fine spatial resolution. This framework was used to determine the effects of terrestrial and marine disturbances on coral reef communities and compare the effects of coastal development coupled with climate change on coral reef benthic communities and their targeted reef fish populations, given different natural disturbance regimes. I then transferred the framework to Kubulau to assess the effects of forest cover change on downstream coral reefs given uncertain climate impacts.

The results revealed that sheltered and dry oceanic environments, such as Kaʻūpūlehu, may be particularly susceptible to reduced water quality impacts. In contrast, exposed areas, like Hāʻena, are less susceptible to anthropogenic activities due to dilution and mixing from higher wave power and freshwater discharge. However, reef fish populations across most study sites became vulnerable to the impact of land-based source pollution when models incorporated climate change. In all cases, terrestrial management actions aimed at improving coastal water quality through wastewater management or forest conservation, coupled with the protection of coral reef nurseries or deep-water refuges, improved coral reef resilience potential. This research demonstrates that locally developed and data-driven models offer a much-needed opportunity for aiding place based management of coral reef social-ecological systems in high oceanic island environments.

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LIST OF ABBREVIATIONS

BROW	Browsers
BRT	Boosted Regression Trees
CCA	Crustose coralline algae
°C	Degrees Celsius
COR	Corals
FERL	Fishery Ecology & research Lab
GRDT	Grazers and detritivores
MAC	Macroalgae
NOAA	National Oceanic and Atmospheric Administration
N	Nitrogen
P	Phosphorus
PISC	Piscivores
TNC	The Nature Conservancy
SCEX	Scrapers and excavators
SCRP	Scrapers
SST	Sea Surface Temperature
TSS	Total Suspended Sediment
TUR	Turf algae
WCS	Wildlife Conservation Society

CHAPTER 1. INTRODUCTION

In the last century, climate change has become one of the most serious risk to coral reefs around the world as it directly impacts corals through bleaching from exposure to elevated sea surface temperature (SST) (Hoegh-Guldberg 1999), ocean acidification (Hoegh-Guldberg et al. 2007), and intensified storms (Webster et al. 2005). At the same time, growing human population has increased the range and intensity of anthropogenic disturbances impacting coral reef ecosystem resilience (Hughes et al. 2010, Nyström et al. 2000). Increases in overfishing and land-based source pollution now threaten over 55% and 25% of the total global reef area, respectively (Burke et al. 2011). Worldwide, humans have altered land use and, consequently, terrestrial fluxes of freshwater (Vörösmarty & Sahagian 2000), sediments (Syvitski et al. 2005), and nutrients (Downing et al. 1999, Elser et al. 2007) to coral reef environments (Kroon et al. 2014). The resulting declines in coastal water quality can impact on the structure, dynamics and diversity of coral reefs (Fabricius 2005, Fabricius et al. 2005), by promoting algal growth and reducing habitat quality (Houk et al. 2014, Smith et al. 2016). Increases in land-based nutrients, coupled with reduced herbivory due to overfishing (Jackson et al. 2001), have become primary concerns as they may interact with natural disturbance cycles to alter coral reefs ability to buffer natural disturbances and increase risk of phase shifts (Connell 1997, Dollar & Grigg 2004, Littler et al. 2006, Nyström et al. 2000). Thus, managing for the resilience of coral reefs has become a priority for conservation planning (Morecroft et al. 2012). In this study, resilience management consists of maintaining the ability of coral reef ecosystems to resist disturbances (resistance), as well as re-organize and re-establish after disturbances (recovery) (Mumby et al. 2014, Nyström et al. 2000).

Ridge-to-reef management has been widely advocated to foster coral reef resilience in a fast changing world (Bridge et al. 2013, Gurney et al. 2013). Consequently, community-based movements across the Pacific and Oceania seek to restore ridge-to-reef resource management systems, such as the ahupuaʻa system in Hawaiʻi (McGregor et al. 2003, Minerbi 1999) and the concept of *vanua* in Fiji (Berkes et al. 1998), as well traditional marine closures, such as *tabu* areas (Johannes 1978, 2002) (Figure 1.1). These ridge-to-reef initiatives aim to promote coral reef ecological and social resilience by protecting their biocultural resources (Minerbi 1999, Winter & Lucas 2017) and restoring abundant coral reef fisheries (Vaughan & Vitousek 2013). However, the degree to which ridge-to-reef management benefits coral reefs can vary among places. This is partly because the impact of human activities on land and at sea vary across space and time depending on their intensity, geology (e.g., soil and reef formation), and geography (e.g., landscape steepness and reef slopes). As a result, the protection of different places on the land and in the sea will have differential impacts on coral reef ecosystems and their fisheries (Klein et al. 2014).

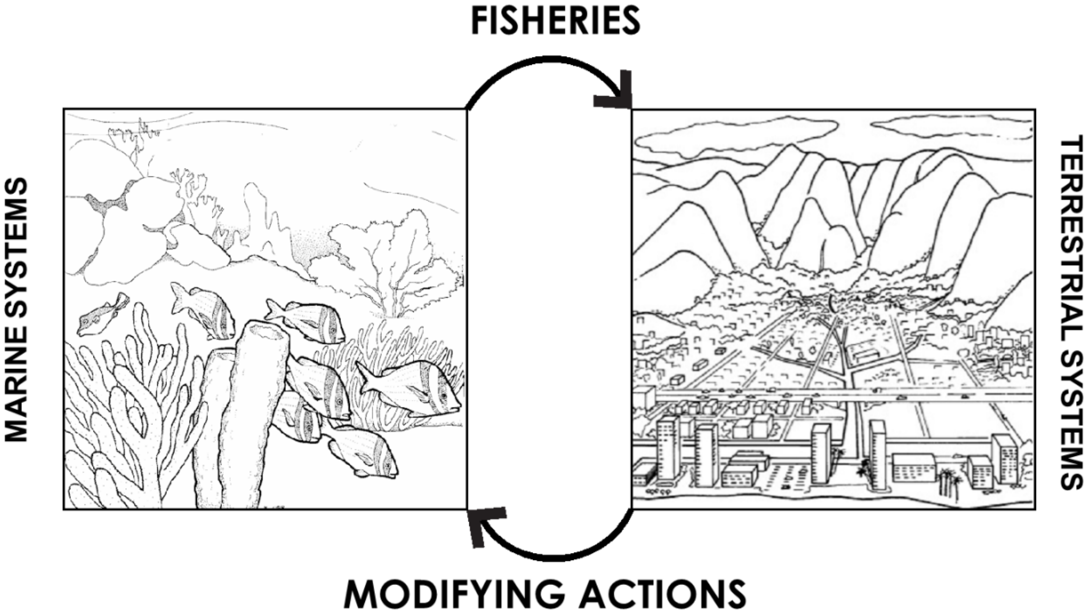

Figure 1.1. Conceptual diagram of a ridge-to-reef Social-Ecological System. Social-ecological systems (SESs) are comprised of an ecological unit, e.g., watersheds and coral reef ecosystems, a social unit, e.g., local coastal communities, and the interactions and feedbacks between them. Ecological systems provide fisheries that support human well-being (I), while social systems feed back on ecological systems through human modifying actions, such as coastal development and fishing activities (II). Adapted from (Kittinger et al. 2012)

In addition, land-sea connections can take multiple pathways, which makes observation and tractability challenging for scientists (Slomp & Van Cappellen 2004), and hinders managers from making informed decisions (Alvarez-Romero et al. 2011, Makino et al. 2013). While streams and storm water runoff are the most obvious lateral pathway to link land and sea (Izuka et al. 2016, Jokiel et al. 1993), groundwater discharge can exceed surface runoff in many coastal regions (Kim et al. 2011, Moore 1996). Groundwater can also be the primary water-borne transport vector for land-based nutrients to coral reefs (Prouty et al. 2016, Street et al. 2008), particularly in dry environments where stream flow is negligible (Knee et al. 2010). Groundwater has been shown to discharge a significant portion of land-based nutrients to coral reef waters compared to surface inputs in ridge-to-reef systems exposed to high rainfall (Garrison et al. 2003). Therefore, decisions about protecting coral reefs or restoring forests need to be supported by spatial conservation prioritization analyses (Klein et al. 2012a) and tools to understand the potential cumulative impacts and multiple outcomes of these decisions (Stamoulis & Delevaux 2015).

High Pacific islands are very susceptible to natural disturbances (Fosberg 1963), which shape the character of ecosystems by changing community structures, physical environments, and resource and space availability (Pickett & White 1985). Exposure to the prevailing trade winds and seasonal large waves combined with the rain shadow from high shield volcanoes result in wet windward sides exposed to high wave action and dry leeward sides sheltered from waves (Fletcher et al. 2008, Giambelluca et al. 2012, Grigg 1998). This is particularly true in high latitude oceanic islands, which often consist of steep topographic relief carved by rainfall (Izuka et al. 2016) and fringed with coral reefs sculpted by oceanic waves (Dollar 1982, Gove et al. 2013, Grigg 1998). As a result of their small size and steep elevational gradients, land and sea are tightly connected through social and ecological processes (Jupiter et al. 2017). Within island geographies are locations subject to different natural disturbances regimes that can be used to compare the effects of natural disturbances on coral reef resilience to human impacts. Therefore, high oceanic islands provide ideal models to understand land-sea and human-environment interactions in disparate natural conditions (Maris 2007).

To manage for coral reef resilience, we need to understand the effects of both natural and anthropogenic disturbances on coral reefs and the interactions between them (Buma 2015, Hughes & Connell 1999). To assess the impacts and recovery of coral reefs subject to disturbances, researchers have generally relied on long-term quantitative measurements (Connell 1997). Ecological and genetic datasets that track changes in coral reef communities across disturbance and recovery periods can help partition the variance associated with marine population dynamics, and attribute causes of change to individual drivers (Houk et al. 2014, Selkoe et al. 2010). However, datasets that provide information on long-term changes in coral reef composition associated with successive disturbances are rare, costly and typically are conducted at very limited temporal and spatial scales (Adjeroud et al. 2008, Chabanet et al. 2005, Hughes et al. 2002). This poses a critical limitation in understanding the roles that natural and human drivers play in coral reef resilience and ecological regime shifts (Hughes et al. 2010, Nyström et al. 2000).

Today's challenge for conservation science and resource management is understanding the cumulative effects of global and local human impacts on ecological systems in order to foster ecosystem resilience and prevent phase shifts (Darling et al. 2010, Nyström et al. 2000). Although, climate change and land-based source pollution have historically been studied and managed in isolation, it is becoming clear that a single-driver perspective is inadequate when managing ecosystems that are subject to multiple co-occurring drivers (Halpern et al. 2008b,a). Gaining knowledge of whether the cumulative effect of multiple human drivers is less than (antagonism), more than (synergism), or equal to the additive effects can have a profound influence on management outcomes (Bruno et al. 2007, Cinner et al. 2016, Hughes & Connell 1999). Of greatest concern to reef health are synergistic interactions among drivers that can result in "ecological surprises" (Folke et al. 2004, Paine et al. 1998), such as coral reefs phase shifts (Connell 1997, Littler et al. 2006). However, these ecosystem shifts are currently difficult to predict and, therefore challenging to manage (Darling & Côté 2008, Thrush et al. 2009).

Social-ecological modeling has proven useful to foster understanding of coral reef ecosystems under multiple co-occurring drivers and alternative human drivers' scenarios to inform management at relevant spatial scales (Gurney et al. 2013, Kouwen et al. 2007). During the last two decades, a series of models have been applied to coral reef ecosystems to explore the influence of natural and human drivers on their community dynamics (Kubicek et al. 2012, McClanahan 1995, Melbourne-Thomas et al. 2011) and provide more effective decision support tools to manage marine ecosystems (Franklin 2010, Stamoulis & Delevaux 2015). Social-ecological predictive modelling can provide insights into (*a*) the drivers and activities that result in shifts within the system (Kenneth 2016), (*b*) the scales they operate on (Halpern et al. 2008a), and (*c*) the interaction between them (Buma 2015, Crain et al. 2008), and thus help to manage cumulative impacts more effectively.

In spite of existing conceptual frameworks to adopt land-sea planning (Alvarez-Romero et al. 2011, Makino et al. 2013), very few practical examples demonstrate how to operationalize ridge-to-reef concepts into marine conservation planning. Some applications have linked the effects of land uses to marine ecosystems at broad spatial resolutions (Halpern et al. 2008b, Jenkins et al. 2010, Klein et al. 2010) to identify regions for more refined analysis (Klein et al. 2014). Others incorporated land and sea connections in the design of protected areas at a fine spatial-resolution (1km^2) and found that priorities for conservation changed after incorporating land-sea connections (Klein et al. 2012b, Tallis et al. 2008, Tulloch et al. 2016). However, these applications remain too coarse to operationalize ridge-to-reef management at the scale relevant for Pacific Islanders- that of a single to a few watersheds and linked reef areas. To address these shortcomings, the goals of this research are to develop a ridge-to-reef modeling framework that links the effects of natural and human drivers to coral reefs at final spatial scale and apply this framework to identify management priorities under different land use and climate change scenarios. To address these goals, my research had three main objectives:

1. Develop a model to determine the effects of terrestrial and marine drivers on coral reef communities and dynamics
2. Compare the effects of coastal development and climate change on coral reefs under different natural disturbance regimes
3. Evaluate the effects of forest conservation in protecting coral reefs from climate change impacts.

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CHAPTER 2. A MODELING FRAMEWORK TO LINK TERRESTRIAL AND MARINE DRIVERS TO CORAL REEF ECOLOGICAL OUTCOMES IN HIGH OCEANIC ISLANDS

ABSTRACT

A cultural renaissance rooted in the concern over declining natural resources around the Pacific seeks to revive traditional ridge-to-reef management approaches to protect land and freshwater and restore abundant reef fisheries in the face of increasing anthropogenic impacts. As a result of their small size and steep elevational gradients, land and sea are tightly connected through social and ecological processes on Pacific high oceanic islands. Effective ridge-to-reef management requires better understanding of the combined effects of terrestrial and marine drivers on coral reef ecosystems under gradients of natural disturbances. Therefore, new tools are needed to inform these efforts over spatial scales relevant to Pacific Islanders. This study focused on two ridge-to-reef systems (Hāʻena and Kaʻūpūlehu) under community-based management, at opposite ends of the main Hawaiian Island chain, which capture a wide spectrum of natural disturbances from rainfall and wave energy influencing high Pacific islands . I developed a novel modeling framework, based on local data from each place, which couples groundwater models with coral reef predictive models at fine spatial resolution. This framework was used to determine the effects of terrestrial drivers (freshwater and nutrients) and marine drivers (habitat and wave power) on coral reef benthic and fish communities under different natural disturbance regimes (freshwater and waves). My results indicate that the high disturbance regime of Hāʻena has shaped a dynamic coral reef community founded on crustose coralline algae and driven by freshwater and wave disturbances, while the low disturbance regime of Kaʻūpūlehu is more dominated by corals and greater habitat structure. For this reason Kaʻūpūlehu may be more sensitive to nutrient inputs due to low rainfall and wave disturbances coupled with high background nitrogen in groundwater. Therefore, Hāʻena should be managed to promote recovery post-disturbances and Kaʻūpūlehu should be managed for resistance to disturbances. The results emphasize how coral reef ecosystems differ due to unique natural disturbance regimes and human activities and thus require place-based, ridge-to-reef approaches to management.

2.1 Introduction

In this chapter, I developed a novel fine-scale modeling framework based on local data, which links the effects of terrestrial (rainfall and nutrients) and marine drivers (wave and habitat) to coral reef ecological outcomes for two ridge-to-reef systems in the Hawaiian archipelago (Hāʻena and Kaʻūpūlehu). Both communities have recently enacted place-based management to foster ahupuaʻa-based management and restore abundant nearshore fisheries (DAR 2016, TNC 2015). Located at opposite ends of the main Hawaiian Island chain, Hāʻena and Kaʻūpūlehu also represent each end of the environmental spectrum (geologic age, rainfall, and wave) governing high oceanic island ecosystems. Hāʻena is an older windward ridge-to-reef system exposed to high rainfall and wave disturbances, while Kaʻūpūlehu is a younger dry leeward ridge-to-reef system sheltered from wave action. To support these and other ridge-to-reef management initiatives, I built a modeling framework that links land use to coral reefs through nutrient enriched groundwater flux, which is the major vector for land-based nutrients to the nearshore environment for both West Hawaiʻi and the North shore of Kauai (Knee et al. 2008, 2010).

My modeling framework couples groundwater models to coral reef predictive models calibrated with local empirical and remote sensing data. I used coral reef benthic and fish functional groups as indicators which support aspects of ecological resilience (Green & Bellwood 2009, Smith et al. 2016) and represent important biocultural resources to native Hawaiians (DAR 2016, Friedlander et al. 2002, Poepoe et al. 2005, TNC 2015). Once calibrated with place-specific empirical data, this framework can provide insights into the effects of terrestrial and marine drivers on the dynamics and structure of coral reef communities. Assuming these fundamental relationships are constant over time, calibrated models can be used to forecast taxa distributions based on habitat suitability and assess the effects of management actions and climate change on these distributions (De'ath & Fabricius 2010, Franklin 2010, Iverson & Prasad 1998). In this study, I used model outputs to characterize the effects of terrestrial-marine linkages on coral reef communities under different natural disturbance regimes represented by freshwater and wave power, to answer the following question: Is Hā'ena coral reef community structure different from Kaʻūpūlehu due to more intense natural disturbances?

2.2 Methods

2.2.1 Site description

The age of the main Hawaiian Islands spans ~6 million years of erosion and exposure to rainfall and wave disturbances. The wind patterns coupled with rain shadows from the high shield volcanoes results in a windward side being wet and a leeward side being dry. Located in the middle of the Pacific Ocean, these high oceanic islands are exposed to large ocean swells. We selected two sites at the opposite ends of this spectrum: Hāʻena and Kaʻūpūlehu ahupuaʻa (Figure 2.1.a).

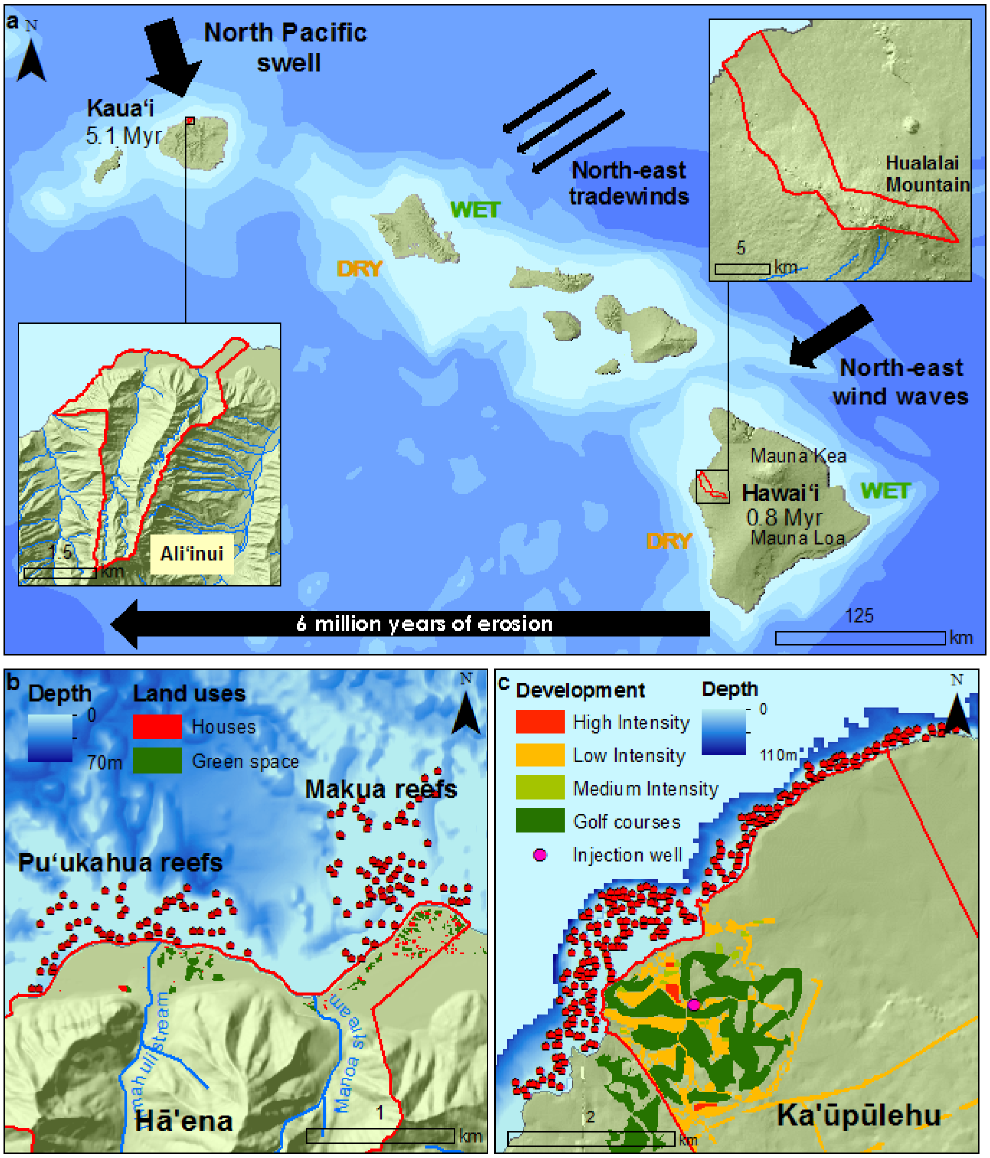

Figure 2.1. Study sites. (a) Location of study sites on Kauaʻi and Hawaiʻi along the main Hawaiian Island chain, with island age and the direction of the prevailing northeast tradewinds indicated. Land cover and reef survey sites are shown for (b) Hāʻena and (c) Kaʻūpūlehu.

2.2.1.1 Windward Kauaʻi ahupuaʻa: Hāʻena

Hāʻena is located on the windward side of Kauaʻi Island (Figure 2.1.a). Due to direct exposure to the prevailing tradewinds, Hāʻena ahupuaʻa receives very high rainfall (4,040 $mm.year^{-1}$), resulting in large fluvial and groundwater inputs (Calhoun & Fletcher 1999). Dominated by steep cliffs, the Hāʻena ahupuaʻa is 7.3 km^2 and spans 1,006 m elevation from the summit of Aliʻinui Mountain to the sea. Two perennial streams, located in Limahuli and Mānoa valleys, flow through Hāʻena. Due to its older geological age combined with marine erosion from wave exposure, the island shelf is wider and shallower compared to Kaʻūpūlehu (Fletcher et al. 2008), resulting in a modeled coral reef domain of 7.6 km^2. Shallow carbonate reef flats form back-reef areas protected from north swell by well-developed reef crests. These back-reef areas exhibit a diverse benthic community with high coral cover and high fish abundance, particularly juveniles (Goodell 2015). On the exposed fore-reefs of Hāʻena, the benthic community is dominated by crustose coralline algae (CCA), and supports high fish biomass, particularly adult fishes (Friedlander et al. 2003, Jokiel et al. 2004). Hāʻena was designated as a Community-based Subsistence Fishing Area by the State of Hawaiʻi in 2006, to protect and reaffirm customary fishing practices for native Hawaiian wellbeing (DAR 2016). With ~140 landowners, the rural ahupuaʻa is mostly owned by the State of Hawaiʻi and the non-profit organization, National Botanical Garden, with a number of private residences along the coast (Figure 2.1.b).

2.2.1.2 Leeward Hawaiʻi ahupuaʻa: Kaʻūpūlehu

Located in the rain shadows of Mauna Loa and Mauna Kea mountains (Figure 2.1.a), Kaʻūpūlehu ahupuaʻa receives much less precipitation (ranging from 1,350 to 260 $mm.yr^{-1}$ from ridge-to-reef) (Izuka et al. 2016) than Hāʻena. This dry ahupuaʻa covers 104 km^2 and spans 2,518 m elevation from the summit of Hualalai Mountain to the sea. Geologically young, the surface is less eroded with poorly developed ephemeral stream channels and groundwater seeping along the coast (Knee et al. 2010). The 7.4 km long shoreline is sheltered from large winter swells. So the fringing reef has not been eroded and forms a narrow band on the slope of the shield volcano, which drops steeply into deep water (Fletcher et al. 2008). Except for a broader, shallow carbonate bench at the southern end of the site, extending the modeled reef area to 3.2km^2. On the reef bench, the benthic community is mostly dominated by turf algae, scattered coral, and pavement, with low structural complexity and low fish abundance (Minton et al. 2015). The reef slope exhibits a more diverse benthic community with high coral cover, structural complexity, and high fish abundance (Minton et al. 2015). Kaʻūpūlehu recently initiated a state-sanctioned 10-year fishing rest period and is developing a set of rules to restore abundant nearshore fisheries and protect groundwater quality (TNC 2015). Kaʻūpūlehu is both commercially and residentially more developed than Hāʻena, with two large luxury resorts, a golf course, three public beach access areas, and several private residences concentrated along the southern end of the coast (Figure 2.1.c). The entire ahupuaʻa is owned by the largest private landowner in the state of Hawaiʻi, Kamehameha Schools.

2.2.2 Ridge-to-reef modeling framework

My modeling framework couples groundwater models to coral reef predictive models calibrated with local empirical and remote sensing data (Figure 2.2). The terrestrial drivers were derived from combining groundwater modeling to quantify groundwater discharge and nutrient flux from natural and human sources with ArcGIS-based modeling to generate maps of nearshore water quality. I applied GIS-based modeling of remotely-sensed bathymetry (Multibeam and LiDAR) (HMRG 2015) and wave models (Stopa et al. 2013) to quantify and develop maps of the marine drivers (habitat and waves). The coral reef indicators were benthic and fish functional groups derived from local empirical data sets (Goodell 2015, Minton et al. 2015). These data sets were first used in a multivariate regression to determine the key terrestrial and marine drivers differentiating the coral reef dynamics of both sites. The coral reef models consisted of Boosted Regression Trees (BRTs) parameterized for the coral reef indicators as response variables with the terrestrial and marine driver data sets used as predictors to derive their empirical relationships (response curves) and map their distributions.

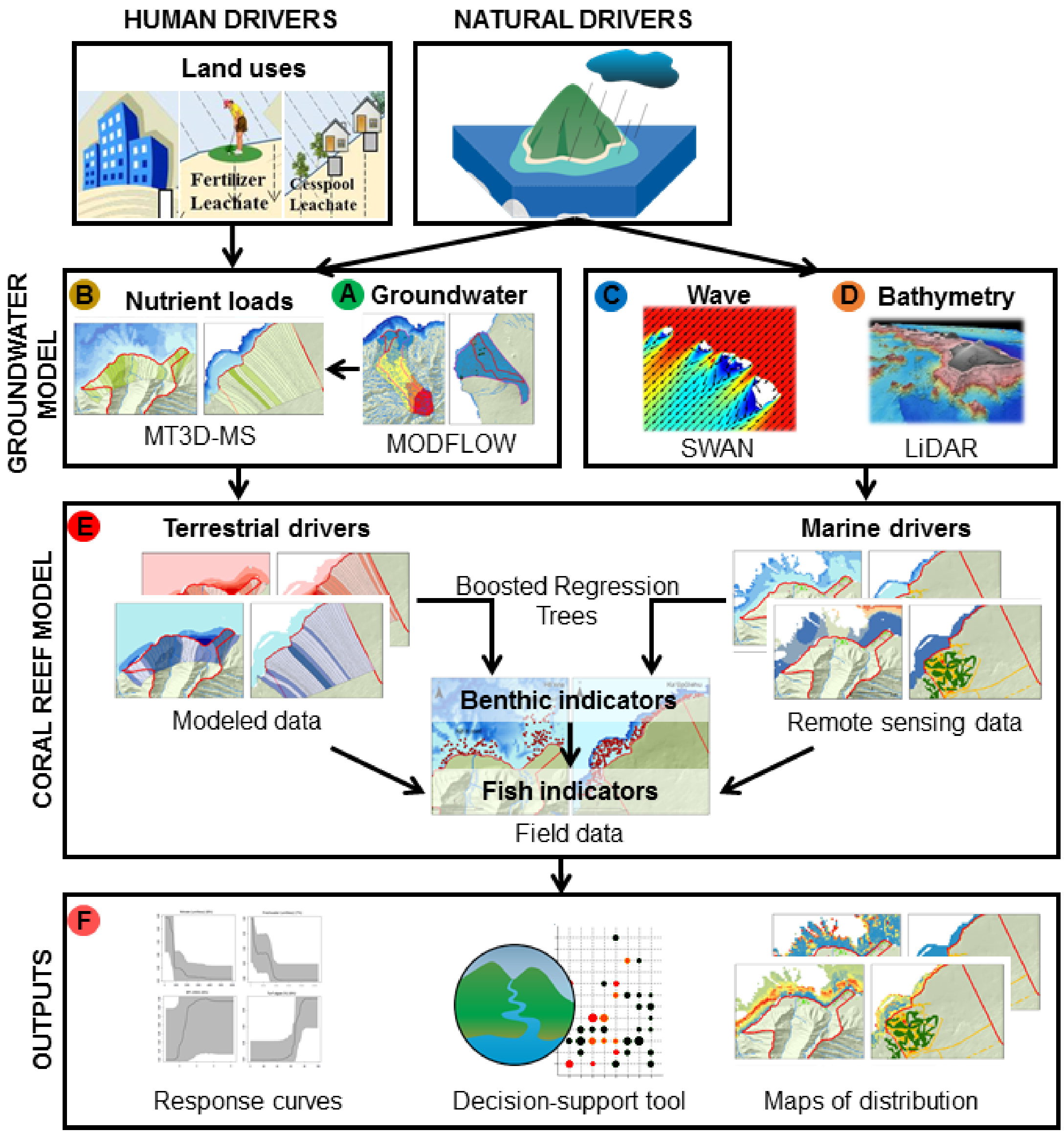

Figure 2.2 Modeling framework for the ridge-to-reef decision support tool[1]. Terrestrial drivers (freshwater and nutrients) derived from groundwater flow model MODFLOW (a) was coupled to the nutrient transport model MT3D-MS (b). Marine drivers (wave energy and habitat structure) were derived from the SWAN wave model (c) and LiDAR bathymetry data (d). Boosted regression trees were used to evaluate the relative contribution of drivers on variability in benthic and fish indicators (e). Response curves created by fitting modeled predictors to empirical measures of indicators can be used to predictively map changes to coral reef indicators under different climate and land use scenarios (f).

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[1] Symbols courtesy of Integration and Application Network (http://ian.umces.edu/symbols/); bathymetry image courtesy of Hawaii Mapping Research Group for bathymetry; wave model image courtesy of Hawaii Coastal Geology Group

2.2.3 Coral reef indicators & field data

2.2.3.1 Coral reef indicators

To determine and compare coral reef community structure and dynamics in the context of resilience to natural disturbances, I considered the abundance of four benthic and four fish groups based on their functional roles and importance as biocultural resources (Table 2.1) (Green & Bellwood 2009, Smith et al. 2016). The benthic functional groups included calcifying organisms (crustose coralline algae [CCA] and coral) and benthic algae (turf algae and macroalgae). CCA and corals are active reef builders (Goreau 1963, Setchell 1930), which can foster larvae recruitment (DeMartini et al. 2010, Harrington et al. 2004, Price 2010) and provide habitat for reef fishes (Green & Bellwood 2009). Excessive benthic algae can be a sign of excessive nutrients or reduced herbivory (Littler et al. 2006, Smith et al. 2010), which can affect coral health through direct or indirect competition for space (Houk et al. 2014, Littler & Littler 2007, Smith et al. 2016), as well as reducing fish larvae settlement (Vermeij & Sandin 2008). Resource fishes identified as important for subsistence and cultural practices by Native Hawaiians (e.g., Surgeonfishes, Parrotfishes, Jacks) (Friedlander et al. 2002, Poepoe et al. 2005) were modeled according to their functional role to track ecological resilience (see Green & Bellwood 2009 for classification): (1) browsers, (2) grazers/detritivores, (3) scrapers/excavators, and (4) piscivores (refer to Table S2.1 for more details on species composition). For instance, Surgeonfishes and most Parrotfishes graze on turf algae or macroalgae, which can help reverse coral-algal phase shifts; and some Parrotfishes free space for CCA and coral larval settlement (Green & Bellwood 2009). I derived the abundance of these indicators from reef survey data collected by the Fisheries Ecology Research Lab (FERL) at the University of Hawaiʻi and The Nature Conservancy of Hawaiʻi (TNC) reef monitoring program.

Table 2.1. Coral reef benthic and fish indicators. Coral reef indicators were used as response variables in the coral reef models.

Type	Code	Metric	Source	Description
Benthic indicators	CCA	Crustose coralline algae	Reef surveys	% cover
	COR	Coral cover	Reef surveys	% cover
	MAC	Macroalgae	Reef surveys	% cover
	TUR	Turf algae	Reef surveys	% cover
Resource fish indicators	BROW	Browsers	Reef surveys	Biomass ($g.m^{-1}$)
	GRDT	Grazers & Detritivores	Reef surveys	Biomass ($g.m^{-1}$)
	SCEX	Scrapers & Excavators	Reef surveys	Biomass ($g.m^{-1}$)
	PISC	Piscivores	Reef surveys	Biomass ($g.m^{-1}$)

2.3.2 Hā`ena field data

For Hāʻena, I used a field dataset comprising 126 survey locations (Figure 2.1.b), collected over two sampling periods, July 2013 and August 2014 (refer to Goodell [2015] for more details). Fish and benthic surveys were randomly stratified by habitat (nearshore, back-reef, and fore-reef areas) and allocated proportionately to area on Mākua and Kēʻē reefs. At each site, a 25 x 5 m belt transect (125-m^2 transect area) were used to collect benthic and fish data. Benthic cover data was collected using quadrat point intercepts (0.5 m^2 quadrats). Two quadrats were randomly placed within each 5 m segment along the transect line resulting in a total of 10 quadrats per transect. Point observations from these transects were classified as “coral”, “CCA”, “macroalgae”, “turf”, or “substrate” from which we calculated the percentage cover of each benthic group. For each belt transect, divers identified, counted, and estimated fork length (FL) of fishes to the nearest centimeter. The biomass for each fish was calculated by applying the length estimates in the length-weight (L-W) expression $W = a \times L^b$, where a and b are constants for the allometric growth equation, L is total length in centimeters, and W is mass in grams, using species-specific a and b parameters obtained from a comprehensive assessment of Hawaiʻi length-weight fitting parameters (FERL, unpublished data) and FishBase (Froese & Pauly 2011).

2.3.3 Ka‘ūpūlehu field data

For Ka‘ūpūlehu, I used a field dataset for comprising 243 survey locations, collected over two sampling periods 2012 (N=166) and 2013 (N=78) by TNC (Figure 2.1.c) (see Minton et al. [2015] for more details). Fish and benthic surveys were randomly stratified across two factors: management status and reef types along Ka‘ūpūlehu-Kiholo coast. Management status included two levels, inside and outside the existing marine managed area (Ka‘ūpūlehu Fisheries Replenishment Area). At each site, two replicate 25 x 5 m belt transect (125-m^2 transect area) were used to collect benthic and fish data. Photo-quadrats were taken every meter and analyzed to estimate the percent cover of CCA, corals, macroalgae, turf algae, and other benthic organisms present. For each belt transect, divers recorded total length (TL) of observed fishes for each species, using 5 cm length classes. The biomass for each fish was calculated by applying the visual mean length of the fish size class in the length-weight (L-W) expression $W = a \times L^b$, where a and b are constants for the allometric growth equation, L is total length in cm, and W is mass in grams.

2.2.4 Modeling terrestrial drivers

To derive maps of coastal water quality at both sites under the Present conditions, we estimated the coastal discharge of groundwater ($m^3.year^{-1}$) and dissolved nutrients loads (Nitrogen [N] and Phosphorus [P] in $kg.year^{-1}$) using the groundwater flow model MODFLOW (Harbaugh 2005) and the nutrient transport model MT3D-MS (Zheng & Wang 1999).

2.2.4.1 Groundwater models boundary conditions

Prior to modeling the terrestrial drivers, we assigned the boundary conditions to groundwater models for Hā‘ena and Ka‘ūpūlehu ahupua‘a. The boundary conditions were defined using MODPATH (Pollock 1994, 2012) and were assigned: (1) a flux representing the groundwater recharge at the upper boundary; (2) no-flow condition at the lateral boundaries; and (3) the elevation of the groundwater head boundaries at the coast (layer 1) and submarine (layer 2). Based on the greater density of seawater, the equivalent freshwater elevation were 0.019 meters above sea level (msl) for layer 1 and 0.075 msl for layer 2. The Hā‘ena model domain comprised four watersheds with perennial streams (i.e., Wainiha River [6,130 ha], Mānoa [253 ha], Limahuli [480 ha] and the Mauna Pūlo‘u [112 ha] watersheds) (Figure 2.3.a). The Ka‘ūpūlehu groundwater model domain included most of the north-central and central part of the Hualalai Aquifer Sector and assumed no inter-aquifer flow between the Kīholo aquifer and the Keauhou Aquifer, due to a rift zone bisecting the modeled area (Figure 2.3.b).

To represent non-point source discharge (Oki et al. 1999), we further sub-divided the groundwater model domains into narrow 'flow tubes' with their respective pour point at the shoreline (Figure 2.3.c & d) using MODPATH (Pollock 1994, 2012). The flow tubes boundaries were established along groundwater flow path lines so very little exchange of groundwater and dissolved nutrient occurs between flow tubes. The path lines were created using the particle tracking model MODPATH (Pollock 1994), which uses MODFLOW groundwater flow solution to model the particles movement along the simulated track to an endpoint (Pollock 2012). The virtual particles were placed at evenly spaced 'pour points' along the shoreline (Figure 2.3.c & d). The reverse tracking option was used to delineate groundwater flow paths from the coast to the zones of recharge, through the modeled area. Upgradient of the coastal zone, the flow tubes were terminated along a groundwater elevation contour. The downgradient boundary for flow tubes was the submarine boundary. The groundwater discharge and nutrient loads were computed for each flow tube using the groundwater utility model, ZONEBUDGET (Harbaugh 1990) and MT3D-MS (Zheng & Wang 1999).

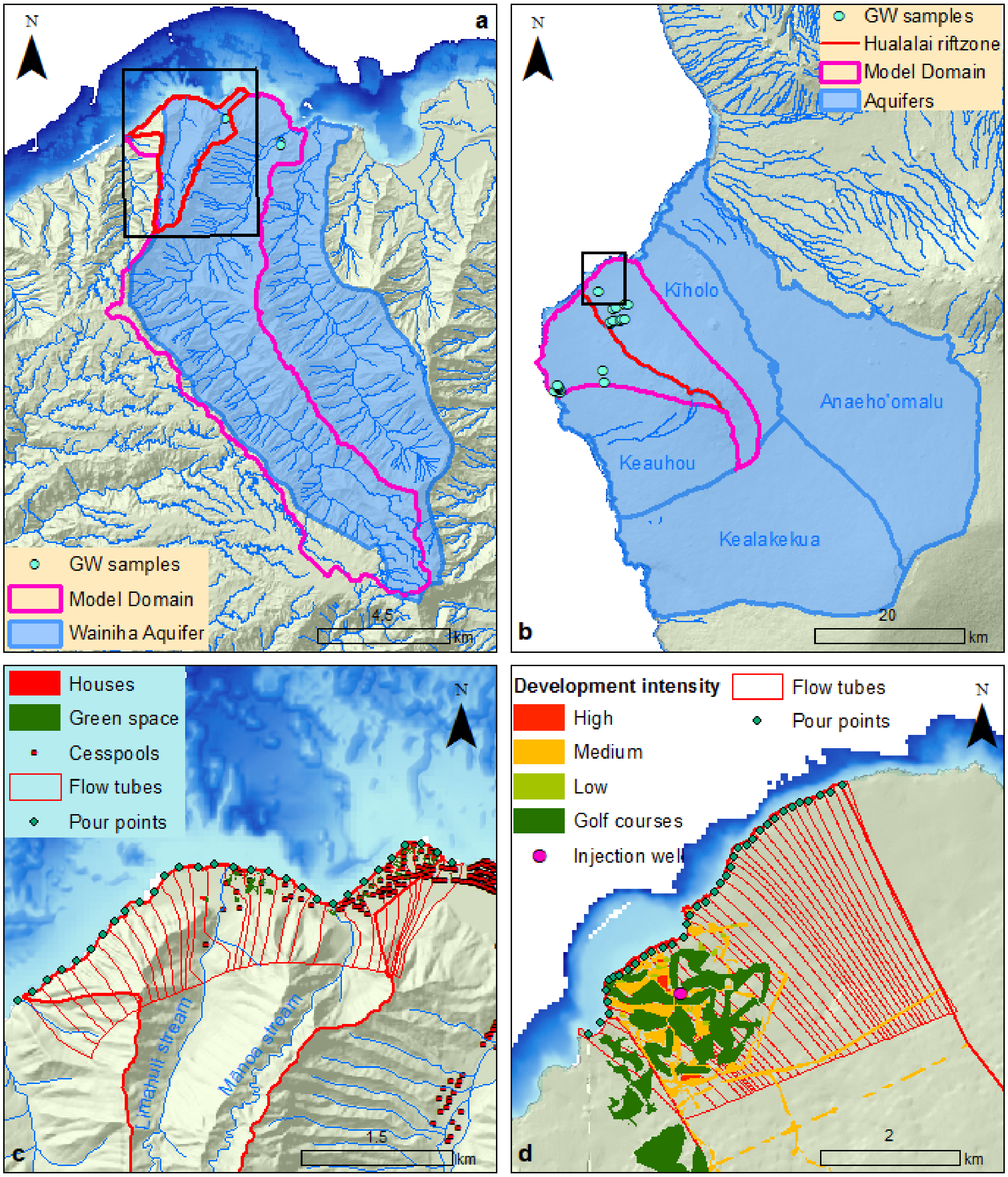


Figure 2.3. Groundwater model domains. (a) Hāʻena model domains (pink outline) overlaps with the Wainiha Aquifer (blue outline). Groundwater recharge is higher in the mountains (red zone) compared to coastal areas (green zone). (b) Kaʻūpūlehu model domains (pink outline), spreading across the Kīholo and Keauhou aquifers and bisected by a rift line (red line). Groundwater recharge is low (blue). (c) Hāʻena & (d) Kaʻūpūlehu key land uses; flow tubes and pour points to link groundwater model outputs to the coastal water quality models.

2.2.4.2 Groundwater flow modeling

On volcanic islands, groundwater is recharged by direct infiltration of rainfall and irrigation water that is not lost to runoff, evapotranspiration, or soil storage, and inflow from upgradient groundwater systems (Oki et al. 1999) (Figure 2.4).

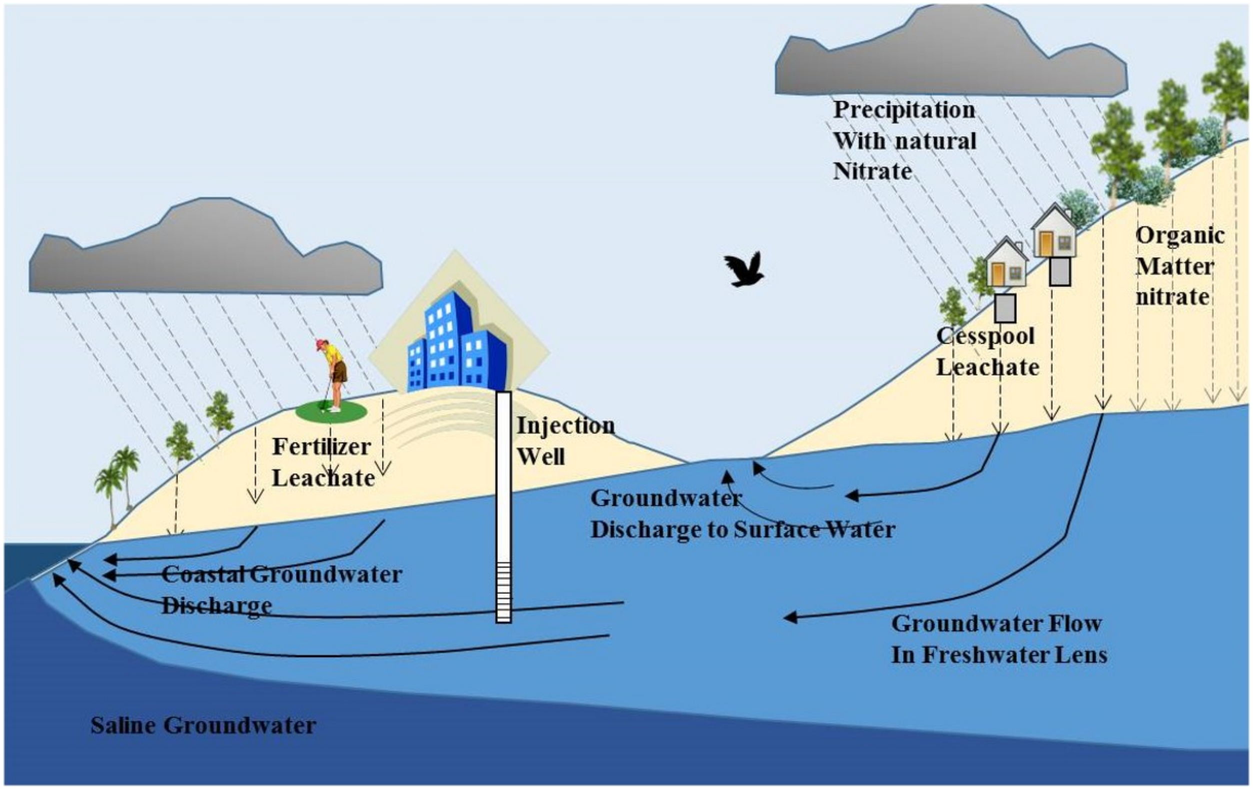


Figure 2.4. Groundwater conceptual model. The groundwater budget represents the sum of the contributions to (e.g., precipitation and injection well) and withdrawals (e.g., evapotranspiration and extraction well) from groundwater.

As summarized in equation 1, the change in groundwater budget (ΔGW) is the sum of the contributions to and withdrawals from groundwater. The groundwater flux ($m^3.d^{-1}$) was computed for individual flow tubes at the upgradient boundary and the coastal and submarine boundaries of both sites. Since groundwater flow was simulated using a steady state model, ΔGW becomes zero and thus the sum of variable in equation 1 also become zero (Izuka et al. 2016) (see Table 2.2 for parameters):

$$\boldsymbol{\Delta GW = R + Inj - ET - Str - Q - Cstl} \qquad (\mathbf{1})$$

where $\boldsymbol{R}$ = groundwater recharge (see Table 2.2 for parameters) and derived from equation 2 (Shade 1995). $\boldsymbol{Inj}$ = water injection volume into the aquifer, $\boldsymbol{ET}$ = evapotranspiration from the aquifer (set to zero because both model domains are deeper than the maximum evapotranspiration depth (1.5 m) (Engott 2011), $\boldsymbol{Str}$ = groundwater discharge to streams, $\boldsymbol{Q}$ = groundwater withdrawal rate (State of Hawai‘i 2014), $\boldsymbol{Cstl}$ = coastal groundwater discharge.

$$\boldsymbol{R = P + I - DR - AE - \Delta SS} \qquad (\boldsymbol{2})$$

where $\boldsymbol{P}$ = precipitation (Giambelluca et al. 2012), $\boldsymbol{I}$ = irrigation (set to zero due to the lack of agriculture in the Hā‘ena modeled domain and the recharge calculations of Engott (2011) was incorporated in model for the Ka‘ūpūlehu), $\boldsymbol{DR}$ = direct runoff (Izuka et al. 2016, Shade 1995), $\boldsymbol{AE}$ = actual evapotranspiration (Giambelluca et al. 2014), and $\boldsymbol{\Delta SS}$ = the change in soil moisture storage (assumed to average out to zero over long term).

Table 2.2. Groundwater budget parameters. For each study site, equations 1 and 2 were parametrized with the following values.

Parameter	**Units**	**Hā‘ena**	**Source**	**Ka‘ūpūlehu**	**Source**
Area	km^2	69.8	Designated	334	Designated
P	$m^3.d^{-1}$	977,000	(Giambelluca et al.	710,000	(Giambelluca et al.
ET	$m^3.d^{-1}$	-161,000	(Giambelluca et al.	395	(Giambelluca et al.
DR	$m^3.d^{-1}$	-528,000	(Shade 1995)	-16,300	(Izuka et al. 2016)
R	$m^3.d^{-1}$	287,000	Computed	272,000	(Izuka et al. 2016)
Q	$m^3.d^{-1}$	-515	(State of Hawai‘i	-51,600	(State of Hawai‘i
Inj	$m^3.d^{-1}$	-	NA	440	(State of Hawai‘i
Str	$m^3.d^{-1}$	-118,000	Modeled	0	NA
Cstl	$m^3.d^{-1}$	-170,000	Modeled	-222,000	Modeled
ΔGW	%	0.1	Computed	-0.6	Computed

For Hā‘ena, groundwater recharge was calculated across the model domain (Figure 2.4.a). Consistent with currently accepted conceptual model of groundwater flow for west Hawai‘i (Wilson Okamoto Corporation 2008), the groundwater model of Ka‘ūpūlehu assumed groundwater recharge occurring on the slopes of Hualalai Mountain and discharge at the coast of the Hualalai Volcano (Figure 2.4.b). The recharge values and distributions were derived from the comprehensive Hawai‘i Island groundwater recharge assessment of Engott (2011) and the resulting GIS maps (Izuka et al. 2016).

For Hā‘ena, groundwater discharge to streams (*Str*) was derived from gaged flow (2007 to present) of Wainiha River (USGS 2017) and estimated at 0.26 $m^3.s^{-1}$ using a flow frequency distribution curve (White & Sloto 1990). The discharge of groundwater to the other streams were estimated by scaling down the Wainiha River baseflow according to the relative watershed area (see Table 2.2 for parameters). For Kaʻūpūlehu, the water budget calibration was simplified by the absence of perennial streams in the modeled domain (see Table 2.2 for parameters). Groundwater coastal discharge ($Cstl$) was computed as the residuals at both sites.

2.2.4.3 Nutrient flux modeling

The nutrient loads were calculated for each ahupuaʻa, in terms of natural and human sources. We simulated the movement of dissolved nutrients in the aquifer and coastal discharge using the steady state transport model MT3D-MS (Zheng & Wang 1999). In the absence of plant uptake at both sites, nitrate was treated as a conservative transport species, which did not bind to soil or alter to another chemical state (Marion 1998, Wiedemeier 1999). Conversely phosphate binds to most soils, so phosphate concentrations reflect the leachable fraction available to the groundwater (Potter et al. 2006, Soldat & Petrovic 2008). The dispersal distance of dissolved nutrients depends on the aquifer heterogeneity, groundwater flow velocity, and molecular diffusion (Freeze & Cherry 1979), and was set to 20 m based on a local study (Bienfang 1980, Glenn et al. 2013).

Natural groundwater nutrient flux

We assigned representative nutrient concentrations to the groundwater recharge (Table 2.3), consistent with local groundwater measurements (Figure 2.3). For Hāʼena, the natural nutrient concentrations were evenly distributed across the modeled area. The background nutrient concentrations were set to 0.5 mg.l^{-1} for nitrogen (Knee et al. 2008) and 0.2 mg.l^{-1} for phosphorus (Fackrell 2016, Glenn et al. 2013, Knee et al. 2008). Given the groundwater nutrient concentrations in the Hualalai Aquifer are spatially variable, partly due to the rift zone (Fackrell 2016), Kaʻūpūlehu model domain was divided into four zones (upland Kaʻūpūlehu, lowland Kaʻūpūlehu, upland Keauhou, and lowland Keauhou) with their respective nutrients concentrations. The natural nutrient loads for the Kaʻūpūlehu model domain were derived from Fackrell (2016). Fackrell (2016) sampled 42 locations to determine the groundwater nutrient content to the coastal environment of west Hawaiʻi Island and divided the Kaʻūpūlehu area into three zones: (1) upland Kaʻūpūlehu wells had a nitrate concentration that varied from 1.6 to 4.2 mg.l^{-1} with an average value of 2.8 mg.l^{-1}; (2) middle Kaʻūpūlehu wells had slightly lower concentrations with an average value of 2.5 mg.l^{-1}; (3) coastal Kaʻūpūlehu nitrate concentration corrected for seawater mixing was 1.5 mg.l^{-1} (Fackrell 2016).

Table 2.3. Annual natural nutrient flux. Groundwater zones were assigned nitrogen and phosphorus concentration with the corresponding concentrations (mg/L/yr) combined with the groundwater recharge rate (R) and equivalent nutrient loads (kg/yr).

Zones	**[N] (mg/L/yr)**	**[P] (mg/L/yr)**	**N Load (kg/yr)**	**P Load (kg/yr)**	**Source**
Hāʻena background	0.50 x R	0.20 x R	7.51/ha	3.00/ha	(Fackrell 2016, Glenn et al. 2013, Knee et al. 2008, State of Hawaiʻi 2016a)
Kaʻūpūlehu Upland background	2.70 x R	0.20 x R	8.55/ha	0.63/ha	(Fackrell 2016, Izuka et al. 2016)
Kaʻūpūlehu Lowland background	0.25 x R	0.10 x R	0.65/ha	0.26/ha	(Fackrell 2016, Izuka et al. 2016)
Keauhou Upland background	1.20 x R	0.15 x R	3.11/ha	0.26/ha	(Fackrell 2016, Izuka et al. 2016)
Keauhou Lowland background	0.25 x R	0.1 x R	0.72/ha	0.29/ha	(Fackrell 2016, Izuka et al. 2016)

Human-derived groundwater nutrient flux

The nutrient loads from human activities was then added to the natural nutrient concentrations. First, we determined the number of houses in the coastal zone, their wastewater treatment systems, and green space areas (i.e., golf courses and lawns) in both *ahupuaʻa*, using aerial photos and existing data. In Hāʻena, the existing coastal development is concentrated along the coastal zone, while in Kaʻūpūlehu it extends further inland and comprises more land use types (Figure 2.1.b & c). We estimated a total of 156 houses on cesspools (Whittier & El-Kadi 2014a) and 0.059 km^2 of green space in the modeled domain of Hāʻena. While Kaʻūpūlehu currently accommodates ~165 houses with 0.18 km^2 of green space, two resorts which disposes of its wastewater after secondary treatment through an injection well, and a golf course (1.87 km^2). We assigned nutrient loading rates to these land use types derived from existing local studies and literature (Table 2.4).

The nutrient flux rates from housing were based on the assumptions that: (1) Each land parcel has a residential unit with three bedrooms at an occupancy rate of 1.5 persons per bedroom; (2) generating 265 $l.d^{-1}$ per person of wastewater or 1,190 $l.d^{-1}$ (435 $m^3.yr^{-1}$) (U.S. EPA 2002); and (3) one onsite wastewater disposal systems (OSDS) served each dwelling. The majority of OSDS in Hāʻena are cesspools (Whittier & El-Kadi 2014b). Cesspool effluent receives no treatment and is disposed of in a deep seepage pit below the evapotranspiration zone, so all effluent is recharged to the groundwater. Nutrient concentrations of the cesspool effluent are assumed to be the same as raw wastewater (Lowe et al. 2009). Currently, the primary method of wastewater disposal in the Kaʻūpūlehu area is through wastewater injection from the Hualalai Resorts. The Hualalai Resorts injects approximately 440,000 $l.day^{-1}$ (or 160,000 $m^3.yr^{-1}$) of secondary treated wastewater into two injection wells located approximately 800 m from the shoreline, resulting in an annual load of 840 and 1,090 kg for nitrogen and phosphorus, respectively (State of Hawaiʻi 2016b). The injection of wastewater was directly simulated in the groundwater flow and transport model. Given phosphorus beneath the soil zone may not get sorbbind with sediment (Glenn et al. 2013), we assumed no sorption for wastewater injection and cesspool discharge.

Typically, green spaces increase the nutrient flux due to increased recharge from irrigation and nutrient leaching from fertilizers. The coastal nutrient flux from green spaces were based on assumed landscaping practices, particularly irrigation (Engott 2011) and fertilization rates. Based on an irrigation rate of 0.00468 $m.d^{-1}$ (5,000 $gpd.ac^{-1}$, CH2MHill 2003), rainfall of 1.01 $mm.d^{-1}$ and an evapotranspiration rate of 0.00371 $m.d^{-1}$, the groundwater recharge rate over green spaces is assumed 0.00191 $m.d^{-1}$ (Engott 2011). For golf courses, fertilizers application rate was assumed at 879 $kg.ha^{-1}$ for nitrogen and 122 $kg.ha^{-1}$ for phosphorus, with a leaching rate of 5% for both nutrients, thereby resulting in an annual load of 49 and 13.5 $kg.ha^{-1}.yr^{-1}$ for nitrogen and phosphorus, respectively (Table 2.4) (Throssell et al. 2009a). Using typical lawn fertilizer applications (Wang et al. 2014) and given soil absorption, a leaching rate of 4.5 $kg.ha^{-1}.yr^{-1}$ and 0.2 $kg.ha^{-1}.yr^{-1}$ were assumed for nitrogen and phosphorus, respectively (Wang et al. 2014) (Table 2.4).

Table 2.4. Annual nutrient flux per land use type. Existing development zones were assigned nitrogen (N) and phosphorus (P) concentration combined with groundwater recharge (R) and the corresponding nutrient loads.

Land use type	**[N] (mg/L/yr)**	**[P] (mg/L/yr)**	**N Load (kg/yr)**	**P Load (kg/yr)**	**Source**
Cesspool	87	19	38 per unit	8.3 per unit	(Lowe et al. 2010, Tasato & Dugan 1980, U.S. EPA 2002)
Wastewater Injection	5.25	6.8	843	1300	(State of Hawai‘i 2016b)
Hā‘ena green space			4.5/ha + R	0.2/ha+ R	(Giambelluca et al. 2012, 2014; Shade 1995)
Ka‘ūpūlehu golf course/green space	7.59	0.54	49/ha	13.5/ha	(Throssell et al. 2009a)

2.2.4.4 Coastal water quality modeling

I diffused the modeled groundwater and nutrient flux from each ‘flow tube’ into the coastal zone to create spatially explicit maps of coastal water quality. In order to represent the non-point source discharge of groundwater on volcanic islands (Oki et al. 1999), I applied an adapted distance based plume model at each ‘pour point’ in ArcGIS (Halpern et al. 2008b). The distance based plume model applies a decay function to a cost surface (Yu et al. 2003) and used 1 km from the shoreline as the maximum threshold for diffusion (Derse et al. 2007). The cost surface was a composite of depth (m), distance from shore (m), and wave power (kW/m). This method allowed me to diffuse groundwater into coastal waters but did not account for nearshore advection that acts to push terrestrial drivers in specific directions. I used these modeled coastal water quality metrics (i.e., freshwater, nitrogen, and phosphorus) as proxies for nutrient-rich groundwater discharge, terrestrial drivers that may influence coral reef dynamics at each site (Table S2.2).

2.2.5 Marine driver modeling

The marine drivers were derived from remote sensing and wave model data available for both sites using GIS-based tools. The selected marine drivers were identified as important drivers of coral reef benthic and fish communities by existing literature and local community input (Table 2.5). Wave disturbance was represented by mean wave power at each site ($kW.m^{-1}$) and derived from the 500 m resolution SWAN hindcast model that spanned 10 years (2000-2009) (Stopa et al. 2013). Depth and distance from shore were used as geographic metrics to account for variation arising from spatial location. Depth was derived from the synthesis of Multibeam sonar and LiDAR bathymetry at 5 m resolution (HMRG 2015) and distance from shore was derived from the statewide coastline map (OP 2000). Three types of habitat drivers, representing direct and indirect effects of seafloor geomorphology on benthic and fish communities, were also derived from the synthesis of Multibeam sonar and LiDAR bathymetry (HMRG 2015): (1) habitat morphology, (2) habitat complexity, and (3) habitat exposure. Habitat morphology, represented by Bathymetric Position Index (BPI) and slope metrics, were computed for two neighborhood sizes (60 m and 240 m radii) to determine depth relative to the reef and surrounding area at different spatial scales (Kendall et al. 2011, Pittman & Brown 2011). Rugosity, plan and profile curvature metrics were computed to estimate habitat complexity. Three metrics of habitat exposure (sine circular mean, cosine circular mean, circular standard deviation), representing the steepest downslope direction (measured in degrees 0°-360°), were used to capture the direct and indirect effects of water flow due to seafloor topography and directionality.

Table 2.5. Description of marine drivers. Refer to Table S2.2 for more information.

Indicator	**Metrics**	**Description**	**Unit**	**References**
Wave	Power	Mean wave power derived from a 10 year (2000-2009) SWAN hindcast wave model.	kW.m^{-1}	(Dollar 1982, Friedlander et al. 2003, Grigg 1998)
Geography	Depth	Mean seafloor depth	m	(Dollar 1982, Fabricius & De'ath 2001, Jouffray et al. 2015)
	Distance to shore	Euclidean distance to the shoreline	m	
Habitat morphology	BPI	Relative topographic position of a point based its elevation and the mean elevation within a neighborhood (m)	m	(Pittman & Brown 2011, Stamoulis et al. 2016)
	Slope	Maximum rate of change in seafloor depth between each grid cell and its neighbors	Degree	
Habitat complexity	Plan curvature	Seafloor curvature perpendicular to the direction of the maximum slope (mean). Value indicates whether flow will converge or diverge over a point.	Radians.m^{-1}	(Darling et al. 2017, Friedlander & Parrish 1998a)
	Profile curvature	Seafloor curvature in the direction of the maximum slope (mean). Value indicates whether flow will accelerate or decelerate over the curve.	Radians.m^{-1}	
	Rugosity	Measure of small-scale variations of amplitude in the height of a surface (mean). Value range from 1 (flat) to infinity.	Unitless	
Habitat exposure	Aspect	Downslope direction of maximum rate of change in seafloor depth between each grid cell and its neighbors (sine circular mean, cosine circular mean, circular standard deviation)	Degree	(Franklin et al. 2013, Knudby et al. 2013)

2.2.6 Identifying terrestrial and marine drivers of coral reefs

To identify and differentiate the effects of terrestrial (groundwater and nutrients) and marine drivers (habitat and wave) on coral reefs between sites, I analyzed the coral reef indicators using distance-based linear modeling (DISTLM) coupled with distance based redundancy analysis (dbRDA), a constrained multivariate multiple regression on principal coordinate axes of environmental drivers (Legendre & Anderson 1999, McArdle & Anderson 2001). This nonparametric technique models the relationship between a multivariate data cloud (coral reef indicators) and environmental drivers (terrestrial and marine). More specifically, it partitions the variation in the data cloud described by the resemblance matrix according to multiple linear regressions (Anderson et al. 2008). An Euclidean distance similarity measure was used to construct a resemblance matrix of the transformed and normalized benthic and fish indicators. Square root and fourth root transformations were applied to the benthic and fish variables, respectively, to improve normality (Costa & Kendall 2016, Stamoulis & Friedlander 2013). Environmental drivers were normalized, with highly correlated (> 0.7) drivers removed from the models. The DISTLIM routine was used to perform the partitioning, while the dbRDA routine was used to perform an ordination of the fitted values of the reef benthic and resource fish communities in PRIMER PERMANOVA+ software (Anderson et al. 2008). Fitted variation >70% is considered a good fit to the model (Legendre & Anderson 1999).

2.2.7 Modeling coral reef dynamics

Tree-based models are effective at modeling nonlinearities, discontinuities (threshold effects), and interactions between variables (Breiman 1996, 2001), which is well suited for the analysis of complex ecological data (De'ath & Fabricius 2000). To determine the important terrestrial and/or marine drivers of each coral reef indicator and obtain a description of these empirical relationships, I applied BRTs (Elith et al. 2008) (Figure 2.2.d).

I calibrated the BRT models for benthic and fish indicators, derived from the field data, as a function of the terrestrial and marine drivers. The calibration process uses an internal ten-fold cross-validation to maximize the model fit and determine the optimal combinations of four parameters: (1) learning rate (lr); (2) tree complexity (tc); (3) bag fraction (bag); and (4) the maximum number of trees (see (Elith et al. 2008) for more details). To control for overfitting, BRTs uses a regularization process that simplifies the selected optimal model, while providing sufficient flexibility to fit complex non-linear relationships. I determined the number of drivers to remove by evaluating how many drivers could be dropped without resulting in a major reduction in PDE (see Elith et al [2008] Appendix S2). Calibrated BRT models provide response curves, which represent the empirical correlation between the indicator and environmental predictor (Figure 2.2.f). The response curves need to be further compared against historical data trends for validation. I used the percent deviance explained (PDE) by the calibration and internal ten-fold cross validation method as performance measures of the model optimum. The optimal models explained the most variation in the response variables (i.e., greatest PDE). During the model-fitting process, BRTs determined the strongest statistical environmental drivers (among the simultaneously tested predictors) and estimate the underlying relationship (response curve) between the modeled indicator and the key environmental drivers (De'ath & Fabricius 2000, 2010; Venables & Ripley 2013). I conducted the model fitting in R software (R Core Team 2014) using the gbm package (Elith et al. 2008, Ridgeway 2007).

The final BRT models of each study sites were used to predict and map the distribution of each coral reef indicator given the environmental drivers' conditions, on a cell-by-cell basis, across the coral reef model domain. First, I spatially predicted the benthic groups as a function of their key environmental drivers. Then, I predicted the resource fishes as a function the environmental drivers, including the predicted benthic groups. Spatial autocorrelation of the response variable was tested using Moran's I Index for both the raw values and the ecological model residuals (Miller 2012). I performed the spatial prediction in the R software (R Core Team 2014) using the dismo (Hijmans et al. 2014) and raster packages (Hijmans 2014).

2.3. Results

2.3.1 Terrestrial drivers

The calculated groundwater recharge for Hāʻena was compared to the Wainiha Aquifer water budget model (Shade 1995) and was within 1% difference. The Kaʻūpūlehu groundwater recharge was derived from the comprehensive Hawaiʻi Island groundwater recharge assessment of Engott (2011) and the resulting GIS maps (Izuka et al. 2016), and therefore did not need further validation. Our groundwater model showed that groundwater recharge was much higher in Hāʻena (ranging from 0.0006 $m.d^{-1}$ to 0.01 $m.d^{-1}$) compared to Kaʻūpūlehu (ranging from 0.0001 $m.d^{-1}$ to 0.0088 $m.d^{-1}$) (Figure 2.5.a & b). Consequently, the groundwater discharge was 2.5 times higher in Hāʻena (57.1 million $m^3.yr^{-1}$ or 10,279 $m^3.m^{-1}.yr^{-1}$ of shoreline) than Kaʻūpūlehu (22.7 million $m^3.yr^{-1}$ or 3,085 $m^3.m^{-1}.yr^{-1}$ of shoreline (Figure 2.6). In Hāʻena, the greatest freshwater flux (~28,200 $m^3.m^{-1}.yr^{-1}$) was through an embayment on the eastern side of the study area (Figure 2.5.c). At Kaʻūpūlehu, the greatest freshwater flux (6,700 $m^3.m^{-1}.yr^{-1}$) occurred through a small embayment near the middle of the study area (Figure 2.5.d).

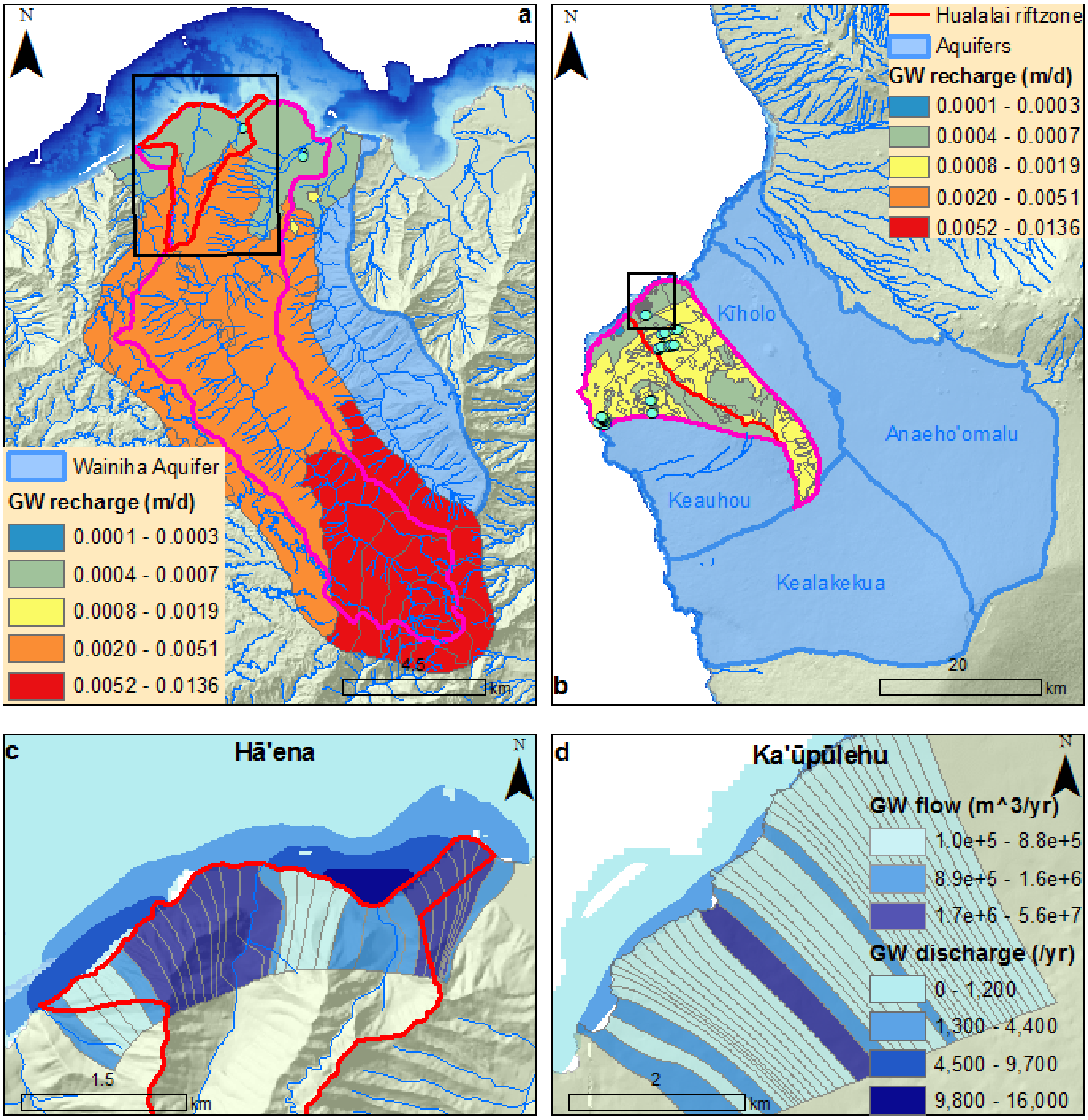


Figure 2.5. Groundwater recharge models. (a) Hāʻena groundwater recharge is higher in the mountains (red zone) compared to coastal areas (green zone). (b) Kaʻūpūlehu groundwater recharge is low throughout the ahupuaʻa (yellow and green zones).

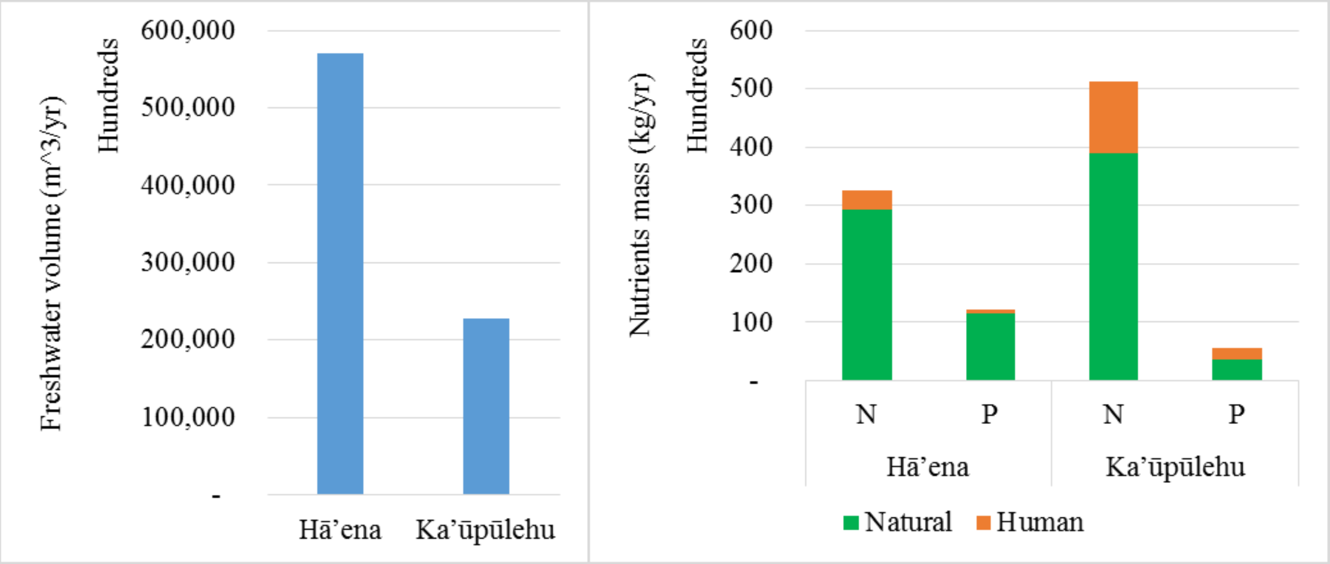


Figure 2.6. Groundwater models outputs. Groundwater discharge (left) and nutrient loads (right) in Hāʻena and Kaʻūpūlehu based on status quo conditions.

In terms of nutrient loads, nitrogen was lower in Hā'ena (29,200 kg.yr^{-1} or 6.02 kg.m^{-1}.yr^{-1}) in comparison to Ka'ūpūlehu (38,900 kg.yr^{-1} or 7.08 kg.m^{-1}.yr^{-1}) (Figure 2.6). Conversely, the phosphorus load for Hāʻena (11,500 kg.yr^{-1} or 2.24 kg.m^{-1}.yr^{-1}) was 3.3 times greater compared to Kaʻūpūlehu (3,510 kg.yr^{-1} or 0.78 kg.m^{-1}.yr^{-1}). The fraction of human-derived nutrient load delivered to the coastal zone was lower at Hāʻena (N=7.8% and P=5.5%), compared to Kaʻūpūlehu (N=24% and P=35%). The key sources of these nutrients were wastewater at Hā'ena and greenspaces, such as golf courses, at Kaʻūpūlehu (Table 2.4). At Hāʻena, the greatest nutrient flux (N=15.4 kg.m^{-1}.yr^{-1} and P=5.9 kg.m^{-1}.yr^{-1}) was through the embayment on the eastern side of the study area (Figure 2.7), located downstream from existing coastal development (Figure 2.1.b). At Kaʻūpūlehu, the greatest nutrients flux (N=18.6 kg.m^{-1}.yr^{-1}and P=4.5 kg.m^{-1}.yr^{-1}) occurred through a small embayment near the middle of the study area (Figure 2.7) and downstream from existing coastal development (Figure 2.1.c). Consequently, coastal nitrogen levels at Kaʻūpūlehu ($\bar{X}$= 1,666; SD=1,776) were higher compared to Hāʻena ($\bar{X}$=933; SD=1,617). Conversely, coastal freshwater and phosphorus levels were higher in Hāʻena (freshwater: $\bar{X}$= 1,445, SD=2,753; P: $\bar{X}$= 336, SD=598) compared to Kaʻūpūlehu (freshwater: $\bar{X}$= 777, SD=746; P: $\bar{X}$= 243, SD=363).

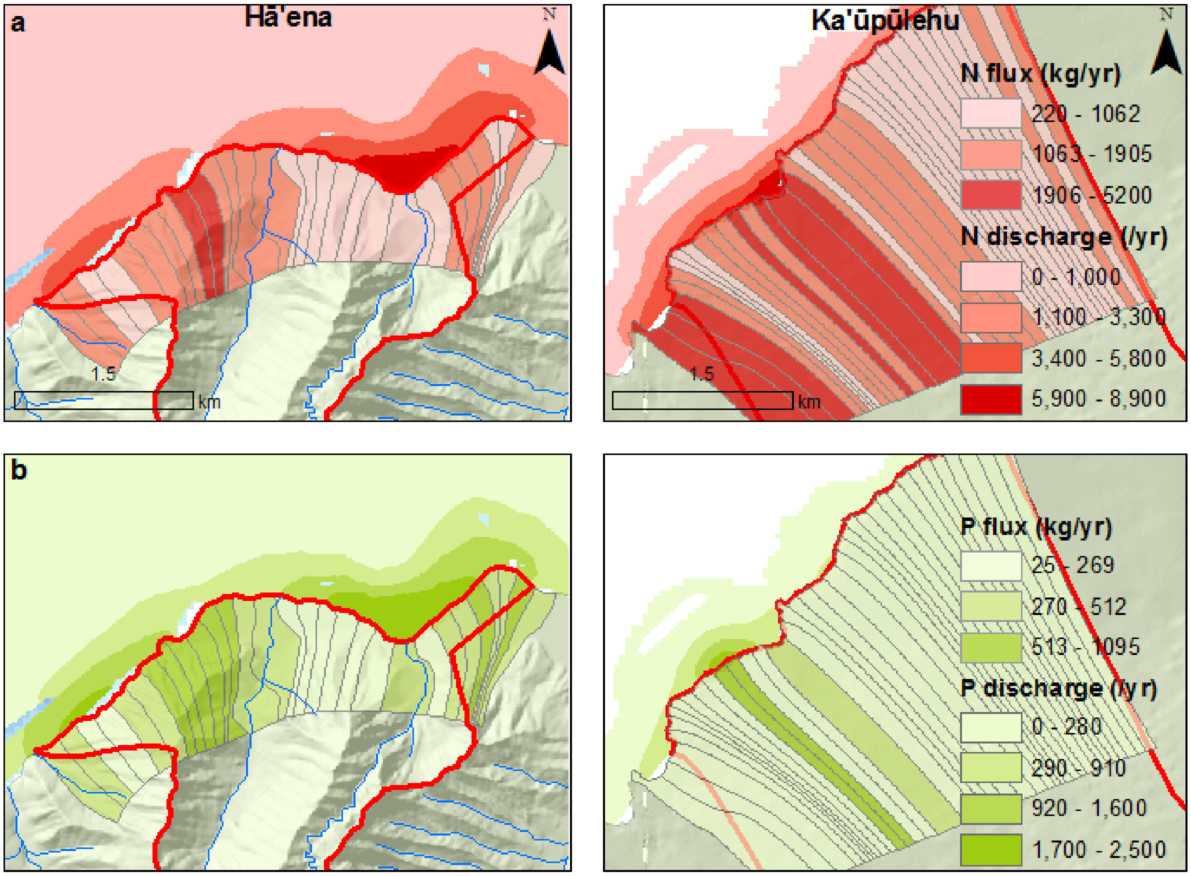


Figure 2.7. Modeled groundwater nutrients flux coupled with modeled coastal water quality in Hāʻena (left) and Kaʻpūlehu (right). a: Groundwater nitrate flux (kg/yr) and coastal plume (/yr). b: Groundwater phosphate flux (kg/yr) and coastal plume (/yr).

2.3.2 Marine drivers

The average and standard deviations of our marine drivers maps across the modeled coral reef domains showed that wave power in Hāʻena is higher than Kaʻūpūlehu by an order of magnitude (Table 2.6) (refer to Figure S2.1 for spatial representation). The island shelf of Hā’ena was wider compared to the narrow island shelf of Kaʻūpūlehu. In terms of habitat morphology, BPI values suggested Hā’ena reef exhibit less ridges and valleys compared to Kaʻūpūlehu at both modeled spatial scales. Similarly, Kaʻūpūlehu reef slopes were steeper and varied more compared to Hāʻena, particularly at the 60m resolution. On the other hand, habitat complexity was higher in Hāʻena compared to Kaʻūpūlehu. In terms of habitat exposure, Hāʻena was more exposed than Kaʻūpūlehu.

Table 2.6. Marine drivers average and standard deviation across Hāʻena and Kaʻūpūlehu modeled areas.

Type	**Marine drivers**	**Hāʻena**	**Kaʻūpūlehu**
Wave disturbance	Wave power	21,697 (4,119)	2,756 (186)
Geographic	Depth	-8.0 (4.4)	-7.3 (5.1)
	Distance to shore	594.5 (422.8)	269.5 (187.1)
Habitat morphology	BPI (60m)	0.2 (0.2)	0.3 (0.4)
	BPI (240m)	0.9 (1.3)	2.7 (3.3)
	Slope (60m)	2.8 (1.8)	3.4 (2.4)
	Slope (240m)	20.0 (6.8)	19.4 (9.2)
Habitat complexity	Plan curvature (mean)	0.0 (1.2)	-0.1 (1.0)
	Plan curvature (std)	18.1 (9.3)	13.8 (9.9)
	Profile curvature	0.0 (0.1)	0.0 (0.1)
	Rugosity	1.0 (0.0)	1.0 (0.0)
Habitat exposure	Aspect (std)	1.1 (0.4)	0.8 (0.5)
	Aspect (cosine)	0.4 (0.4)	0.5 (0.4)
	Aspect (sine)	-0.1 (0.5)	-0.5 (0.4)

2.3.3 Coral reef drivers

The distance-based redundancy analysis (dbRDA) showed that Hāʻena and Kaʻūpūlehu coral reef communities are well separated in ordination space based on key terrestrial drivers (freshwater, nitrogen, and phosphorus) and marine drivers (wave, distance from shore and depth) (Figure 2.8). The first axis was positively correlated with wave power and accounted for 57.8% of the fitted variation (34.1% of the total variation), separating the exposed waters of Hāʻena from the sheltered waters of Kaʻūpūlehu. The second axis accounted for 29% of the fitted variation, equivalent to 17.1% of the total variation. It showed a positive correlation with distance from shore and a negative correlation with depth, thereby separating the wider and shallower eroded island shelf of Hā'ena from the narrow and deeper island shelf of Kaʻūpūlehu. The second axis was also negatively correlated with the terrestrial drivers, highlighting the higher levels of nitrogen in Kaʻūpūlehu compared to Hāʻena, as opposed to higher levels of freshwater and phosphorus in Hāʻena compared to Kaʻūpūlehu.

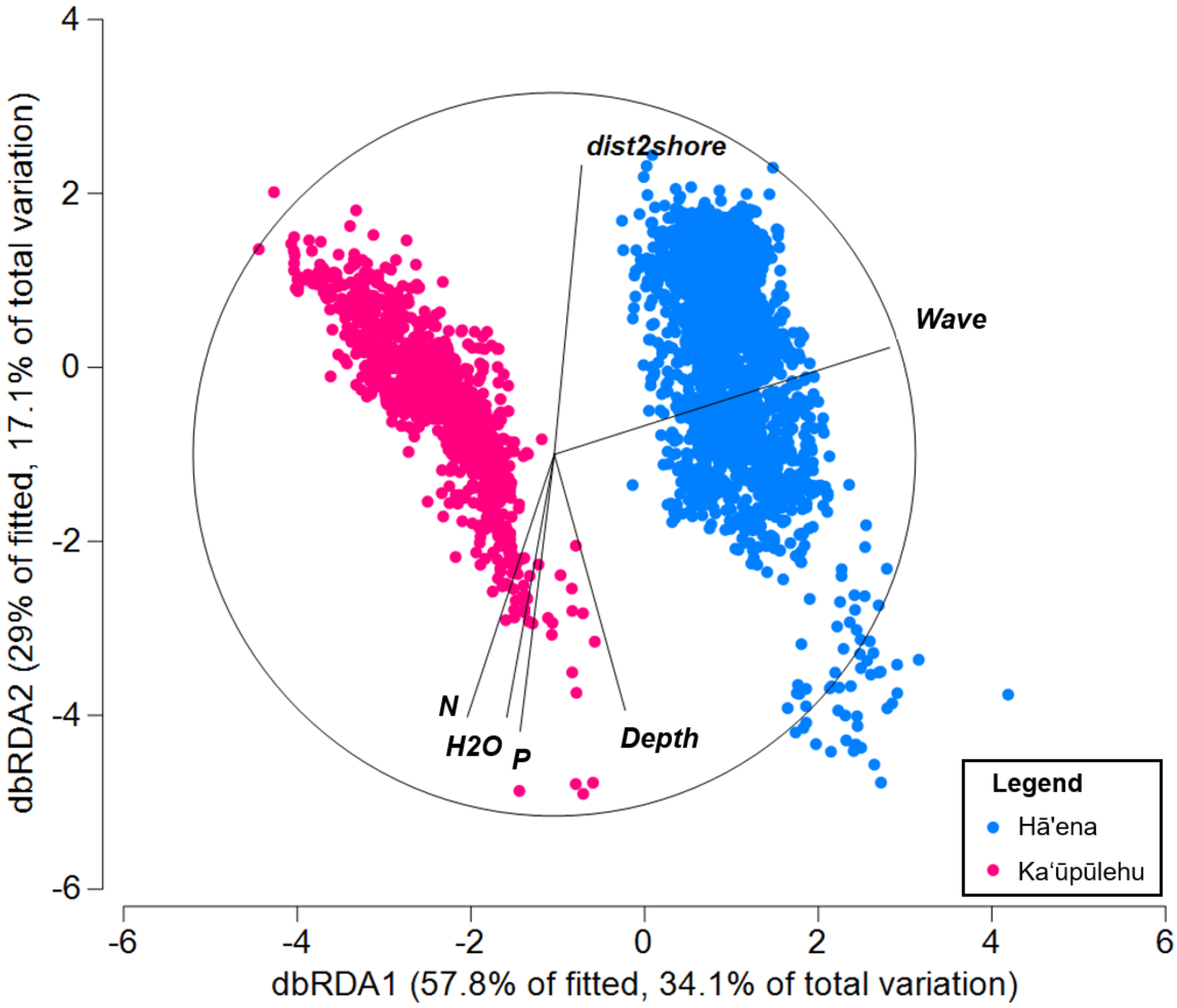


Figure 2.8. dbRDA of the coral reef communities. Ordination plot illustrating the relationship between terrestrial and marine drivers that best explain the variation of benthic and fish indicators (a) in Hāʻena (blue dots) and (b) Kaʻūpūlehu (pink dots). The dbRDA vectors overlays are shown for the environmental drivers explaining a significant proportion of the variation: Wave, distance to shore (dist2shore), depth, groundwater (H2O) and nutrients (N and P) are the key drivers differing Hāʻena from the Kaʻūpūlehu coral reef communities.

The calibration and cross-validation of coral reef models of Hāʻena explained 34-74% and 10-51% of the deviance, respectively (Table 2.7). At Kaʻūpūlehu, the calibration and cross-validation of coral reef models explained 21-60% and 5-26% of the deviance, respectively. Analysis of the residuals from the final coral reef models showed no spatial autocorrelation (Moran's I Index p > 0.1).

Table 2.7. Coral reef model performance. The percent deviance explained (PDE) by the BRT models for the calibration and cross-validation (CV) processes and the final number of predictors (Pi) is shown for Hāʻena and Kaʻūpūlehu.

Reef indicators	**Hāʻena**			**Kaʻūpūlehu**		
	PDE (%)	**CV PDE (%)**	**Pi**	**PDE (%)**	**CV PDE (%)**	**Pi**
CCA	74	51	4	22	5	4
Corals	67	47	4	60	26	4
Macroalgae	50	27	7	28	7	4
Turf algae	44	10	6	33	10	6
Browsers	34	12	5	21	5	6
Grazers & Detritivores	49	25	7	50	16	6
Scrapers & Excavators	41	10	6	50	20	5
Piscivores	41	10	6	32	10	7

The final coral reef models found that Hāʻena is mostly structured by natural disturbances (wave and freshwater) and distance from shore, while Kaʻūpūlehu is mostly driven by local drivers, like habitat structure and land-based nutrients (Figure 2.9). The response curves characterizing those relationships showed group-specific responses to key drivers, as well as similarities and differences between the two geographical locations (Figures S2.2 & S2.3). Those empirically derived relationships influence the distribution of the benthic and fish indicators at each site (Figures 2.10 & 2.11).

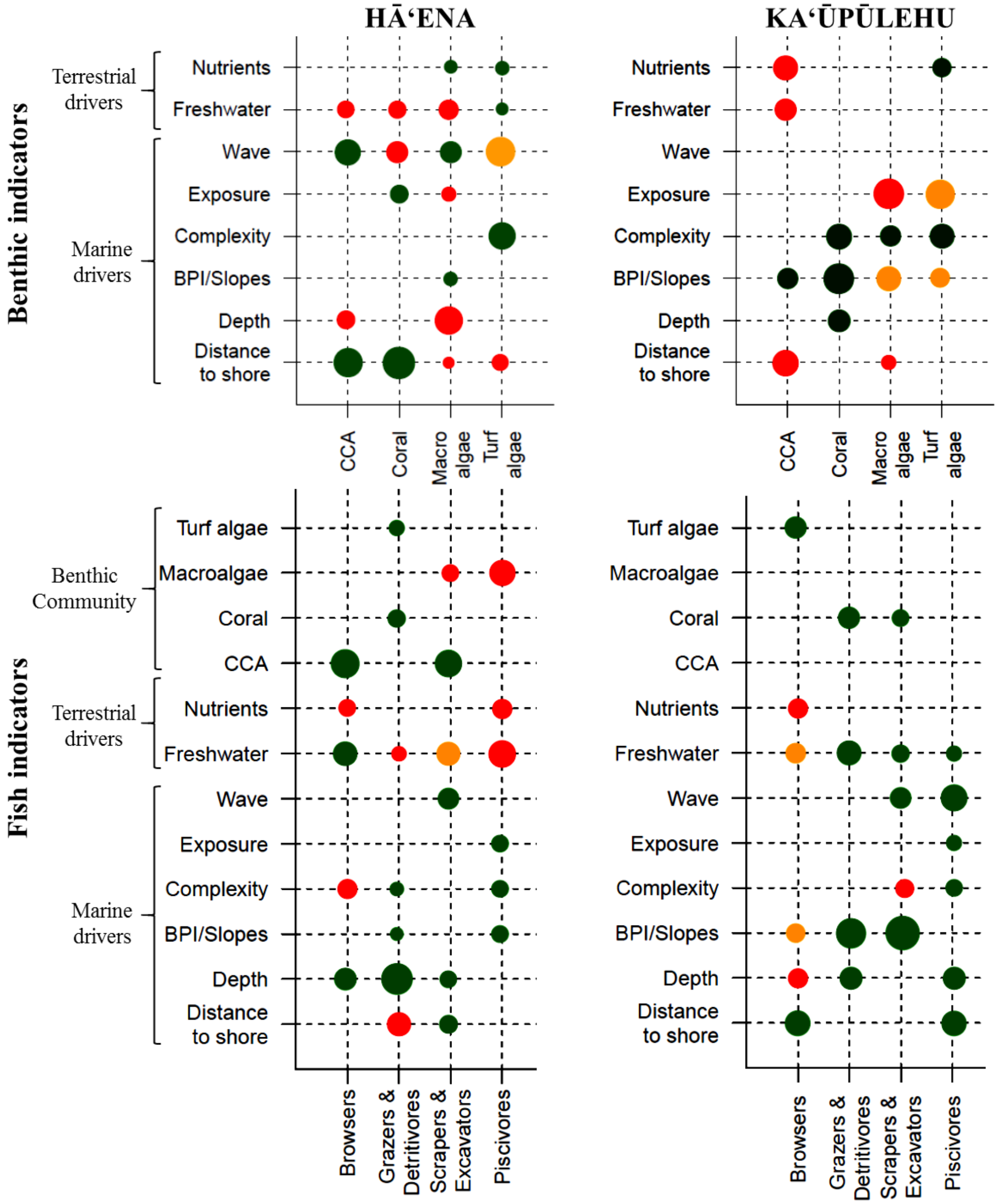


Figure 2.9. Coral reef models and key drivers of benthic and fish indicators. The BRT models identify the key drivers of the benthic and fish indicators. The benthic (top) and fish (bottom) indicators are represented along the X axes. The terrestrial drivers, marine drivers, and benthic community for the fish indicator only are represented on the Y axes. The bubble size represents the relative percent contribution of each driver and the color indicates whether the relationship between the indicator and the driver is positive (green), convex or concave or unchanged (yellow), or negative (red).

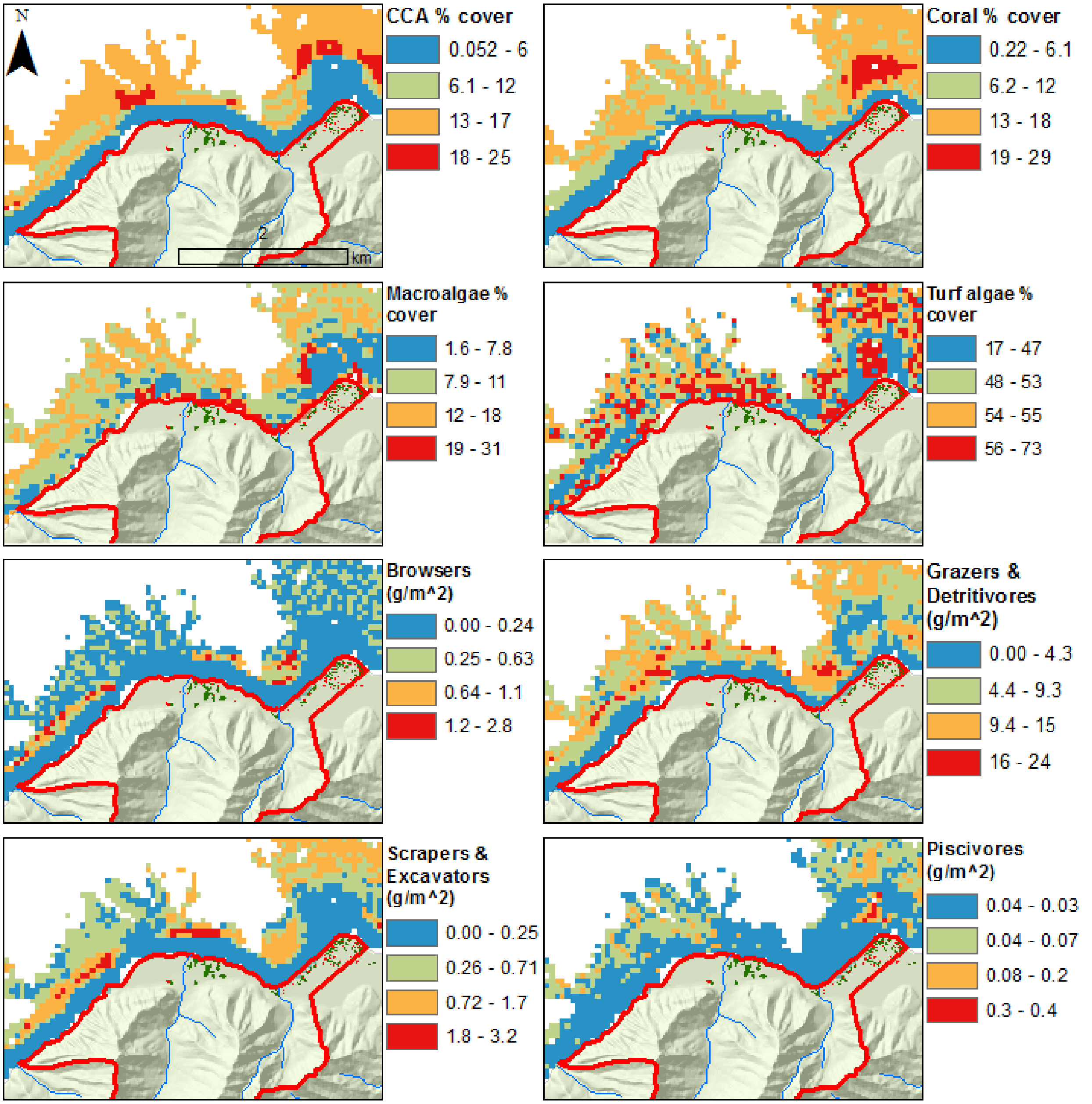


Figure 2.10. Predicted distribution of the coral reef indicators at Hāʻena. Benthic groups are measured in % cover and the fish indicators are measured in g/m^2

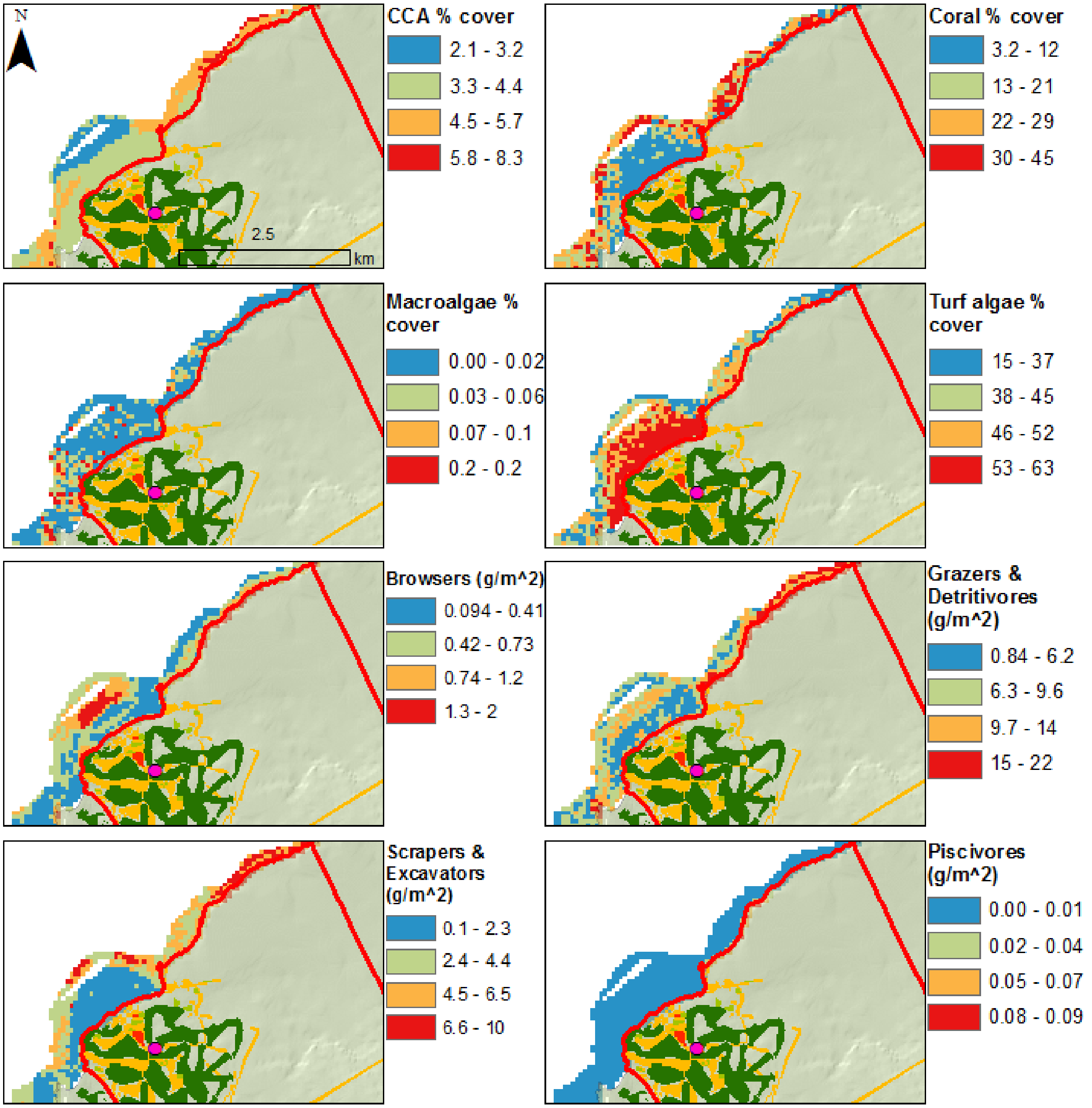


Figure 2.11. Predicted distribution of the coral reef indicators at Kaʻūpūlehu. Benthic groups are measured in % cover and the fish indicators are measured in g/m^2

2.3.3.1 Effect of groundwater discharge on coral reefs

The coral reef models identified groundwater discharge (represented by freshwater) as a more important driver of the benthic community at Hāʻena, compared to Kaʻūpūlehu (Figure 2.9). In both sites, CCA was negatively related with groundwater discharge. In Hāʻena only, coral and macroalgae were negatively related to groundwater discharge, while turf algae showed a positive association. The effects of groundwater discharge varied across fish functional groups, as well as between sites. The relationship between browsers and grazers/detritivores with groundwater discharge were reversed between sites, while the piscivores were negatively related with groundwater discharge at both sites.

2.3.3.2 Effect of wave power on coral reefs

Wave power was an influential marine driver of the benthic community at Hāʻena, but not at Kaʻūpūlehu (Figure 2.9). In Hāʻena, CCA and macroalgae were positively associated with wave power, while coral cover and turf algae responded negatively to wave power. As a result, predicted coral cover was lower and CCA was more abundant and widespread in Hāʻena (Figure 2.10), whereas predicted CCA was lower and coral cover was more abundant and broadly distributed in Kaʻūpūlehu (Figure 2.11). In response to these benthic indicators, fish biomass (for browsers and scrapers/excavators) was higher with CCA at Hāʻena, while fish biomass (for grazers/detritivores and scrapers/excavators) was higher with corals at Kaʻūpūlehu (Figure 2.9). Fish biomass of scrapers/excavators was also positively associated with higher levels of wave power at both sites and piscivores at Kaʻūpūlehu only.

2.3.3.3 Effect of habitat conditions on coral reefs

The geographic metrics (depth and distance from shore) were important predictors in both sites (Figure 2.9). In Hāʻena, CCA and corals were predicted to be more abundant in areas away from the shore, while macroalgae and turf algae are more abundant in areas close to shore (Figure 2.10). In Kaʻūpūlehu, CCA and macroalgae were predicted to be more abundant in nearshore areas, while coral cover was predicted to be higher in deeper waters (Figure 2.11). In both sites, fish biomass was predicted to be higher in deeper waters, with the exception of browsers in Kaʻūpūlehu (Figures 2.10 & 2.11). Fish biomass was also predicted to be higher in areas away from the shore in both sites, with the exception of grazers/detritivores in Hāʻena (Figures 2.10 & 2.11).

The geomorphology metrics (BPI and slope) were more important drivers for the Kaʻūpūlehu coral reef community than for that of Hāʻena (Figure 2.9). In Kaʻūpūlehu, the abundance of CCA, coral, grazers/detritivores, and scrapers/excavators were all positively associated with the reef slopes. Consequently, the biomass of these fish groups was predicted to be higher along the reef slopes of Kaʻūpūlehu (Figure 2.11). Macroalgae, turf algae and browsers were positively associated with flat areas, so higher biomass of browsers is predicted to be found on the reef flats of Kaʻūpūlehu. Surface complexity of the reef was also a positive driver of benthic and fish abundance at both sites, but this was particularly true for the benthic community at Kaʻūpūlehu (Figure 2.9).

2.3.3.4 Effect of land-based nutrients on coral reefs

The coral reef models indicated that nutrients were more important at Kaʻūpūlehu, compared to Hāʻena (Figure 2.9). In Hāʻena, macroalgae and turf algae were weakly but positively related with nutrients (nitrate [Figure S2.2]). Similarly in Kaʻūpūlehu, turf algae responded positively to nutrients (phosphate [Figure S2.3]), whereas CCA was negatively related to nutrients (nitrate [Figure S2.3]). As a result, turf algae, and particularly macroalgae, were predicted to be more abundant in the nearshore and eastern areas of Hāʻena (Figure 2.10), where nutrients discharge from coastal development was higher (Figure 2.7). In Kaʻūpūlehu, turf algae distribution is predicted to be concentrated near higher sources of nutrients, such as golf courses, while CCA abundance is predicted to be higher in areas away from nutrients inputs (Figure 2.11). In response to these benthic communities, fishes were more strongly associated to macroalgae at Hāʻena (scrapers/excavators and piscivores), while fishes were more dependent on turf algae at Kaʻūpūlehu (browsers) (Figure 2.9). Fish biomass was also negatively associated with higher levels of nutrients at both sites (Figure 2.9). More specifically, browsers and piscivores were negatively associated with nitrate in Hāʻena (Figure S2.2), while browsers were negatively related with phosphate in Kaʻūpūlehu (Figure S2.3).

2.4. Discussion

I present a novel integrated framework that links fine-scale land use to coral reef dynamics through groundwater, to support ridge-to-reef management at the (sub) watershed-scale on small oceanic islands. I used this approach to characterize the dynamics of two oceanic island environments subject to very different disturbance regimes. Over time, exposure to natural disturbances have sculpted a diverse gradient of ridge-to-reef systems along the Hawaiian Islands chain. My results suggest that exposure to rainfall and wave power can influence whether coral reef communities are primarily structured by natural disturbances or local drivers. The coral reef dynamics of Hāʻena characterize an old oceanic island environment eroded by freshwater and wave disturbances, while young Kaʻūpūlehu represents a sheltered and dry oceanic island environment shaped by local drivers, such as marine habitat conditions and human activities (coastal development) (Figure 2.1). Consistent with previous studies (Dollar 1982, Engels et al. 2004, Friedlander & Parrish 1998a, Grigg 1998), my results show that the high wave energy environment of Hāʻena has shaped a coral reef community founded on CCA, while the low wave energy environment of Kaʻūpūlehu has allowed for the accretion of a coral driven community. In response, the fish-habitat linkages of Hā'ena is more strongly related to CCA, while in Kaʻūpūlehu fishes is more strongly associated to corals and habitat structure. With the exception of wave sheltered back-reef areas, the benthic community of Hā'ena may benefit from dilution and mixing of land-based source nutrients attributable to high rainfall and wave power. In contrast, the Kaʻūpūlehu benthic community may be more vulnerable to land-based sources of nutrients due to naturally high levels of dissolved nutrient in groundwater, combined with low dilution and mixing from limited rainfall and wave action. Below I discuss the mechanisms by which the most important drivers found in this study may influence reef benthic and fish communities.

2.4.1 Effect of natural disturbances on coral reefs

2.4.1.1 Effect of groundwater discharge on coral reefs

Our groundwater models reflect the different rainfall patterns (Giambelluca et al. 2012), where recharge and discharge at Hāʻena are much higher than at Kaʻūpūlehu and consequently play a higher role in structuring reef communities at Hāʻena. Groundwater discharge can reduce salinity (Jokiel et al. 1993) and/or temperature in shallow waters (Bienfang 1980, Knee et al. 2010).. Consistent with the ecology and salinity tolerance of CCA on coral reefs (Adey 1986), CCA responded negatively to groundwater discharge in both sites. Similarly, and also consistent with their ecology (Bahr et al. 2015, Jokiel et al. 1993), coral cover was lower in areas exposed to high groundwater inputs. Results for CCA and corals in Hāʻena suggest that groundwater discharge may hinder their distribution in nearshore areas (Figure 2.10). Conversely, turf algae were positively related to freshwater input (Figure 2.9). Decreases in salinity can directly promote intrinsic turf algae growth or indirectly hinder competition for space by other species (Duarte et al. 2010). Freshwater input had a mixed effect on the distribution of reef fishes, which may be due to the fact that reef fishes may tolerate a wider range of salinity than expected (Wu & Chung 1995).

2.4.1.2 Effect of wave power on coral reefs

Wave disturbance is a key marine driver controlling coral growth, reef development and the structure of Hawaiian benthic reef communities (Dollar 1982, Fletcher et al. 2008). On small high oceanic islands, coral reefs grow as narrow fringing reefs on the subsiding slopes of shield volcanoes. In geologically young islands, sheltered from wave power, coral reefs form relatively narrow fringes, which can drop quickly in deeper waters (Fletcher et al. 2008), such as in Kaʻūpūlehu. In geologically older islands exposed to wave power, coral reefs form wider and shallower reef flats eroded by wave action (Fletcher et al. 2008), such as are found in Hāʻena. In Hāʻena, wave power has restricted coral growth to sheltered backreef areas (Figure 2.10) like the Makua reef complex (Figure 2.1) (Goodell 2015). By contrast, Kaʻūpūlehu coral growth is not limited by wave power (Fletcher et al. 2008, Grigg 1998) and therefore was more widespread across the reef slopes (Figure 2.11). Coral cover was higher in deeper waters at Kaʻūpūlehu and in areas away from the shore at Hāʻena, both demonstrating association with well mixed waters (Friedlander & Brown 2006). Similar to coral reefs in exposed settings (Fletcher et al. 2008), CCA abundance was greater in the high-wave environment of Hāʻena (Figure 2.10), where it stabilizes the reef structure (Smith et al. 2016) and promotes recovery post-disturbances through coral larval recruitment (Harrington et al. 2004, Price 2010). The coral and CCA abundance patterns in both sites indicate that CCA may be out-competed by coral under wave conditions suited to coral growth, but flourish in wave conditions adverse to coral growth (Figures 2.10 & 2.11) (Engels et al. 2004, Friedlander & Parrish 1998a, Friedlander et al. 2014, Jokiel et al. 2004). These patterns have also been observed across the Hawaiian archipelago (Dollar & Grigg 2004, Grigg 1998, Jokiel 1978), where coral reefs in exposed settings are dynamic, subject to renewal, and often suppressed to a thin veneer (Grigg 1983), while coral reefs in sheltered areas can accrete slowly over time and are more stable (Dollar 1982, Grigg 1983). These different benthic community dynamics have implications for habitat conservation and coral reef resilience management.

The effect of wave disturbance on reef fish community structure in Hawaiʻi is not well studied, due to the challenges of conducting field work in high wave environments (DeMartini et al. 1996, Friedlander & Parrish 1998b, Friedlander et al. 2003). My results implied that wave energy indirectly influences fish through habitat association: at Hāʻena, browser, scraper and excavator biomass have positive association with CCA cover, which dominate in the high wave energy environment, while at Kaʻūpūlehu, scraper and excavator biomass has positive association which coral, which is more dominant in deeper, sheltered areas. Fish biomass for scrapers and excavators was also higher in more exposed wave environments and deeper reefs in both sites (Figure 2.9). These results suggested that fishes seek refuge in deeper waters at Hāʻena to avoid the metabolic costs of operating in high wave energy environments (Friedlander & Parrish 1998b), while in Kaʻūpūlehu fishes may seek deeper areas to avoid fishing pressure (Goetze et al. 2011) and may benefit from reduced human access due to wave action (Stamoulis et al. 2016).

2.4.2 Effect of habitat conditions on coral reefs

Owing to their geological ages coupled with erosion from natural disturbances (Fletcher et al. 2008), coral reefs of Hāʻena and Kaʻūpūlehu exhibit very different habitat geomorphology and complexity. Many studies have shown that habitat geomorphology and complexity are primary marine drivers controlling coral reefs in Hawaiʻi (Friedlander & Parrish 1998a, Friedlander et al. 2003, Friedlander & Brown 2006, Stamoulis et al. 2016). The results for Kaʻūpūlehu in particular are consistent with these findings, with benthic and resource fish communities depending strongly on the reef geomorphology and habitat complexity, as opposed to Hāʻena (Figure 2.9). The reef calcifying groups are more abundant along the reef slopes while the benthic algae are on the reef flats (Figure 2.9). Resource fish biomass is generally higher along reef slopes, with high structure, such as spur and grooves carved by water circulation (Friedlander & Brown 2006) (Figure 2.10 & 2.11). The disparate importance of habitat structure between both sites implied that natural disturbances are the primary drivers of coral reef communities in exposed settings, while habitat conditions play a more important role in protected settings.

2.4.3 Effect of land-based nutrients on coral reefs

Our nutrient transport model results highlighted that Kaʻūpūlehu has relatively high natural nutrient loads, consistent with leaching from agricultural activities (Fackrell et al. in press), though the land cover types above the groundwater flow path only consists of barren rock, grass lands, shrub land, and some native forests (Engott 2011). Therefore, groundwater provides a large fraction of the coastal nitrogen load. Some have hypothesized that groundwater in this region may be geothermally altered (Fackrell et al. in press), but the exact source of these background nutrients remains unknown. Compounded with lower groundwater recharge, the concentrations of dissolved nitrogen in Kaʻūpūlehu are much higher, compared to Hāʻena (Figure 2.6). Kaʻūpūlehu results are consistent with other areas on the dry leeward side of Hawaiʻi Island, where coastal groundwater nutrient fluxes were estimated as high as 2,000 and 200 kg/ha/yr for nitrogen and phosphorus, respectively (Street et al. 2008). These values are high compared to other less dry high latitude oceanic islands, such as South Korea (N:1,100 and P:20 kg/ha/yr) (Street et al. 2008). Results for Hāʻena are consistent with other wet and rural ahupuaʻa on the windward side of Kauai (Knee et al. 2008), Oʻahu (Garrison et al. 2003) and south side of Molokaʻi (Street et al. 2008). In Hanalei Bay, groundwater provides over 2.7 times more nutrients to the coastal environment than Hanalei River (Knee et al. 2008). Nutrient fluxes in Kahana Bay, on the windward side of Oʻahu, were estimated as 170 and 19 kg/ha/yr for nitrogen and phosphorus, respectively (Garrison et al. 2003). On other tropical oceanic islands where surface water runoff is negligible, submarine groundwater discharge has been identified as a major source of nutrients to coral reefs, including Reunion Island (Cuet et al. 2011), and Mauritius Island, and were partly linked to sewage pollution (Gendre et al. 1994) and agriculture (Povinec et al. 2012).

In addition to the natural nutrient loads, groundwater can be enriched by human activities (Amato et al. 2016, Lapointe et al. 1999). This study identified wastewater disposal via cesspools for Hāʻena as the major source of human-derived nutrients (Table 2.4). Sewage on coral reefs has been recognized as a major environmental problem in Hawaiʻi (Amato et al. 2016, Smith et al. 1981) as well as in regions such as the Red Sea (Walker & Ormond 1982), Florida Keys (Lapointe et al. 2005), and the Great Barrier Reef (Bell 1992) Cesspools represent the most prevalent wastewater disposal system across the main Hawaiian Islands and have been recognized as a primary driver of groundwater and nearshore water quality degradation (Whittier & El-Kadi 2014a). Although, the Hawaiʻi Department of Health revised wastewater regulations to ban new cesspools for the entire state in 2016 (HAR Title 11, Chapter 62), cesspools still account for 76% and 84% of the OSDS currently used on Kauaʻi and Hawaiʻi Island, respectively (Whittier & El-Kadi 2014a). For Kaʻūpūlehu, we identified green spaces, such as golf courses, as the major source of human-derived nutrients (Table 2.4). Studies elsewhere in Hawaiʻi have showed that nutrient concentrations can be significantly higher in proximity to golf courses (Derse et al. 2007, Dollar & Atkinson 1992, Knee et al. 2010), thereby calling for best management practices for fertilizer application.

2.4.3.1 Marine sinks of land-based nutrients

Macroalgae and turf algae responded positively to nitrate in Hāʻena, while turf algae was positively related to phosphate and CCA was negatively related to nitrate in Kaʻūpūlehu (Figures 2.9, S2.2, & S2.3). These ecological responses to nutrients suggest that coral reef waters are nitrogen limited in Hāʻena, as was shown in nearby Hanalei Bay (Derse et al. 2007). Phosphate could be a limiting nutrient in Kaʻūpūlehu, as was found in Honokōhau Bay also located on the Kona coast (Prouty et al. 2016). Known to be abundant on healthy reefs (Barott et al. 2009), turf algae can also proliferate rapidly and lead to phase shifts when exposed to land-based nutrients (Fabricius 2005, Vermeij et al. 2010). These results suggest that macroalgae, but particularly turf algae may have a competitive advantage over corals and CCA under nutrient enriched waters, such as Kaʻūpūlehu. Vermeij et al. (2010) showed that local nutrient enrichment can foster turf algae overgrowth, reduce CCA and coral recovery capacity after disturbances, through loss of space availability (Smith et al. 2006). Delivery of nutrient enriched groundwater can negatively affect coral reef calcifiers while promoting benthic algae growth (Fabricius 2005, Littler et al. 2006, Pastorok & Bilyard 1985, Smith et al. 2010, Vermeij et al. 2010).

On coral reefs, herbivores structure benthic communities by controlling the abundance of turf and macroalgae (Littler et al. 2006, Smith et al. 2010, Vermeij et al. 2013) and freeing space for recruitment of coral reef calcifiers (Green & Bellwood 2009). Consistent with Hanalei Bay (Friedlander & Parrish 1998a), macroalgae appear to have been reduced by grazing from herbivores in Hāʻena, given their cover showed a negative relationship with herbivore biomass (Figure 2.9). In this study, grazers/detritivores in Hāʻena and browsers in Kaʻūpūlehu were positively associated with turf (Figure 2.9). The extent to which a reef system possesses these functional groups is fundamental to determine its capacity to resist phase shifts and recover in the face of disturbance (Bellwood et al. 2004).

2.4.4 Management implications

The similarity and differences identified in these ridge-to-reef systems are applicable to other oceanic island environments comprised within this spectrum of natural disturbances. This study confirms the need for ridge-to-reef management grounded in the dynamics of the place. In ridge-to-reef environments exposed to natural disturbances, as represented by Hāʻena, it is critical to adopt management practices that promote coral reef recovery post-disturbances. An appropriate management strategy would be to protect habitats located away from the influence of terrestrial disturbances (Bridge et al. 2013) and those protected from wave power, such as the Makua reef complex, which can act as nursery grounds to replenish coral and fish populations (Figure 2.1) (Goodell 2015). Additionally, upgrading existing cesspools could reduce the nutrients being discharged upstream from Makua reefs complex, which may negatively impact the fish community or the habitat quality (Figure 2.10) of this nursery ground. In addition, the protection of key herbivores, such as scrapers and excavators, can foster CCA and coral recruitment after natural disturbances (Bellwood et al. 2004).

Dry ridge-to-reef environments sheltered from natural disturbances, as represented by Kaʻūpūlehu, call for ridge-to-reef management actions, that which promote coral reef resistance to natural and human disturbances. The coral reef community along the narrow fringing reef appears seems to be susceptible to increases in land-based nutrients (Figure 2.11). Therefore, land-based activities should minimize nutrient inputs into groundwater or coastal waters given the naturally high groundwater nutrient loads (Street et al. 2008). Marine actions should focus on protecting deep water habitats, which can act as refuge for corals and fish populations from human disturbances (land-based nutrients and fishing pressure) (Bridge et al. 2013) coupled with the protection of herbivores to offset the effect of nutrients on turf algae (Bellwood et al. 2004, Littler et al. 2006, Smith et al. 2010).

2.5. Conclusions

With a growing human population and a trend away from traditional ridge-to-reef resource-management practices, managers need to better understand the impact of land-based activities on coral reefs in order to manage them more effectively. Empirical data provide a snapshot of the coral reef at the time of the data collection, but fail to provide future predictions to inform decision making (Stamoulis & Delevaux 2015). Tools to project and anticipate potential impacts are needed to better manage coral reefs (Gurney et al. 2013, Melbourne-Thomas et al. 2011). The linked land-sea models I produced here can help managers evaluate the relative influence of terrestrial and marine drivers on reef communities to better direct strategical investment to maintain system resilience. Furthermore, they can be used to predict downstream responses to future land use and climate change. Although these ridge-to-reef models were built to understand the dynamics specific to these places, many of the effects we described can be generalized and adapted to oceanic island environments comprised within this spectrum of environmental conditions.

Supplementary Material

Table S2.1. Fish species composition per functional groups.

Function	Scientific name	Common name	Hawaiian name
Browsers	*Calotomus carolinus*	Stareye parrotfish	ponuhunuhu
	Naso lituratus	Orangespine unicornfish	umaumalei
	Naso unicornis	Bluespine unicornfish	kala
Grazers & Detritivores	*Acanthurus achilles*	Achilles Tang	paku'iku'i
	Acanthurus blochii	Ringtail surgeonfish	pualu
	Acanthurus dussumieri	Eyestripe surgeonfish	palani
	Acanthurus guttatus	Whitespotted surgeonfish	api
	Acanthurus leucopareius	Whitebar surgeonfish	maikoiko
	Acanthurus nigricans	Goldrim surgeonfish	
	Acanthurus nigrofuscus	Brown surgeonfish	ma'i'i'i
	Acanthurus nigroris	Bluelined surgeonfish	maiko
	Acanthurus olivaceus	Orangeband surgeonfish	na'ena'e
	Acanthurus triostegus	Convict surgeonfish	manini
	Acanthurus xanthopterus	Yellowfin surgeonfish	pualu
	Ctenochaetus hawaiiensis	Black surgeonfish	
	Ctenochaetus strigosus	Goldring surgeonfish	kole
	Zebrasoma flavescens	Yellow tang	lau'ipala
	Zebrasoma veliferum	Sailfin tang	mane'one'o
Scrapers & Excavators	*Chlorurus perspicillatus*	Spectacled parrotfish	uhu uliuli
	Chlorurus spilurus	Pacific bullethead parrotfish	uhu
	Scarus dubius	Regal parrotfish	lauia
	Scarus psittacus	Palenose parrotfish	uhu
	Scarus rubroviolaceus	Ember parrotfish	palukaluka
Piscivores	*Caranx melampygus*	Bluefin trevally	omilu
	Parupeneus cyclostomus	Blue goatfish	moano kea
	Scomberoides lysan	Doublespotted queenfish	lai

Table S2.2. Modeling framework predictor variables description and processing methods. Description of all the predictor variables modeled in the coral reef models. Each metric was classified by type (terrestrial drivers or marine drivers) and coded for modeling. Data source and analytical tool used to generate each metric are provided. Refer to Stamoulis et al. 2016 for more details.

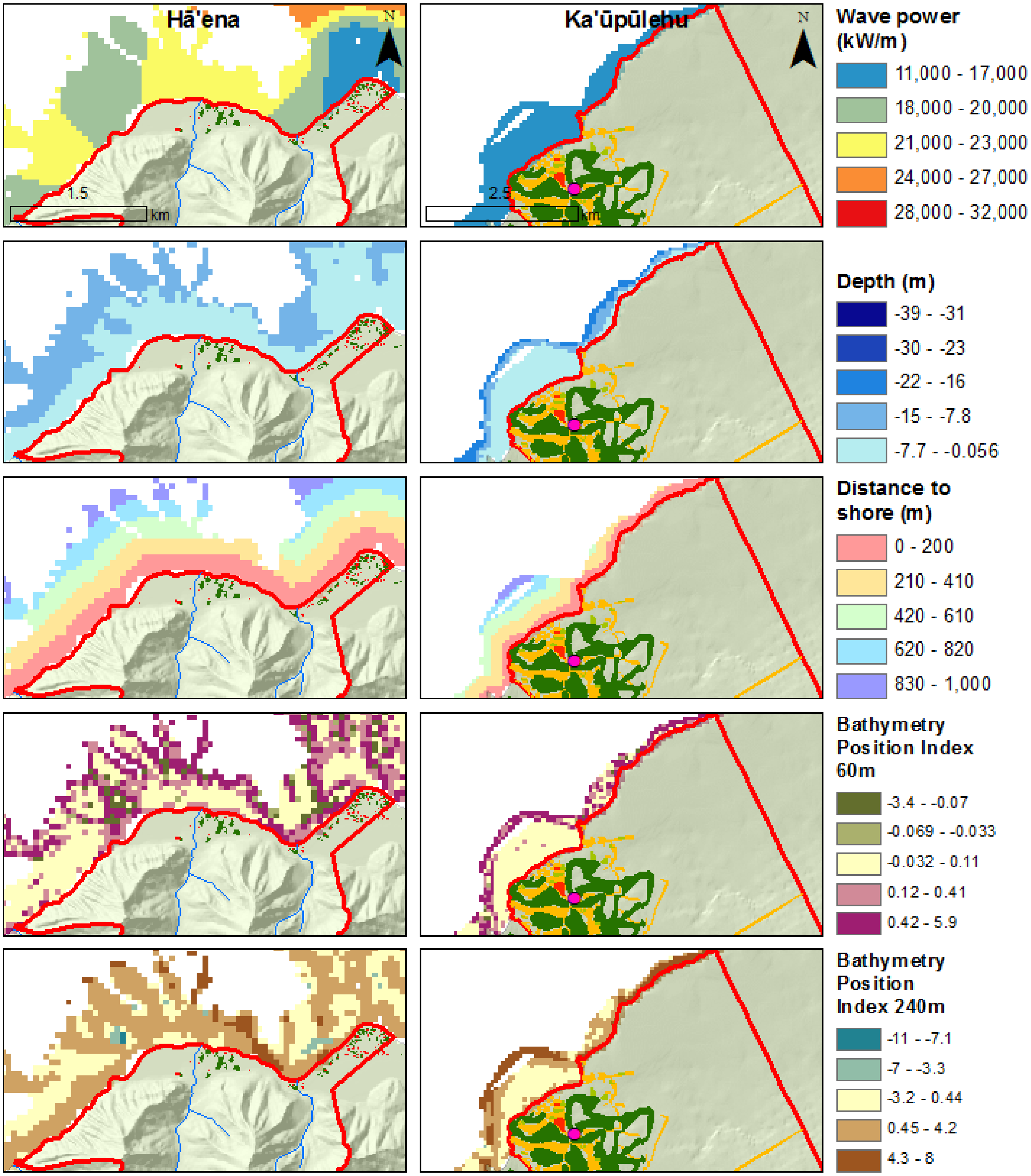
Type	Code	Metric	Source	Description	Analytical tool
Terrestrial drivers	H2O	Freshwater	Groundwater models	Proxy for salinity (/yr)	GIS-based models
	N	Nitrate	Groundwater models	Proxy for land-based source dissolved nitrogen (/yr)	GIS-based models
	P	Phosphate	Groundwater models	Proxy for land-based source dissolved phosphorus (/yr)	GIS-based models
Marine driver (Wave)	wav	Wave power	SWAN wave model[1]	Wave power (kW.m-1)	(Stopa et al. 2013)
Marine drivers (Geography)	Depth	Depth	Bathymetry[2]	Average depth (m)	ArcGIS Spatial Analyst tools (ESRI 2011)
	dist2shore	Distance to shore	Coastline[3]	Distance to nearest land (m)	ArcGIS Spatial Analyst Euclidean Distance tool (ESRI 2011)
Marine drivers (Morphology)	bpi	Bathymetric position index (60m, 240m)	Bathymetry[2]	Mean values indicate a location's position relative to the surrounding area; values can be positive (ridges), negative (valleys), or zero (flat or constant slope)	Benthic Terrain Modeler tool (Wright et al. 2005)
	slp	Slope (60m, 240m)	Bathymetry[2]	Maximum rate of change from a cell to its neighbors	ArcGIS Slope tool (ESRI 2011) ArcGIS Focal Statistics tool (ESRI 2011)
Marine drivers (Exposure)	asp_sd	Surface aspect (standard deviation)	Bathymetry[2]	Slope direction (degree)	ArcGIS Aspect tool (ESRI 2011)

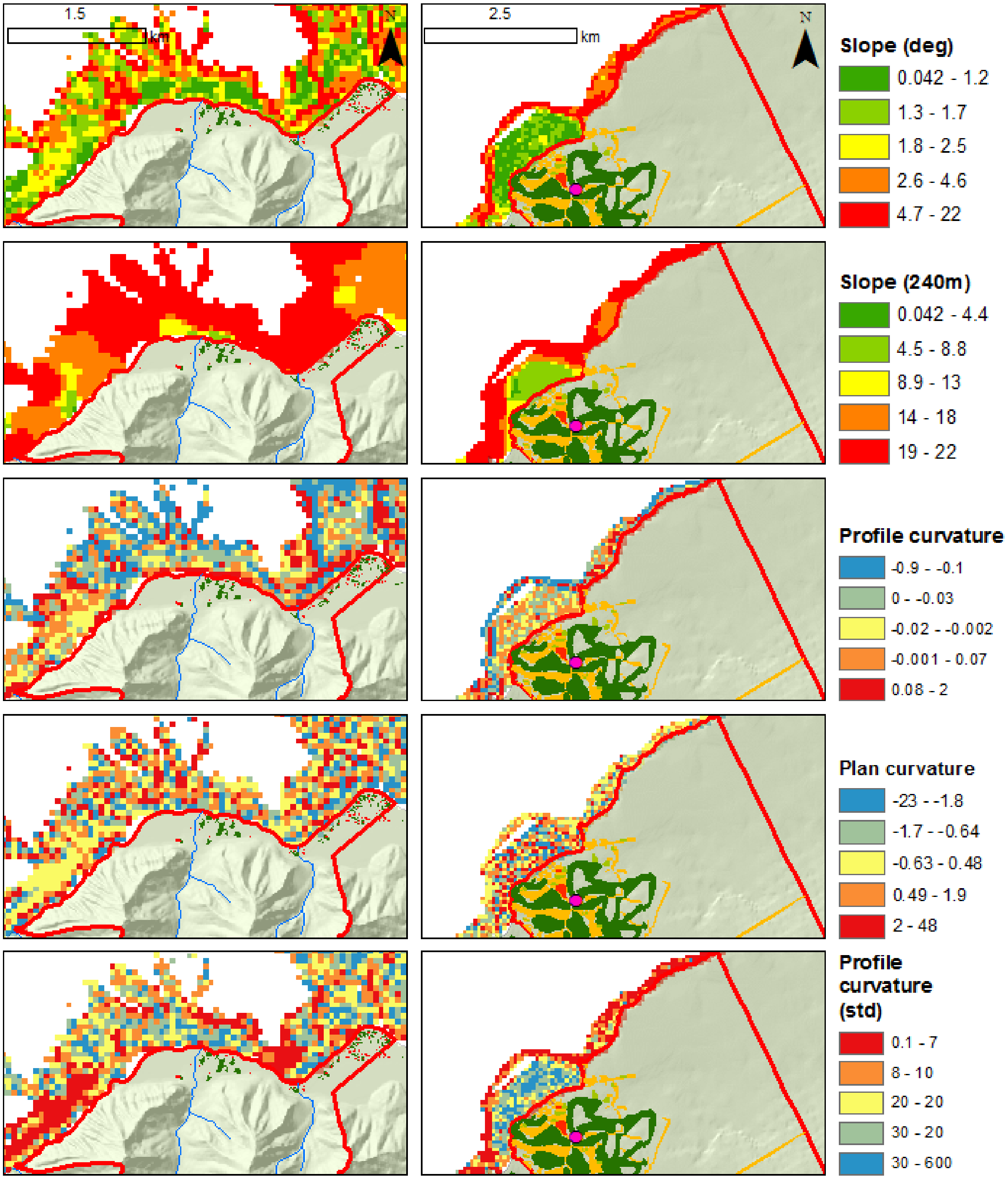
	asp_sin	Sine aspect	Bathymetry^2	Sine of slope direction (derived from transforming the mean aspect into “eastness”) (degree)	ArcGIS Spatial Analyst tools (sine function) (ESRI 2011)
	asp_cos	Cosine aspect	Bathymetry^2	Cosine of slope direction (derived from transforming the mean aspect into “northness”) (degree)	ArcGIS Spatial Analyst tools (cosine function) (ESRI 2011)
Marine drivers (Complexity)	curv_pro	Profile curvature (mean)	Bathymetry^2	Curvature values can be + (concave), - (convex), or 0 (flat). A proxy for spur and groove effects on water flow.	DEM Surface Tools Curvature tool (Jenness 2013)
	curv_plan	Planar curvature (mean)	Bathymetry^2	Curvature values can be – (concave) to + (convex), or 0 (flat) (mean). A proxy for spur and groove effects on water flow.	DEM Surface Tools Curvature tool (Jenness 2013)
	rug	Rugosity	Bathymetry^2	Value range from 1 (flat) to infinity.	DEM Surface Tools Curvature tool (Jenness 2013)
Benthic community	CCA	Crustose coralline algae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	COR	Coral cover	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	MAC	Macroalgae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	TUR	Turf algae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions

[1] SWAN hindcast wave model at 500m native resolution (Stopa et al. 2013)

[2] Bathymetry synthesis at 5m native resolution (HMRG 2015)

[3] Coastline (OP 2000)


Hā'ena
Ka'ūpūlehu
N
N
1.5
km
2.5
km
Wave power (kW/m)
11,000 - 17,000
18,000 - 20,000
21,000 - 23,000
24,000 - 27,000
28,000 - 32,000
Depth (m)
-39 - -31
-30 - -23
-22 - -16
-15 - -7.8
-7.7 - -0.056
Distance to shore (m)
0 - 200
210 - 410
420 - 610
620 - 820
830 - 1,000
Bathymetry Position Index 60m
-3.4 - -0.07
-0.069 - -0.033
-0.032 - 0.11
0.12 - 0.41
0.42 - 5.9
Bathymetry Position Index 240m
-11 - -7.1
-7 - -3.3
-3.2 - 0.44
0.45 - 4.2
4.3 - 8


1.5
km
N
2.5
km
N
Slope (deg)
0.042 - 1.2
1.3 - 1.7
1.8 - 2.5
2.6 - 4.6
4.7 - 22
Slope (240m)
0.042 - 4.4
4.5 - 8.8
8.9 - 13
14 - 18
19 - 22
Profile curvature
-0.9 - -0.1
0 - -0.03
-0.02 - -0.002
-0.001 - 0.07
0.08 - 2
Plan curvature
-23 - -1.8
-1.7 - -0.64
-0.63 - 0.48
0.49 - 1.9
2 - 48
Profile curvature (std)
0.1 - 7
8 - 10
20 - 20
30 - 20
30 - 600

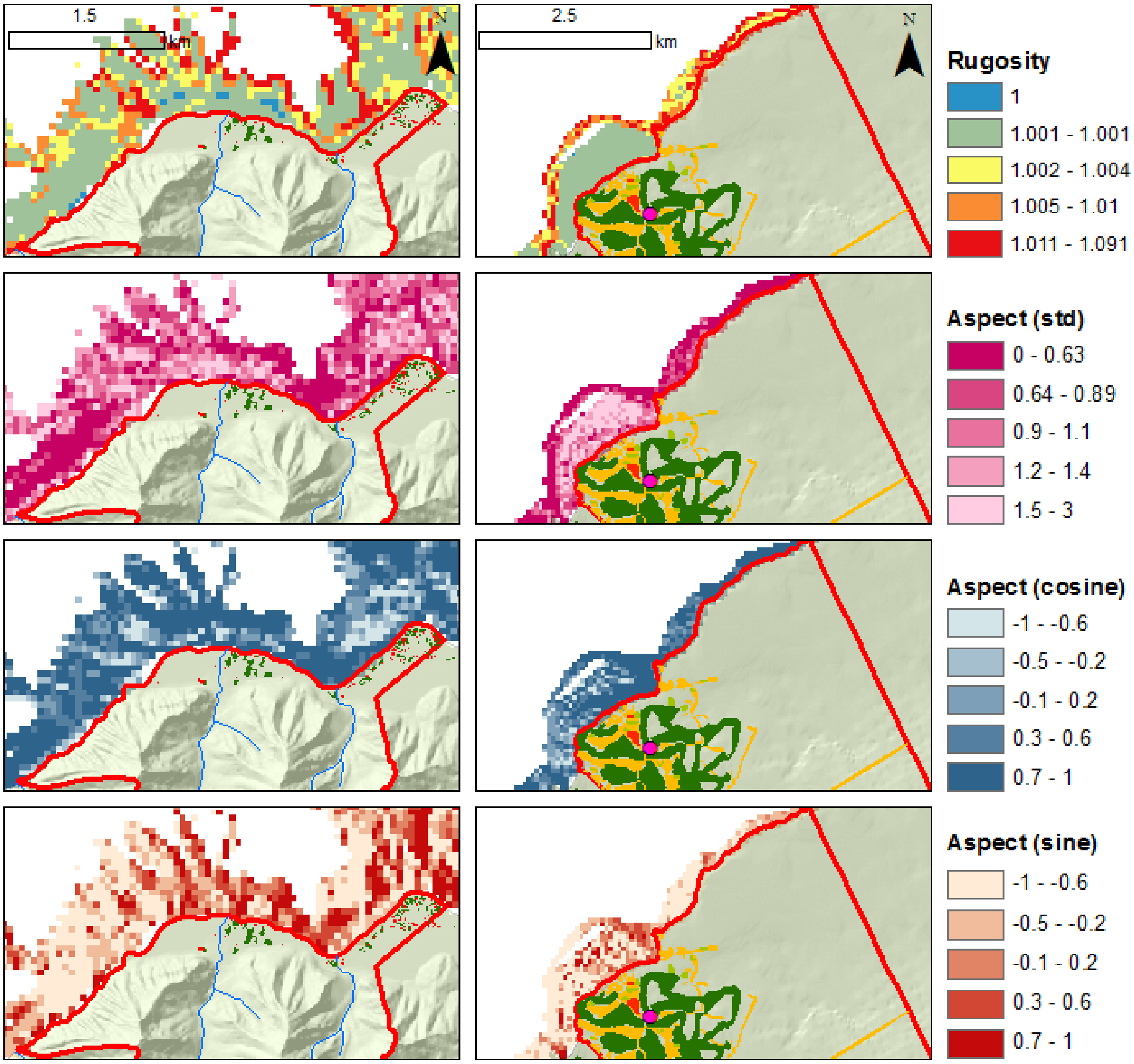
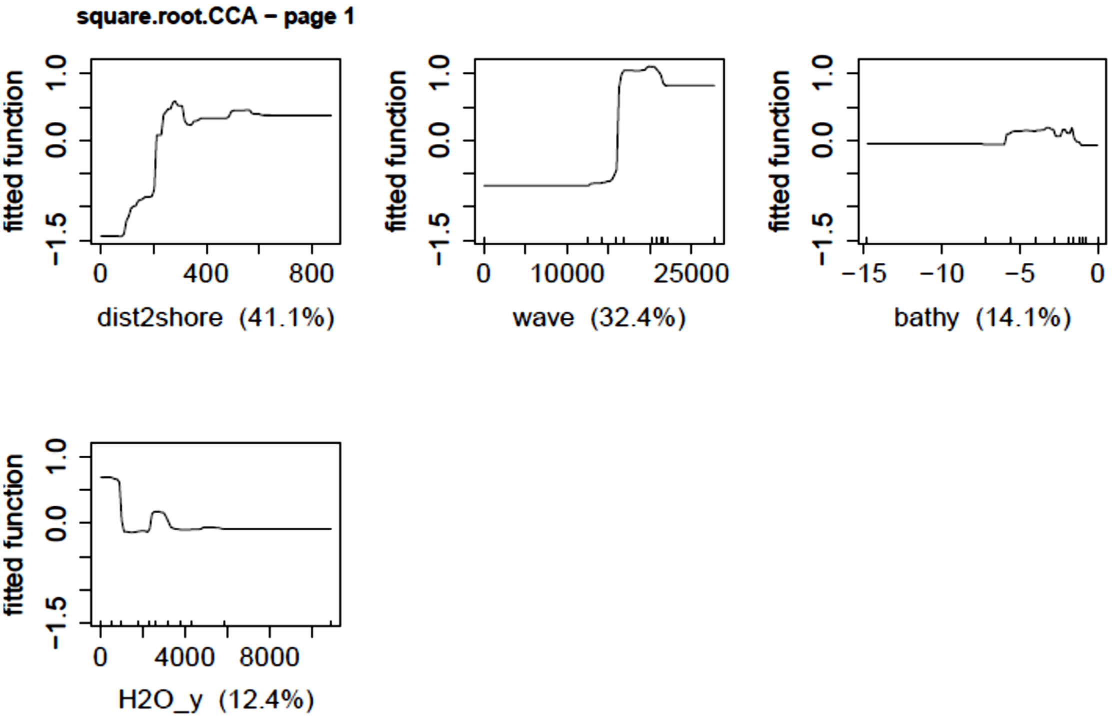
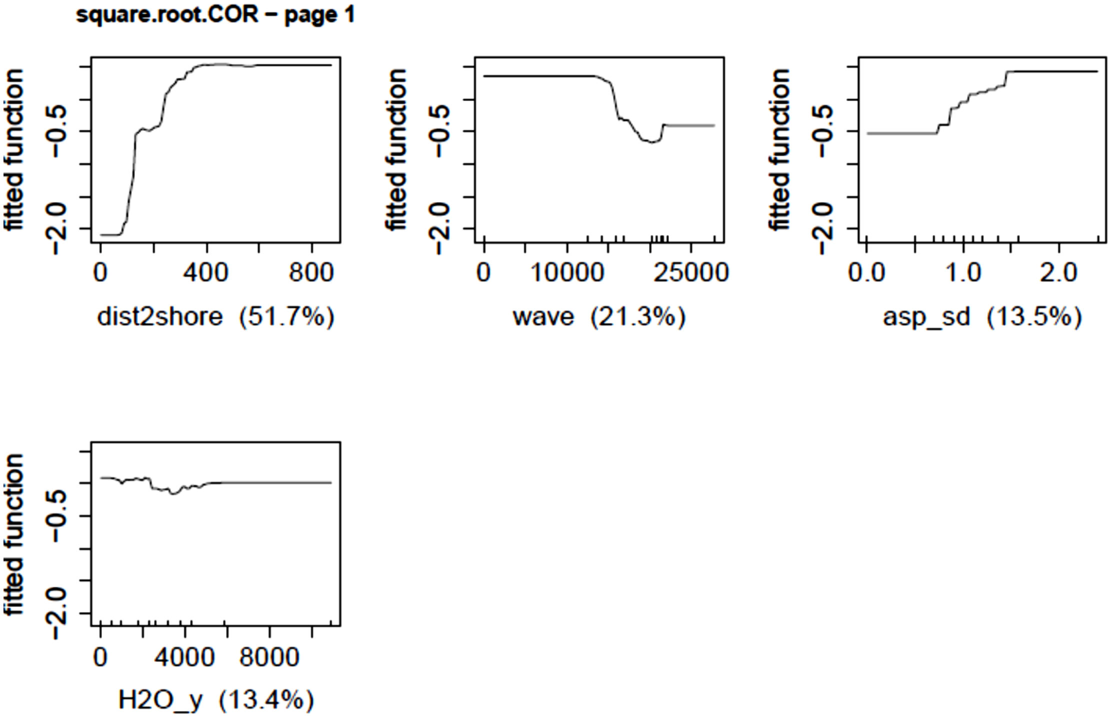
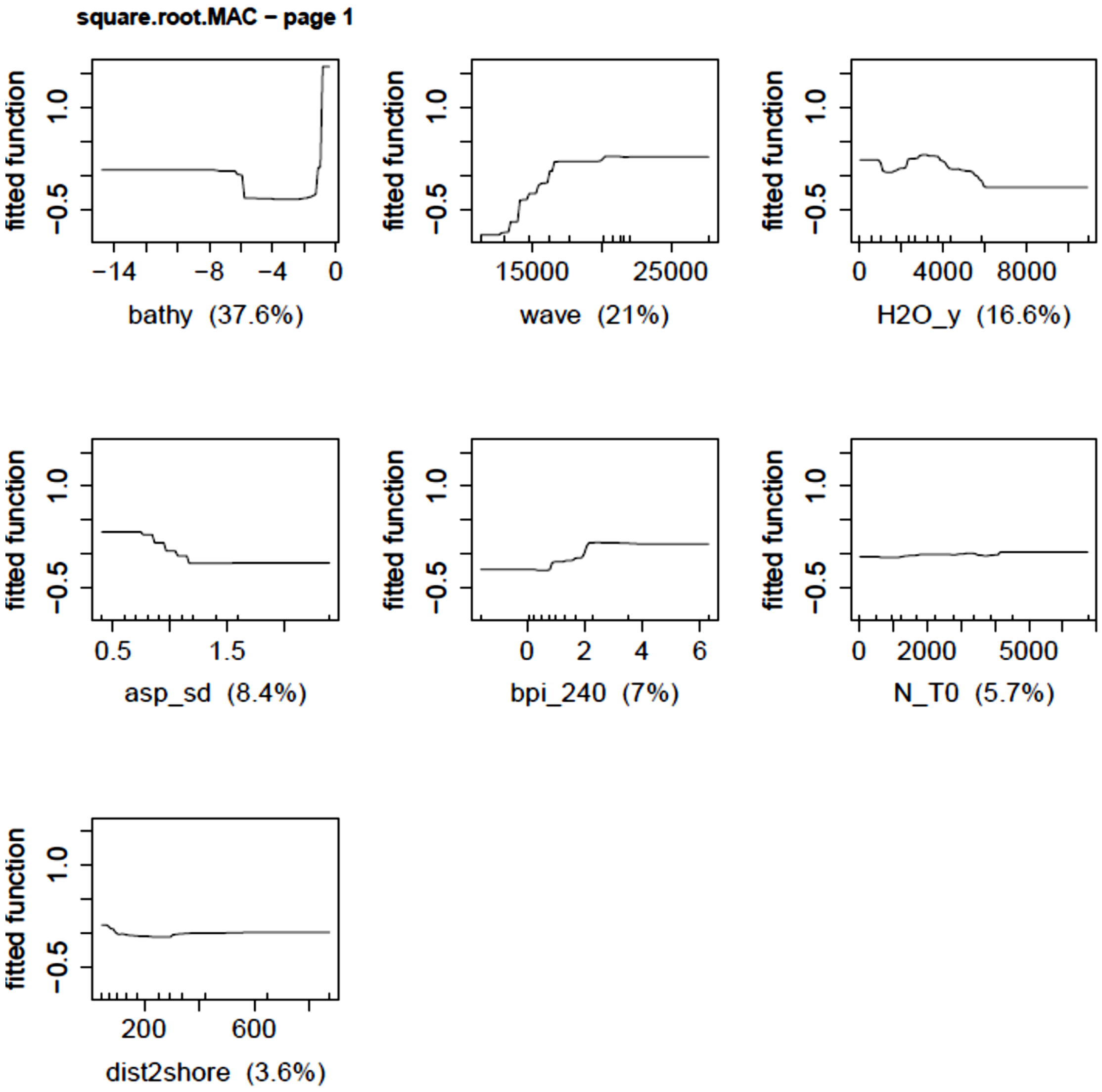
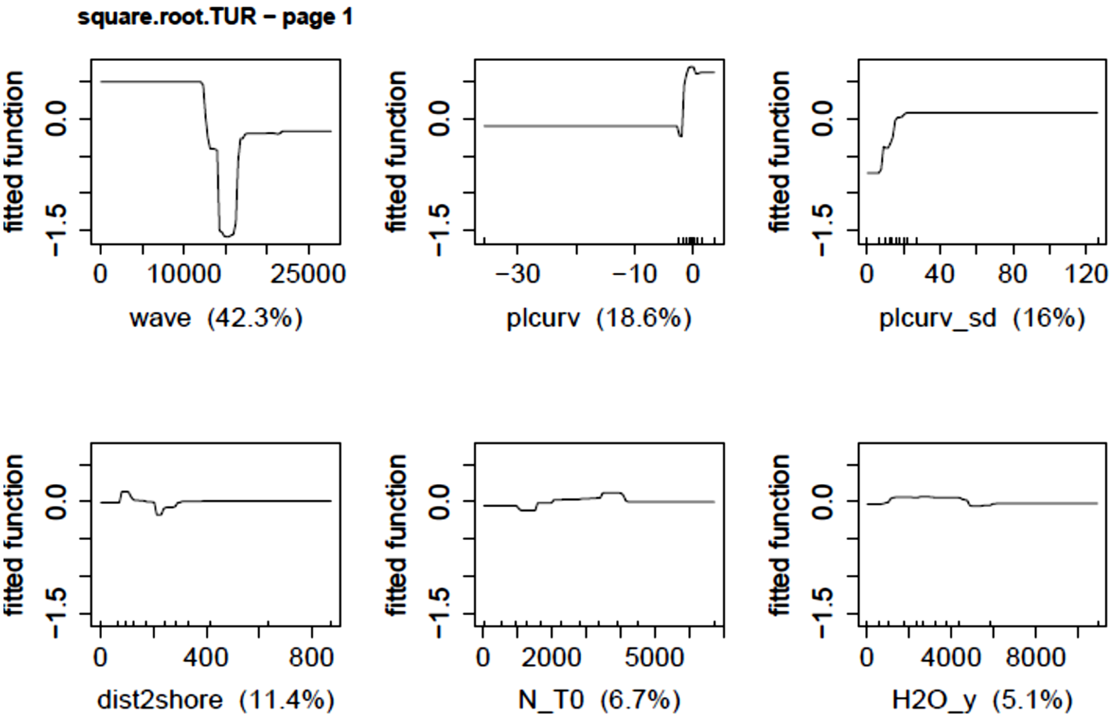


Figure S2.1. Spatial representation of the marine drivers at Hāʻena (left) and Kaʻūpūlehu (right).

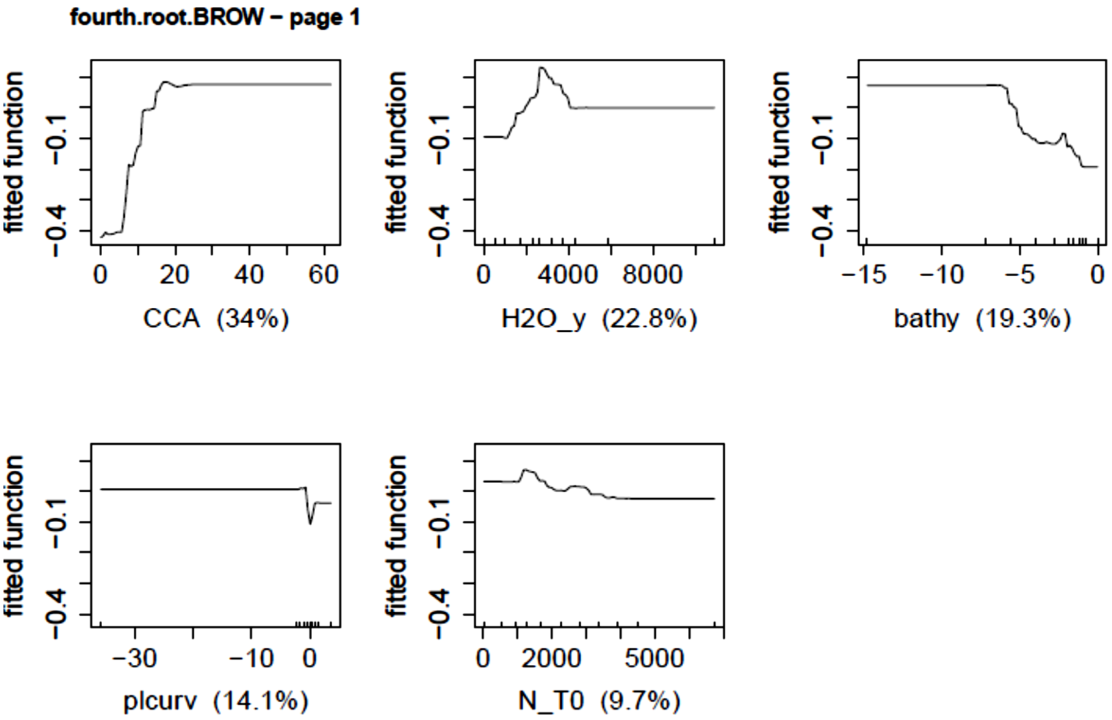

square.root.CCA – page 1


square.root.COR – page 1

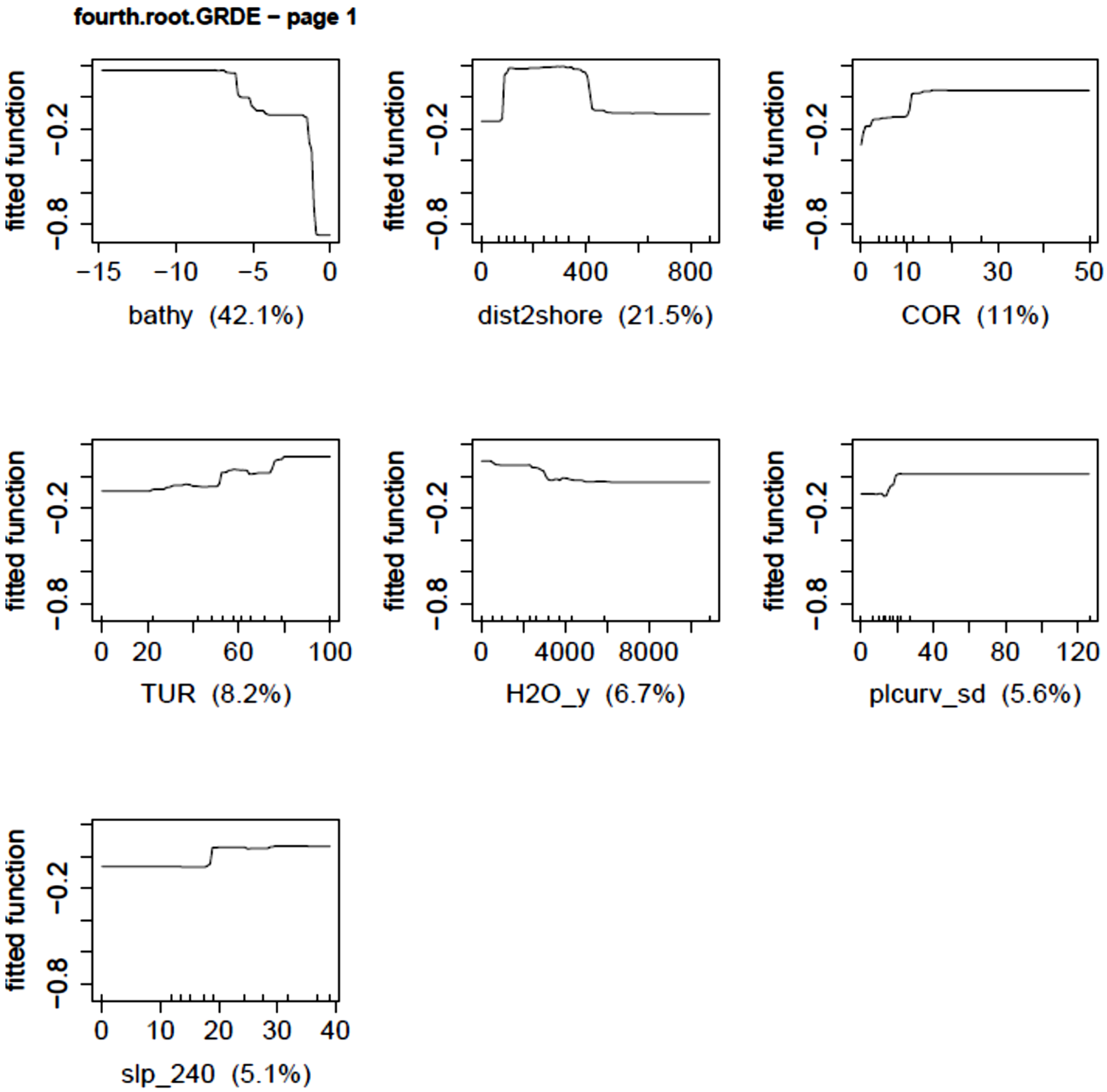

square.root.MAC – page 1
fitted function
−0.5
1.0
−14
−8
−4
0
bathy (37.6%)
15000
25000
wave (21%)
0
4000
8000
H2O_y (16.6%)
0.5
1.5
asp_sd (8.4%)
0
2
4
6
bpi_240 (7%)
0
2000
5000
N_T0 (5.7%)
200
600
dist2shore (3.6%)



square.root.TUR – page 1



fourth.root.BROW – page 1



fourth.root.GRDE – page 1

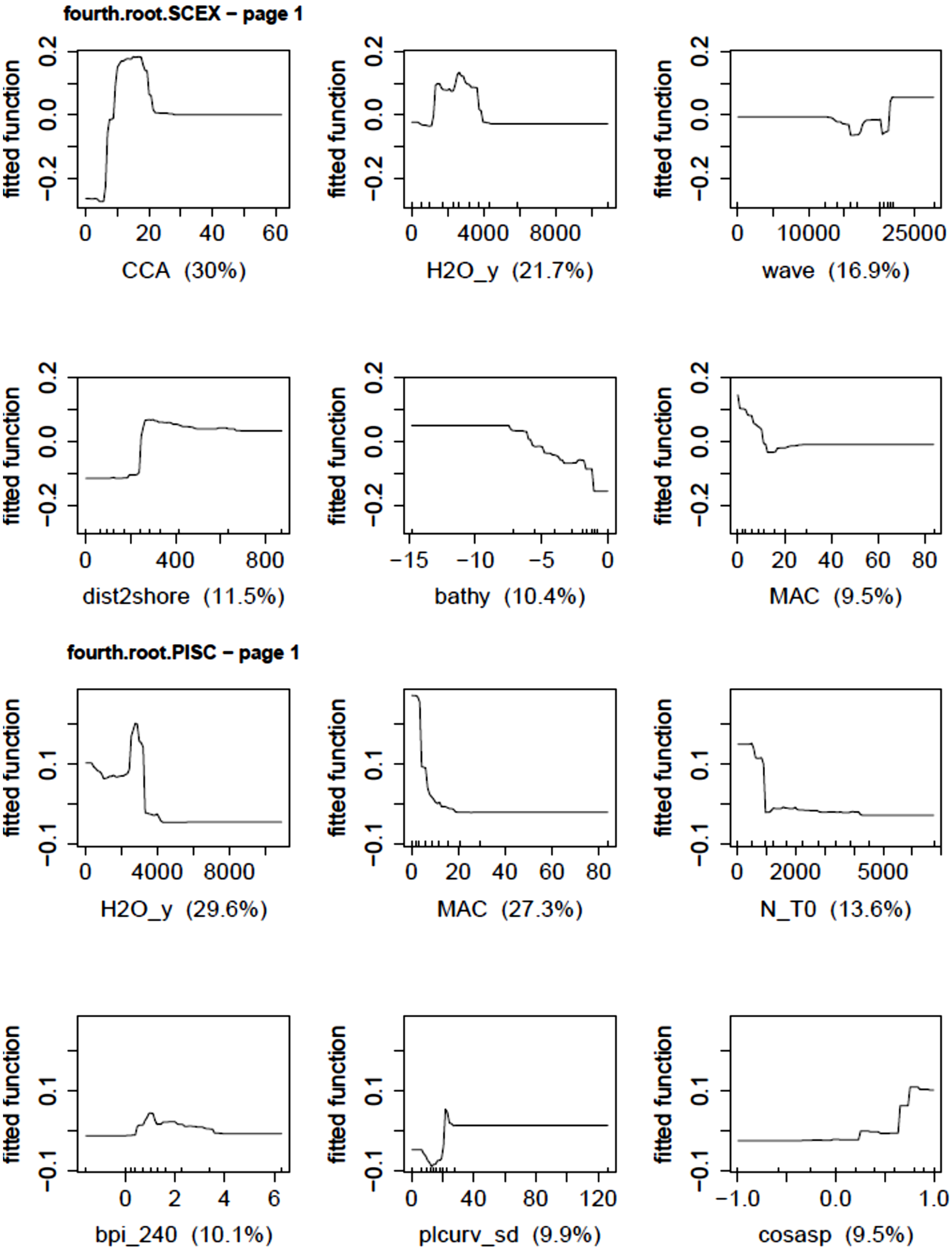
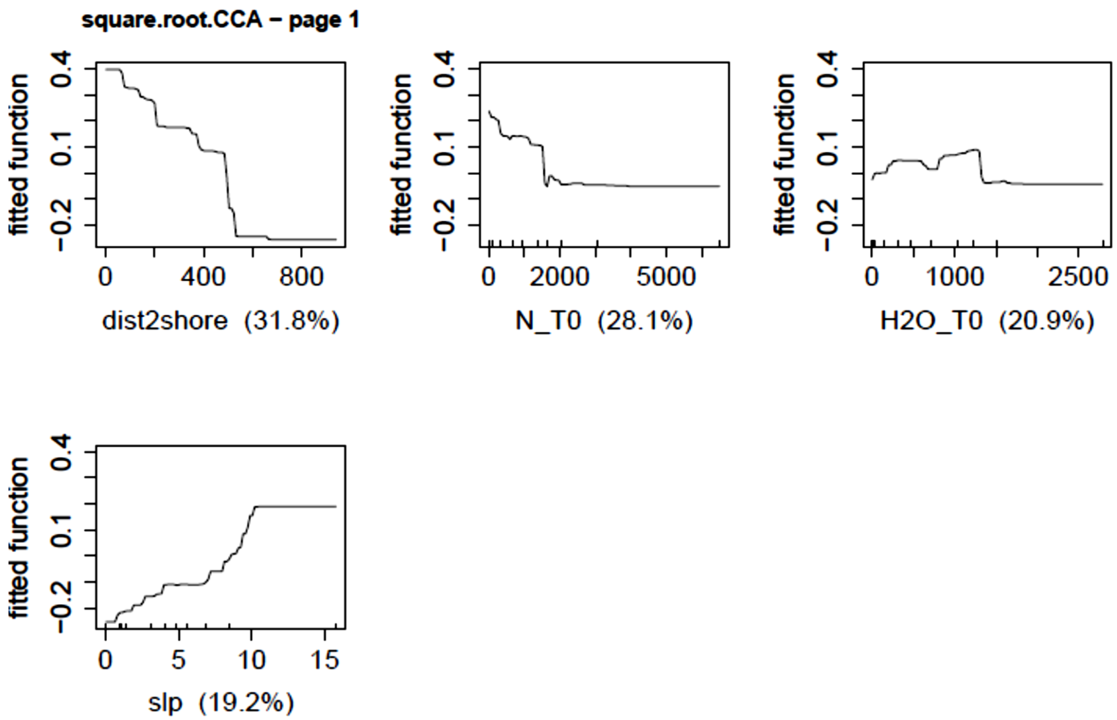
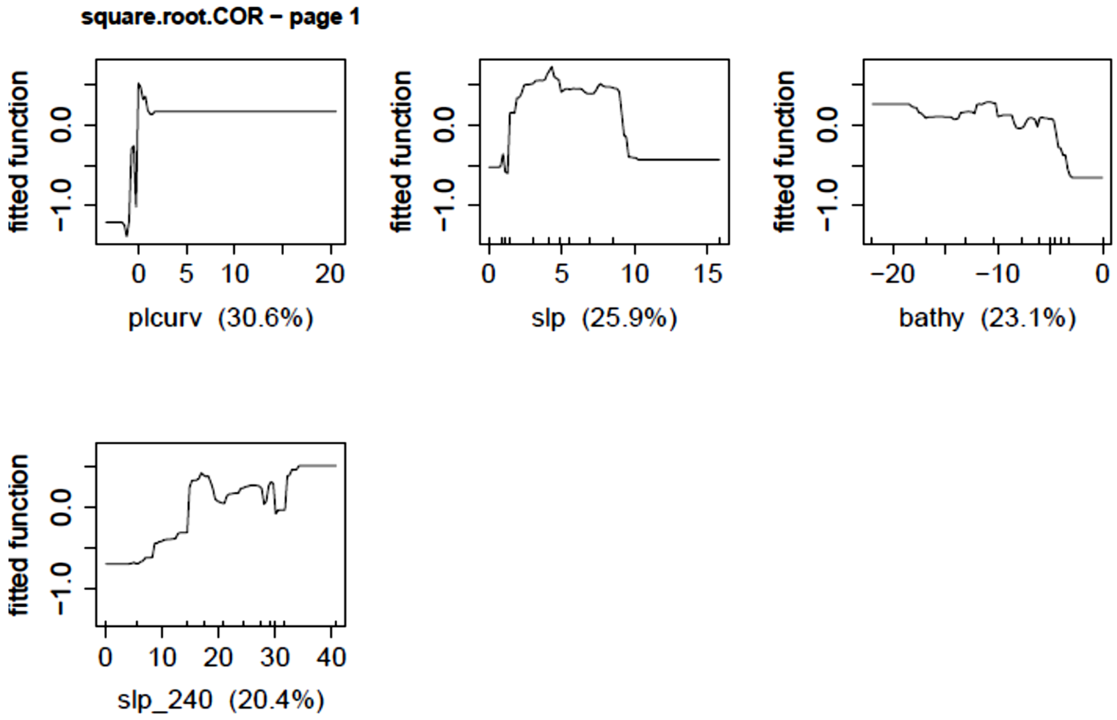
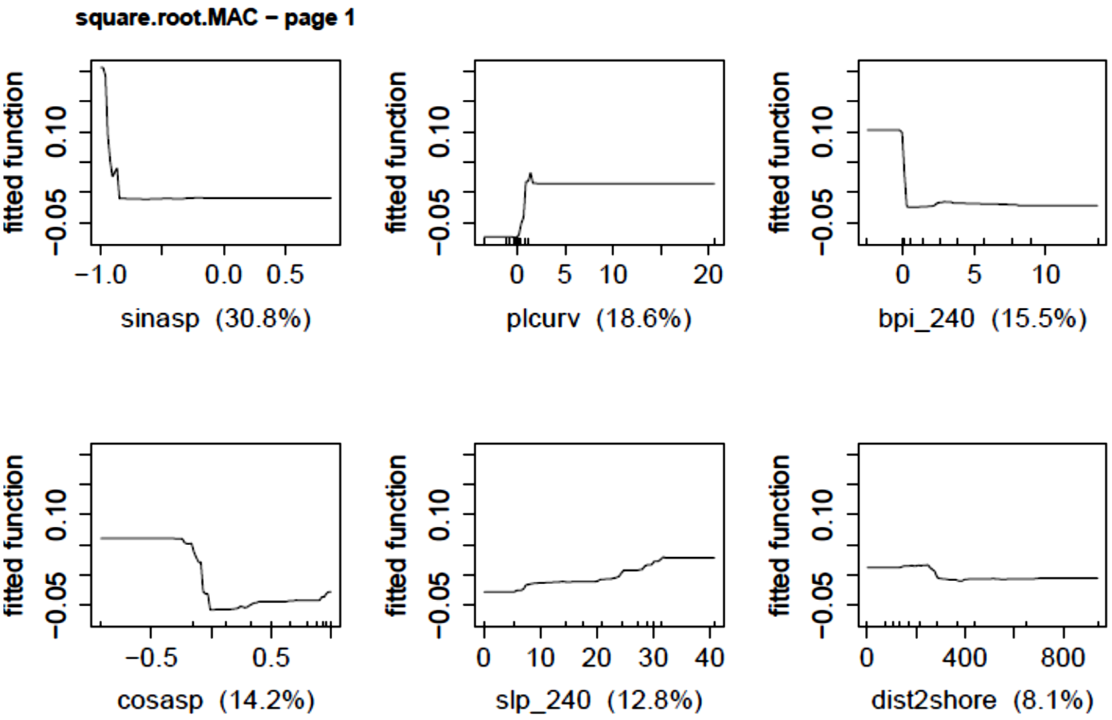
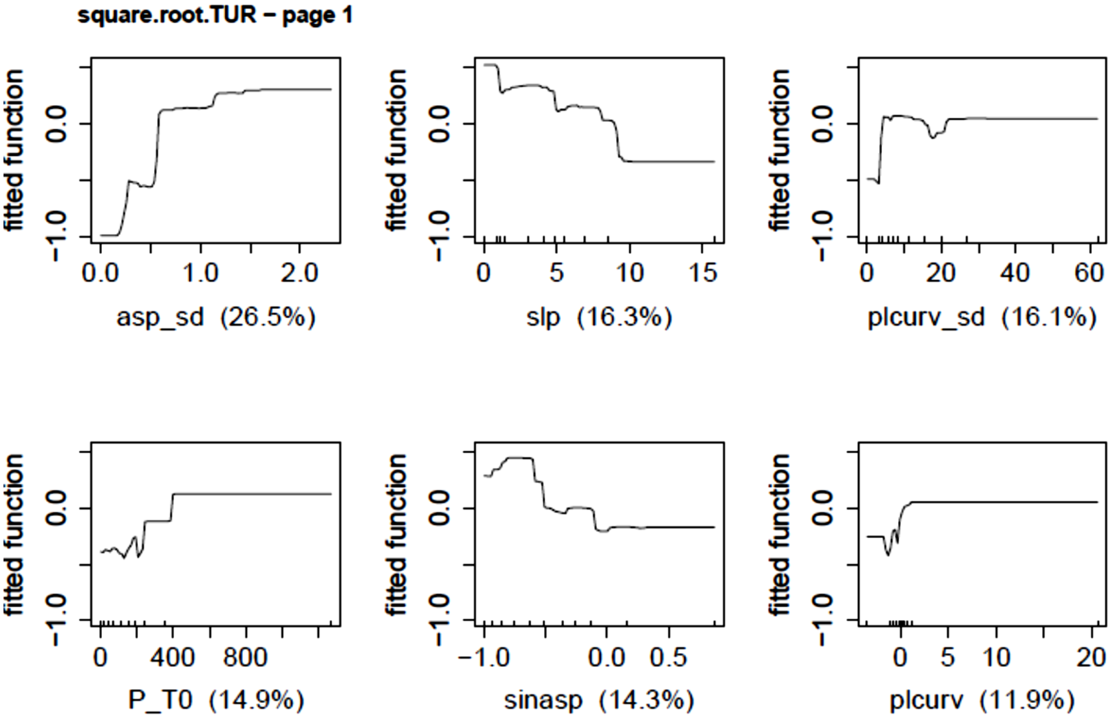


Figure S2.2. Response curves of coral reef indicators at Hāʻena. The y-axis is the fitted function for the modeled coral reef indicator and the x-axis represents the terrestrial or marine drivers

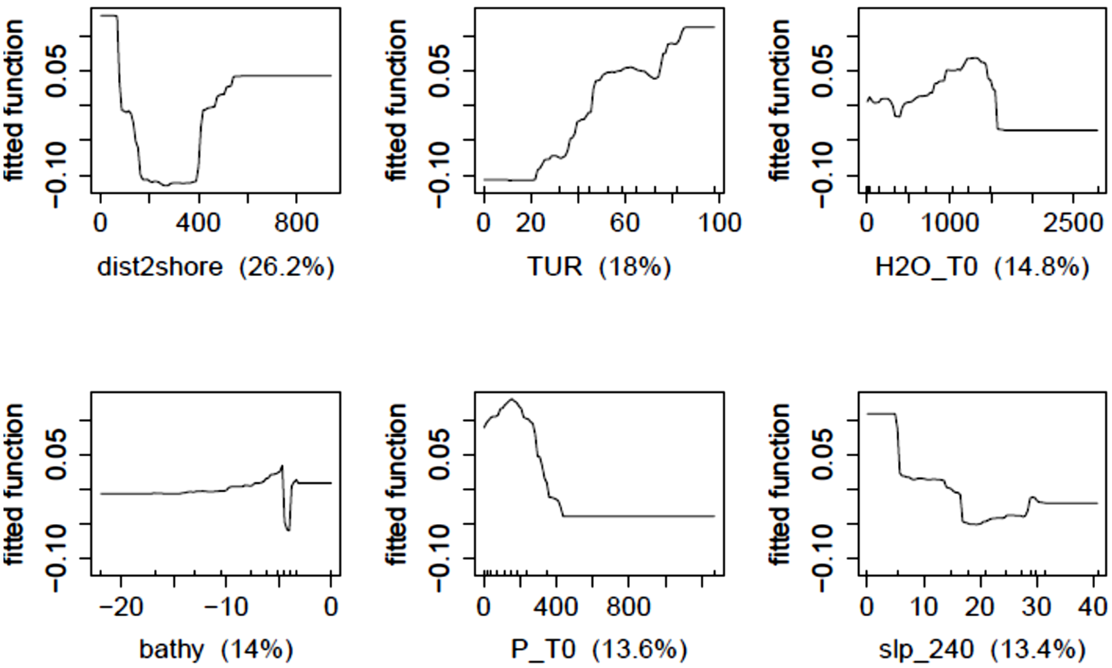

square.root.CCA – page 1
fitted function
0.4
0.1
−0.2
0
400
800
dist2shore (31.8%)
0
2000
5000
N_T0 (28.1%)
0
1000
2500
H2O_T0 (20.9%)
0
5
10
15
slp (19.2%)


square.root.COR – page 1
fitted function
0.0
−1.0
0
5
10
20
plcurv (30.6%)
0
5
10
15
slp (25.9%)
−20
−10
0
bathy (23.1%)
0
10
20
30
40
slp_240 (20.4%)

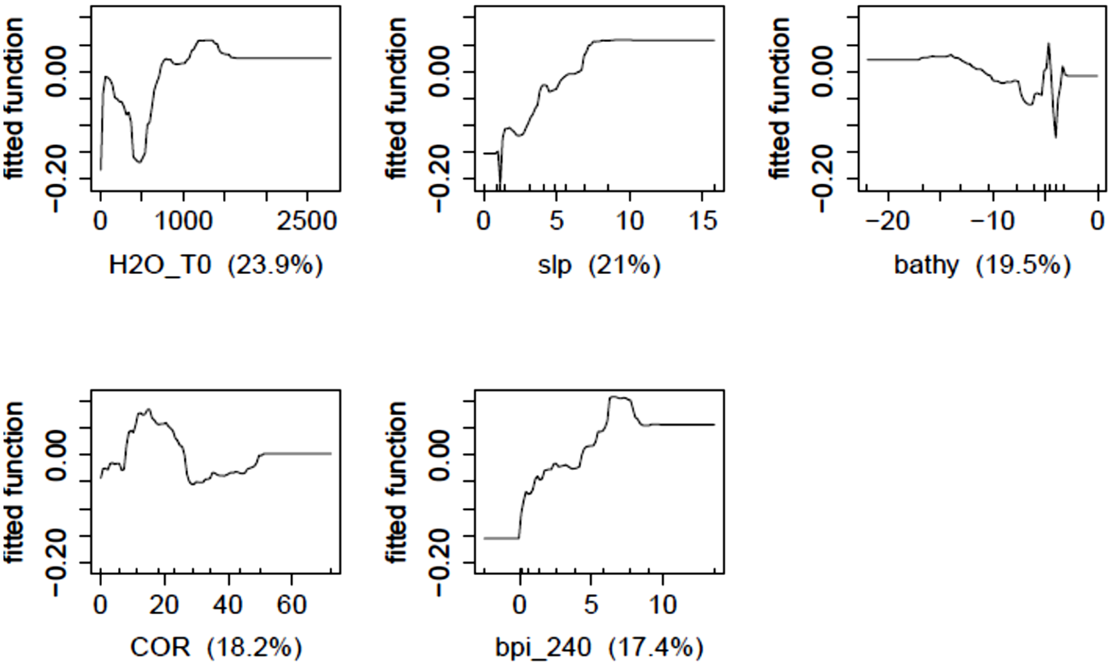

square.root.MAC – page 1

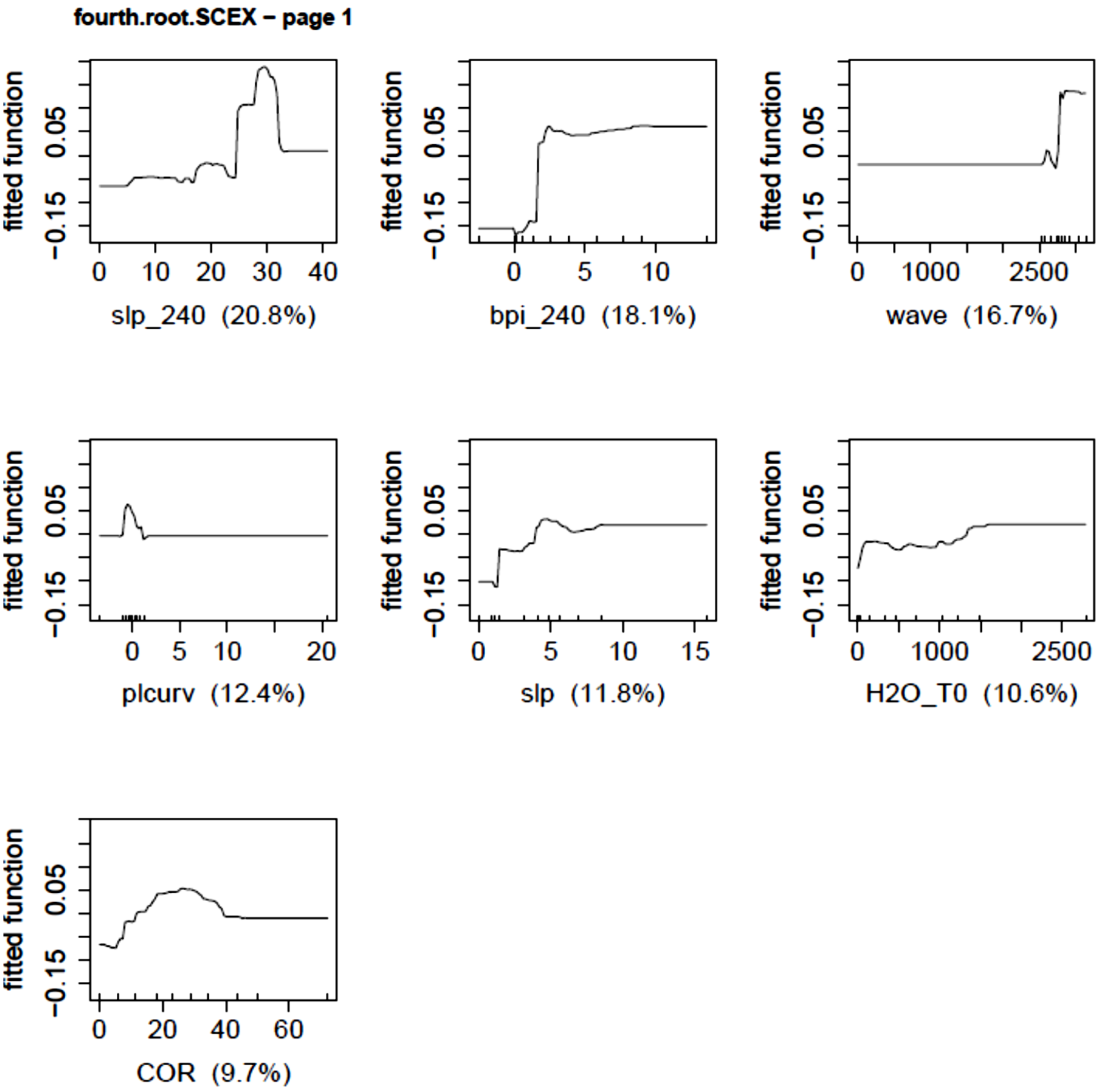

square.root.TUR – page 1

fourth.root.BROW – page 1



fourth.root.GRDE – page 1




fourth.root.SCEX – page 1
fitted function
−0.15
0.05
0
10
20
30
40
slp_240 (20.8%)
0
5
10
bpi_240 (18.1%)
0
1000
2500
wave (16.7%)
0
5
10
20
plcurv (12.4%)
0
5
10
15
slp (11.8%)
0
1000
2500
H2O_T0 (10.6%)
0
20
40
60
COR (9.7%)

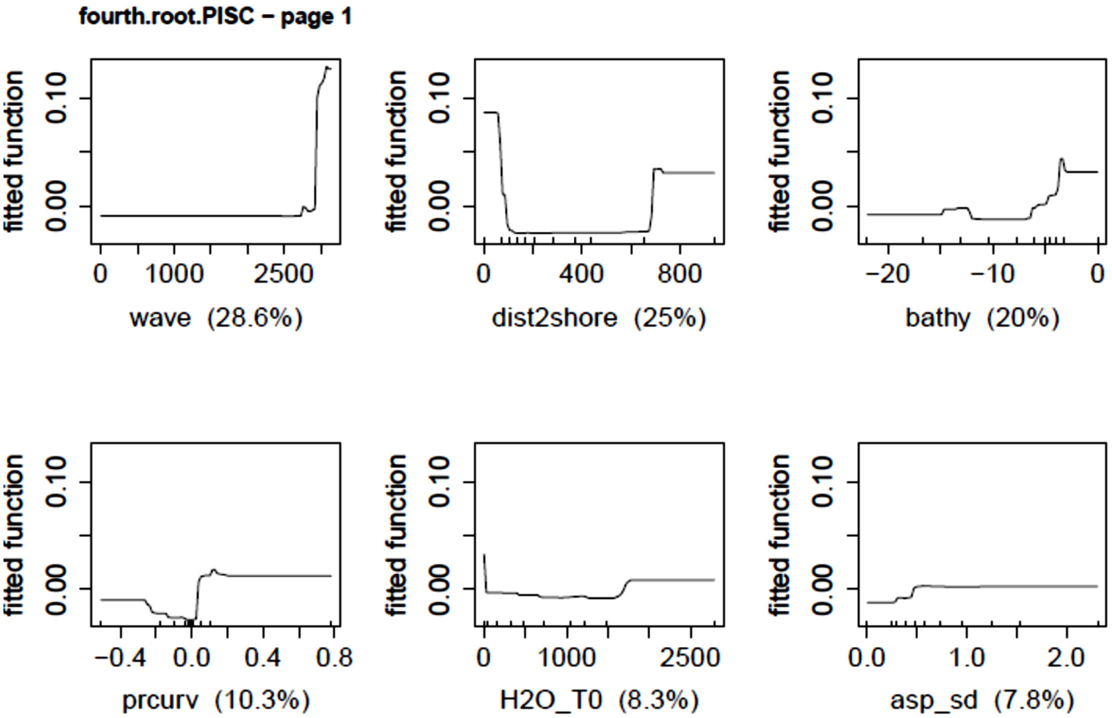


Figure S2.3. Response curves of coral reef indicators at Ka‘ūpūlehu. The y-axis is the fitted function for the modeled coral reef indicator and the x-axis represents the terrestrial or marine drivers

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CHAPTER 3. CORAL REEF RESILIENCE TO HUMAN DRIVERS IN OCEANIC ISLAND ENVIRONMENTS

ABSTRACT

High latitude coral reefs on oceanic islands are subject to a large range of natural disturbances that shape the character of these ecosystems. In the last century, climate change has emerged as a global threat to coral reefs, which can interact with natural disturbance cycles and local human drivers (fishing and land-based source pollution). To promote resilience to climate change, management of local human drivers has been widely advocated. However, the extent of its effectiveness remains unclear because the combined effects of co-occurring human and natural disturbances on coral reefs and their fisheries remain poorly understood which in turn hinders resilience management. To address this knowledge gap, this study focused on two ridge-to-reef systems (Hāʻena and Kaʻūpūlehu) under community-based management, at opposite ends of the main Hawaiian Island chain, thus capturing a wide spectrum of natural disturbances governing high Pacific islands (geologic age, rainfall and waves). I applied a novel ridge-to-reef modeling framework, which links fine-scale land use to coral reef ecological outcomes through groundwater, to assess the cumulative effects of land-based nutrients and climate induced bleaching on coral reefs. My results indicate that Kaʻūpūlehu, on Hawaiʻi Island is more susceptible to coastal development and climate change, partly due to low rainfall and wave power, compounded with naturally high nitrogen in groundwater. Although Hāʻena, on Kauaʻi, benefits from dilution and mixing attributable to high rainfall and wave disturbances, critical nursery habitats seem vulnerable to climate change impacts and could benefit from reduced nutrient inputs and increased herbivory to promote recovery post-bleaching events. This study suggests that managing human drivers from ridge-to-reef using a place-based approach aimed at improving water quality, protecting important habitat (refuges and nurseries), and fostering herbivory can promote coral reef resilience in the face of climate change. Lastly, I demonstrate that locally developed models offer a critical and much needed opportunity for aiding local-scale and place based management of coral reefs in high oceanic island environments.

3.1 Introduction

Native Hawaiians, as the original inhabitants of the Hawaiian Islands, traditionally nurtured and regulated the resources available from ridge-to-reef by subdividing the land into ahupuaʻa management units to sustain their wellbeing (McGregor et al. 2003). The ahupuaʻa management system integrated the terrestrial, freshwater and nearshore marine resources based on the fundamental linkages from ridges to reefs (Jokiel et al. 2010, McGregor et al. 2003). Following the 1800s, the modern socio-economic and political context, specifically land and water privatization, led to breakdown of the traditional ahupuaʻa system (Minerbi 1999, Vaughan & Vitousek 2013). Today, a Hawaiian Cultural Renaissance, rooted in the recognition of declining important biocultural resources, has brought the ahupuaʻa into the contemporary framework of ecosystem-based management and seeks to re-establish the cohesive links between land and sea, encompassing both ecological and social processes along that continuum (Friedlander et al. 2013, Jokiel et al. 2010). Two leading examples are the ahupuaʻa of Hāʻena (Winter & Lucas 2017) and Kaʻūpūlehu, which recently enacted place-based management to restore Hawaiian values and an ahupuaʻa-based approach to managing coral reef fisheries (DAR 2016, TNC 2015). Located at opposite ends of the main Hawaiian Island chain, Hāʻena and Kaʻūpūlehu also represent each end of the environmental spectrum (geologic age, rainfall, and wave) governing high oceanic island ecosystems. Hāʻena is an older windward ridge-to-reef system exposed to high freshwater inputs (Calhoun & Fletcher 1999) and high wave disturbance (Hoeke et al. 2013), while Kaʻūpūlehu is a younger dry leeward ridge-to-reef system sheltered from wave action (Chapter 1).

In order to support these and other ridge-to-reef management initiatives, I applied the fine-scale modeling framework developed for these locations, which links the effects of land use to coral reef ecological outcomes through groundwater flux (Chapter 1). More specifically, this study applied these ridge-to-reef models in order to: (1) investigate the effects of costal development and climate change on coral reefs and resource fishes; (2) examine the effect of different natural disturbance regimes on coral reef resilience; (3) and inform resilience management using a place-based approach. Assuming the fundamental ecological relationships are constant over time, these models were applied to forecast benthic and fish resilience indicator distributions under different coastal development, climate change, and combined scenarios. Then I assessed and compared the predicted changes of the benthic and fish communities to current conditions in each place in order to answer the following questions:

1. Can ridge-to-reef management foster coral reef resilience to climate change in oceanic island ecosystems with different natural disturbance regimes?
2. Do high natural disturbance regimes, such as in Hāʻena, increase or decrease resilience to local human impacts and climate change, compared to Kaʻūpūlehu?

3.2. Methods

This chapter also focused on Hāʻena and Kaʻūpūlehu ahupuaʻa. Refer to Section 2.1 for more information.

3.2.1 Modeling approach

In order to determine the effects of co-occurring human drivers on coral reefs and their targeted fish populations, I applied two spatially explicit ridge-to-reef models developed independently for Hāʻena and Kaʻūpūlehu (Chapter 1). The modeling framework coupled groundwater models and coral reef predictive models, calibrated on locally available data (Figure 3.1). First, we designed and modeled several coastal development scenarios, based on local communities' inputs; and climate change based on projected coral bleaching for the region (Hoeke et al. 2011). The groundwater models were used to quantify the change in nutrient loads under each coastal development scenario, and were coupled with ArcGIS-based modeling to derive maps of nearshore water quality. I then simulated the change in distribution of benthic and fish indicators under those coastal development and climate change scenarios, using the predictive coral reef models calibrated on georeferenced benthic and fish survey data contributed by the Fisheries Ecology Research Lab (FERL) and The Nature Conservancy of Hawaiʻi (TNC). The outputs of the coral reef spatial predictive models were used to evaluate potential changes in the benthic and fish community structure under the projected scenarios compared to present conditions at 60-m2 spatial resolution.

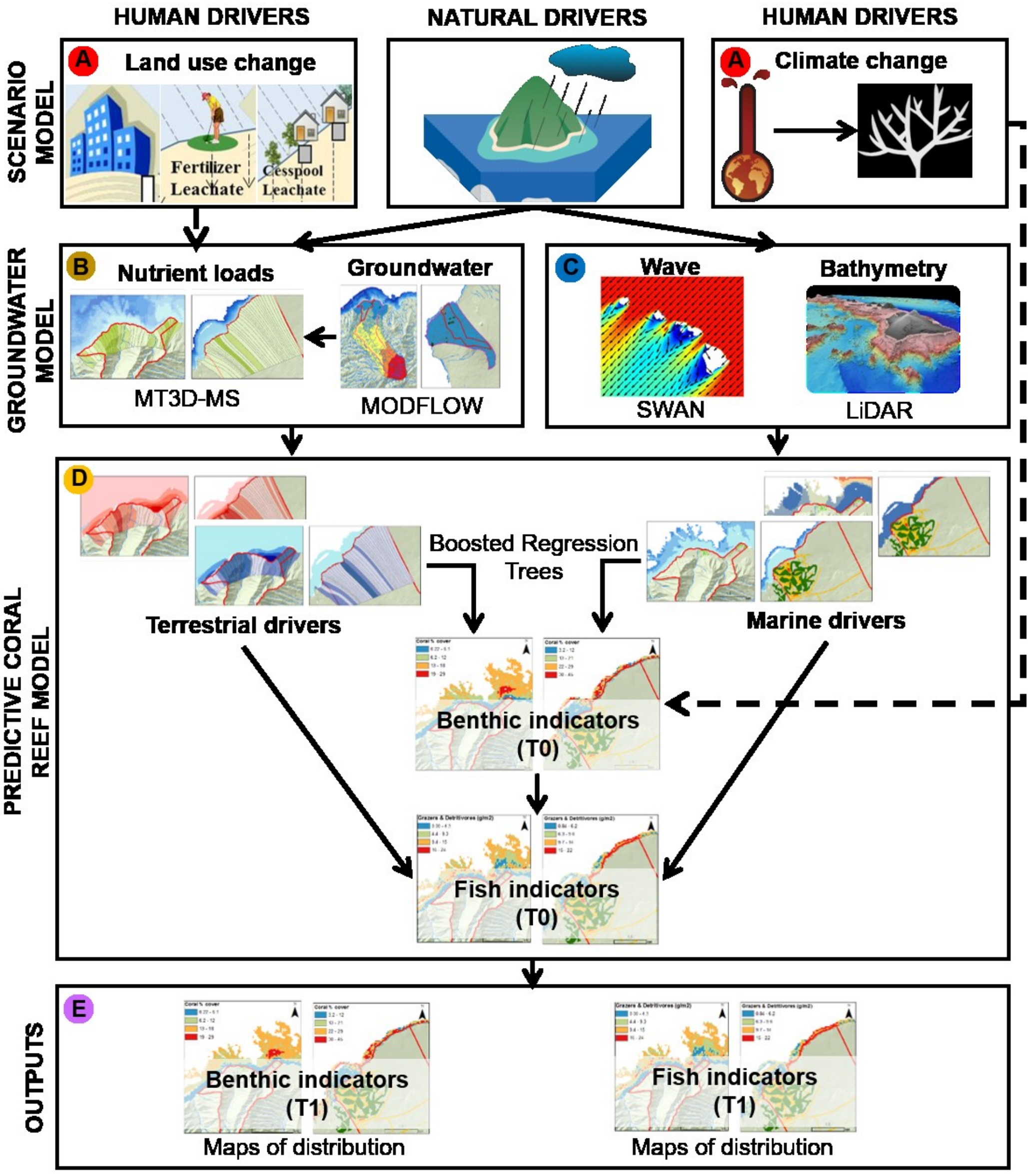

Figure 3.1. Modeling framework[2]**.** A: Coastal development and climate change scenarios were designed for each study site. B. Change in nitrogen and phosphorus coastal discharge was modeled using calibrated groundwater models under each coastal development scenario. C: Marine drivers were derived from existing remote sensing data. D: Change in coral reef indicators distribution were modeled using the calibrated coral reef models as a function of terrestrial (freshwater and

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[2] Symbols courtesy of Integration and Application Network (http://ian.umces.edu/symbols/); bathymetry image courtesy of Hawaii Mapping Research Group for bathymetry; wave model image courtesy of Hawaii Coastal Geology Group.

nutrients) and marine drivers (habitat and wave). E: Model outputs included maps of coral reef indicators distribution under each scenario.

3.2.2 Coral reef indicators

To assess dimensions of coral reef social-ecological resilience, we considered the change in the distribution of benthic (% cover) and fish (biomass) indicators modeled in chapter 1, respectively. These indicators were quantified by reef survey data collected by the Fisheries Ecology Research Lab (FERL) at the University of Hawai‘i and The Nature Conservancy of Hawai‘i (TNC) reef monitoring program (refer to Section 2.2.3 for more details).

3.2.3 Modeling natural drivers

The key natural terrestrial and marine drivers were identified for these coral reefs during the development and calibration of this modeling framework (Table 3.1). The natural terrestrial drivers included groundwater discharge and nutrients loads, derived from groundwater modeling (Figure 3.1.B); and the marine drivers included wave and habitat structure, derived from wave models (Stopa et al. 2013) and remotely-sensed bathymetry (Multibeam and LiDAR) (HMRG 2015) (Figure 3.1.C). The predicted abundance of the benthic indicators were used as drivers for the fish indicators (Figure 3.1.D). To test the effect of human drivers on coral reef communities, we assumed that these natural drivers’ remained constant over time, except for the benthic community indicators.

Table 3.1. Description of the natural drivers used as predictors for the coral reef models. Refer to **Section 2.2.4** and **Table S2.2** for more details on the processing methods of the terrestrial and marine drivers, respectively.

Indicator	Metrics	Description	Unit
TERRESTRIAL DRIVERS			
Groundwater discharge	Freshwater[1]	Volume of freshwater discharged yearly	$m^3.yr^{-1}$
	N[1]	Mass of dissolved nitrogen.	$kg.yr^{-1}$
	P[1]	Mass of dissolved phosphorus.	$kg.yr^{-1}$
MARINE DRIVERS			
Wave	Power[2]	Mean wave power derived from a 10 year (2000-2009) SWAN hindcast wave model.	$kW.m^{-1}$
Geography	Depth[3]	Mean seafloor depth	m
	Distance to shore[4]	Euclidean distance to the shoreline	m
Habitat morphology	BPI[3]	Difference in seafloor depth and the mean seafloor depth in an annular neighborhood of specified inner and outer radii; mean values indicate a location's position relative to the surrounding area; values can be positive (ridges), negative (valleys), or zero (flat or constant slope)	m
	Slope[3]	Maximum rate of change in seafloor depth between each grid cell and its neighbors	Degree
Habitat complexity	Plan curvature[3]	Seafloor curvature perpendicular to the line of maximum slope; value indicates whether flow will converge or diverge over a point; values can be – (concave), + (convex), or 0 (flat) (mean). A proxy for spur and groove effects on water flow.	$Radians.m^{-1}$
	Profile curvature[3]	Seafloor curvature along the line of maximum slope; value indicates whether flow will accelerate or decelerate over the curve; values can be + (concave), - (convex), or 0 (flat) (mean). A proxy for spur and groove effects on water flow.	$Radians.m^{-1}$

	Rugosity[3]	Measure of small-scale variations of amplitude in the height of a surface (mean). Value range from 1 (flat) to infinity.	Unitless
Habitat exposure	Aspect[3]	Downslope direction of maximum rate of change in seafloor depth between each grid cell and its neighbors (sine and cosine circular mean, circular standard deviation)	Degree
Benthic groups (applied to the fish models only)	CCA[5]	Spatially predicted abundance of crustose coralline algae	% cover
	Coral[5]	Spatially predicted abundance of coral.	% cover
	Macroalgae[5]	Spatially predicted abundance of macroalgae	% cover
	Turf algae[5]	Spatially predicted abundance of turf algae	% cover

[1] Groundwater models (**Section 2.2.4**)
[2] SWAN hindcast wave model (Stopa et al. 2013)
[3] Bathymetry synthesis (HMRG 2015)
[4] Coastline (OP 2000)
[5] Coral reef models (**Section 2.2.7**)

3.2.4 Modeling human drivers

3.2.5.1 Local human drivers: Coastal development scenarios

Three Coastal Development scenarios, ranging from Moderate, to Severe and Extreme were designed (Table 3.2.a) and implemented using the groundwater models calibrated on current conditions (Chapter 1). The total nutrient load delivery to the coast was calculated for each coastal development scenario based on the nutrient loading rates associated with each land use type (Table 3.2.b, Figure 2.1 & Section 2.2.4.3 for more details). For all coastal development scenarios at Hāʻena, it was assumed that the cesspools in the coastal zone were converted to septic tanks based on the recent statewide cesspool ban (Table 3.2a) (HAR Title 11, Chapter 62). At Kaʻūpūlehu, all proposed coastal development scenarios assumed low intensity development and two wastewater disposal types were considered (Table 3.2.a). For each parcel of light intensity development, a 0.4 ha lot with 60 percent green space, and 4.5 persons per residence was assumed. The moderate scenario assumed that wastewater was collected by sewer system, delivered to a wastewater treatment plant and disposed of through an injection well (Table 3.2.a). The nutrient quality of the effluent was scaled to the proposed development and assumed the same loading and discharge rates as the existing injection well (Table 3.2.b). The severe and extreme scenarios assumed that the wastewater was disposed of through septic tanks (Table 3.2.a).

In addition to increases in housing, each scenario considered increases in lawns and golf courses (Table 3.2.a). Typically, green spaces increase the nutrient flux due to increased recharge from irrigation and nutrient leaching from fertilizers. The coastal nutrient flux from green spaces were based on assumed landscaping practices, particularly irrigation (Engott 2011) and fertilization rates. At Hāʻena, the groundwater recharge over green spaces was computed and assumed no irrigation given high rainfall in the area. Based on an irrigation rate of 0.00468 $m.d^{-1}$ (5,000 $gpd.ac^{-1}$, CH2MHill 2003), rainfall of 1.01 $mm.d^{-1}$ and an evapotranspiration rate of 0.00371 $m.d^{-1}$, the groundwater recharge rate over green spaces in Ka'ūpūlehu was assumed 0.00191 $m.d^{-1}$ (Engott 2011).

Table 3.2.a. Coastal development scenarios. Moderate and severe scenarios considered different coastal development scenarios at each site. The extreme scenario proposed similar coastal development intensity to enable comparisons between sites.

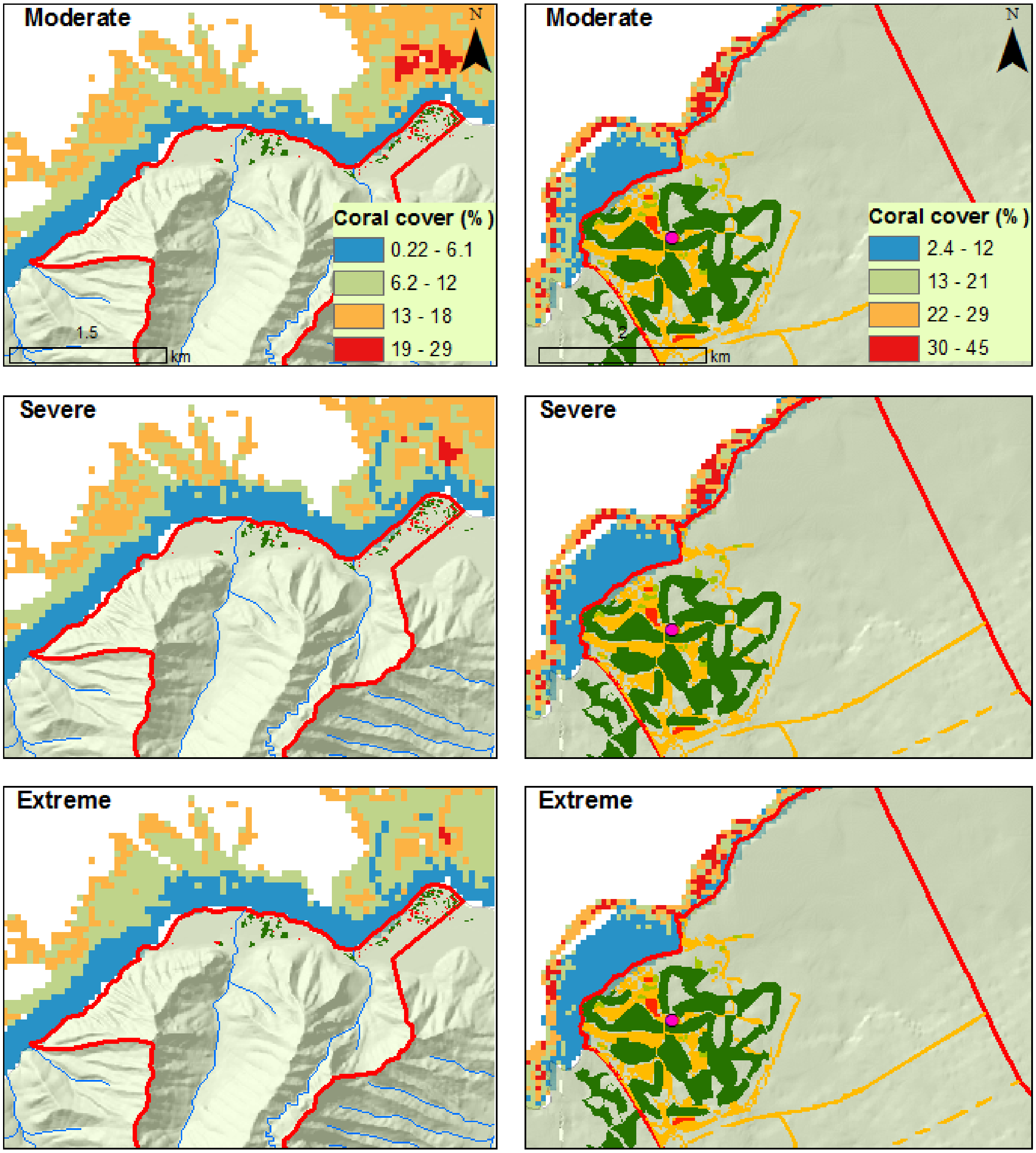
Sites	**Scenarios**	**Coastal development**	
		Houses (units)	**Green space / Golf course (km^2)**
Hāʻena	Present	156 houses (on cesspool)	Green space (0.06 km^2)
	Moderate	260 houses (130 on cesspool and 206 on septic tanks)	Green space (0.2 km^2)
	Severe	336 houses (130 on cesspool and 130 on septic tanks)	Green space (0.3 km^2)
	Extreme	500 houses (130 on cesspool and 370 on septic tanks)	Green space (0.7 km^2) & 1 golf course
Kaʻpūlehu	Present	165 houses (1 wastewater injection well)	Green space (0.18 km^2) & 1 golf course (1.87 km^2)
	Moderate	201 houses (2 wastewater injection well)	Green space (1.4 km^2) & 1 golf course (1.87 km^2)
	Severe	201 houses (septic tanks)	Green space (1.4 km^2) & 1 golf course (1.87 km^2)
	Extreme	500 houses (septic tanks)	Green space (3 km^2) & 2 golf courses

Table 3.2.b. Nutrient loading rates per land use type.

Land Use type	**N Load (kg/yr)**	**P Load (kg/yr)**	**Wastewater Discharge (m^3/yr/OSDS)**	**Source**
House (cesspool)	38	8.3	435	(Lowe et al. 2010, Tasato & Dugan 1980, U.S. EPA 2002)
House (septic tank)	15	0.5	435	(Lowe et al. 2010, Tasato & Dugan 1980, U.S. EPA 2002)
Wastewater Injection (current)	843	1300	160,600	(State of Hawaiʻi 2016b)
Wastewater Injection (future)	460	596	87,600	(State of Hawaiʻi 2016b)
Hāʻena green space	4.5/ha + R	0.2/ha+ R	na	(Giambelluca et al. 2012, 2014; Shade 1995)
Kaʻūpūlehu golf courses/green space	49/ha	13.5/ha	na	(Throssell et al. 2009b)

3.2.5.2 Global human driver: Climate change scenarios

Climate change scenarios were designed and implemented to spatially represent the potential effect on coral bleaching. An average greenhouse gas emissions scenario (A1) was assumed for the years 2000–2099 A.D. (21st century), which corresponds to a future with very rapid economic growth, global population peaks in mid-century and declines thereafter, a rapid introduction of new and more efficient technologies, and an energy system with no heavy dependence on one particular source (see IPCC [2007] for more details). Based on SST and atmospheric carbon dioxide (CO_2) projections, shallow-water scleractinian coral cover loss due to bleaching was estimated based on a combination of growth and mortality models (Hoeke et al. 2011). Based on a projected increase in global temperatures of 2-4° C over the coming century (per Scenario A1B) with a threshold for heat stress increasing by 0.1° C every decade (IPCC 2007); the model suggests a coral cover decline of 25% to 75% for the main Hawaiian Islands by the end of the century (Hoeke et al. 2011). These scenarios should not be considered quantitative forecasts of percent coral cover change for these specific locations and should be considered as large-scale probability-based estimates of the relative impact of predicted increases in SST and CO_2 on corals in the main Hawaiian Archipelago over the next 100 years (Hoeke et al. 2011). In spite of large uncertainties and debate surrounding coral adaptation to heat stress (Baker et al. 2008), this analysis quantitatively illustrated the potential for large decline in coral cover in the 21st century (Hoeke et al. 2011). Based on these projections and given that deeper waters are cooler and can reduce the impact of increase in SST (Bridge et al. 2013), we designed 3 scenarios: a Moderate and a Severe Bleaching scenario which forced a negative 25% and 50% scaling factor respectively, on all current coral cover for reef areas shallower than 5 m, and an Extreme Bleaching scenario which forced a 50% scaling factor on coral cover in reef areas between 0 and 5m and a 25% scaling factors for areas between 5 and 10m (Figure 3.2).



Moderate

Moderate

Severe

Severe

Extreme

Extreme

Figure 3.2. Maps of coral cover per climate change scenario. Each map shows the change in coral cover under proposed climate change bleaching scenario at Hāʻena (left) and Kaʻūpūlehu (right).

3.2.5 Modeling scenarios impacts

I applied the spatial predictive coral reef models developed in Chapter 1 to simulate the benthic and fish communities under coastal development and climate change scenarios for Hāʻena and Kaʻūpūlehu. For each site, the calibrated coral reef models were used to predict the potential distribution of each benthic and fish indicator for each 60 m^2 grid cell according to future scenario. The modeled predictions were used to produce maps of benthic and fish indicator distributions under future scenarios. First, the benthic groups were spatially predicted as a function of the natural drivers (Table 3.1) and projected human scenarios. Then the resource fishes were predicted as a function of the natural drivers (including the predicted benthic community) and future human driver scenarios. Spatial predictions were performed in R (R Core Team 2014) using the dismo (Hijmans et al. 2014) and raster (Hijmans 2014) packages.

3.2.6 Scenario analysis

The predicted spatial distribution of benthic and fish indicators under each coastal development, climate change, and combined scenarios were compared against present distributions using a permutational multivariate analysis of variance (PERMANOVA) (McArdle & Anderson 2001) in Primer PERMANOVA+ software (Anderson et al. 2008). PERMANOVA partitions and tests simultaneously multiple response variables, represented in an Euclidean distance resemblance matrix, as a function of one or more environmental drivers in an analysis of variance (ANOVA), including fixed factors and interactions treatments (i.e., scenarios) (Anderson et al. 2008). The PERMANOVA tested for significant differences in terms of mean distribution and composition of the benthic and fish assemblages for each site. The permutation p-values provided an exact test of each individual null hypothesis (Anderson et al. 2008) and were not corrected for multiple comparisons since *ad hoc* experiment-wise corrections, such as Bonferroni, are known to be overly conservative for PERMANOVA analyses (Day & Quinn 1989). P-values were calculated based on 9,999 permutations of the residuals under a reduced model, thus avoiding the assumption of normally distributed errors (Anderson et al. 2008).

By assessing the main effect and how interactions between human drivers can manifest within coral reef benthic and fish communities, we determined if and how benthic and fish communities differed from present conditions under each independent and combined human driver scenarios. Significant p-values indicated whether projected future benthic and fish community structure significantly differed from present community structures, in terms of mean composition. This can be interpreted as detecting whether the current coral reef community is likely to undergo a significant change under alternative human drivers' scenarios. This study sought to identify environmental conditions that may potentially lead to phase shifts or broad-scale changes in species composition and function, so p-values less than 0.1 were reported as significantly different from present conditions to identify potential ecosystem change and buffer against model uncertainty.

3.3. Results

3.3.1 Effect of coastal development on groundwater nutrient flux

Our groundwater models results showed that the type of wastewater technology employed can influence the nutrient load discharge (Figure 3.3). Under the Moderate Coastal Development, existing coastal houses and new houses were assumed to switch from cesspool to septic tanks, which resulted in a 50% decrease from present conditions in human-derived nutrients at Hāʻena. At Kaʻūpūlehu, the Moderate Coastal Development scenario assumed wastewater was discharged through an injection well, which resulted in 8% and 35% increase in nitrogen and phosphorus, respectively. Under the Severe Coastal Development scenario, the proposed development combined with the upgraded wastewater technology resulted in a 16% and 22%, respectively of human-derived nitrogen and phosphorus loads at Hāʻena. At Kaʻūpūlehu, the Severe Coastal Development scenario assumed wastewater was discharged through septic tanks, which resulted in three times more nitrogen and a 34% increase in phosphorus compared to the Moderate Coastal Development (wastewater injection well). Under the Extreme Coastal Development scenario, the increase in nutrients was larger at Hāʻena (N: 500% and P: 278%) than Kaʻūpūlehu (N: 61% and P: 44%), when compared to Present conditions. The change in nutrient fluxes in groundwater resulted in change in coastal water quality (Figures 3.4 and 3.5).

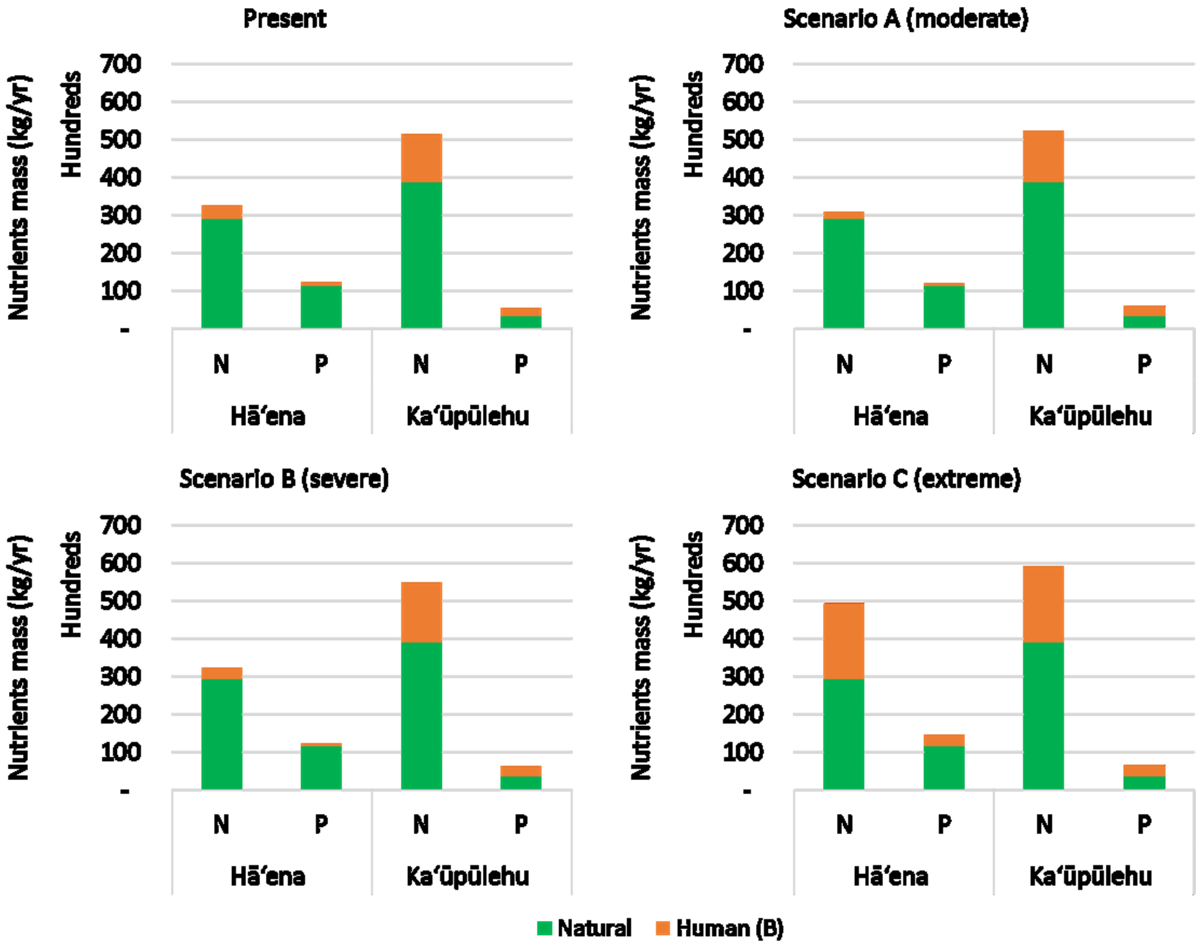


Figure 3.3. Coastal nutrients export per coastal development scenario. Nutrient fluxes are expressed in terms of natural (green) and human-derived (orange) sources.

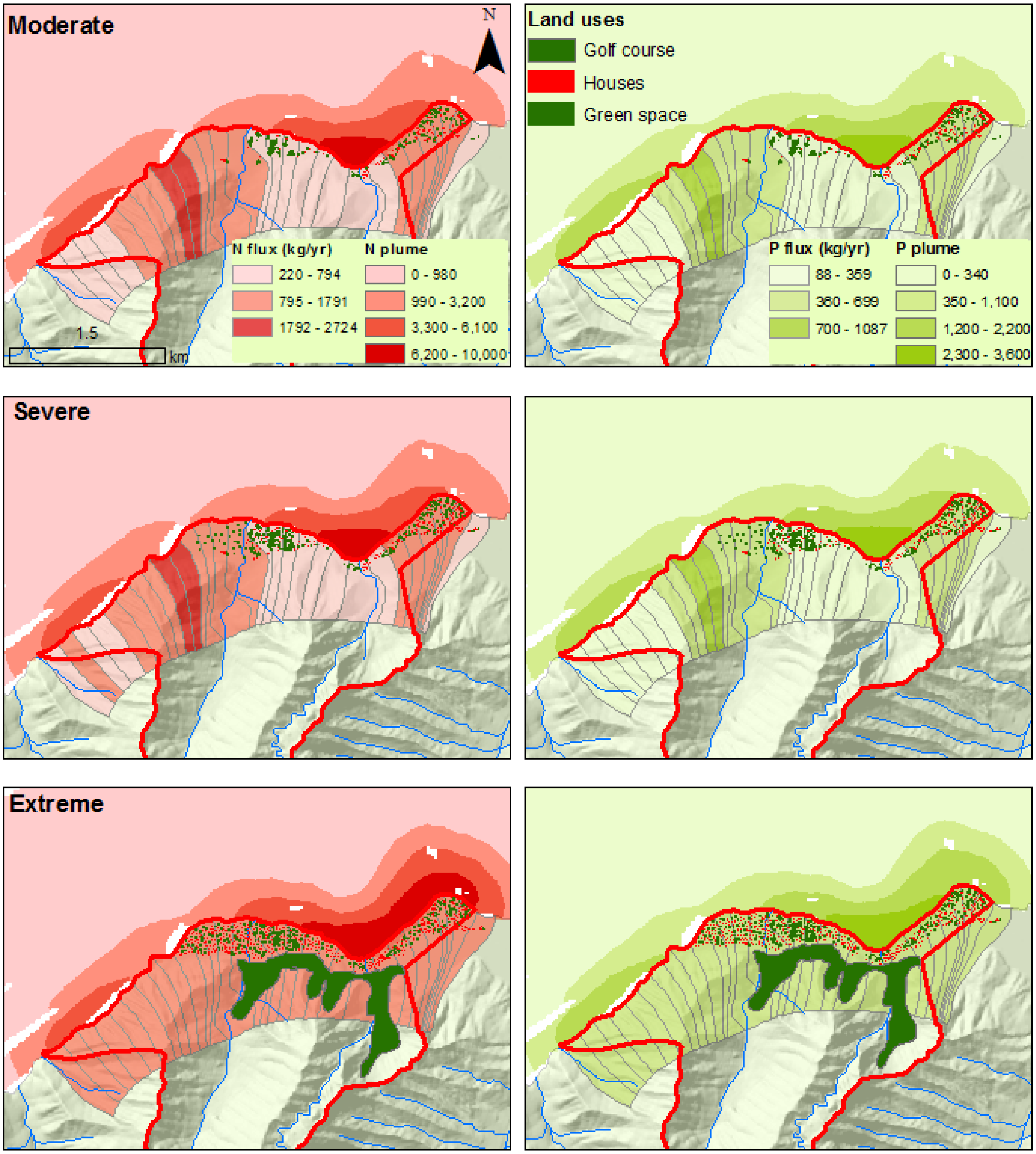


Figure 3.4. Coastal development scenarios at Hāʻena. Each map represents the modeled flux of nitrate and phosphate combined with modeled coastal plume for each coastal development scenario.

Figure 3.5. Coastal development scenarios at Ka‘ūpūlehu. Each map represent the modeled flux of nitrate and phosphate combined with modeled coastal plume for each coastal development scenario.

3.3.2 Effect of coastal development on coral reefs

The projected mean composition of the benthic community of Hāʻena did not differ significantly from present conditions under all coastal development scenarios, while Kaʻūpūlehu differed significantly under the Extreme Coastal Development scenario (Table 3.4). The differences detected in the Kaʻūpūlehu benthic community was attributed to a projected decrease in CCA and an increase in turf algae (Figures 3.6 & S3.3). Similarly, the fish community of Kaʻūpūlehu significantly differed from present conditions under the Extreme Coastal Development scenario, while the fish community of Hāʻena did not differ for any of the coastal development scenarios (Table 3.4). The differences detected in the fish community of Kaʻūpūlehu was attributed to a decrease in browser biomass (Figures 3.6 & S3.3).

Table 3.4. PERMANOVA pseudo-F values for the benthic and fish communities per scenario. Coastal development (DVMT), climate change (CLIM), and combined (CLIMxDVMT) scenarios with 3 levels of intensity (A = Moderate, B = Severe, and C = Extreme). P-values < 0.05* and <0.01** are reported as significantly different from present conditions.

Reef	**Sites**	**Hāʻena**			**Kaʻūpūlehu**		
	Scenarios	**A**	**B**	**C**	**A**	**B**	**C**
Benthic	DVMT	0.07	0.04	0.17	0.23	0.33	2.39**
	CLIM	2.58**	3.73**	5.29**	3.15**	6.59**	8.29**
	CLIMxDVMT	2.58**	3.73**	5.3**	6.62**	6.62**	8.62**
Fish	DVMT	0.34	0.21	1.31	0.21	0.35	2.51**
	CLIM	0.6	0.87	1.25	0.85	1.76*	1.78*
	CLIMxDVMT	0.7	0.9	1.77*	0.88	1.80*	3.00**

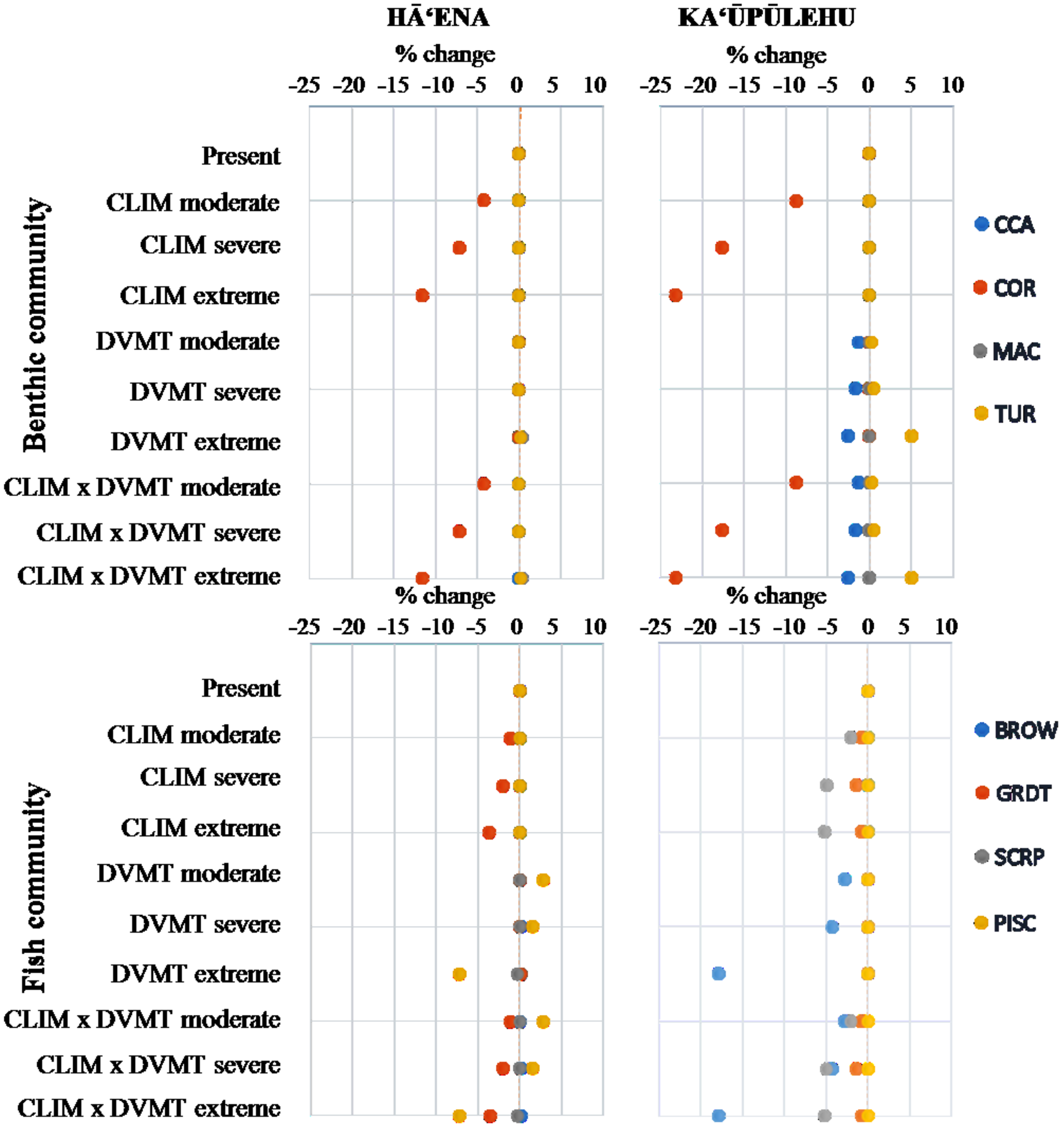


Figure 3.6. Average percent change of coral reef indicators per scenario. The x-axis represents the percent change from current conditions (marked by the red dashed line). Climate change scenarios (CLIM) and coastal development scenarios (DVMT) range from moderate, severe, and extreme. Refer to Figure S3.5 for the distribution of these predictions.

3.3.3 Effect of climate change on coral reefs

The projected effect of climate change on the benthic community was similar in Hāʻena and Kaʻūpūlehu and differed significantly under all climate change scenarios at both sites (Table 3.4, Figures S3.2 & S3.3). These differences are due to the specific coral cover loss imposed as a proxy for climate change bleaching impacts in the region. Coral cover loss was higher in shallower and backreef areas at Hāʻena and along the reef slopes at Kaʻūpūlehu (Figure 3.6). Under all Bleaching scenarios, the fish community of Hāʻena did not differ significantly from present conditions, while Kaʻūpūlehu significantly differed from present conditions under the Severe and Extreme Bleaching scenarios (Table 3.4). The effect detected in the Kaʻūpūlehu fish community was attributed to a decrease in grazers/detritivores and scrapers/excavators (Figures 3.6 & S3.4).

3.3.4 Effects of coastal development and climate change on coral reefs

At both sites, the benthic community significantly differed from the present community under all the combined coastal development and climate change bleaching scenarios. However, no significant interaction was detected at Hāʻena because climate change was the dominant driver (Table 3.4). Conversely, at Kaʻūpūlehu a significant interaction was detected in the benthic community under the combined Extreme Coastal Development and Bleaching scenario (Table 3.4). Kaʻūpūlehu benthic community also differed significantly under both the Extreme Coastal Development and Extreme Bleaching scenarios independently, which we can interpret a significant interaction. The differences detected in the benthic community of Kaʻūpūlehu can be attributed to a decrease in CCA and coral cover, combined with an increase in turf algae (Figures 3.6 & S3.3).

For the fish community, significant differences were detected at both sites. At Hāʻena, a significant interaction was detected under the Extreme combined scenarios, (Table 3.4), attributable to an increase in grazers/detritivores biomass combined with a decrease in scrapers/excavators and piscivores biomass (Figures 3.6 & S3.2). At Kaʻūpūlehu, the fish community differed significantly under the Severe and Extreme combined scenarios (Table 3.4), due to a projected decrease in biomass for all herbivores functional groups (browsers, grazers/detritivores, and scrapers/excavators) (Figures 3.6 & S3.3). Under the Severe combined scenario, no interactions were detected and climate change was the dominant driver, while an interaction was detected under the Extreme combined scenario.

3.4. Discussion

This study used predictive ridge-to-reef social-ecological models calibrated using local data to determine the potential effect of multiple co-occurring human impacts on coral reefs, under different natural disturbance regimes in Hāʻena and Kaʻūpūlehu (Chapter 1). The results support two important principles when managing coral reefs on high oceanic islands in the face of climate change. First, it is critical to consider the combined impact of multiple human and natural drivers, and potential interactions between them, to develop effective management actions (Crain et al. 2008, Halpern et al. 2008a, Hughes et al. 2007, Nyström et al. 2000). Second, ridge-to-reef management actions that improve water and habitat quality can play a significant role in promoting coral reef resilience under the anticipated effects of climate change (Gurney et al. 2013, Maina et al. 2013). Our findings reveal that Hāʻena coral reef community may be more resilient to increases in human drivers compared with Kaʻūpūlehu, due to more intense and variable natural disturbances (waves and freshwater) (Chapter 1). Conversely, the lack of natural disturbances to dilute and mix land-based nutrients and the stronger dependence on habitat conditions and water quality (Chapter 1), renders Kaʻūpūlehu more vulnerable to human impacts. However, changes in the coral reef community were detected at both sites under Extreme Coastal Development and Bleaching scenarios, implying that although Hāʻena may have a higher buffer against climate change and/or coastal development impact, both sites can become vulnerable to a large increase in these human disturbances. My analyses also revealed that managing local human drivers could support higher quality habitat, which can act both as refuge from bleaching for coral reefs sheltered from natural disturbances and nurseries for coral reefs subject to intense natural disturbance regimes. Managing local human drivers can also support higher reef fish biomass in both types of oceanic island environments.

3.4.1 Human driver effects on coral reefs

3.4.1.1 Effect of coastal development on coral reefs

The results of this study imply that Hāʻena coral reef community is less sensitive to coastal development compared to Kaʻūpūlehu (Table 3.4). These findings suggest that coral reef systems largely governed by natural drivers, like Hāʻena, may be more resilient to local human drivers compared to coral reef systems governed by habitat and local drivers, such as Kaʻūpūlehu (Chapter 1). The observed difference between study sites in resilience to land-based nutrients could be a result of Hāʻena benefiting from dilution and mixing attributable to high wave power and freshwater discharge. Kaʻūpūlehu is notable for naturally high nutrient concentrations in its groundwater (Fackrell 2016) combined with human derived nutrient inputs from existing coastal development (Chapter 1). Vermeij et al. (2010) showed that local nutrient enrichment can foster turf algae overgrowth and reduce CCA and coral recovery capacity after disturbances, through loss of space availability (Smith et al. 2006). Therefore delivery of nutrient enriched groundwater can negatively affect coral reef calcifiers and promote benthic algae growth (Fabricius 2005, Pastorok & Bilyard 1985, Vermeij et al. 2010), particularly in dry ridge-to-reef systems sheltered from natural disturbances. Although the scenario analysis did not reveal a significant impact from coastal development on Hāʻena coral reef community, Chapter 1 identified positive relationships between land-based nutrients and benthic algae (macroalgae and turf algae) (Figure 2.9) and found higher levels of turf and macroalgae in the nearshore and back-reef areas of the Makua reef complex (Figure S3.2). This suggests that increases in land-based nutrients in groundwater due coastal development upstream from these ecologically important areas could negatively impact these habitats, particularly during summer when wave action is reduced (Hoeke et al. 2013). Given that turf algae can proliferate rapidly and lead to phase shifts when exposed to land-based nutrients (Fabricius 2005, Vermeij et al. 2010), these results suggest that turf algae may have a competitive advantage over corals and CCA under nutrient enriched waters at both sites but particularly Kaʻūpūlehu.

3.4.1.2 Effect of climate change on coral reefs

The results of this study suggest that Kaʻūpūlehu is more sensitive to bleaching from climate change compared to Hāʻena (Table 3.4). Based on projected SST and associated bleaching for the region (Hoeke et al. 2011), the coral populations of both Hāʻena and Kaʻūpūlehu are likely to be impacted. At both sites, the imposed coral cover loss from bleaching under the Moderate Bleaching scenario represented a significant impact when compared to the current coral population. Bleaching impact seems to particularly affect corals in back reef area of the Makua complex at Hāʻena and corals in the shallow areas of Kaʻūpūlehu (Figure 3.2). The results for the fish community implied that Hāʻena community is not significantly affected by the loss of coral cover to bleaching alone, while Kaʻūpūlehu community was significantly impacted under both Severe and Extreme Bleaching conditions. This difference of susceptibility to climate change likely results from the different benthic communities among locations resulting from different wave and freshwater disturbance regimes (Chapter 1). In terms of reef calcifiers, differences in coral and CCA abundance patterns among sites indicate that CCA is out-competed by coral under wave conditions suited to coral growth, but flourish in wave conditions adverse to coral growth (Engels et al. 2004, Friedlander & Parrish 1998a, Friedlander et al. 2014, Jokiel et al. 2004). At Hāʻena, corals are restricted to back reef areas away from freshwater influence, which are protected from high wave power (Figure 2.10) (Chapter 1, Goodell 2015). Conversely, the coral population at Kaʻūpūlehu is not limited by large freshwater runoff and high wave power, and is therefore more widespread and provides important habitat for resource fishes (Figure 2.11) (Chapter 1). As a result, the fish community, particularly scrapers and excavators, are more vulnerable to coral bleaching and habitat loss at Kaʻūpūlehu, compared to Hāʻena, where reef fishes are more dependent on CCA (Figure 2.9).

3.4.1.3 Effect of coastal development and climate change on coral reefs

Under the combined effects of coastal development and climate change, the projected benthic community showed no significant interactions at Hāʻena but indicated a shift at Kaʻūpūlehu. At Hāʻena, the significant difference detected in the benthic community resulted from the dominant effect of climate change. Given the weak but positive relationships between land-based nutrients and benthic algae (macroalgae and turf algae) (Figure 2.9) and the higher abundance of benthic algae in the nearshore and back-reef areas of the Makua reef complex (Figure 2.10), our results suggest that coral cover loss from bleaching combined with land-based nutrients could promote benthic algae growth, particularly during summer when wave action is reduced (Hoeke et al. 2013). Based on projected changes, the ecological shift at Ka‘ūpūlehu can be characterized by a decrease in CCA and coral cover combined with an increase in turf algae (Figure 3.5). CCA can promote coral settlement (Harrington et al. 2004, Price 2010) and corals provide habitat for reef fishes (Green & Bellwood 2009), while turf algae compete for space with coral reef calcifiers (McCook 2001, Vermeij et al. 2010) and inhibit settlement of fish larvae (Vermeij & Sandin 2008, Vermeij et al. 2009). Thus, the projected changes in the benthic community at Ka‘ūpūlehu suggests recovery from bleaching events may be hindered by the effects of increased coastal development.

The results for the fish community suggest that some synergistic effects may be taking place under the extreme combined scenarios at both sites (Table 3.4). At Hā‘ena, the difference in the fish community structure can be attributed to an increase of grazers/detritivores and a decrease in scrapers/excavators and piscivores biomass (Figure 3.5). While at Ka‘ūpūlehu, the difference stems from a decrease in total herbivore biomass (browsers, grazers/detritivores, and scrapers/excavators) (Figure 3.5). On coral reefs, herbivores can structure benthic communities by controlling the abundance of turf and macroalgae (Littler et al. 2006, Smith et al. 2010). Therefore, the extent to which a reef system possesses these functional groups is fundamental in determining its capacity to resist phase shifts and recover in the face of disturbance (Bellwood et al. 2004). Because the fish community did not change under climate change alone at Hā‘ena, this study suggests that in places with high natural disturbances, managing local human drivers can minimize climate change impacts on resource fishes. This differs from Ka‘ūpūlehu where the fish community was impacted by climate change alone, indicating that in places with low natural disturbances there is a need to protect deep water habitats which are removed from bleaching impacts.

3.4.2 Management implications

Although managing local human drivers has been widely advocated to promote resilience of coral reefs in the face of climate change (Hughes et al. 2007), the degree to which managing these local drivers can benefit coral reefs remains challenging to quantify and differs among places. This research supports the paradigm that managing local-scale human drivers is critical to the resilience of coral reefs in face of climate change (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). The consequences for coral reefs due to the interactions between climate change and coastal development can be used to illustrate the potential for local management to alleviate cumulative impacts (Kenneth 2016). We found that the impacts on resource fish biomass from coral bleaching could be minimized through ridge-to-reef management aimed at providing better water and habitat quality to foster coral reef resistance to disturbances and/or recovery post-disturbances. However, the extent to which improving water quality can influence coral reef resilience varies among locations and natural disturbance regimes. At Hāʻena, the benthic community is likely to be impacted by projected climate induced coral bleaching alone, particularly in back-reef areas where water circulation and depth are more restricted, while the fish community becomes vulnerable to climate change when combined with extreme coastal development. At Kaʻūpūlehu, the benthic and the fish communities are both vulnerable to coastal development and climate change alone and in combination, particularly in shallow areas. This analysis of the cumulative impacts of climate induced bleaching and water quality indicate that management of local human drivers can significantly influence coral reef resilience under a changing climate.

The major source of human-derived nutrients are wastewater disposal via cesspools for Hāʻena and green spaces or golf courses for Kaʻūpūlehu (Chapter 1). In both sites, avoiding groundwater contamination through the use of more effective OSDS adapted to volcanic islands and proper maintenance of existing OSDS (Babcock et al. 2014), can reduce land-based nutrients and improve nearshore water quality and thereby reduce coral reef vulnerability to projected climate change impacts. Improvement in water quality could also be achieved by regulating landscaping practices and fertilizer applications to green spaces and golf courses (Richmond 1993, Valiela & Bowen 2002). In addition, identifying and accounting for the nutrient ratios and limiting nutrients can reduce the risk of coral reef phase shifts (Derse et al. 2007, Prouty et al. 2016). For instance, the ecological responses of benthic algae to different nutrients at each site suggest that coral reef waters are nitrogen limited in Hāʻena, as was shown in nearby Hanalei Bay (Derse et al. 2007) and phosphate could be a limiting nutrient in Kaʻūpūlehu, as was found in Honokōhau Bay also located on the Kona coast (Prouty et al. 2016). Therefore, adopting land use practices that reduce exposure of watersheds and coral reefs to degraded coastal water quality could reduce coral reefs vulnerability to climate change impacts and promote recovery post-bleaching events, especially in dry regions or shallow back-reef areas with limited water circulation.

Management actions that protect key habitats (Bridge et al. 2013) and prevent loss of herbivores (Bellwood et al. 2004) can alleviate risks of coral reef phase shifts under nutrient enrichment (Kenneth 2016) and climate change. To foster coral reef resilience to climate change, it is important to identify and protect reef areas where environmental conditions reduce the likelihood of temperature-related bleaching and mortality (i.e., areas naturally resistant to bleaching) and reef areas that are more likely to recover after bleaching and mortality (i.e., areas naturally resilient) (Bridge et al. 2013). In Hāʻena, protecting shallow backreef areas away from land-based influence that are protected from high wave power, provides habitats for coral settlement and fosters recovery of coral reef communities after natural and human disturbance events. The backreef habitats of Makua form a lagoon (named Kai Kua`au o Hā`ena) and were identified as an important nursery area for fishes (Goodell 2015) and granted greater protection from human activities under the CBSFA rules (DAR 2016). At Kaʻūpūlehu, the geomorphology and coral reef dynamics call for protection of deep water areas (Chapter 1), which can act as refuges from land-based influence and climate change (Bridge et al. 2013) by providing habitat for corals and shelter for key resource fishes. However, these coral refuges can work more effectively when coupled with land-based practices that minimize land-based source pollution, otherwise the depth range of coral distribution may be reduced to a narrower euphotic zone (Bahr et al. 2015). In addition to habitat management, protection of herbivores can potentially compensate for some of the lost competitive ability of calcifying organisms (CCA and coral) over benthic algae (macro- and turf algae) under climate change (Adam et al. 2015). By consuming benthic algae, herbivores also free space for CCA and coral larvae recruitment (Bellwood et al. 2004, Green & Bellwood 2009), which is important in the context of coral reef resistance and recovery from climate change.

3.5. Conclusions

Chapter 1 highlighted the different disturbance regimes of these two ridge-to-reef systems and the need for place-based management actions. This chapter demonstrated the pivotal role that human disturbances can play in different oceanic island environments when considering ride-to-reef management. Our results confirm that coral reefs managed from ridge-to-reef have a much better chance of withstanding impacts from climate change. This study also helps identify land and sea pathways as well as management actions that can foster the resilience of these ridge-to-reef systems to multiple human drivers, via effective management “levers” (Kenneth 2016), such as key sources of nutrients and areas important for coral reef resilience. In addition, I illustrate the utility of decision support tools to environmental management by creating models, which can estimate future ecosystem structure under alternative management and climatic scenarios.

Supplementary Material

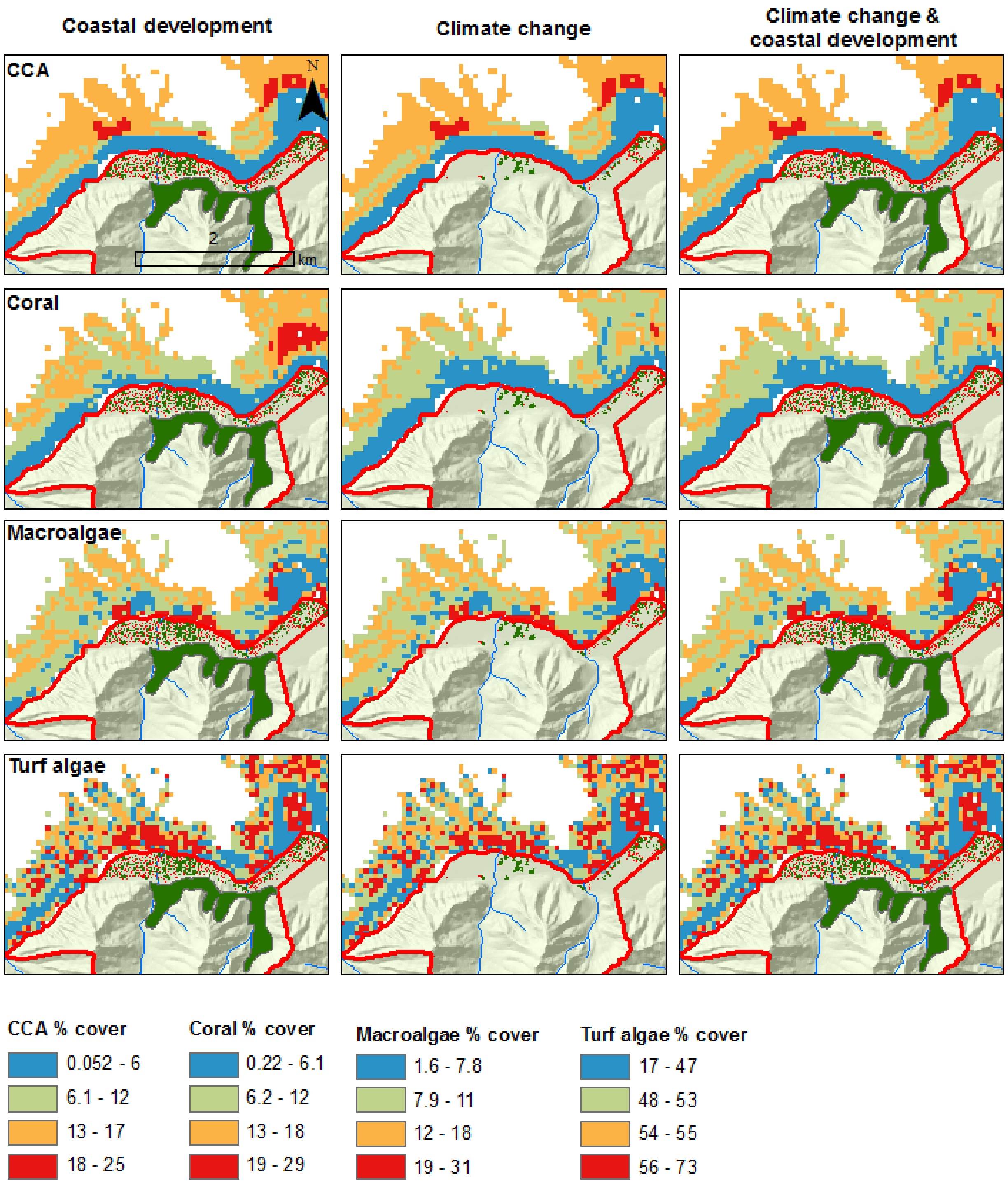


Figure S3.1. Hāʻena benthic indicators distribution per extreme scenarios. The benthic reef indicators are shown in each row and each column represents Extreme Coastal Development, Climate Change and their combination.

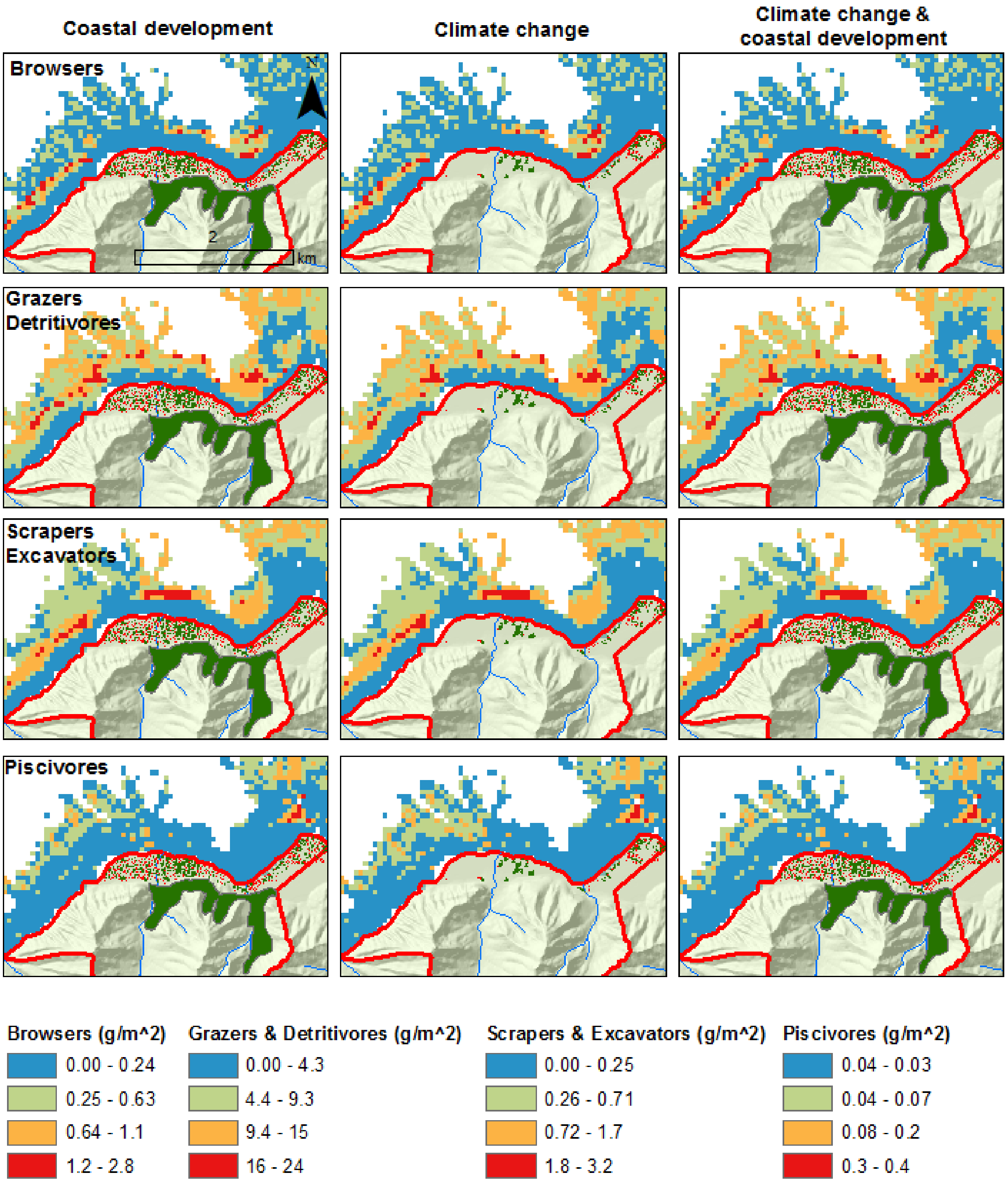


Figure S3.2. Hā‘ena resource fish indicators distribution per extreme scenario. The reef fish indicators are shown in each row and each column represents Extreme Coastal Development, Climate Change and their combination.

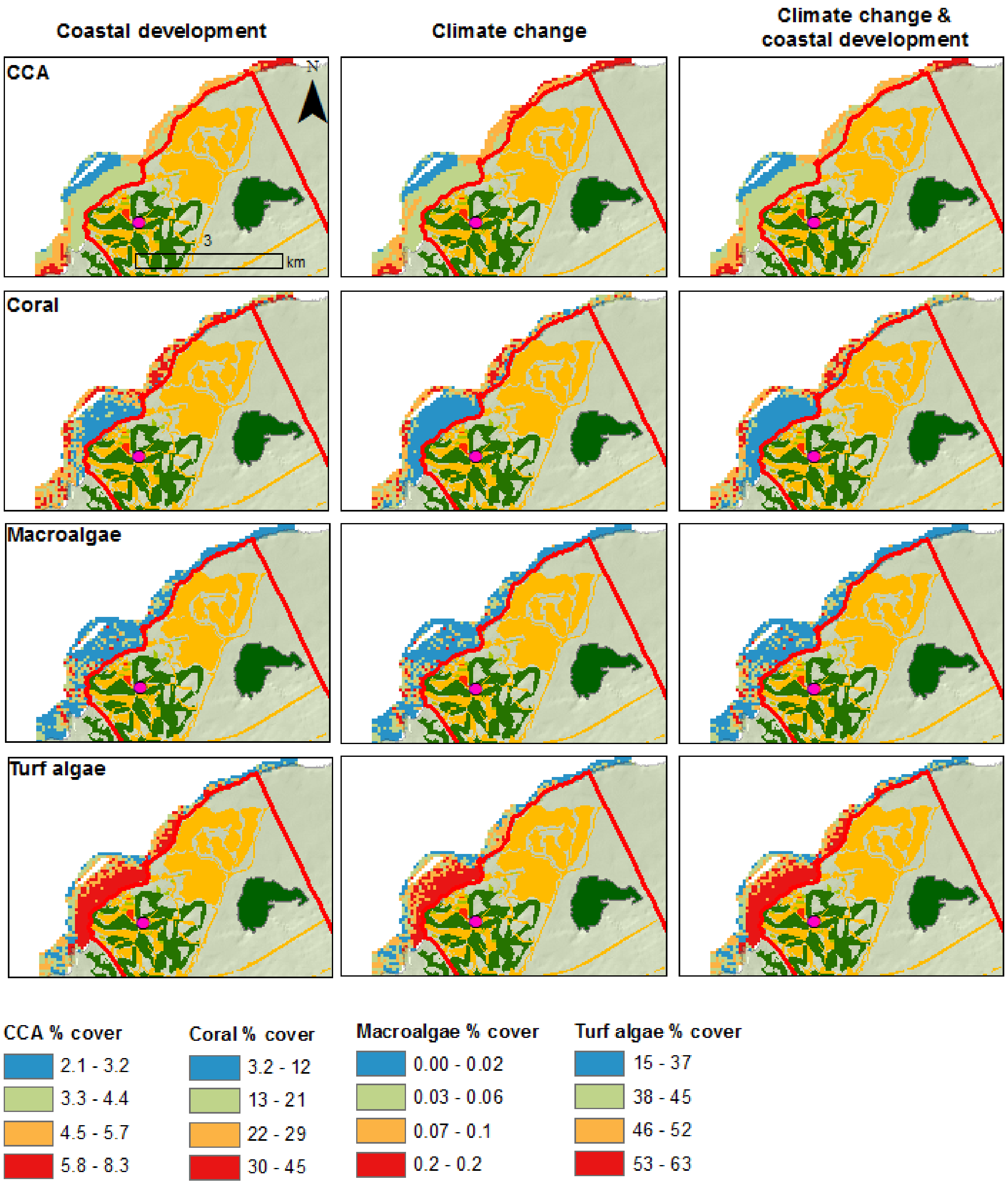


Figure S3.3. Kaʻūpūlehu benthic indicators distribution per extreme scenarios. The benthic reef indicators are shown in each row and each column represents Extreme Coastal Development, Climate Change and their combination.

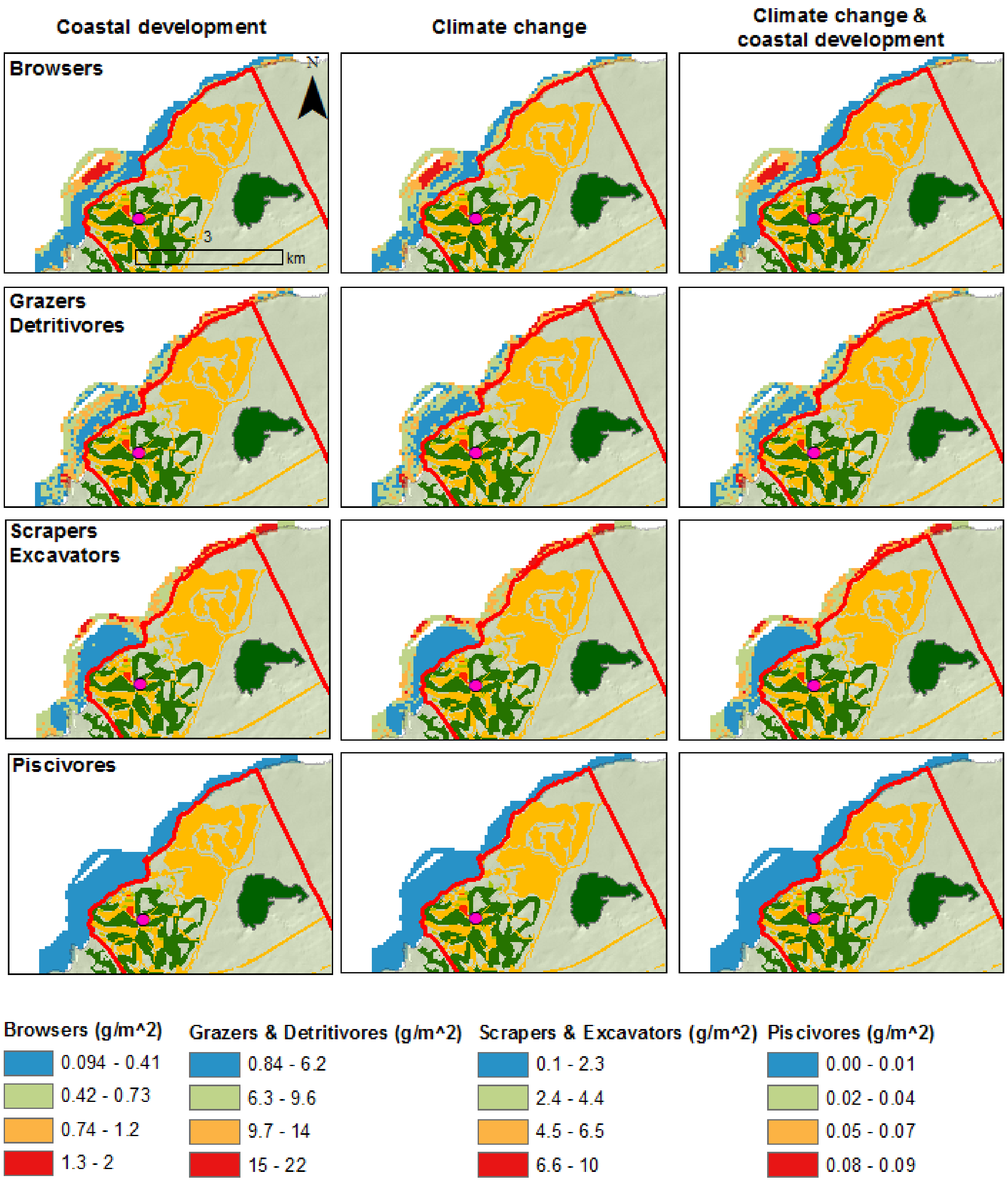


Figure S3.4. Kaʻūpūlehu resource fish indicators distribution per extreme scenario. The reef fish indicators are shown in each row and each column represents Extreme Coastal Development, Climate Change and their combination.

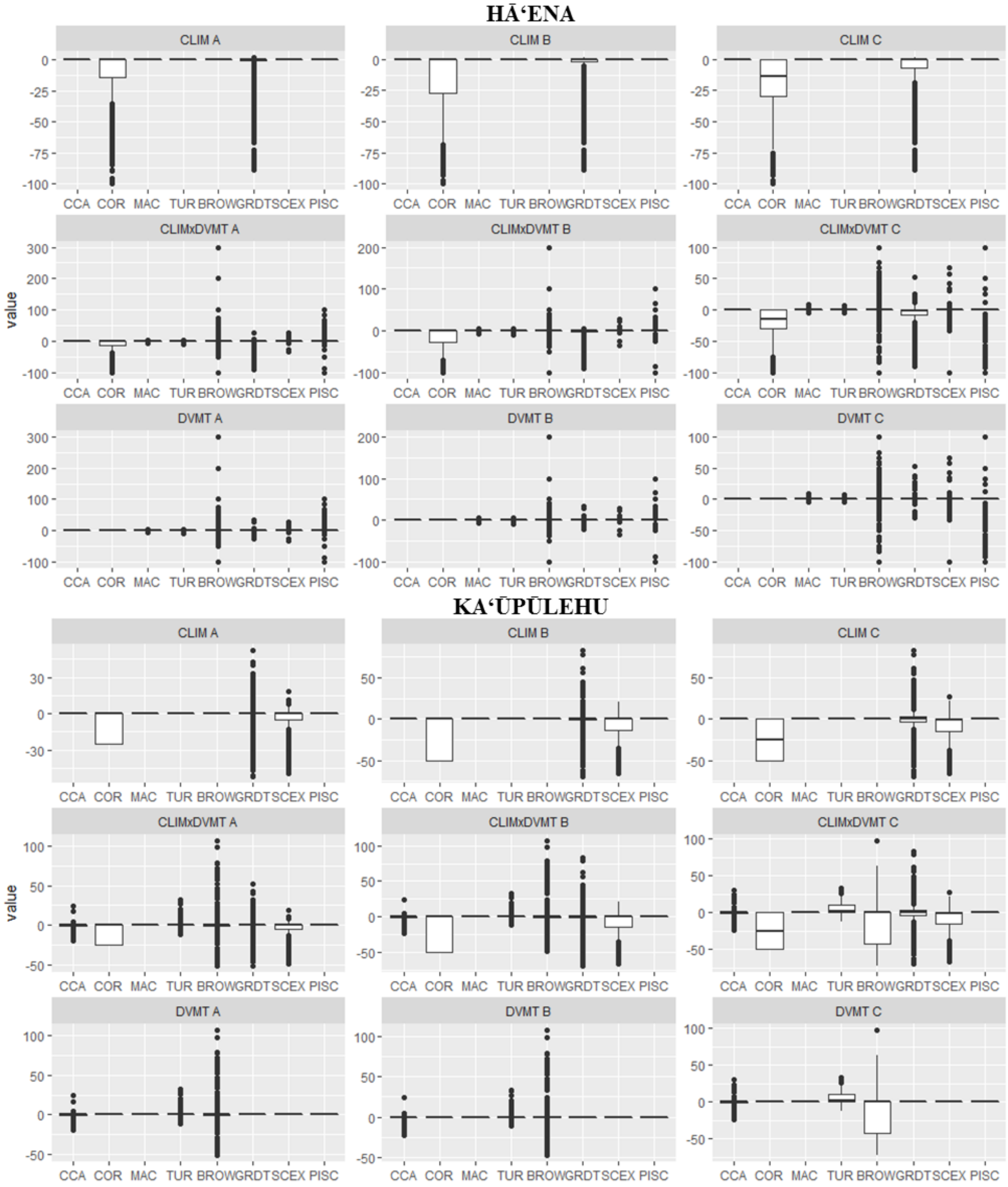


Figure S3.5. Coral reef indicators abundance change per scenario in Hā‘ena (top) and Ka‘ūpūlehu (bottom). Climate change scenarios (CLIM) and coastal development scenarios (DVMT) range from Moderate (A), Severe (B), and Extreme (C).

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CHAPTER 4. MANAGING FOR ISLAND RESILIENCE THROUGH SCENARIO PLANNING WITH LINKED LAND-SEA MODELS

ABSTRACT

Around Oceania, a cultural renaissance rooted in the concern over declining natural resources seeks to revive traditional ridge-to-reef management approaches to promote social and ecological resilience in the face of climate change. However, the differential effectiveness specific of ridge-to-reef management measures remain unclear due to a poor understanding of the individual and cumulative effects of human and natural disturbances. Therefore, new tools are needed to inform resilience management over spatial scales relevant to Oceania islanders. This research focused on a network of 35 watersheds located in Kubulau District (Fiji). Based on local data, I used a novel predictive modeling framework to evaluate differential effects of terrestrial (sediment) and marine (habitat composition and structure) drivers on coral reef communities under various future land cover and climate scenarios. I modeled the effects of three bleaching scenarios (moderate, severe and extreme), combined with deforestation and restoration scenarios, on coral reefs. The results revealed that coral reefs more exposed to chronic sediment disturbance are more resilient to modeled future climate change and deforestation impacts. In contrast, coral reefs more dependent on marine drivers, such as coral cover and habitat conditions, are more susceptible to climate change impacts. Under scenarios of climate change impacts coupled with future deforestation, targeted fish biomass is reduced at marine-driven reefs exposed to plumes from large watersheds. By linking land and sea spatially, we show multiple disturbances operating within ridge-to-reef systems can have cumulative impact on resources important to coastal communities. Therefore, forest conservation actions aimed at reducing sedimentation can promote coral reef resilience to climate change. This research demonstrates that locally developed and data-driven models offer a much-needed opportunity for aiding place-based management of coral reef social-ecological systems in high oceanic island environments.

4.1 Introduction

Protected areas have played a critical role in terrestrial and marine conservation as they are amongst the most effective strategies at mitigating threats to species and habitats (Halpern 2003, Klein et al. 2014). Historically, terrestrial and marine ecosystems have been managed and protected in isolation, where terrestrial protected areas (TPAs) and marine protected areas (MPAs) were often designed without consideration of downstream or upstream activities (Alvarez-Romero et al. 2011, Margules & Pressey 2000). However, TPAs can foster downstream benefits when accounting for land and sea linkages, while the ability of MPAs to promote coral reef resilience beyond their boundaries depends on their design and the cumulative impacts of existing upstream and marine anthropogenic drivers (Grorud-Colvert et al. 2014, Halpern et al. 2008a, Klein et al. 2012b, Stamoulis & Friedlander 2013). In some cases, MPAs may not be effective at addressing land-based source pollution impacts on coral reefs (Fredston-Hermann et al. 2016, Halpern et al. 2013), but may be useful in face of climate change by protecting important functional groups (Bellwood et al. 2004). Therefore, a more coordinated effort in the placement of TPAs and MPAs could help increase benefits and resilience of both terrestrial and marine ecosystems under a changing climate (Klein et al. 2014).

In Fiji, the Government is committed to protecting 30% of its inshore waters and 17% of its land by 2020, and therefore seeks to identify what and where to protect to achieve its goal (including financial mechanisms) (Jupiter et al. 2011). During the Fiji Islands Marine Ecoregion assessment, Kubulau District on Vanua Levu and its traditionally managed fishing grounds (*qoliqoli*) were declared as areas of global significance within the Vatu-i-Ra seascape (Jupiter et al. 2012, WWF 2004). In 2005, numerous community-based marine closures (*tabu*) were combined with three large, permanent no-take MPAs (Namena, Namuri, Nasue) in a network designed based on ecosystem-based management principles (Jupiter & Egli 2011, Weeks & Jupiter 2013). Concurrently, the forests of Kubulau District with a well-preserved hydrological connectivity between land and sea (Jenkins et al. 2010), were also identified as a national priority area for conservation (Olson et al. 2010). In 2009, the high council of chiefs (*Bose Vanua*) endorsed the first comprehensive ridge-to-reef ecosystem based management for Kubulau, which seeks to integrate the management of terrestrial, freshwater, estuarine, coastal, and marine ecosystems throughout the district (Jupiter et al. 2012). Given the importance of land and sea connections, greater understanding of when and how terrestrial and marine conservation can benefit coral reef ecosystems and their fisheries is needed to support these efforts.

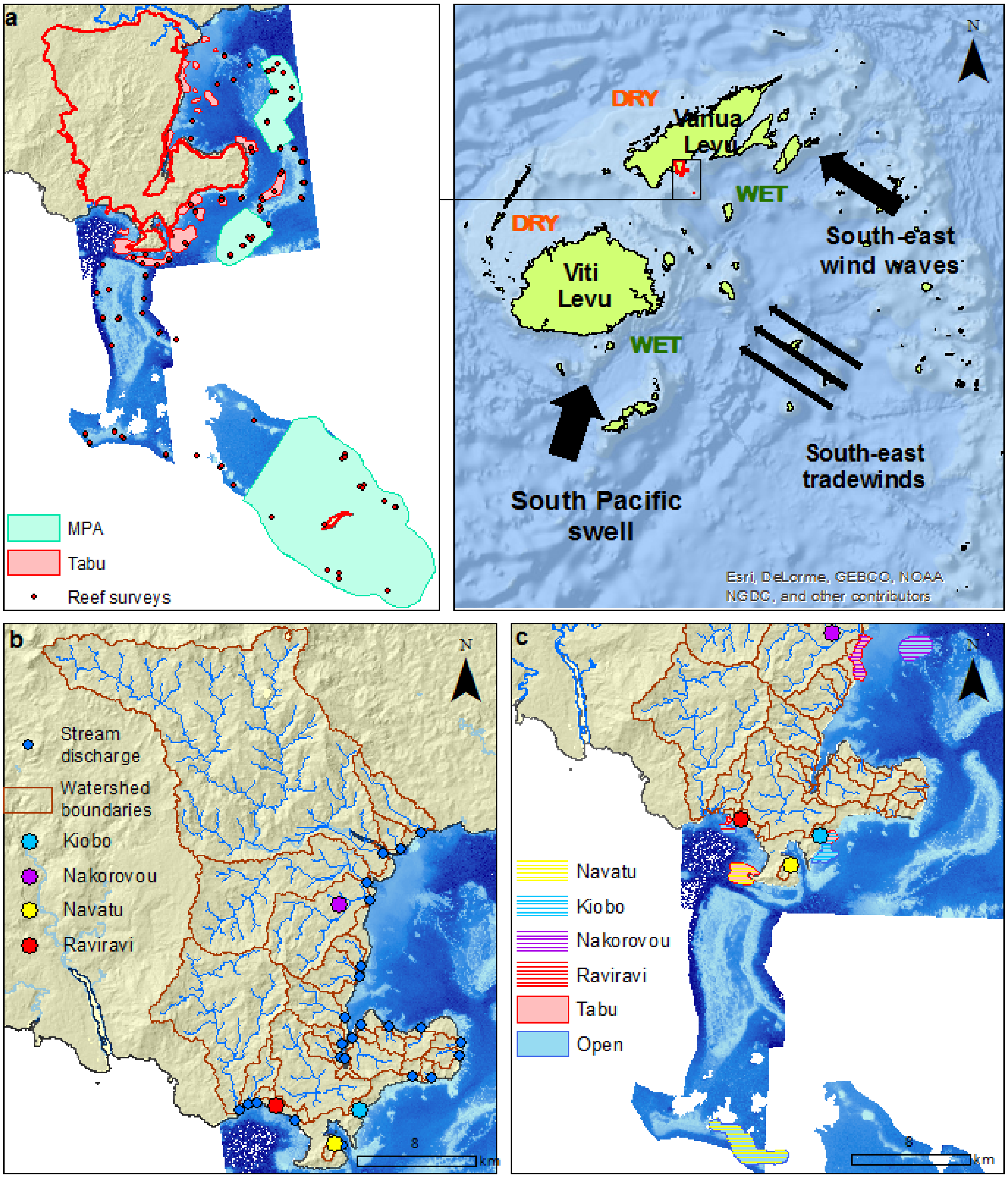
I address this knowledge gap by adapting and scaling up the integrated ridge-to-reef framework developed in Chapter 1 coupled with a scenario analysis for the Kubulau region. Streams and rivers are the most obvious lateral pathway to link land and sea when assessing the effects of forest conservation on sedimentation (Kim et al. 2011, Moore 1996). Therefore, I modified the framework developed in Chapter 1 to spatially link the effects of forest conservation actions to coral reef resilience potential through streams and sedimentation. My aim was to identify spatial management priorities and determine how forest and marine conservation actions can promote coral reef ecosystem resilience and fisheries in Oceania. I used Kubulau as a case study to answer the following questions relevant to ridge-to-reef management effectiveness in the context of deforestation and climate change:

(1) What are the relative effects of terrestrial and marine drivers on coral reef dynamics?
(2) In what context does forest conservation reduce impact of sediment runoff on coral reefs and their associated targeted fish populations?

4.2. Methods

4.2.1 Site description: Kubulau, Fiji

The Fiji archipelago consist of over 300 islands, surrounded by fringing and barrier coral reefs, with Viti Levu and Vanua Levu being the two largest islands. Both islands are mountainous with peaks rising to 1300 m, which combined with the prevailing south-east trade winds result in wet windward southeastern sides (originally covered in dense tropical rainforest) and drier leeward western sides (Neall & Trewick 2008). Kubulau District is located on Vanua Levu (Figure 4.1.a), in Bua Province. The watersheds of Kubulau District have between 70%–80% forest cover (Jupiter & Egli 2011) with relatively intact hydrologic connectivity between terrestrial, freshwater, and marine areas (Jenkins et al. 2010). Several perennial streams discharge into the nearshore waters of Kubulau (Figure 4.1.b). The complex geomorphology of Kubulau offers a spectrum of ridge-to-reef systems, ranging from small to large watersheds, which discharge in small to large bays or narrow lagoons. The diverse marine geomorphology of the area includes fringing and inshore reefs, lagoons, midshelf reefs and a barrier reef (Figure 4.1.c). The population of the district is ~1,000 people spread between ten villages, seven of which are located on the coast.



Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors

Figure 4.1. Study site. (a) Location of Kubulau study site in the Fijian Archipelago, with the direction of the prevailing southeast trade winds indicated. Village locations are shown within (b) the landscape (watersheds and stream discharge points). Important fishing grounds (tabu and open

areas) for Navatu, Kiobo, Nakorovou and Raviravi villages and reef survey sites are shown in the (c) seascape.

4.2.2 Modeling approach

In order to determine the effects of terrestrial and marine drivers combined with anthropogenic drivers on coral reefs and targeted reef fish population in Kubulau District, we adapted and applied the predictive ridge-to-reef modeling framework developed in Chapter 1. The modified modeling framework, coupled sediment models and coral reef predictive models and was calibrated on locally available data (Figure 4.2). First, we designed and modeled three forest management scenarios (Present, Deforestation, and Restoration) based on the input of local communities and three climate change scenarios (Moderate, Severe, and Extreme Bleaching) derived from recorded and projected coral bleaching impacts for the region (Hoeke et al. 2011, Lovell et al. 2004). Important fishing grounds for coastal villages were identified and digitized (Jupiter et al. 2010) and mapped with existing tabu areas (Jupiter & Egli 2011). Sediment modeling was used to quantify the downstream sediment discharge resulting from land cover change, coupled with ArcGIS-based modeling to derive maps of coastal water quality. For the marine drivers, I applied GIS-based modeling of remotely-sensed bathymetry (IKONOS/Quickbird and LiDAR) (Knudby et al. 2011) to quantify and develop maps of the marine habitat structure and composition. The predictive coral reef models were parameterized for a suite of benthic and fish indicators as response variables, derived from reef survey data collected by the Wildlife Conservation Society Fiji Program. The modeled indicators were benthic and fish functional groups that support aspects of coral reef ecological resilience (Green & Bellwood 2009, Smith et al. 2016) and represent important cultural resources (Jupiter & Egli 2011). Boosted Regression Trees (BRTs) were used to characterize the responses of benthic and fish indicators as a function of the terrestrial and marine driver data sets across the Kubulau seascape and map their predicted distributions. Once adapted and calibrated, I applied this framework as a decision support tool to assess the potential benefits of forest conservation on coral reefs marine closures and fishing grounds of 4 villages (Kiobo, Nakorovou, Navatu and Raviravi) by simulating the benthic and fish communities under forest cover and climate change scenarios. The outputs of the coral reef models were used to evaluate potential changes in the benthic and fish communities under projected scenarios compared to present conditions.

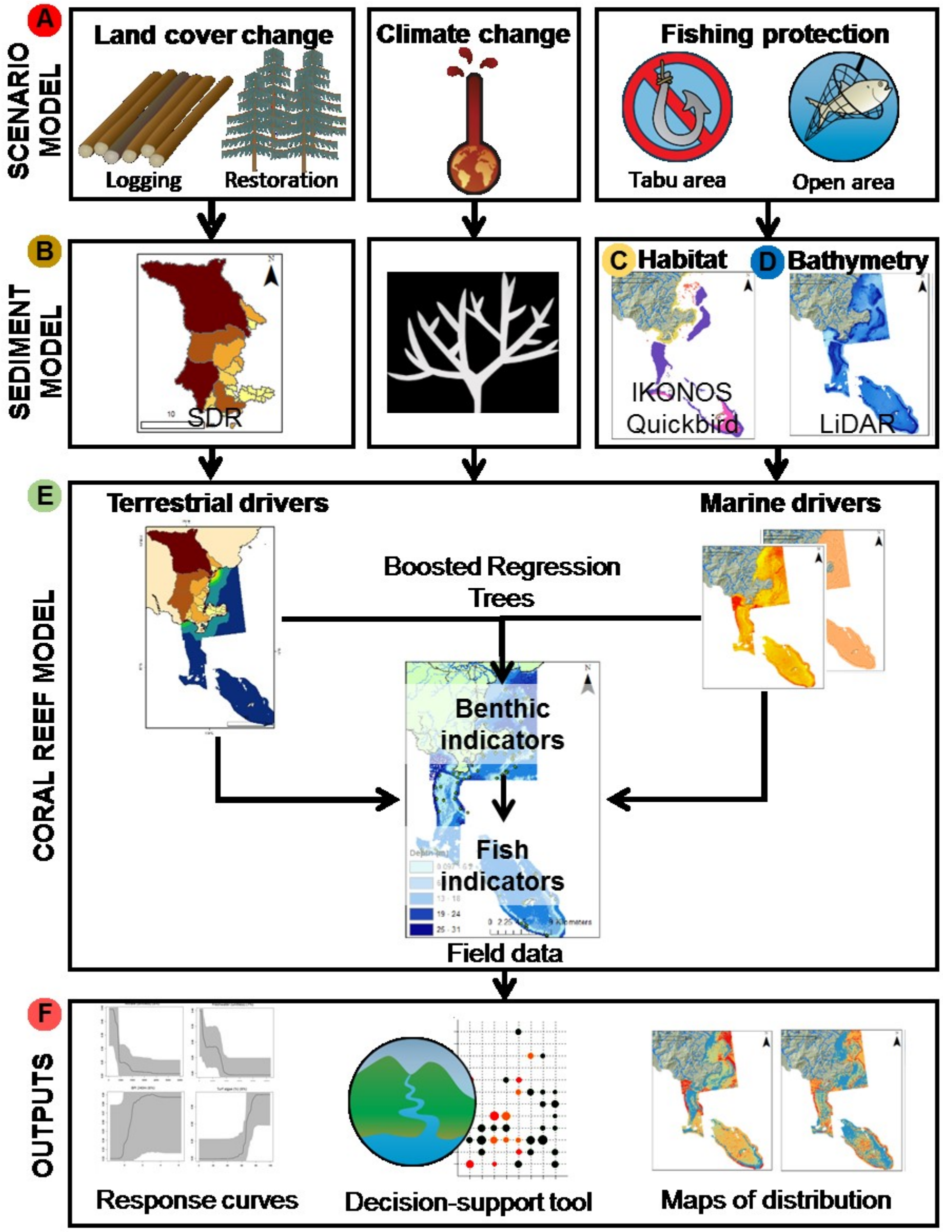


Figure 4.2. Modeling framework for the ridge-to-reef decision support tool[3]. Terrestrial drivers (total suspended sediment [TSS]) derived from sediment model SDR (a). Marine drivers (habitat composition and structure) were derived from habitat map (c) and bathymetry data (d). Boosted regression trees were used to evaluate the relative contribution of drivers on variability in

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[3] Symbols courtesy of Integration and Application Network (http://ian.umces.edu/symbols/)

benthic and fish indicators (e). Response curves created by fitting modeled predictors to empirical measures of indicators can be used to predictively map changes to coral reef indicators under different climate and land use scenarios (f).

4.2.3 Coral reef indicators

To assess coral reef dynamics and predicted ecological responses to sedimentation and bleaching, I considered the abundance of four benthic (% cover) and four fish (kg/ha) groups based on their functional roles and importance as biocultural resources (Table 4.1) (Green & Bellwood 2009, Smith et al. 2016). The benthic functional groups included calcifying organisms (crustose coralline algae [CCA] and coral) and benthic algae (turf algae and macroalgae) (refer to Section 2.3 for more details). Resource fishes identified as important for subsistence and cultural practices by the local Fijian communities (e.g., Acanthuridae, Carangidae, Carcharhinidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Serranidae, Siganidae, Sphyraenidae) (Jupiter & Egli 2011) were modeled according to their functional role to track ecological resilience (see Green & Bellwood 2009 for classification): (1) browsers, (2) grazers/detritivores, (3) scrapers/excavators, and (4) piscivores (refer to Table S4.1 for information on the species composition). The extent to which a reef system possess these functional groups is fundamental to determine its capacity to resist phase shifts and recover in the face of disturbance (Edwards et al. 2014). We derived the abundance of these indicators from reef survey data collected by the Wildlife Conservation Society (WCS) Fiji Program.

Table 4.1. Coral reef benthic and fish indicators for coral reef models. These indicators were used as response variables in the BRT coral reef models.

Type	Code	Metric	Source	Description
Benthic indicators	CCA	Crustose coralline algae	Reef surveys	% cover
	COR	Coral cover	Reef surveys	% cover
	MAC	Macroalgae	Reef surveys	% cover
	TUR	Turf algae	Reef surveys	% cover
Resource fish indicators	BROW	Browsers	Reef surveys	Biomass (kg.ha^{-1})
	GRDT	Grazers & Detritivores	Reef surveys	Biomass (kg.ha^{-1})
	SCEX	Scrapers & excavators	Reef surveys	Biomass (kg.ha^{-1})
	PISC	Piscivores	Reef surveys	Biomass (kg.ha^{-1})

4.2.3.1 Field datasets

We obtained three field datasets totaling 163 survey locations, collected over three sampling periods, April and September 2009 and April 2010 contributed by WCS Fiji (see WCS [2010] for more details). Fish and benthic surveys were stratified by depth (deep [12-15 m], shallow [5-8 m], top [0.5-2 m]), habitat (forereef and backreef areas), and management (open or closed to fishing) (Figure 4.1.a). Generally, two forereef and two backreef sites were surveyed within each management treatment, with 3-5 replicate transects nested within depth categories and depth nested within sites. At each site, 50 x 5 m belt transects (250-m^2 transect area) were used to collect fish data. Benthic life-form categories were recorded along the same 50 m transects at 0.5 m intervals using lifeform categories adapted from English et al. (1994) (Jupiter & Egli 2011). Life-form classes were reclassified according to the following 8 functional strata: crustose coralline algae (CCA, including coralline algae with structure); live hard scleractinian coral (COR: *Acropora* spp., branching, corymbose, encrusting, foliose, massive, and submassive corals); macroalgae (MAC: all fleshy macroalgae >2 cm, dead coral with fleshy algae); turf algae (TUR: ≤2 cm height on reef pavement); filter feeders (FLF: sponge, soft corals, zooanthids), hard bottom (HB: rubble, non-carbonate rock); soft bottom (SB: sand, silt); and other substrate (OT: including *Halimeda* spp., microbial and other biota). For the purposes of this study, we calculated the percentage cover of each benthic group. For each belt transect, divers recorded total length (TL) of observed fishes for each targeted species, using 5 cm length classes for fishes < 40 cm and exact size for fishes ≥40 cm (Jupiter & Egli 2011). As many of the L-W conversions required fork length (FL), a length-length (LL) conversion factor was obtained from FishBase where necessary to convert from total length (TL) recorded during the surveys to FL before biomass estimation (Jupiter & Egli 2011). To calculate the biomass for each fish, we applied length estimates in the length-weight (L-W) expression $W = a \times L^b$, where a and b are constants for the allometric growth equation, L is total length in cm, and W is mass in kg, using species-specific a and b parameters obtained from FishBase (Froese & Pauly 2011) with a and b parameter values preferentially selected from sites closest to Fiji (e.g., New Caledonia). Because the L-W formula resulted in some grossly overestimated weights for fishes that substantially change morphology as they age, maximum weights were used for certain species when these fish were sighted above threshold sizes.

4.2.4 Modeling human drivers

4.2.4.1 Global human drivers: Coral bleaching scenarios

Climate change scenarios were designed and modeled to spatially represent the potential effects on coral reefs, including mortality from coral bleaching. Based on sea surface temperature (SST) and atmospheric carbon dioxide (CO_2) projections, shallow-water scleractinian coral cover loss due to bleaching was estimated based on a combination of growth and mortality models (Hoeke et al. 2011). Based on a projected increase in global temperatures of 2-4^o C over the coming century with a threshold for heat stress increasing by 0.1^o C every decade; the model suggested a coral cover decline of 25% to 75% for the main Hawaiian Islands by the end of the century (Hoeke et al. 2011, IPCC 2007). Based on coral reef monitoring post bleaching events in Fiji (Cumming et al. 2002, Lovell et al. 2004), we confirmed similar levels of impact between Hawai‘i and Fiji, so we transferred the bleaching scenarios developed for the Hawai’i sites to Kubulau. I implemented Moderate and Severe Bleaching scenarios, where negative 25% and 50% scaling factors, respectively, were forced on current coral cover for all reef areas shallower than 5 m (Figure 4.3) and an Extreme Bleaching scenario that forced a 50% scaling factor on coral cover in all reef areas between 0 and 5m and a 25% scaling factor for areas between 5 and 10m (Figure 4.3). In spite of large uncertainties and debate surrounding coral adaptation to heat stress (Baker et al. 2008), this analysis quantitatively illustrates the potential impacts from large declines in coral cover in the 21st century (Hoeke et al. 2011).

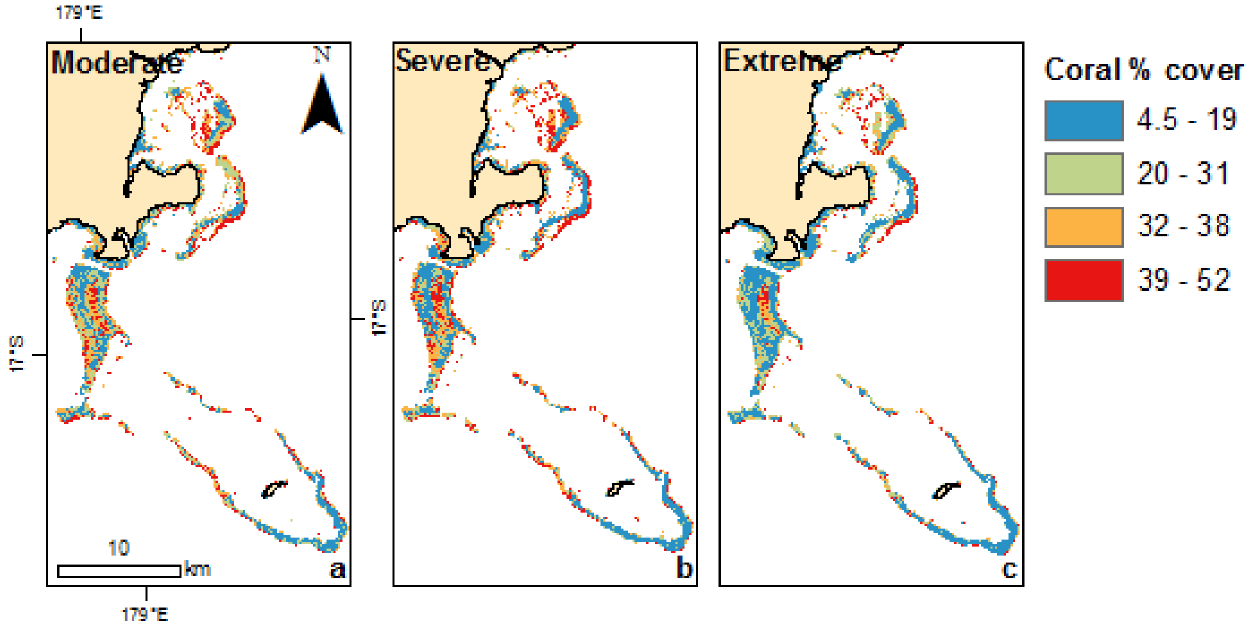


Figure 4.3. Maps of coral cover per climate change scenario. The Moderate (a), Severe (b), and Extreme (c) Bleaching scenarios represent different levels of coral cover loss.

4.2.4.2 Local human drivers: Forest cover change scenarios

Three land cover scenarios were considered: (1) Conservation (present land cover), (2) Deforestation, and (3) Reforestation. Present land cover was defined using a land cover map derived from satellite imagery (Figure 4.4) (Ministry of Agriculture *unpublished data*). A land use capability classification (Land Use Planning Section et al. 2012) was used to determine areas suitable for agriculture (classes 1-4); forestry (classes 1-7); and conservation/natural forest only (class 8). The Deforestation scenario assumed all areas within designated current and proposed logging areas within logging concessions (WCS *unpublished data*) were converted to pine with the exception of land use capability class 8. Outside of logging concession areas, all areas suitable for agriculture (classes 1-4) were converted to taro (*Colocasia esculenta*) and kava (*Piper methysticum*), whereas classes 5-8 remained forest. The forest Restoration scenario (or Reforestation) assumed all native forest was conserved and all areas currently in pine were restored to native forest.

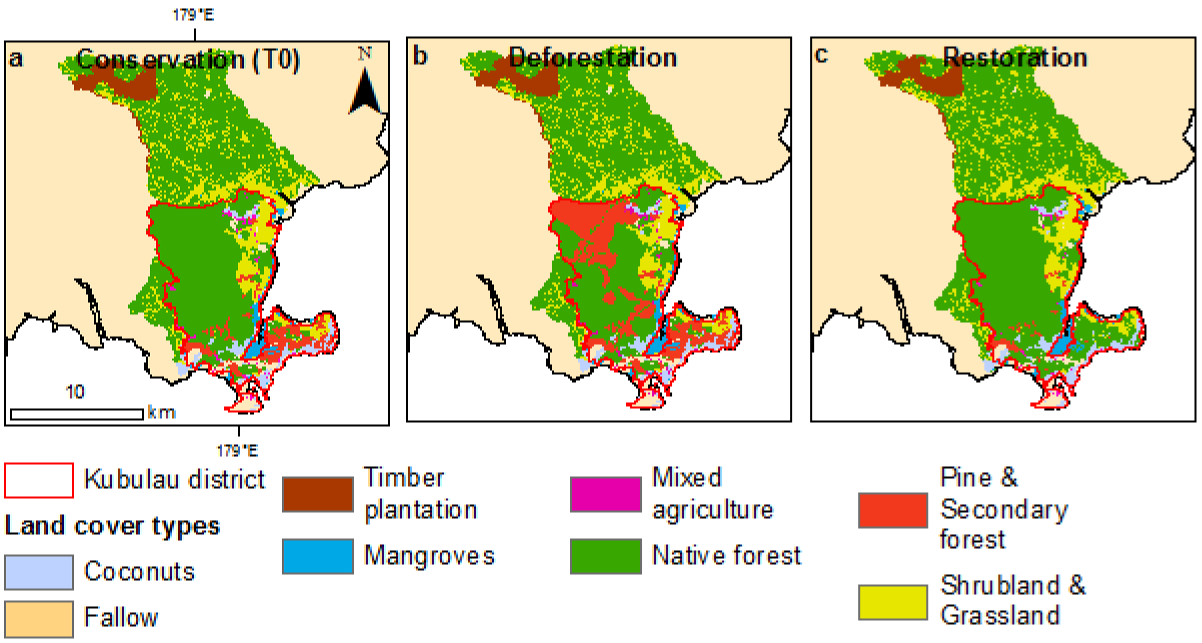


Figure 4.4. Maps of forest cover change per scenario. The Conservation scenario (a) represents current conditions. Also considered were: Deforestation (b) and Reforestation (b) land cover change scenarios.

4.2.5 Modeling terrestrial drivers

4.2.5.1 Sediment models

Sediment export was modeled for each land use scenario to quantify the total sediment discharge downstream. First gross erosion was estimated per cell using the empirical Revised Universal Soil Loss Equation (RUSLE) method (Renard et al. 1997), and then the sediment delivery from each cell to the hydrologic network was estimated using a sediment delivery ratio (SDR) approach (Borselli et al. 2008). We used the InVEST Sediment Delivery Ratio (SDR) model to conduct these calculations (The Natural Capital Project 2015). Ground-truth data were unavailable, but the connectivity of the model was verified using available stream maps by comparing predicted stream outputs to an existing stream layer. The model parameterization included a streamflow accumulation parameter of 100, a Borselli k-factor of 5.0 and an IC_0 of 0.3. The maximum allowable SDR was set to 0.8. Subwatersheds were created using the Basins function with ArcGIS 10.2. Discharge points to the coast were hand-edited for accuracy in comparison to satellite imagery (Figure 4.1).

Input data to the spatial model included a digital elevation model (DEM) (30 m resolution), land cover, rainfall erosivity, and soil erodibility (**K**). The rainfall erosivity (**R**) map was created at a 100-m resolution by using available annual precipitation averages (**P**) and converting to erosivity using the Bols method, which has also been applied in Indonesia (Bols 1978).

$$\boldsymbol{R} = \frac{\mathbf{2.5\ x\ } \boldsymbol{P}^{\mathbf{2}}}{(\mathbf{100}\ \boldsymbol{x}\ (\mathbf{0.07}\boldsymbol{P} + \mathbf{0.73}))} \qquad (\mathbf{1})$$

Soil erodibility was derived from the New Zealand Soil Survey dataset (Leslie et al. 1998), and used a value of K of 0.002 ton ha hr MJ^{-1} ha^{-1} mm^{-1} to fill in missing values that were not available in the tables. In addition, for each land use class, an estimate of vegetation cover (C-factor) and management practice effectiveness (P-factor) was required for the model. We adopted the biophysical table that includes the C-factor and P-factor shown in Table 4.2. C-factors for taro were taken from published FAO rice values, and forest values were separated by degraded and secondary forests following Lianes (2009). All P-factors were kept at 1, lacking information to suggest otherwise.

Table 4.2. Sediment model calibration factors. See Falinski 2016 for more details.

Land Cover type	**C factor**	**P factor**
Coconuts	0.02	1
Fallow	0.12	1
Fish pond	0.001	1
Grassland	0.009	1
Mangroves	0.001	1
Monoculture taro	0.2	1
Monoculture kuta	0.05	1
Monoculture kuta and taro	0.05	1
Monoculture rice	0.2	1
Natural forest	0.006	1
Pine	0.007	1
Polyculture	0.3	1
Secondary forest	0.007	1
shrubland	0.013	1
Tilaka	0.2	1
Village	0.2	1
Wetland	0.001	1

4.2.5.2 Coastal water quality modeling

The modeled sediment discharge from each watershed was distributed to each coral reef through a distance-based plume model developed in in ArcGIS, following Halpern et al. (2008a). The distance based plume model applied a decay function to a cost-path surface (Yu et al. 2003). The cost-path surface was a composite of factors that promoted or hindered sediment dispersion and included geomorphic features (i.e., fringing reef, inner reef flats, reef crests, reef slopes, lagoon) derived from a geomorphic zoning map (Roelfsema et al. 2013), as well as depth (m), distance from shore (m), and wave exposure (degree). Based on the distance measured between river mouths and locations where sediment impacts on coral reefs has been recorded in the past (Jupiter et al. 2010), the maximum threshold for diffusion from the shoreline was set to 2.5 km. This method enabled the creation of spatially explicit maps of nearshore water quality. I used this modeled coastal water quality metric as a proxy for total suspended sediment dispersion from stream discharge (TSS thereafter) that may influence coral reef dynamics.

4.2.6 Modeling marine drivers

The marine drivers were derived from remote sensing and wave model data available for both sites using GIS-based tools. The selected marine drivers were identified as important predictors of coral reef benthic and fish communities by chapter 1 (Table 3). Depth and distance from shore were used as geographic metrics to account for variation arising from spatial location. A bathymetric depth at 4 m resolution was used (Knudby et al. 2011), which was derived from passive remote sensing techniques and distance from shore was derived from the archipelago-wide coastline map (Fiji Department of Lands, unpublished data). Three types of habitat drivers represented direct and indirect effects of seafloor geomorphology on benthic and fish communities: (1) habitat morphology, (2) habitat complexity, and (3) habitat exposure. Habitat morphology, represented by Bathymetric Position Index (BPI) and slope metrics, were computed for two neighborhood sizes (60 m and 240 m radii) to determine depth relative to the reef and surrounding area at different spatial scales (Kendall et al. 2011, Pittman & Brown 2011). Terrain ruggedness, slope of slope, and plan and profile curvature metrics were computed to estimate topographic complexity. Three metrics of habitat exposure (aspect sine circular mean, aspect cosine circular mean, aspect circular standard deviation), representing the steepest downslope direction (measured in degrees 0°-360°), were used to capture the direct and indirect effects of water flow due to seafloor topography and directionality. Four types of habitat connectivity metrics, representing direct and indirect effects of habitat composition and fragmentation on benthic and fish communities, were derived from the benthic habitat map at 10-m resolution (Roelfsema et al. 2013) in FRAGSTATS software (McGarigal et al. 2002): (1) contiguity, (2) fractal dimension, (3) proximity, and (4) Shannon diversity index (McGarigal et al. 2009).

Table 4.3. Description of marine drivers. Supporting references are listed that indicate the importance of each variable on fish communities. Refer to Table S4.2 for more information.

Indicator	**Metrics**	**Description**	**Unit**	**References**
Geography	Depth	Mean seafloor depth	m	(Dollar 1982, Fabricius & De'ath 2001, Jouffray et al. 2015)
	Distance to shore	Euclidean distance to the shoreline	m	
Habitat morphology	BPI	Relative topographic position of a point based its elevation and the mean elevation within a neighborhood	m	(Pittman & Brown 2011, Stamoulis et al. 2016)
	Slope	Maximum rate of change in seafloor depth between each grid cell and its neighbors	Degree	
Habitat complexity	Plan curvature	Seafloor curvature perpendicular to the direction of the maximum slope (mean). Value indicates whether flow will converge or diverge over a point.	Radians.m^{-1}	(Darling et al. 2017, Friedlander & Parrish 1998a)
	Profile curvature	Seafloor curvature in the direction of the maximum slope (mean). Value indicates whether flow will accelerate or decelerate over the curve.	Radians.m^{-1}	
	VRM	Measure of terrain ruggedness variations (mean). Value range from 0 (flat) to 1 (complete variation).	Unitless	
Habitat exposure	Aspect	Downslope direction of maximum rate of change in seafloor depth between each grid cell and its neighbors (sine circular mean, cosine circular mean, circular standard deviation)	Degree	(Franklin et al. 2013, Knudby et al. 2013)
Habitat composition	Contiguity Index	Mean spatial connectedness of patches	Unitless	(McGarigal et al. 2009)

	Fractal dimension	Mean patch complexity at the landscape level	Unitless	(McGarigal et al. 2009)
	Proximity index distribution	Measure of patch isolation	Unitless	(McGarigal et al. 2009)
	Shannon diversity index	Diversity of benthic cover types in the landscape	Unitless	(McGarigal et al. 2009)

4.2.7 Coral reef predictive models

For the coral reef models, I calibrated BRT models using the empirical benthic and fish data for Kubulau collected by WCS Fiji (Figure 4.2.E) as a function of the terrestrial and marine drivers for Kubulau (Figure 4.1.C & D) (see Elith et al. (2008) for more details). I used the percent deviance explained (PDE) by the calibration and internal ten-fold cross validation method as performance measures of the model optimum. The optimal models explained the most variation in the response variables (i.e., greatest PDE). To control for overfitting, we determined the number of drivers to remove by evaluating how many drivers could be dropped without resulting in a major reduction in PDE (see [Elith et al. 2008] Appendix S2). The final BRT models determined the strongest statistical environmental drivers (among the simultaneously tested predictors) and estimated the underlying relationship (response curve) between the modeled indicators and the key environmental drivers (Venables & Ripley 2013). I conducted the model fitting in R software (R Core Team 2014) using the gbm package (Elith et al. 2008, Ridgeway 2007).

I applied the calibrated spatial predictive coral reef models to simulate projected changes to simulate the benthic and fish communities under forest cover and climate change scenarios. The calibrated coral reef models were used to predict the potential distribution of each benthic and fish indicator for each 60 m^2 grid cell according to future conditions. The modeled predictions were used to produce maps of benthic and fish indicator distributions under future scenarios. First, the benthic groups were spatially predicted as a function of the terrestrial and marine drivers (Table 4.3) and projected human scenarios. Then resource fishes were predicted as a function of the natural drivers, including the predicted benthic community (Table 4.3) and future human driver scenarios. Spatial predictions were performed in R (R Core Team 2014) using the dismo (Hijmans et al. 2014) and raster (Hijmans 2014) packages.

4.2.8 Modeling of scenario impacts and analysis

The scenario analysis focused on the tabu and fished areas important to four villages (Raviravi, Navatu, Nakorovou, and Kiobo) to capture a range of exposure and environmental conditions (Figure 4.1) (Jupiter et al. 2010). For each of these important fishing grounds, the predicted spatial distribution of benthic and fish indicators under each forest cover, climate change, and combined scenario were compared against present distributions using a permutational multivariate analysis of variance (PERMANOVA) (McArdle & Anderson 2001) in Primer PERMANOVA+ software (Anderson et al. 2008) (refer to Section 3.2.6 for more details).

4.3. Results

4.3.1 Terrestrial drivers

The sediment export model results for present conditions showed that current land cover in Kubulau resulted in relatively low sediment loads (2,452 tons or 11.9 t/km^2) (Figure 4.5). A large percentage of the total sediment budget (ranging from 43 to 55%) discharging in the eastern bay, originated from the watershed just north of Kubulau. The largest difference between deforestation and restoration scenarios occurred within two large watersheds, which discharged in the eastern and southern bays of Kubulau. The southern bay received discharge of 550 ton/yr under the deforestation scenario, compared to 383 ton/year under the restoration scenario. These differences corresponded to a 50% and 2.8% increase from status quo conditions for deforestation and restoration, respectively. The southern bay received discharge of 280 ton/yr under the deforestation scenario, compared to 63 ton/year under the restoration scenario. These differences correspond to a 330% increase and 0.5% decrease from Present conditions for Deforestation and Restoration, respectively. In terms of sediment discharge, Raviravi (Tabu: $\bar{X}$= 208.1, SD=11.5; Open: $\bar{X}$= 182.0, SD=32.1) and Nakorovou (Tabu: $\bar{X}$= 182.9, SD= 99.4; Open: $\bar{X}$=13.3, SD= 10.8) were the most exposed to sedimentation discharge, with the exception of Nakorovou open fishing areas (Table S4.3). The fished areas of Kiobo (Tabu: $\bar{X}$=23.7, SD=4.5; Open: $\bar{X}$= 31.2, SD=7.4) and Navatu (Tabu: $\bar{X}$= 4.2 , SD= 1.2; Open: $\bar{X}$= 0.0, SD=0.0) were the least exposed to sediment influence.

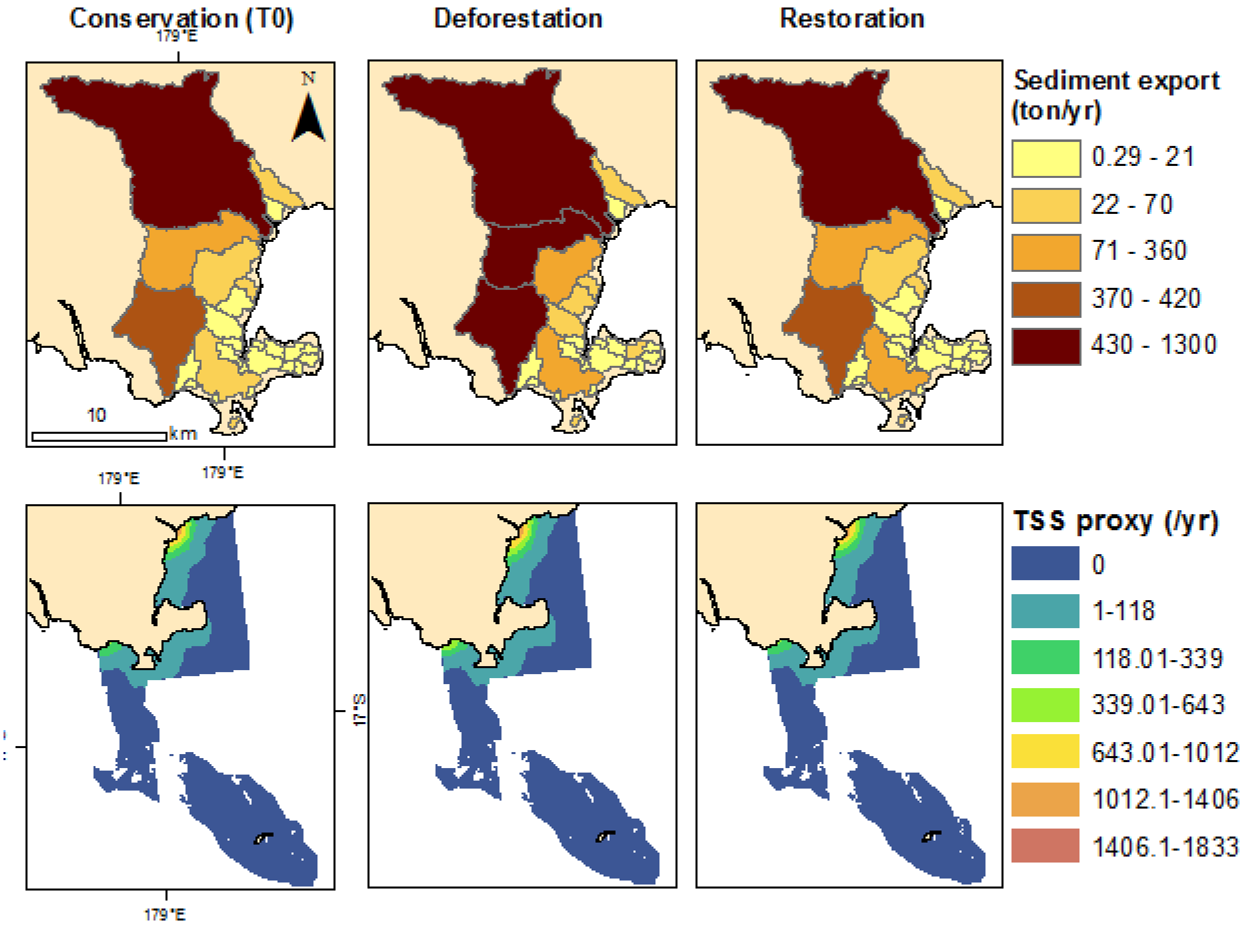


Figure 4.5. Modeled sedimentation coupled with modeled coastal water quality per forest cover scenario. Present (left), Deforestation (middle) and Restoration (right) scenarios.

4.3.2 Marine drivers

Our marine driver maps showed that most tabu and open areas were shallow reef areas and located closer to shore (Table S4.3) (refer to Figure S4.1 for spatial representation). Generally, tabu areas were shallower (6.3 – 7.9m deep) and closer to shore (<280 m from shore), while the open areas were deeper (7.4 – 11.7m) and located further offshore, particularly Kiobo and Nakorovou open areas (>330m from shore). Tabu areas located in Kiobo and Navatu exhibited less reef slopes and supported less habitat complexity than the open areas. On the other hand, Nakorovou and Raviravi tabu exhibited more reef slopes and habitat complexity than the open areas. Tabu areas located in Kiobo and Navatu also showed higher exposure, compared to the open areas, while the open areas located in Nakorovou and Raviravi showed higher exposure than the tabu areas. In terms of habitat connectivity, tabu areas showed more contiguity compared to the open areas, except for Kiobo, which showed the opposite trend. Fractal dimension and habitat proximity were generally higher in the tabu areas compared to the open areas, except for Kiobo and Navatu, respectively. Habitat diversity was similar in tabu and open areas for most villages, except for Navatu where the open area showed higher diversity than the tabu area.

4.3.3 Coral reef communities in tabu and open areas

The benthic group abundance and resource fish biomass varied between villages and type of fishing grounds (tabu and open areas) (Figure S4.4). Compared to the tabu areas, the areas open to fishing showed higher abundance of reef calcifiers (CCA and coral) and less benthic algae (macroalgae and turf algae) across most villages. In areas open to fishing, CCA and corals were more abundant in Nakorovou and Navatu, while benthic algae were more prevalent in Kiobo and Raviravi. In tabu areas, CCA and corals were more abundant in Kiobo and Navatu, while benthic algae were more abundant in Nakorovou and Raviravi. With the exception of browsers, resource fish indicators biomass was higher in the areas open to fishing, compared to the tabu areas across all villages. In areas open to fishing, browser biomass was higher in Kiobo and Navatu; the scrapers and piscivores biomass was higher in Nakorovou, and Navatu supported higher biomass of grazers/detritivores. In tabu areas, resource fish biomass was higher for most indicators in Kiobo. One exception was the browsers biomass, which was higher in Nakorovou and Raviravi compared to other villages.

4.3.4 Coral reef drivers and seascape dynamics

The calibration and cross-validation of coral reef models of Kubulau explained 38-73% and 11-40% of the deviance, respectively, with the exception of the turf algae model, which performed poorly (Table 4.4). Analysis of the residuals from the final coral reef models showed no spatial autocorrelation (Moran’s I Index $p > 0.1$).

Table 4.4. BRT model calibration and cross-validation (CV) percent deviance explained (PDE). The final number of predictors (Pi) is also indicated.

Reef indicators	PDE (%)	CV PDE (%)	Pi
CCA	64	40	6
Corals	60	29	6
Macroalgae	43	11	8
Turf algae	3	-1	8
Browsers	54	10	7
Grazers & Detritivores	63	35	6
Scrapers	38	15	6
Piscivores	73	36	8

The final coral reef models identified TSS as a key terrestrial driver and habitat complexity and connectivity as the key marine drivers, as well as exposure and depth (Figure 4.6). For the terrestrial driver, TSS was negatively correlated with the reef calcifiers and positively correlated with benthic algae. As a result, the reef calcifiers were less abundant and benthic algae were more abundant in areas more exposed to sediment influence (Figure 4.7). Except for scrapers, most resource fish biomass was negatively related to TSS. In terms of fish-habitat linkages, most fish groups were positively associated with coral cover and higher biomass was predicted in areas with higher coral cover, except for browsers. Browsers and piscivores biomass was positively related to CCA, while grazers/detritivores and scrapers were negatively related to macroalgae. The final coral reef models also identified reef morphology (represented by BPI and slopes) and topographic complexity as the most common and important marine drivers of the benthic and fish communities, followed by habitat exposure and connectivity. Most resource fishes and benthic calcifiers were positively correlated with reef slopes and topographic complexity. As a result, higher fish biomass was predicted along the reef slopes. Corals were positively correlated with more exposed habitats, while all the algae groups were negatively related to exposure (Figure 4.6). Those trends were reversed for habitat connectivity, where corals were abundant in patchy habitats, while the algae groups were more abundant in contiguous habitats (Figure 4.6). Lastly, depth was positively related to reef calcifiers and scrapers (Figure 4.6).

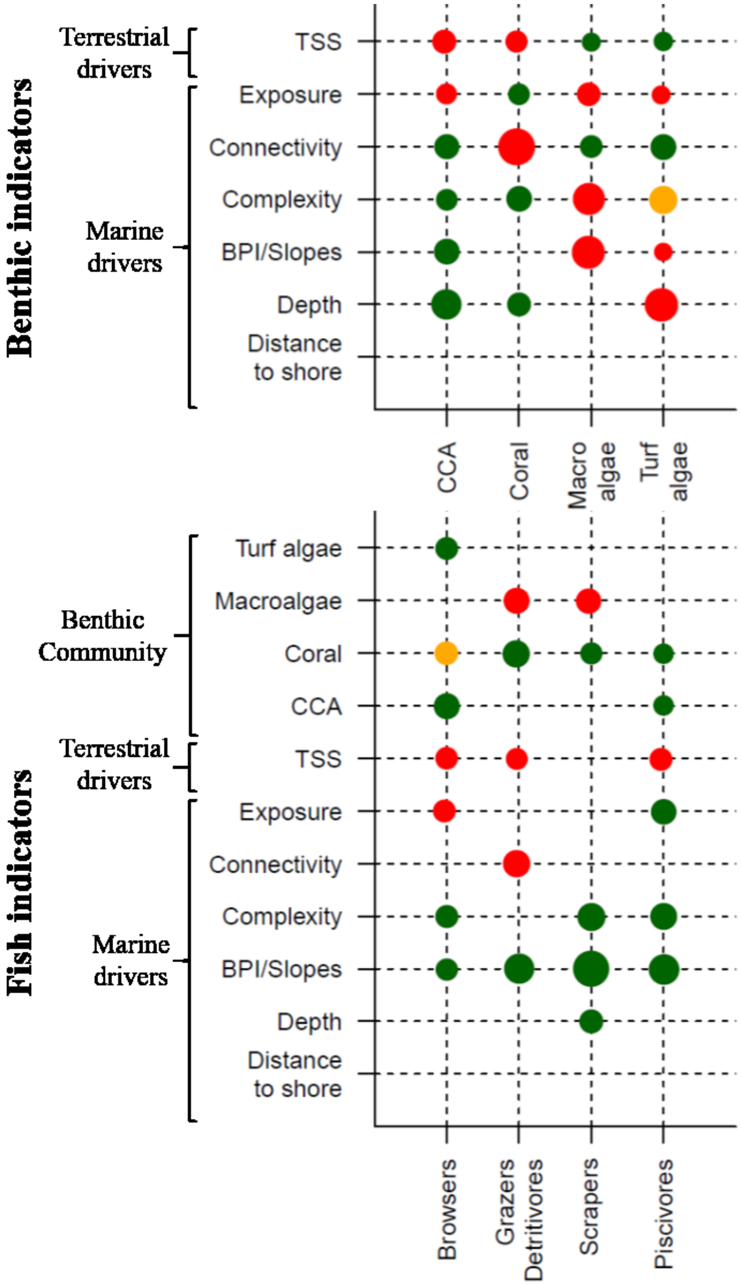


Figure 4.6. Coral reef models and key drivers of benthic and fish indicators. The BRT models identify the key drivers of the benthic and fish indicators. The benthic (top) and fish (bottom) indicators are represented along the x-axes. The terrestrial drivers, marine drivers, and benthic community predictors for the fish indicators only are represented on the y-axes. The bubble size represents the relative percent contribution of each driver and the color indicates whether the relationship between the indicator and the driver is positive (green); convex, concave, or unchanged (yellow); or negative (red).

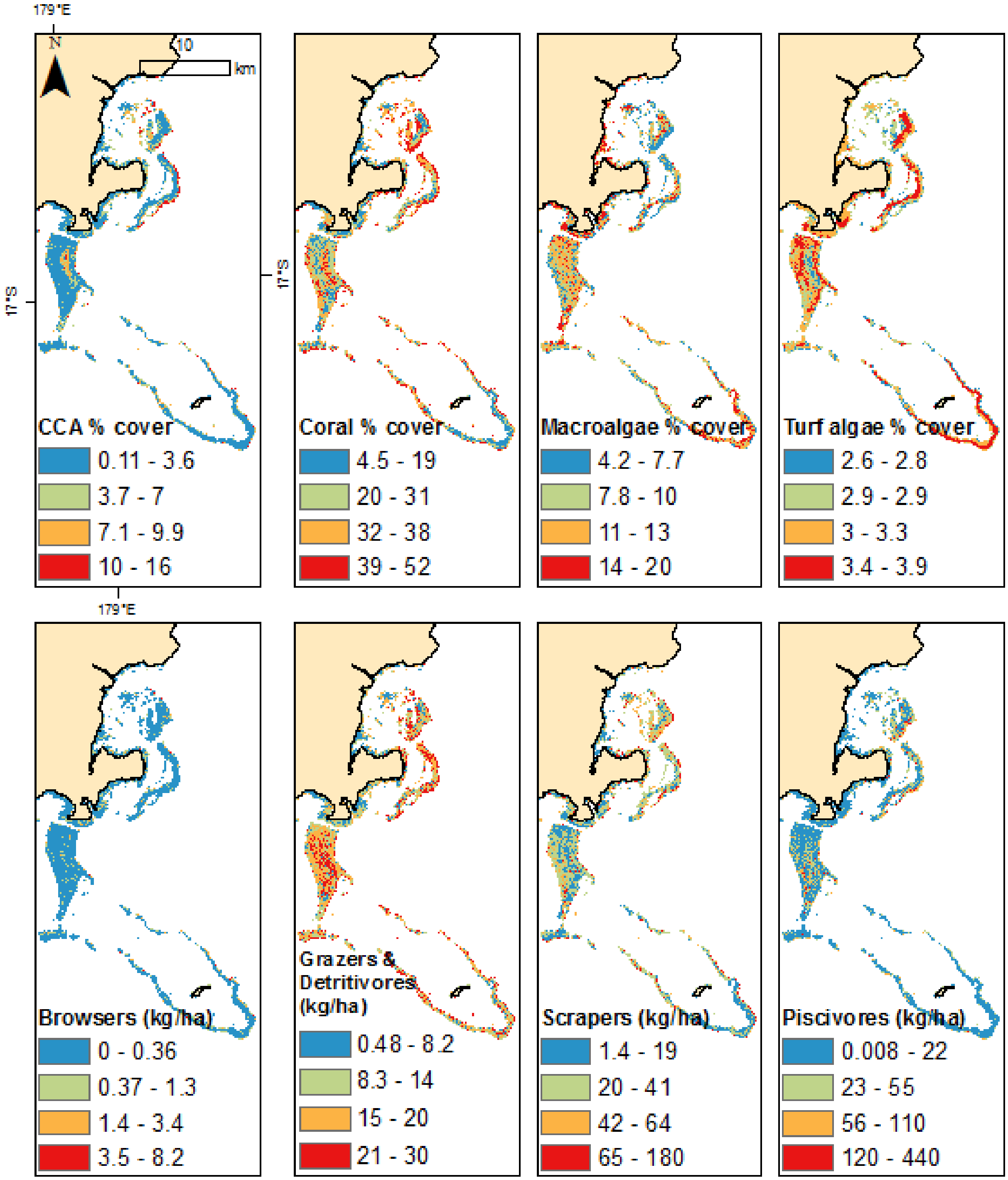


Figure 4.7. Predicted distribution of the coral reef indicators. Benthic groups are measured in % cover and the fish indicators are measured in kg/ha

4.3.5 Effect of human drivers on on coral reefs

The PERMANOVA results for Kiobo indicated that the benthic community significantly differed from Present conditions under climate change scenarios ranging from Severe to Extreme, particularly when combined with the Deforestation scenario (Table 4.5). In the tabu area, the benthic community significantly changed from Present conditions under the combined Moderate Bleaching and Deforestation scenario and did not change under the combined Moderate Bleaching and Reforestation scenario. When climate change scenarios were Severe and Extreme, the benthic community in the open area significantly differed under all combined scenarios. Climate change was the dominant effect and the difference was mostly attributed to a decrease in coral cover (Figure 4.8 & 4.9). For Nakorovou, the PERMANOVA results showed that the benthic community significantly differed from Present conditions in the tabu areas under the Extreme Bleaching scenario, regardless of forest cover change. In the fished area of Nakorovou, the PERMANOVA results showed that the benthic community significantly differed from Present conditions in the tabu areas under the Extreme Bleaching scenario and in combination with Deforestation only. The difference was attributed to a decrease in CCA and coral cover and a slight increase in macroalgae (Figure 4.8). In Navatu, the PERMANOVA results indicated that benthic community significantly differed from Present conditions under all the climate change scenarios alone, as well as when combined with forest cover change. The benthic community significantly changed under the Moderate and Extreme Bleaching scenarios in the tabu and fished areas, respectively. The difference was mostly attributed to a decrease in coral cover (Figure 4.8 & 4.9). When combined with a forest cover change scenarios, climate change was the dominant effect. In Raviravi, the benthic community did not significantly differ from Present conditions under all scenario considered, except for the Extreme Bleaching combined with Deforestation scenario. For the fish community, the PERMANOVA results of Kiobo, Nakorovou and Raviravi did not significantly differ from present conditions under all scenario. In the fished area of Navatu, the PERMANOVA results indicated that the fish community did not significantly differ from Present conditions under all scenario considered. On the other hand, the fish community in the tabu area significantly differed from Present conditions under the combined Extreme Bleaching and Deforestation scenario. This difference was due to a decrease in all fish groups, with the exception of browser biomass (Figure 4.8).

Table 4.5. PERMANOVA F-values for the fished and tabu areas per village. P-values < 0.1* are reported as significantly different from present conditions. Current forest cover (Present), Deforestation and Reforestation (R) scenarios were combined with the bleaching scenarios and compared to present coral reef conditions in Kiobo (K), Nakorovou (O), Navatu (A), and Raviravi (R).

Fishing areas	**Forest cover scenarios**	**Bleaching scenarios**	**BENTHIC**				**FISH**			
			K	**O**	**A**	**R**	**K**	**O**	**A**	**R**
TABU	Deforestation	Present	0.22	0.00	0.17	0.01	0.05	0.01	0.97	0.00
	Reforestation	Present	0.43	0.00	0.00	0.01	0.13	0.01	0.03	0.00
	Present	Moderate	1.52	0.26	**2.28***	0.16	0.23	0.09	0.49	0.03
	Deforestation	Moderate	**1.73***	0.26	**2.17***	0.16	0.27	0.09	1.27	0.03
	Reforestation	Moderate	1.12	0.26	**2.28***	0.16	0.11	0.09	0.50	0.03
	Present	Severe	**3.14***	0.55	**4.75***	0.34	0.50	0.17	1.12	0.04
	Deforestation	Severe	**3.35***	0.55	**4.64***	0.34	0.53	0.17	**1.79***	0.04
	Reforestation	Severe	**2.78***	0.55	**4.75***	0.34	0.39	0.17	1.13	0.04
	Present	Extreme	**4.73***	**3.82***	**7.03***	1.60	0.60	0.77	1.27	0.26
	Deforestation	Extreme	**4.93***	**3.82***	**6.92***	**1.60***	0.65	0.77	**1.98***	0.26
	Reforestation	Extreme	**4.35***	**3.82***	**7.03***	1.60	0.56	0.77	1.28	0.26
OPEN	Deforestation	Present	0.12	0.35	0.00	0.00	0.05	0.71	0.00	0.00
	Reforestation	Present	0.21	0.01	0.00	0.00	0.08	0.01	0.00	0.00
	Present	Moderate	0.90	0.00	0.33	0.11	0.05	0.00	0.02	0.04
	Deforestation	Moderate	1.02	0.35	0.33	0.11	0.09	0.71	0.02	0.04
	Reforestation	Moderate	0.69	0.01	0.33	0.11	0.06	0.01	0.02	0.04
	Present	Severe	**1.96***	0.00	0.70	0.24	0.23	0.00	0.05	0.07
	Deforestation	Severe	**2.08***	0.35	0.70	0.24	0.25	0.71	0.05	0.07
	Reforestation	Severe	**1.75***	0.01	0.70	0.24	0.21	0.01	0.05	0.07
	Present	Extreme	**4.19***	**1.49***	**5.18***	1.39	0.44	0.06	0.78	0.26
	Deforestation	Extreme	**4.31***	**1.64***	**5.18***	1.39	0.47	0.75	0.78	0.26
	Reforestation	Extreme	**3.97***	1.49	**5.18***	1.39	0.41	0.06	0.78	0.26

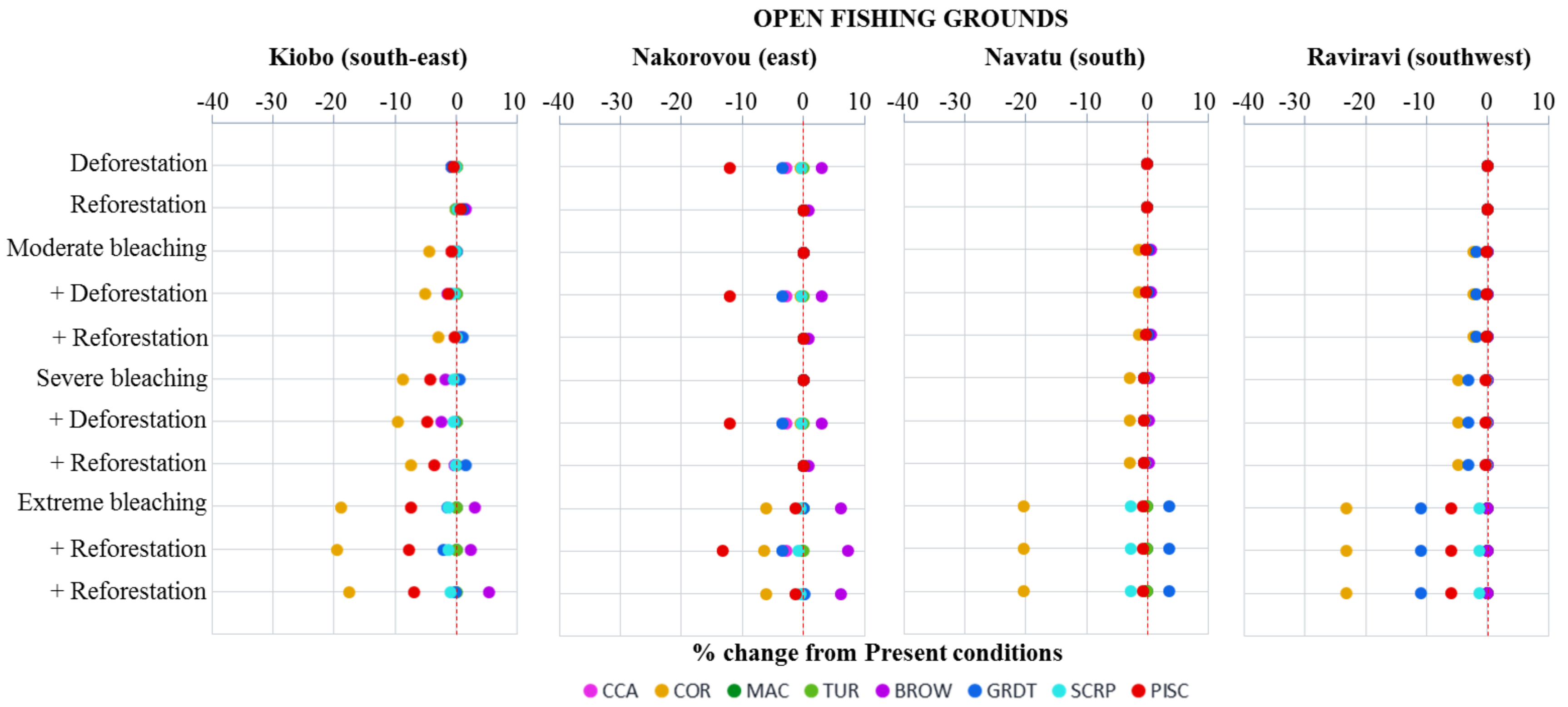


Figure 4.8. Coral reef community percent change from present conditions in areas open to fishing. The x-axis represents the percent change from current conditions (marked by the red dashed line). Each scenario combination is represented along the y-axis. Bleaching scenarios range from Moderate, Severe, and Extreme, and two forest cover scenarios were considered (Deforestation and Reforestation).

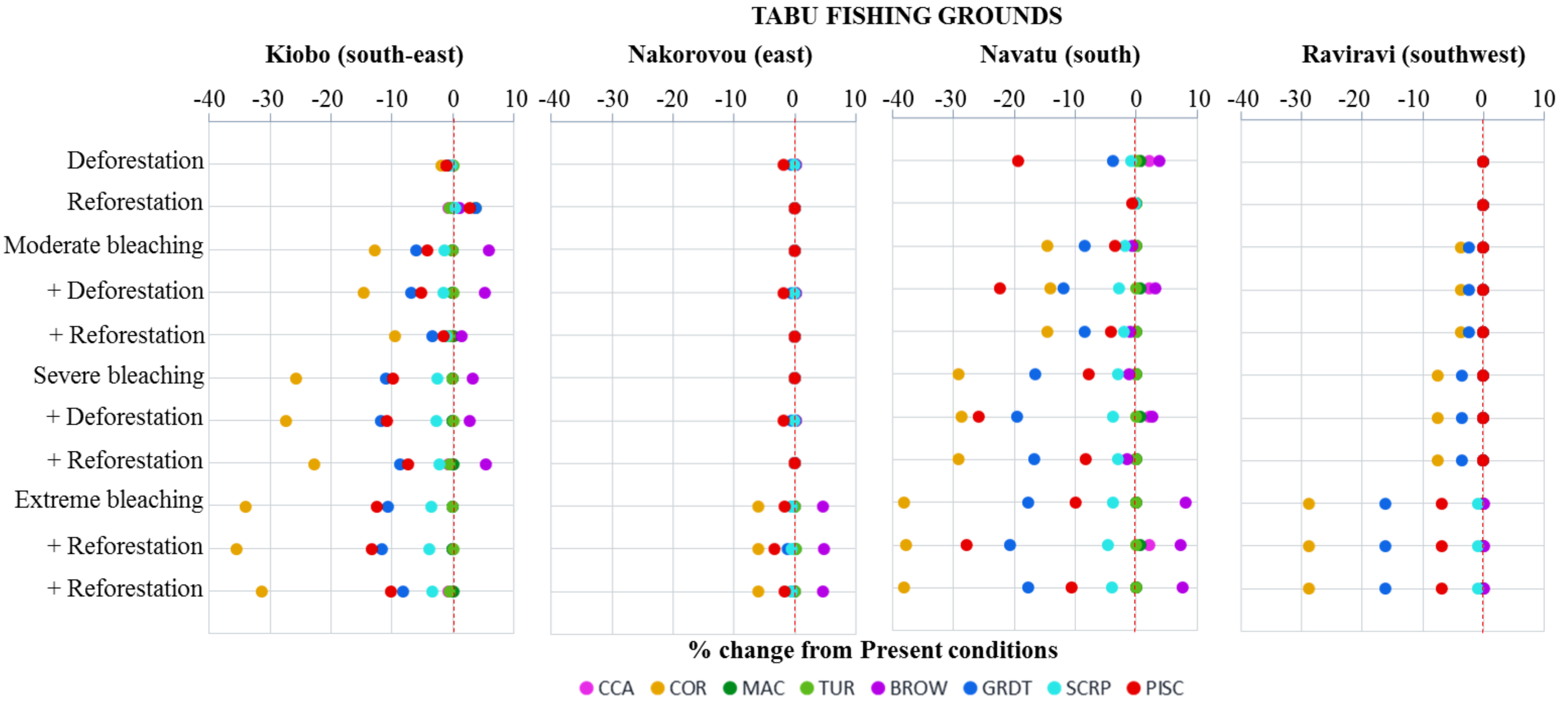


Figure 4.9. Coral reef community percent change from present conditions in areas tabu to fishing. The x-axis represents the percent change from current conditions (marked by the red dashed line). Each scenario combination is represented along the y-axis. Bleaching scenarios range from Moderate, Severe, and Extreme, and two forest cover scenarios were considered (Deforestation and Reforestation).

4.4. Discussion

To support ridge-to-reef management on oceanic islands, I modified and scaled up a novel methodology to link fine-scale land cover to coral reef dynamics through stream sedimentation in a single modeling framework (see Chapter 1 for more details). Kubulau, Fiji represents a range of Indo-Pacific reef types, including fringing, patch, lagoon, and barrier and atoll reefs (Roelfsema et al. 2013). I used this modeling framework to characterize the dynamics of the landscape and seascape linkages of Kubulau District. The coral reef models identified habitat structure and connectivity, coral cover, and sedimentation as the primary drivers of coral reef communities. The scenario analysis of tabu and open areas revealed that coral reef ecological outcomes varied under different scenarios due to differing land-sea dynamics and the geomorphology of the land and the reefs. Ridge-to-reef systems such as Nakorovou and Raviravi, which span large watersheds and discharge in semi-enclosed bays, are more exposed to chronic sediment disturbances. Consequently, the tabu and open areas appear more resistant to increased exposure to sedimentation and/or climate change. Conversely, Navatu is located on a small nearshore island and represents a short ridge-to-reef system more exposed to waves and currents. Located across the bay from Raviravi, the tabu area of Navatu becomes vulnerable to climate change, when deforestation in the Raviravi watershed takes place, thereby revealing connectivity across ridge-to-reef systems. Similarly, Kiobo is located downstream from several small watersheds that discharge in a narrow and deep lagoon. Although, the fish community appears more resilient to climate change and deforestation, the benthic community seems more vulnerable to climate change modeled impacts, particularly when coupled with deforestation.

4.4.1 Effects of terrestrial and marine drivers on ridge-to-reef dynamics

4.4.1.1 Effects of terrestrial drivers on coral reefs

Although, these sediment results support that the current state of the watersheds and stream systems mainly consists of unaltered hydrological systems and forested areas (Jenkins et al. 2010, Jupiter et al. 2012), my coral reef models revealed that TSS was an important driver for reef calcifiers, and to a lesser extent benthic algae (Figure 4.6). Results for CCA and corals suggested that TSS hinders their distribution in areas near river mouths or subject to high TSS. The adverse impact of sedimentation, nutrient enrichment, and turbidity on coral reefs at local scales has been well established (Fabricius 2005). Even if coral reefs in turbid waters can flourish (Anthony 1999), they are restricted to the top 4-10 m depth range (Fabricius et al. 2005, Yentsch et al. 2002), and typically support fewer species, slower growth rates, and poorer recruitment (Rogers 1990). Consequently, abundance of reef calcifiers were lower in tabu areas exposed to high sediment inputs, and higher in well exposed and deeper fished areas, demonstrating association with well mixed waters.

Conversely, results for macroalgae and turf algae showed a positive relationship with TSS (Figure 4.6). Increases in sediment can directly promote macroalgae and turf algae growth through increases in nutrients bounded to sediments (Fabricius 2005, Umar et al. 1998) or indirectly hinder competition for space by reef calcifiers (Smith et al. 2016, Szmant 2002). These results suggested that benthic algae, may have a competitive advantage over reef calcifiers under high levels of sediments and/or turbidity (Pastorok & Bilyard 1985). McCook et al. (2001) also showed that large-scale shifts from corals to algae usually indicates coral mortality due to external disturbances, rather than competitive overgrowth, and can lead to competitive inhibition of coral recruitment, with implications for coral reef recovery. In Kubulau, increase in sedimentation and TSS can reduce reef calcifiers abundance, and indirectly promote benthic algae growth, which inhibits recovery capacity after disturbances through loss of space availability. Consequently, abundance of benthic algae were higher in tabu areas exposed to high sediment inputs, and lower in fished areas which are exposed and deeper.

Sedimentation had a direct negative effect on coral reef fish biomass in Kubulau (Figure 4.6). Reef fishes can be adversely affected by sedimentation and turbidity through altered foraging patterns (Johansen & Jones 2013). Sedimentation also indirectly affects reef fishes by altering the benthic community structure and composition (Pratchett et al. 2008, Rogers 1990). Given the effects of TSS on all these benthic groups and the dependence of the fishes on these benthic communities, fishes are likely to also be indirectly affected by TSS through the benthic community. The degree of dependence on different benthic groups may influence the susceptibility of fishes to habitat impacts from sedimentation, and can have implications for coral reef recovery. For instance, research has shown that fish recruitment decreases in sediment impacted habitat compared to coral-dominated habitats (DeMartini et al. 2013). Browsers were positively associated with CCA and turf algae, while grazers/detritivores and scrapers were negatively related to macroalgae. Consistent with findings in Hawaiʻi (Friedlander & Parrish 1998a), macroalgae appeared to have been reduced by grazing from herbivores, and their cover showed a negative relationship with grazer/detritivore and scraper biomass. Consequently, biomass of targeted reef fishes were lower in tabu areas where reef calcifiers' abundance was lower and higher in open areas where reef calcifiers' abundance was higher.

4.4.1.2 Effects of marine drivers on coral reefs

Many studies have shown that habitat morphology and complexity are primary marine drivers controlling coral reefs community structure in oceanic island environments (Graham & Nash 2013, Wilson et al. 2010). Owing to its proximity to the Australian-Pacific plate boundary, the complex geological history of Fiji has resulted in diverse coral reef geomorphology and habitat structure (Hoffmeister & Ladd 1944, Neall & Trewick 2008). Across the Kubulau seascape, my benthic models indicated that coral reef calcifiers associated with steeper reef slopes and complex habitats, while benthic algae groups correlated with reef valleys and flats (Figure 4.6). The fish community was also strongly structured by BPI and reef slopes (Figure 4.6). Resource fish biomass was generally higher along reef slopes, like spur and groove habitats, which are carved by wave action (Figure 4.7) (Arias-González et al. 2006, Sheppard 1981). Structurally complex reef habitats also supported higher resource fish biomass (Figure 4.6), indicating that fishes may be seeking refuge in habitat structure (Almany 2004, Friedlander & Parrish 1998a, Gratwicke & Speight 2005). In the tabu areas, habitat complexity was lower compared to the fished areas. Consequently, biomass of targeted reef fishes were lower in tabu areas where habitat complexity is lower and higher in fished areas where habitat complexity is higher. These trends revealed that habitat conditions play an important role in structuring the coral reef community of Kubulau.

4.4.2 Effects of human drivers on coral reefs

Management of multiple human drivers requires an understanding of how interactions between local and global drivers manifests itself in different places (Chapter 2). My scenario analysis revealed that coral reef ecological outcomes in tabu and open areas varied under different combinations of scenarios, due to their different geographical location, exposure to terrestrial drivers, and habitat structure and composition (Table 4.1). The results of this study suggest that the benthic communities of Kiobo, Nakorovou, and Navatu are more sensitive to bleaching from climate change, particularly when combined with deforestation, compared to Raviravi. The degree of dependence of resource fishes on the benthic community may influence the level of vulnerability of coral reef fish populations to coral bleaching and habitat degradation (Pratchett et al. 2008, Wilson et al. 2010). This analysis identified that when forest restoration was combined with climate change, the fish population of Navatu tabu area was not impacted, while deforestation combined with climate change resulted in a shift of the fish community structure (Table 4.1). This shift in the fish community resulted from a decrease of most functional fish groups' biomass and an increase in browser biomass (Figure 4.9). Although some areas exhibit higher levels of resilience to global and local drivers, these results imply that the Kubulau coral reef benthic and fish communities are likely to be impacted by climate change, particularly if combined with deforestation, based on projected sea surface temperature and associated bleaching (Cumming et al. 2002, Hoeke et al. 2011).

4.4.3 Management implications

The differences in resilience to sedimentation between tabu and open areas could result from the spatial differences in combined influences of terrestrial and marine drivers. The tabu areas of Nakorovou and Raviravi are located downstream of large watersheds that discharge in semi-enclosed bays, while Navatu and Kiobo are located downstream from small watersheds that discharge in areas more exposed to waves and currents. Fishing grounds located in enclosed bays, which are naturally exposed to more sedimentation, may have developed higher tolerance to sediment over time (Figures 4.1 and 4.5) (Jupiter et al. 2010). While areas that are naturally less exposed to sediments, such as the tabu area of Navatu, are more vulnerable to deforestation by being located across from large watersheds. These results also reveal that coral reefs more resilient to sediment disturbance are also more resilient to climate change. While coral reefs less exposed to sedimentation and more influenced by marine drivers appear to be more vulnerable to bleaching impacts, particularly when they are located offshore from large watersheds. At the larger land-seascape scale, these spatially complex connections show that in larger and geologically more diverse oceanic islands, ridge-to-reef systems where sediment discharge from some watersheds can impact coral reefs in nearby watersheds.

This study supports the paradigm that managing local-scale human drivers can promote coral reef resilience to climate change (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011). The interactions between climate change and forest cover and consequences for coral reefs can be used to illustrate the potential for management actions that can alleviate cumulative impacts. The results for the benthic community in Kiobo and the open area of Nakorovou reveal that forest conservation or restoration can prevent climate change impacts. In the tabu area of Navatu, I found that coral bleaching impacts on coral reef fish populations could also be minimized through forest conservation or restoration. By managing local drivers of deforestation in areas where local drivers outweigh global drivers, reduced sedimentation provides better water quality to foster post-bleaching recovery (McCook et al. 2001, Szmant 2002). Similarly in Madagascar, deforestation has been showed to outweigh the projected impacts of climate change on coral reefs (Maina et al. 2013). In areas where global drivers outweigh local drivers, adopting marine conservation actions that protect herbivores or foster marine habitat quality can foster recovery post-bleaching events. This cumulative impacts analysis of bleaching and forest cover change indicate that local forest conservation actions can significantly influence coral reef futures in the face of climate change, thereby calling for more ridge-to-reef management strategies.

4.5. Conclusions

Chapter 1 demonstrated that natural disturbance regimes can shape different ridge-to-reef systems, which calls for place-based management. Similarly, this chapter showed that spatial arrangement and exposure to terrestrial and marine drivers influence the dynamics and resilience potential to local and global changes of important coral reef resources to local communities. My results demonstrated that coral reefs managed from ridge-to-reef have a much better chance of withstanding bleaching impacts. I identified drivers of coral reef fish biomass degradation and provided guidance on appropriate management actions and locations where they could be more effective. This study also helped identify where terrestrial and marine management actions can foster the resilience of these ridge-to-reef systems by strategically placing protected areas in terrestrial and marine ecosystems. Areas which are naturally more exposed to sedimentation, have evolved more resilience to both sedimentation and climate change. Conversely, areas not naturally exposed to sediments are more vulnerable and should be prioritized for land and sea management to minimize sediment impacts and promote resilience to climate change.

Supplemental material

Table S4.1. Fish species composition per functional groups.

Function	Family	Scientific name	Common name
Browsers	Acanthuridae	*Naso annulatus*	Whitemargin unicornfish
		Naso brachycentron	Humpback unicornfish
		Naso lituratus	Orangespine unicornfish
		Naso sp.	Unicornfish spp.
		Naso tonganus	Bulbnose unicornfish
		Naso tuberosus	Humpnose unicornfish
		Naso unicornis	Bluespine unicornfish
	Kyphosidae	*Kyphosus bigibbus*	Brown chub
		Kyphosus cinerascens	Blue sea chub
		Kyphosus sp.	Chubs spp.
		Kyphosus vaigiensis	Brassy chub
Grazers & Detritivores	Acanthuridae	*Acanthurus auranticavus*	Orange-socket surgeonfish
		Acanthurus blochii	Ringtail surgeonfish
		Acanthurus fowleri	Fowler's surgeonfish
		Acanthurus grammoptilus	Finelined surgeonfish
		Acanthurus leucocheilus	Palelipped surgeonfish
		Acanthurus leucopareius	Whitebar surgeonfish
		Acanthurus lineatus	Lined surgeonfish
		Acanthurus maculiceps	White-freckled surgeonfish
		Acanthurus nigricans	Goldrim surgeonfish
		Acanthurus nigricauda	Epaulette surgeonfish
		Acanthurus nigrofuscus	Brown surgeonfish
		Acanthurus nigroris	Bluelined surgeonfish
		Acanthurus olivaceus	Orangeband surgeonfish
		Acanthurus pyroferus	Chocolate surgeonfish
		Acanthurus sp.	Surgeonfish spp.
		Acanthurus triostegus	Convict surgeonfish
		Acanthurus xanthopterus	Yellowfin surgeonfish
		Zebrasoma flavescens	Yellow tang
		Zebrasoma scopas	Twotone tang
		Zebrasoma sp.	Tang spp.
		Zebrasoma veliferum	Sailfin tang
	Siganidae	*Siganus argenteus*	Rabbitfish
		Siganus doliatus	Barred spinefoot
		Siganus guttatus	Orange-spotted spinefoot
		Siganus punctatissimus	Peppered spinefoot
		Siganus punctatus	Goldspotted spinefoot
		Siganus sp.	Spinefoot spp.
		Siganus spinus	Little spinefoot

		Siganus stellatus	Brown-spotted spinefoot
		Siganus uspi	Bicolored foxface
		Siganus vermiculatus	Vermiculated spinefoot
Scrapers & Excavators	Scaridae	*Cetoscarus bicolor*	Bicolour parrotfish
		Chlorurus bleekeri	Bleeker's parrotfish
		Chlorurus frontalis	Pacific slopehead parrotfish
		Chlorurus japanensis	Palecheek parrotfish
		Chlorurus microrhinos	Steephead parrots
		Chlorurus sordidus	Pacific bullethead parrotfish
		Chlorurus sp.	Parrotfish spp.
		Hipposcarus longiceps	Pacific longnose parrotfish
		Hipposcarus sp.	
		Scarus altipinnis	Filament-finned parrotfish
		Scarus chameleon	Chameleon parrotfish
		Scarus dimidiatus	Yellowbarred parrotfish
		Scarus forsteni	Forsten's parrotfish
		Scarus frenatus	Bridled parrotfish
		Scarus ghobban	Blue-barred parrotfish
		Scarus globiceps	Globehead parrotfish
		Scarus guttatus	Blue-barred parrotfish
		Scarus japanensis	Palecheek parrotfish
		Scarus longipinnis	Highfin parrotfish
		Scarus niger	Dusky parrotfish
		Scarus oviceps	Dark capped parrotfish
		Scarus prasiognathos	Singapore parrotfish
		Scarus psittacus	Palenose parrotfish
		Scarus rivulatus	Midnight parrotfish
		Scarus rubroviolaceus	Ember parrotfish
		Scarus schlegeli	Yellowband parrotfish
		Scarus sp.	Parrotfish spp.
		Scarus spinus	Greensnout parrotfish
Piscivores	Carangidae	*Alectis ciliaris*	Threadfin trevally
		Carangoides ferdau	Blue trevally
		Carangoides fulvoguttatus	Yellowspotted trevally
		Carangoides gymnostethus	Bludger
		Carangoides oblongus	Coachwhip trevally
		Carangoides plagiotaenia	Barcheek trevally
		Caranx ignobilis	Giant trevally
		Caranx melampygus	Bluefin trevally
		Caranx papuensis	Brassy trevally
		Caranx sexfasciatus	Bigeye trevally

	Caranx sp.	Trevally spp.
	Elagatis bipinnulata	Rainbow runner
	Gnathanodon speciosus	Golden trevally
	Scomberoides lysan	Doublespotted queenfish
	Seriola rivoliana	Almaco jack
	Trachinotus baillonii	Smallspotted dart
	Trachinotus blochii	Snubnose pompano
	Uraspis helvola	Whitetongue jack
Carcharhinidae	*Carcharhinus amblyrhynchos*	Blacktail reef shark
Labridae	*Epibulus insidiator*	Sling-jaw wrasse
	Oxycheilinus bimaculatus	Two-spot wrasse
	Oxycheilinus digrammus	Cheeklined wrasse
	Oxycheilinus orientalis	Oriental maori wrasse
	Oxycheilinus sp.	Wrasse spp.
Lethrinidae	*Lethrinus atkinsoni*	Pacific yellowtail emperor
	Lethrinus erythracanthus	Orange-spotted emperor
	Lethrinus erythropterus	Longfin emperor
	Lethrinus harak	Thumbprint emperor
	Lethrinus laticaudis	Grass emperor
	Lethrinus lentjan	Pink ear emperor
	Lethrinus microdon	Smalltooth emperor
	Lethrinus miniatus	Trumpet emperor
	Lethrinus nebulosus	Spangled emperor
	Lethrinus obsoletus	Orange-striped emperor
	Lethrinus olivaceus	Longface emperor
	Lethrinus semicinctus	Black blotch emperor
	Lethrinus sp.	Emperor spp.
	Lethrinus xanthochilus	Yellowlip emperor
Lutjanidae	*Aphareus furca*	Small-toothed jobfish
	Aprion virescens	Green jobfish
	Lutjanus argentimaculatus	Mangrove red snapper
	Lutjanus biguttatus	Two-spot banded snapper
	Lutjanus bohar	Two-spot red snapper
	Lutjanus ehrenbergii	Blackspot snapper
	Lutjanus fulviflamma	Dory snapper
	Lutjanus fulvus	Blacktail snapper
	Lutjanus gibbus	Humpback red snapper
	Lutjanus johnii	John's snapper
	Lutjanus kasmira	Common bluestripe snapper
	Lutjanus monostigma	One-spot snapper
	Lutjanus quinquelineatus	Five-lined snapper

	Lutjanus rivulatus	Blubberlip snapper
	Lutjanus russeli	Russell's snapper
	Lutjanus semicinctus	Black-banded snapper
	Lutjanus sp.	Naso
Mullidae	*Mulloidichthys flavolineatus*	Yellowstripe goatfish
	Mulloidichthys sp.	Goatfish spp.
	Mulloidichthys vanicolensis	Yellowfin goatfish
	Parupeneus cyclostomus	Blue goatfish
Serranidae	*Anyperodon leucogrammicus*	Slender grouper
	Belonoperca chabanaudi	Arrowhead soapfish
	Cephalopholis argus	Blue spotted grouper
	Cephalopholis leopardus	Leopard hind
	Cephalopholis miniata	Coral trout
	Cephalopholis sexmaculata	Sixblotch hind
	Cephalopholis sp.	Grouper spp.
	Cephalopholis urodeta	Darkfin hind
	Gracila albomarginata	Masked Grouper
	Plectropomus areolatus	Squaretail coralgrouper
	Plectropomus laevis	Blacksaddled coralgrouper
	Plectropomus leopardus	Leopard coralgrouper
	Plectropomus maculatus	Spotted coralgrouper
	Plectropomus pessuliferus	Roving coralgrouper
	Variola albimarginata	White-edged lyretail
	Variola louti	Yellow-edged lyretail
Sphyraenidae	*Sphyraena barracuda*	Great barracuda
	Sphyraena flavicauda	Yellowtail barracuda
	Sphyraena qenie	Blackfin barracuda
	Sphyraena sp.	Barracuda spp.

Table S4.2. Modeling framework predictor variables description and processing methods. Description of all the predictor variables modeled in the coral reef models of this modeling framework. Each metric was classified by type (terrestrial drivers or marine drivers) and coded for modeling. Data source and analytical tool used to generate each metric. Refer to Stamoulis et al. 2016 for more details on processing methods.

Type	**Code**	**Metric**	**Source**	**Description**	**Analytical tool**
Terrestrial drivers	TSS	Sedimentation	Sediment model	Proxy for TSS (/year)	GIS-based models
Marine drivers (Geography)	Depth	Depth	Bathymetry[1]	Average depth (m)	ArcGIS Spatial Analyst tools (ESRI 2011)
	dist2shore	Distance to shore	Coastline[2]	Distance to nearest land (m)	ArcGIS Spatial Analyst Euclidean Distance tool (ESRI 2011)
Marine drivers (Morphology)	bpi	Bathymetric position index (60m, 240m)	Bathymetry[1]	Mean values indicate a location's position relative to the surrounding area; values can be positive (ridges), negative (valleys), or zero (flat or constant slope)	Benthic Terrain Modeler tool (Wright et al. 2005)
	slp	Slope (60m, 240m)	Bathymetry[1]	Maximum rate of change from a cell to its neighbors	ArcGIS Slope tool (ESRI 2011) & ArcGIS Focal Statistics tool (ESRI 2011)
Marine drivers (Exposure)	asp_sin	Sine aspect	Bathymetry[1]	Sine of slope direction (derived from transforming the mean aspect into "eastness") (degree)	ArcGIS Spatial Analyst tools (sine function) (ESRI 2011)
	asp_cos	Cosine aspect	Bathymetry[1]	Cosine of slope direction (derived from transforming the mean aspect into "northness") (degree)	ArcGIS Spatial Analyst tools (cosine function) (ESRI 2011)

Marine drivers (Complexity)	curv_pro	Profile curvature (mean)	Bathymetry[1]	Curvature values can be + (concave), - (convex), or 0 (flat). A proxy for spur and groove effects on water flow.	DEM Surface Tools Curvature tool (Jenness 2013)
	curv_plan	Planar curvature (mean)	Bathymetry[1]	Curvature values can be – (concave) to + (convex), or 0 (flat) (mean). A proxy for spur and groove effects on water flow.	DEM Surface Tools Curvature tool (Jenness 2013)
	slpslp	Slope of slope	Bathymetry[1]	Second derivative of slope	ArcGIS Spatial Analyst tools (ESRI 2011)
	vrm	Terrain ruggedness	Bathymetry[1]	Variation in 3D orientation of grid cells value indicates topographic roughness (0 = no variation to 1 = complete variation).	Benthic Terrain Modeler tool (Wright et al. 2005)
Habitat connectivity	contig_mn	Contiguity Index	Habitat composition[3]	Mean spatial connectedness of patches. Patch shape based on the spatial connectedness of cells within a patch; large contiguous patches will result in larger contiguity index values (unitless).	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2 (McGarigal et al. 2002)
	frac_mn	Fractal dimension (mean)	Habitat composition[3]	Mean patch complexity at the landscape level (unitless)	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2 (McGarigal et al. 2002)
	prox_mn	Proximity index	Habitat composition[3]	Measure of patch isolation (unitless)	Exhaustive sampling using a 60m radius moving window

		distribution (mean)			analysis in Fragstats v4.2 (McGarigal et al. 2002)
	shdi	Shannons habitat diversity index	Habitat composition[3]	Diversity of benthic cover types in the landscape (unitless)	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2 (McGarigal et al. 2002)
Benthic community	CCA	Crustose coralline algae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	COR	Coral cover	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	MAC	Macroalgae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions
	TUR	Turf algae	Coral reef model	Spatially-explicit predicted % cover	Coral reef model predictions

Table S4.3. Marine drivers average and standard deviation in each tabu and open areas per village.

Marine drivers	Fishing ground	Kiobo	Nakorovou	Navatu	Raviravi
Depth	TABU	5.7 (+/-3.1)	7.9 (+/-2.0)	5.1 (+/-2.7)	6.3 (+/-1.0)
	OPEN	8.7 (+/-3.3)	11.7 (+/-2.3)	8.3 (+/-2.4)	7.4 (+/-2.5)
Distance to shore	TABU	189.3 (+/-137.8)	87.6 (+/-95.7)	262.1 (+/-100.2)	106.6 (+/-93.9)
	OPEN	331.6 (+/-185.0)	368.5 (+/-99.1)	285.1 (+/-97.6)	107.5 (+/-11.6)
Aspect (sd)	TABU	106.8 (+/-10.5)	95.7 (+/-10.6)	100.2 (+/-11.3)	93.9 (+/-12.5)
	OPEN	102.6 (+/-8.3)	99.1 (+/-9.5)	97.6 (+/-14.0)	107.5 (+/-11.6)
BPI (60)	TABU	0.3 (+/-0.3)	0.1 (+/-0.2)	0.2 (+/-0.4)	0.2 (+/-0.1)
	OPEN	0.2 (+/-0.5)	-0.2 (+/-1.0)	0.2 (+/-0.3)	0.2 (+/-0.2)
BPI (240)	TABU	0.3 (+/-1.1)	0.2 (+/-0.5)	-0.5 (+/-1.4)	-0.4 (+/-0.6)
	OPEN	0.2 (+/-1.3)	-1.8 (+/-1.8)	-0.9 (+/-1.5)	-0.6 (+/-1.1)
Slope (60)	TABU	5.1 (+/-2.5)	2.9 (+/-1.5)	5.4 (+/-2.8)	4.6 (+/-1.4)
	OPEN	5.9 (+/-3.2)	9.2 (+/-2.1)	6.6 (+/-1.5)	5.0 (+/-1.5)
Slope (240)	TABU	5.3 (+/-0.5)	2.7 (+/-1.0)	5.6 (+/-1.8)	4.7 (+/-0.3)
	OPEN	5.4 (+/-1.2)	6.5 (+/-0.6)	6.1 (+/-0.3)	5.2 (+/-0.7)
Slope of slope	TABU	22.2 (+/-8.9)	13.1 (+/-6.2)	22.6 (+/-9.7)	19.8 (+/-5.7)
	OPEN	24.4 (+/-10.8)	34.1 (+/-6.2)	26.2 (+/-4.8)	21.4 (+/-5.4)
Plan curvature	TABU	0.1 (+/-0.3)	0.0 (+/-0.1)	0.2 (+/-0.3)	0.1 (+/-0.2)
	OPEN	0.0 (+/-0.3)	0.0 (+/-0.3)	0.1 (+/-0.3)	0.1 (+/-0.2)
Profile curvature	TABU	0.1 (+/-0.3)	0.0 (+/-0.1)	0.2 (+/-0.3)	0.1 (+/-0.2)
	OPEN	0.0 (+/-0.3)	0.2 (+/-0.3)	0.1 (+/-0.4)	0.1 (+/-0.2)
VRM	TABU	0.0 (+/-0.0)	0.0 (+/-0.0)	0.0 (+/-0.0)	0.0 (+/-0.0)
	OPEN	0.0 (+/-0.0)	0.0 (+/-0.0)	0.0 (+/-0.0)	0.0 (+/-0.0)
Contiguity	TABU	0.4 (+/-0.3)	0.6 (+/-0.3)	0.6 (+/-0.3)	0.9 (+/-0.1)
	OPEN	0.6 (+/-0.3)	0.1 (+/-0.2)	0.3 (+/-0.2)	0.7 (+/-0.3)
Fractal dimension	TABU	0.6 (+/-0.4)	0.8 (+/-0.4)	0.8 (+/-0.4)	1.0 (+/-0.1)
	OPEN	0.8 (+/-0.4)	0.1 (+/-0.3)	0.6 (+/-0.5)	0.8 (+/-0.4)
Proximity	TABU	0.8 (+/-1.3)	0.3 (+/-0.7)	1.1 (+/-1.8)	0.0 (+/-0.0)
	OPEN	0.7 (+/-1.3)	0.1 (+/-0.5)	1.6 (+/-2.0)	0.0 (+/-0.0)
SHDI	TABU	0.2 (+/-0.2)	0.2 (+/-0.2)	0.2 (+/-0.2)	0.0 (+/-0.0)
	OPEN	0.2 (+/-0.2)	0.0 (+/-0.1)	0.4 (+/-0.3)	0.0 (+/-0.0)
TSS	TABU	23.7 (+/-4.5)	182.9 (+/-99.4)	4.2 (+/-1.2)	208.1 (+/-11.5)
	OPEN	31.2 (+/-7.4)	13.3 (+/-10.8)	0.0 (+/-0.0)	182.0 (+/-32.1)

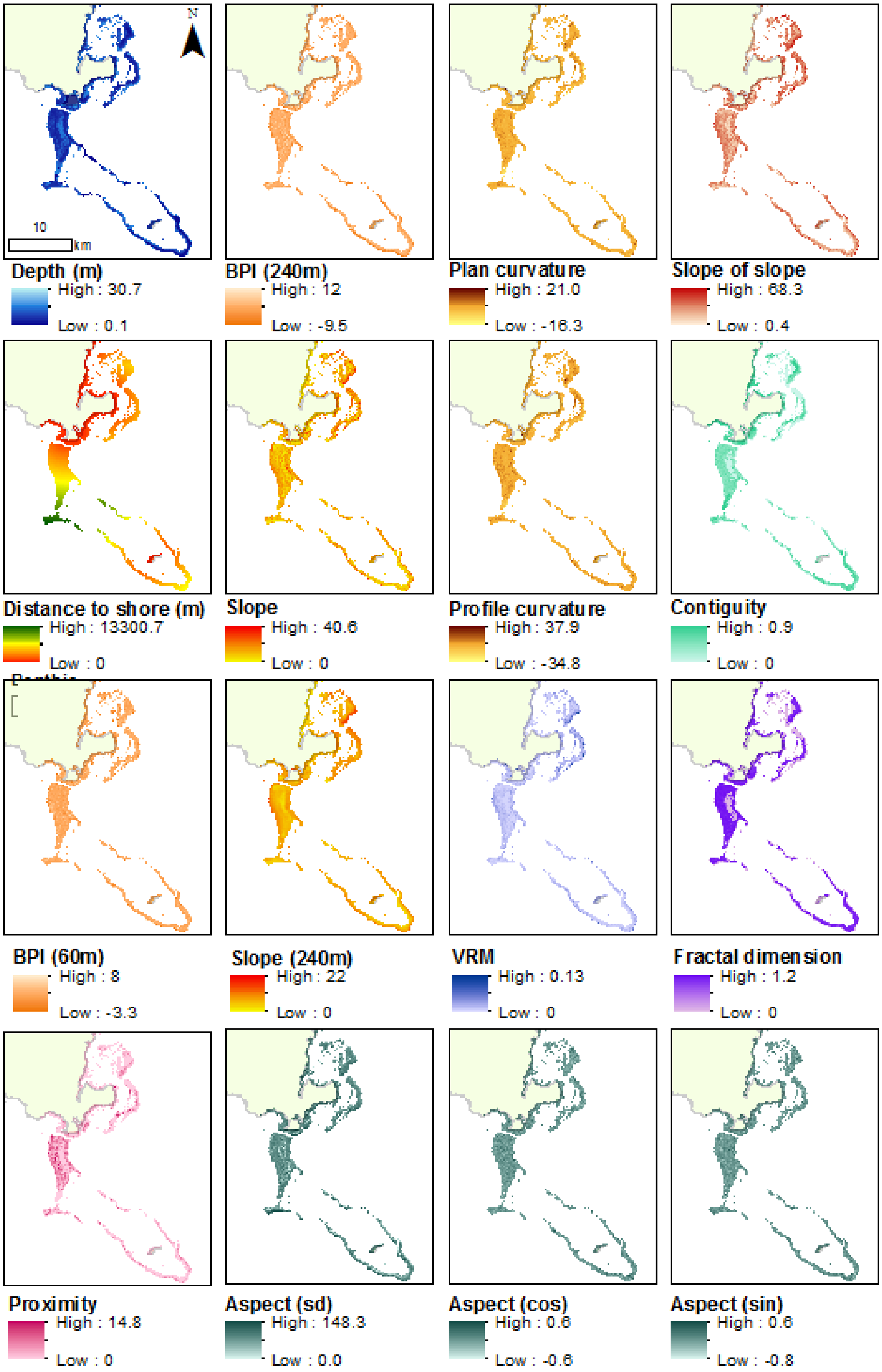
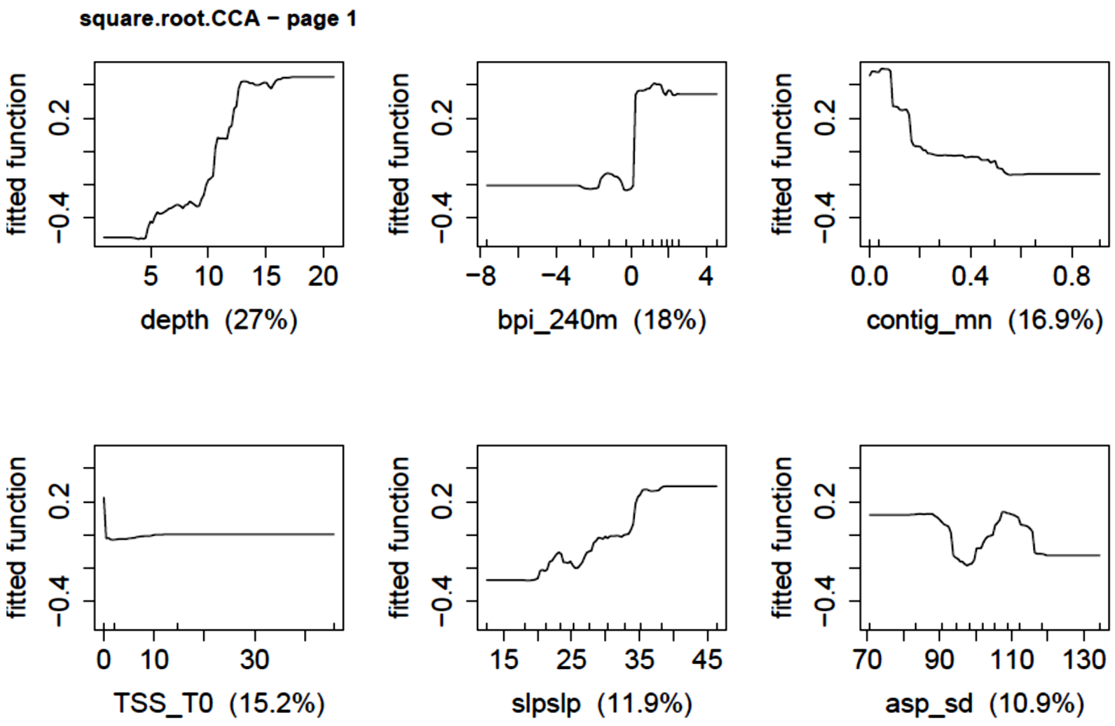


Figure S4.1. Spatial representation of marine drivers.


square.root.CCA – page 1
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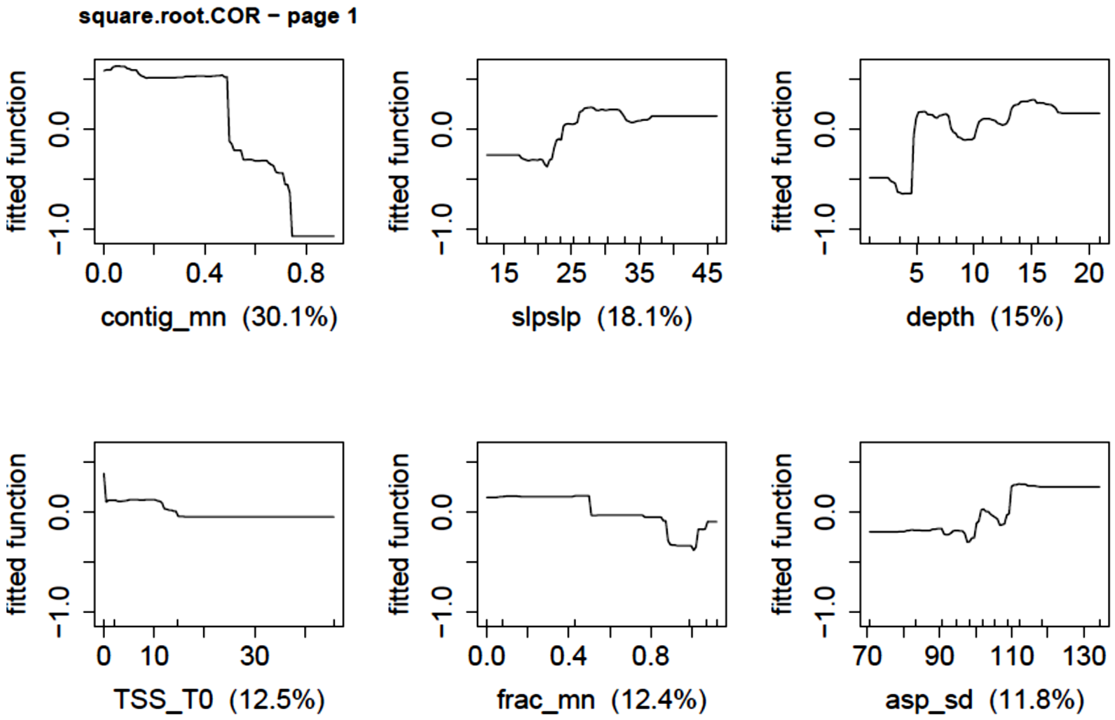
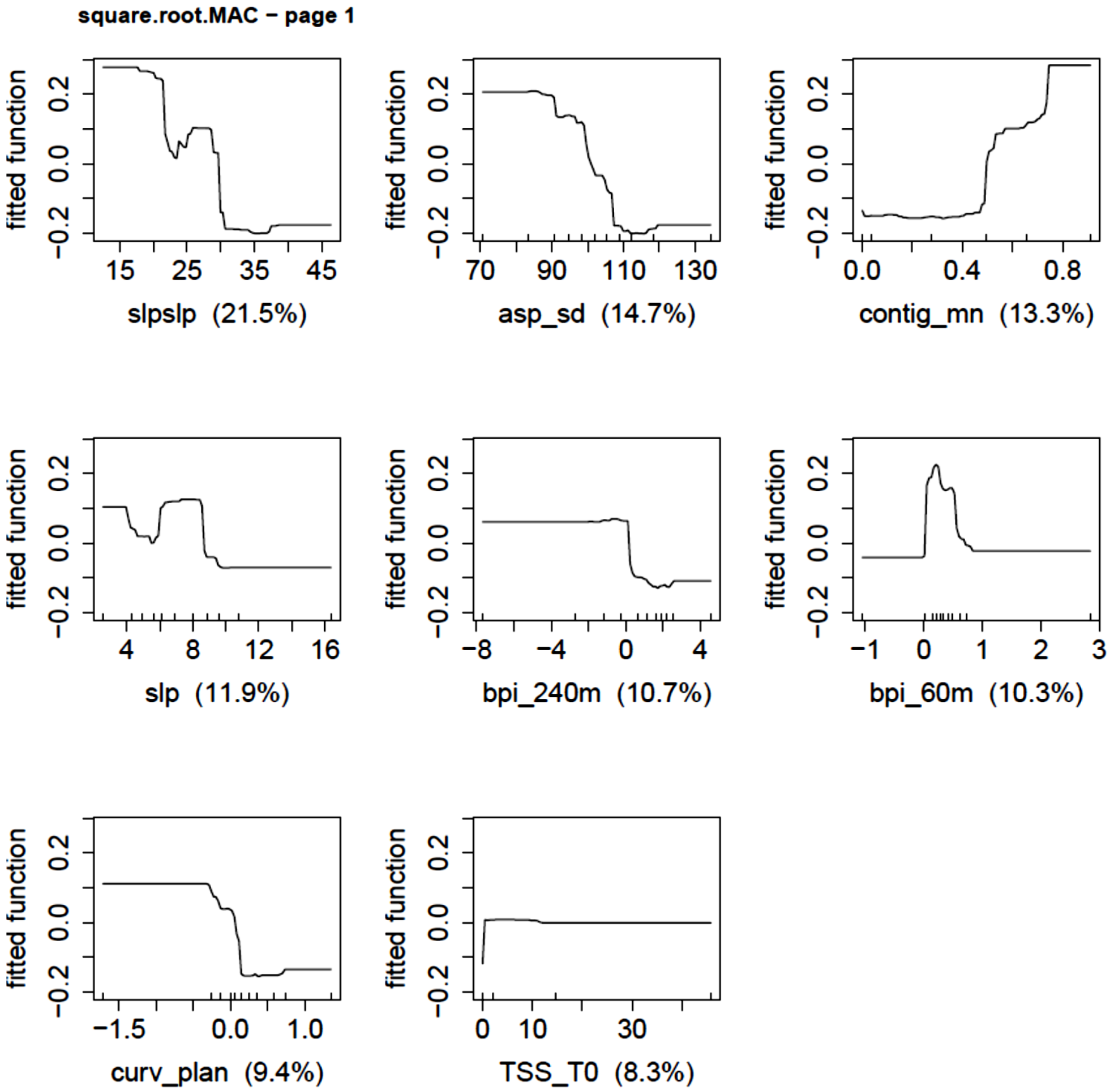
-0.4
0.2
5
10
15
20
depth (27%)
-8
-4
0
4
bpi_240m (18%)
0.0
0.4
0.8
contig_mn (16.9%)
0
10
30
TSS_T0 (15.2%)
15
25
35
45
slpslp (11.9%)
70
90
110
130
asp_sd (10.9%)


square.root.COR – page 1
fitted function
-1.0
0.0
0.0
0.4
0.8
contig_mn (30.1%)
15
25
35
45
slpslp (18.1%)
5
10
15
20
depth (15%)
0
10
30
TSS_T0 (12.5%)
0.0
0.4
0.8
frac_mn (12.4%)
70
90
110
130
asp_sd (11.8%)


square.root.MAC – page 1
fitted function
−0.2
0.0
0.2
15
25
35
45
slpslp (21.5%)
70
90
110
130
asp_sd (14.7%)
0.0
0.4
0.8
contig_mn (13.3%)
4
8
12
16
slp (11.9%)
−8
−4
0
4
bpi_240m (10.7%)
−1
0
1
2
3
bpi_60m (10.3%)
−1.5
0.0
1.0
curv_plan (9.4%)
0
10
30
TSS_T0 (8.3%)

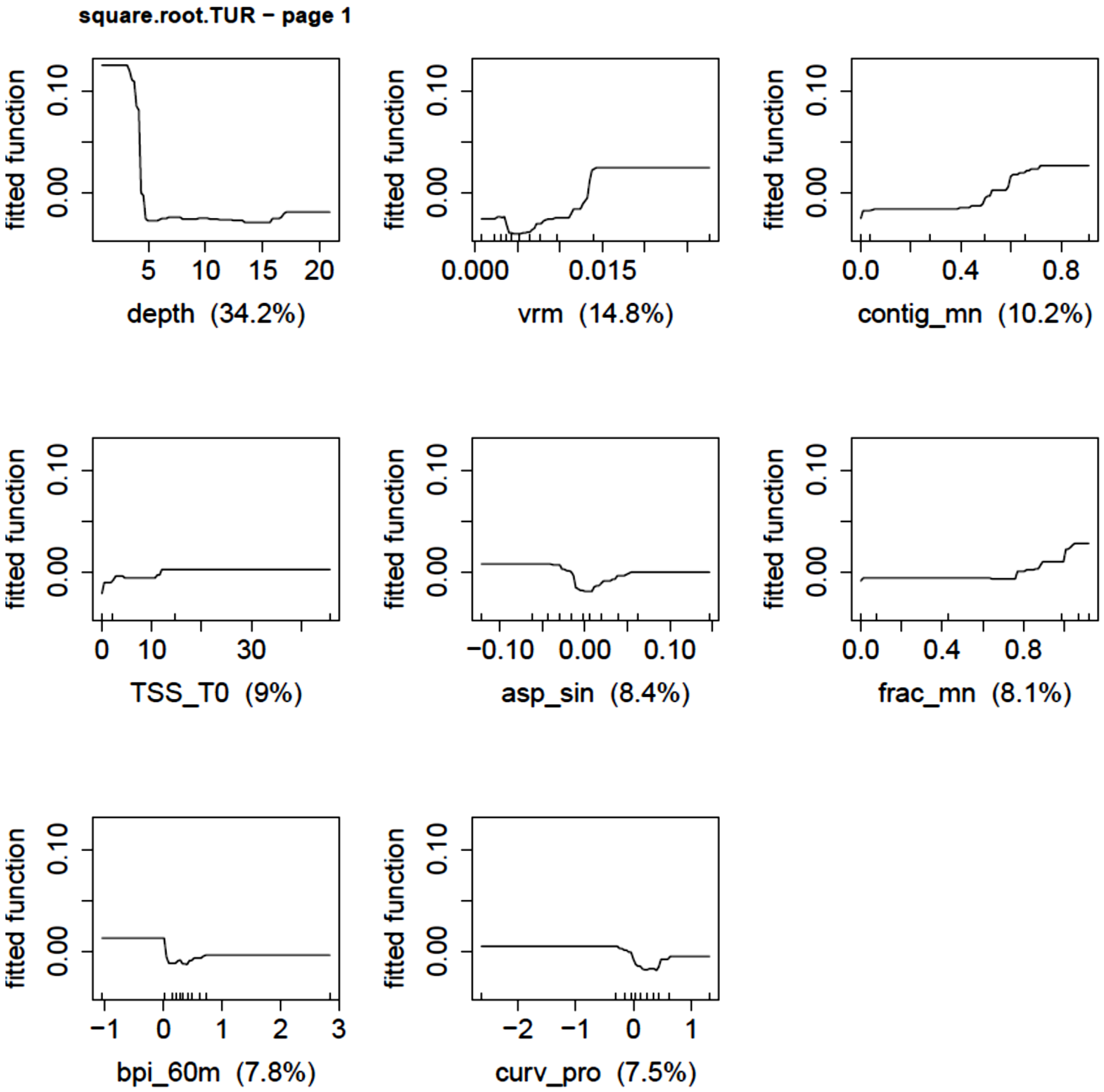
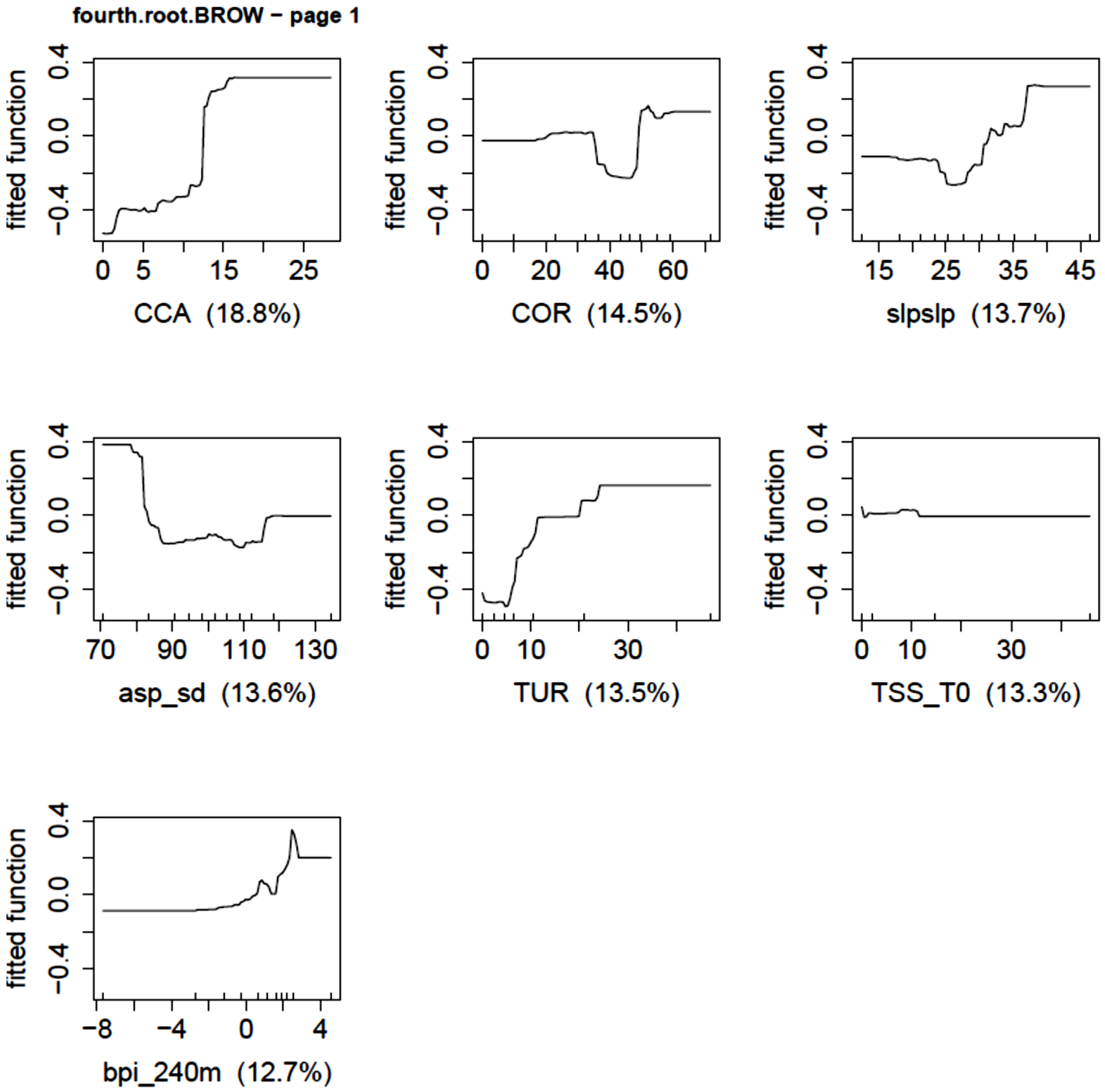
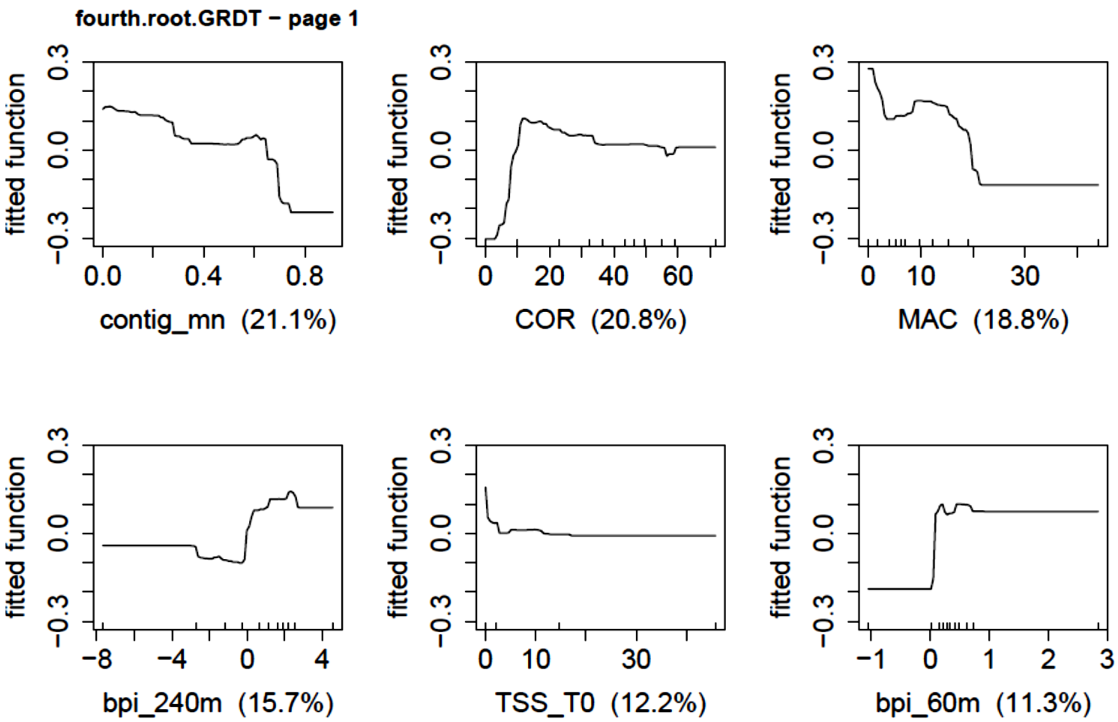
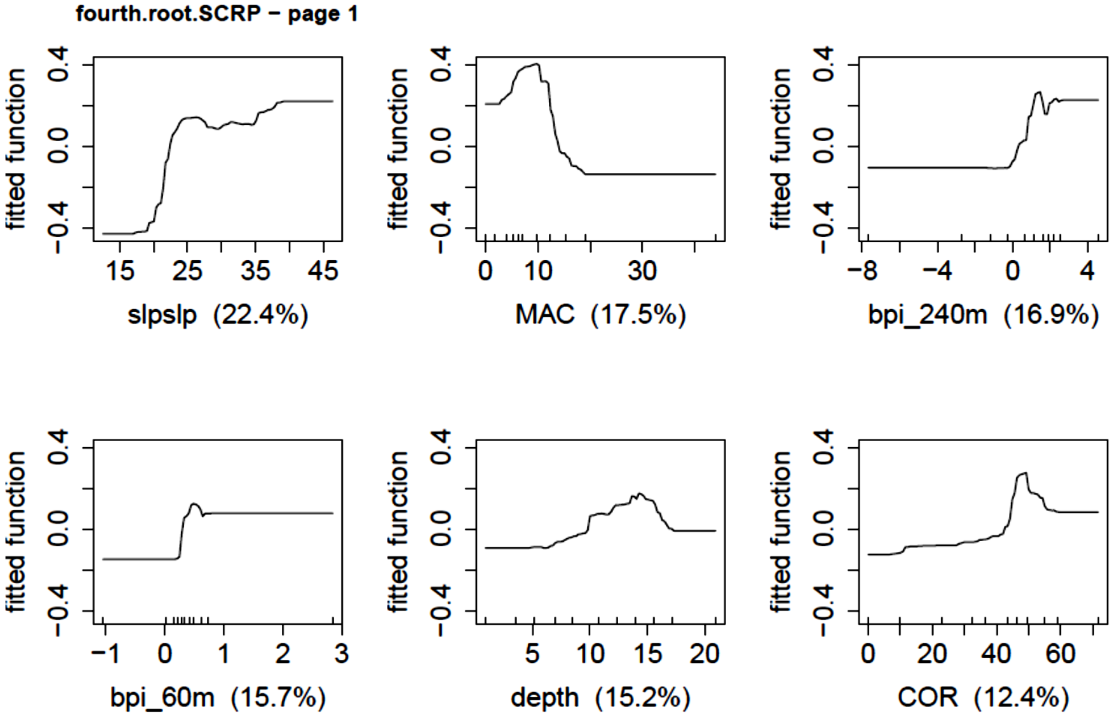


Figure S4.2. Response curves of benthic indicators.


fourth.root.BROW − page 1
fitted function
0.4
0.0
−0.4
0
5
15
25
CCA (18.8%)
0
20
40
60
COR (14.5%)
15
25
35
45
slpslp (13.7%)
70
90
110
130
asp_sd (13.6%)
0
10
30
TUR (13.5%)
0
10
30
TSS_T0 (13.3%)
−8
−4
0
4
bpi_240m (12.7%)


fourth.root.GRDT – page 1
fitted function
−0.3
0.0
0.3
0.0
0.4
0.8
contig_mn (21.1%)
0
20
40
60
COR (20.8%)
0
10
30
MAC (18.8%)
−8
−4
0
4
bpi_240m (15.7%)
0
10
30
TSS_T0 (12.2%)
−1
0
1
2
3
bpi_60m (11.3%)


fourth.root.SCRP – page 1
fitted function
−0.4
0.0
0.4
15
25
35
45
slpslp (22.4%)
0
10
30
MAC (17.5%)
−8
−4
0
4
bpi_240m (16.9%)
−1
0
1
2
3
bpi_60m (15.7%)
5
10
15
20
depth (15.2%)
0
20
40
60
COR (12.4%)

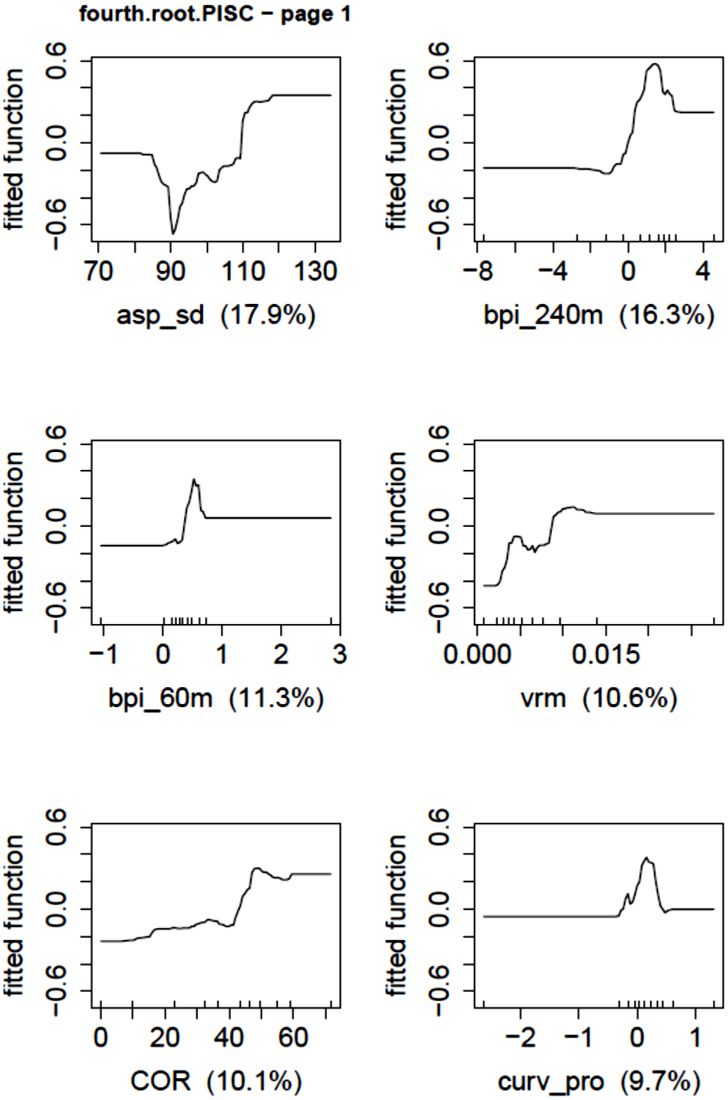
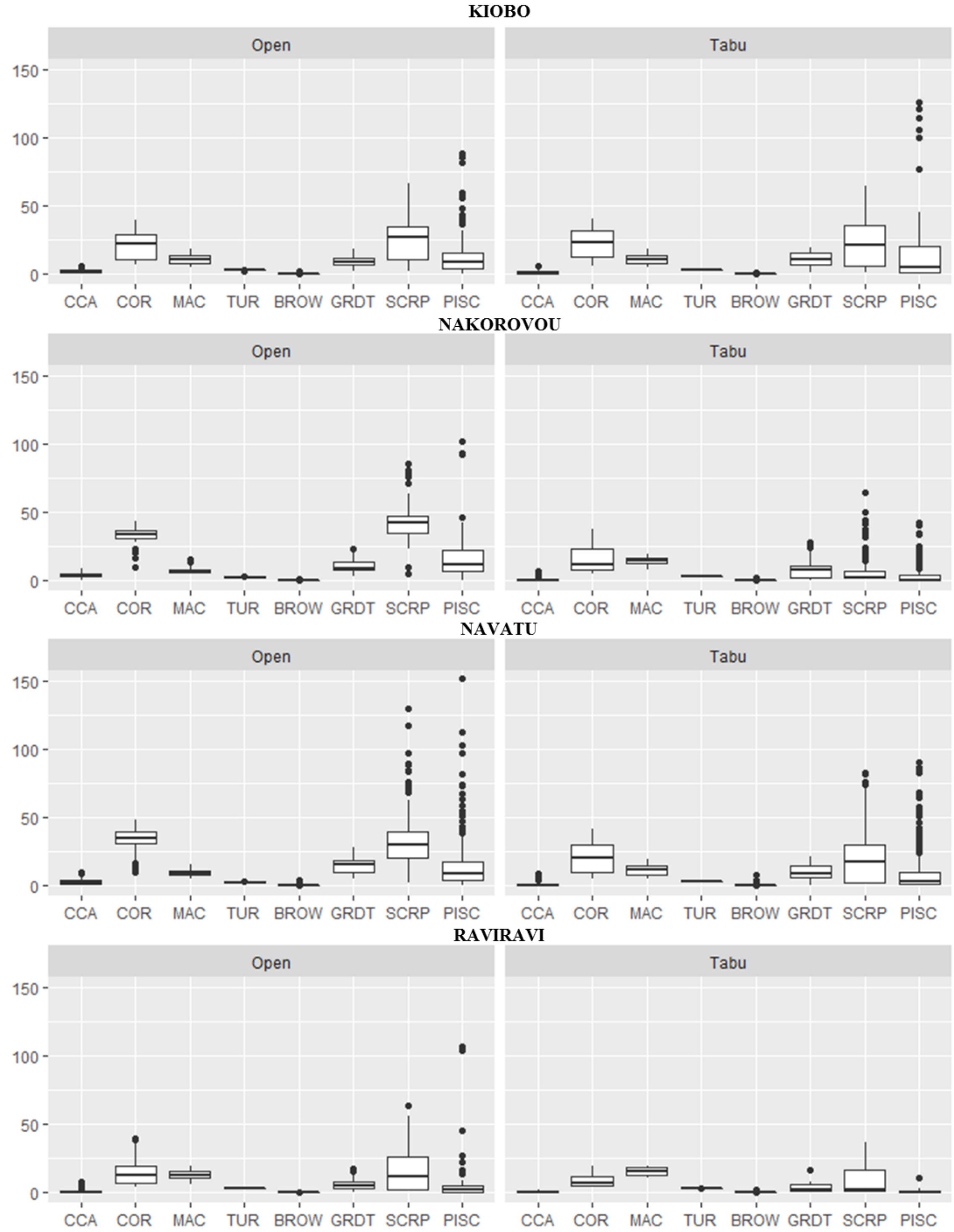


Figure S4.3. Response curves of fish indicators.



KIOBO

NAKOROVOU

NAVATU

RAVIRAVI

Figure S4.4. Boxplots of coral reef indicators values for Present by fishing ground per village. Benthic indicators (Crustose coralline algae [CCA], coral [COR], macroalgae [MAC], turf algae [TUR]) are expressed in % cover and resource fishes (browsers [BROW], grazers and detritivores [GRDT], scrapers [SCRP], and piscivores [PISC]) are expressed in kg/ha.

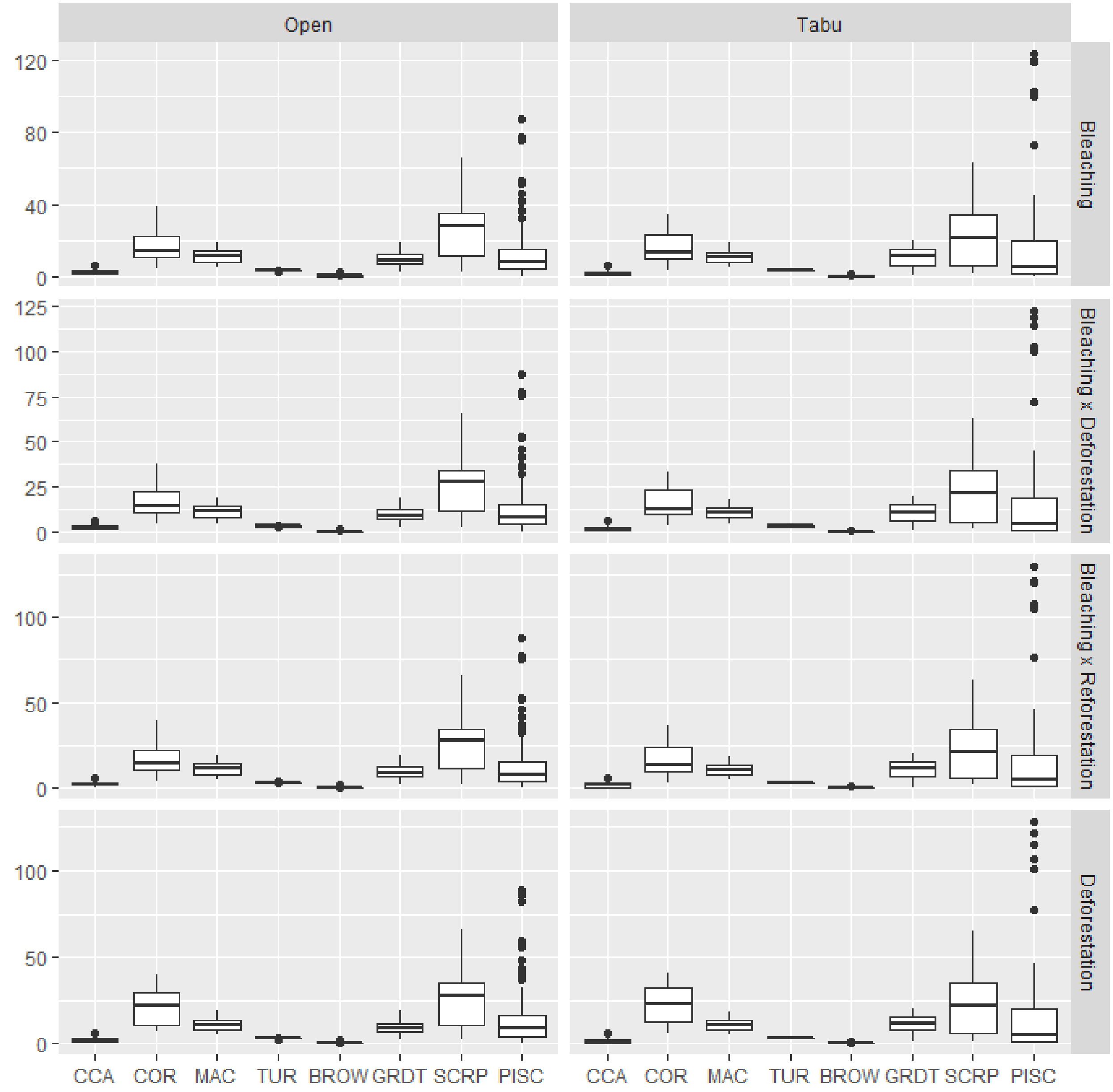


Figure S4.5. Coral reef indicators abundance percent change from present conditions in Kiobo open (left) and tabu (right) areas per scenario. Extreme climate change scenarios (bleaching), forest cover change scenarios (deforestation and reforestation) and their combination are shown.

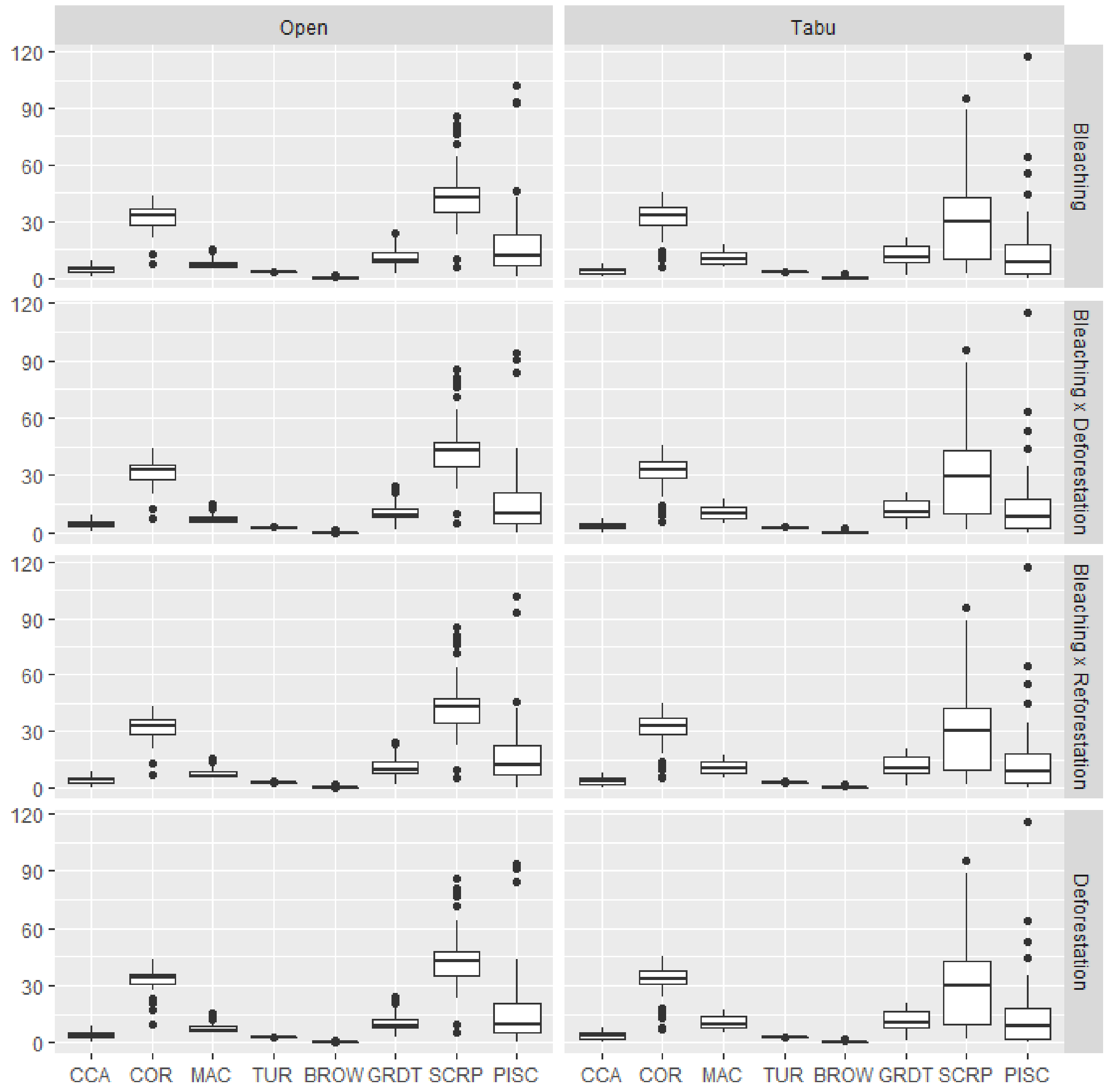


Figure S4.6. Coral reef indicators percent abundance change from present conditions in Nakorovou open (left) and tabu (right) areas per scenario. Extreme climate change scenarios (bleaching), forest cover change scenarios (deforestation and reforestation) and their combination are shown.

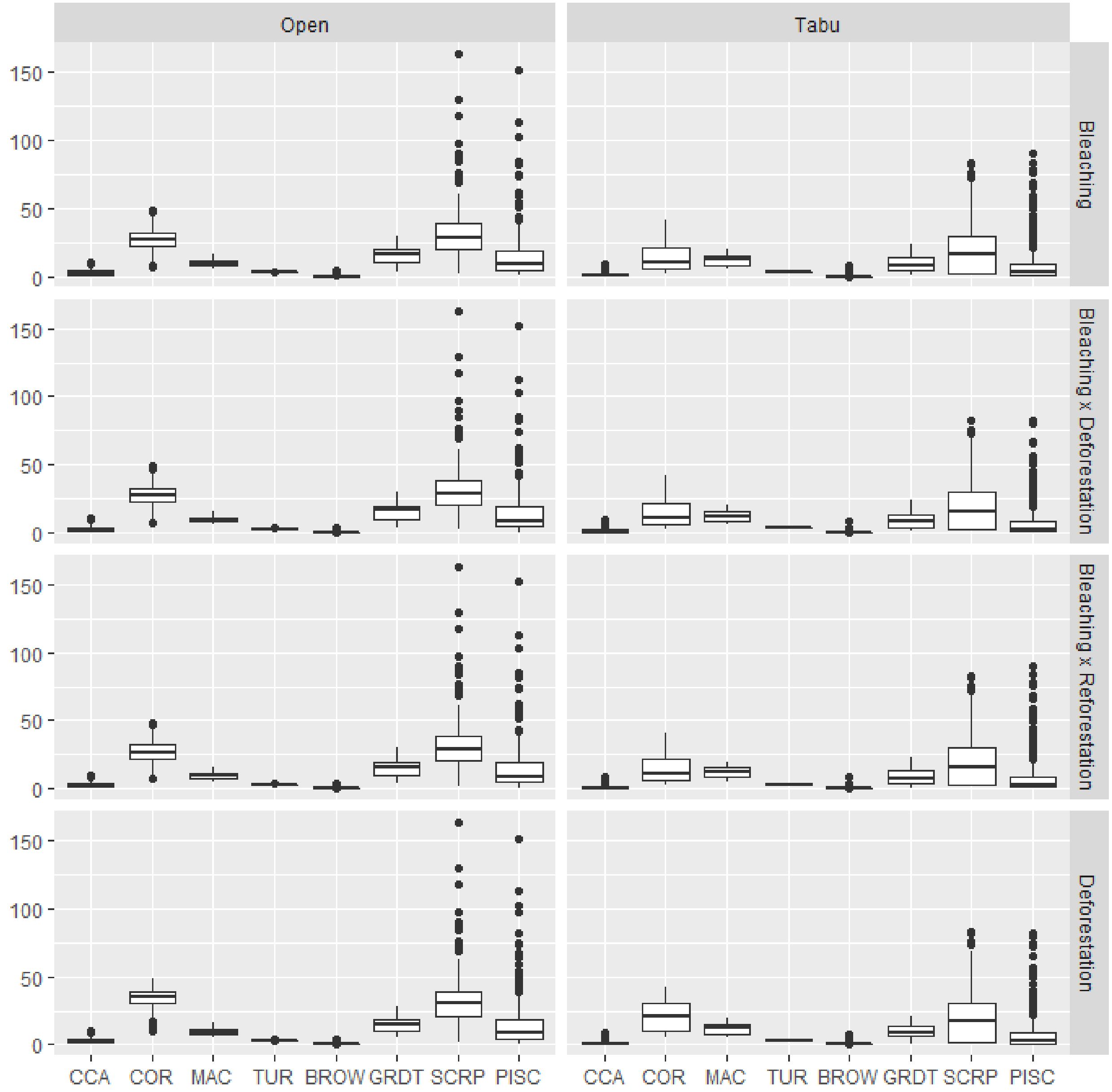


Figure S4.7. Coral reef indicators abundance percent change from present conditions in Navatu open (left) and tabu (right) areas per scenario. Extreme climate change scenarios (bleaching), forest cover change scenarios (deforestation and reforestation) and their combination are shown.

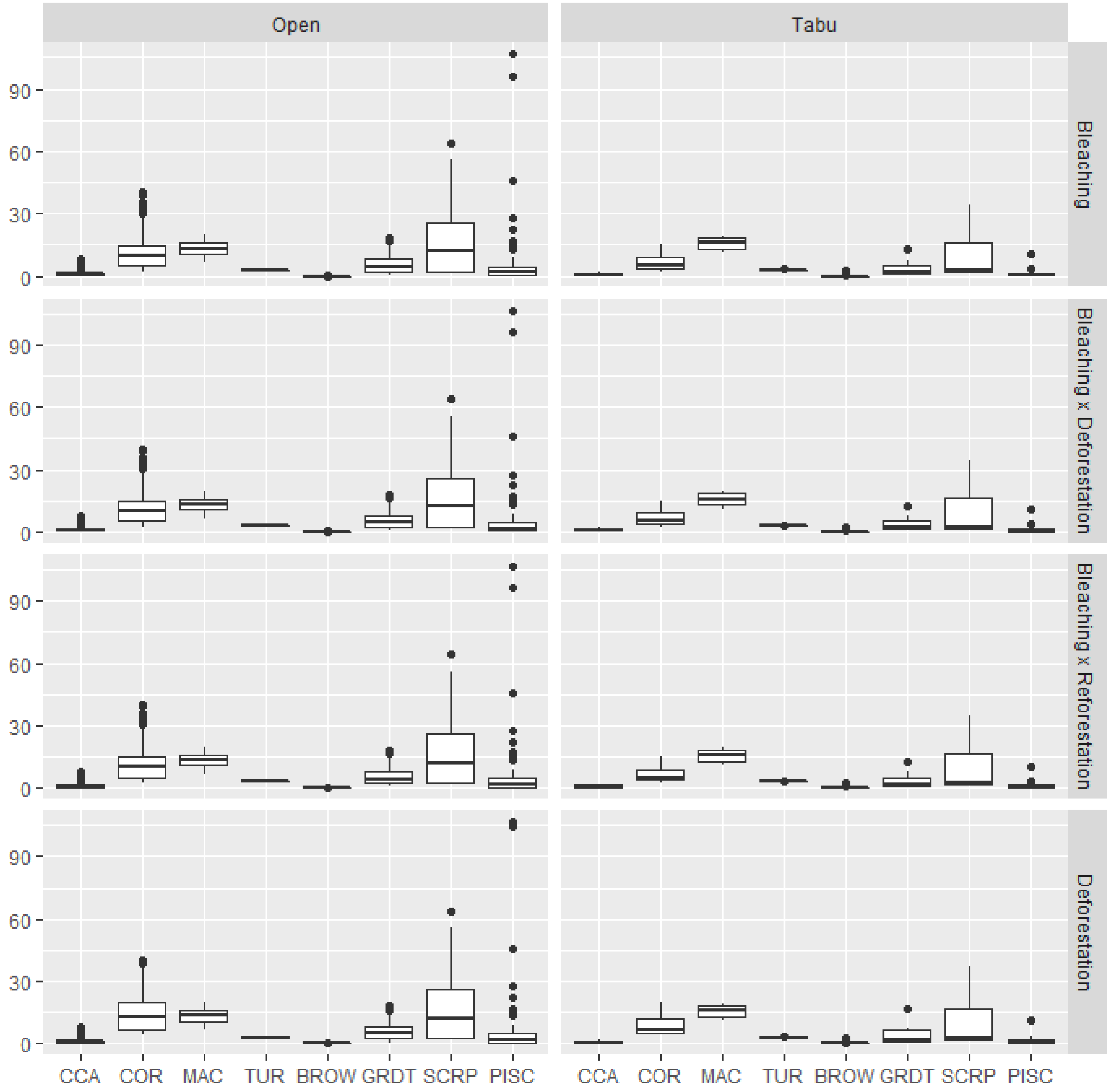


Figure S4.8. Coral reef indicators abundance percent change from present conditions in Raviravi open (left) and tabu (right) areas per scenario. Extreme climate change scenarios (bleaching), forest cover change scenarios (deforestation and reforestation) and their combination are shown.

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CHAPTER 5. CONCLUSION

There is a large body of literature arguing that land and sea linkages are important factors influencing the dynamics of coral reefs and the resilience of these ecosystems (Alvarez-Romero et al. 2011, Gurney et al. 2013, Jupiter et al. 2017, Klein et al. 2010), however, very few practical examples demonstrate how to operationalize ridge-to-reef concepts into marine conservation planning. This is partly because land-sea connections can take multiple pathways and forms, which makes observation and tractability challenging for scientists, and hinders managers from making informed decisions (Alvarez-Romero et al. 2011, Makino et al. 2013). This study has developed the first ridge-to-reef modeling framework that links land-based activities to coral reef ecological outcomes at fine spatial resolution for high oceanic islands.

Uncertainty is inherent to modeling complex systems (Reichert & Borsuk 2005) and arises at all stages of the modeling process (Gurney et al. 2013). A predictive model calibrated for current conditions can be used to forecast potential species distribution and abundance at another point in time (Franklin 2010), but requires a number of assumptions. One of the foremost assumptions associated with predicting futures is that species distributions are in equilibrium with current conditions and the identified relationships will not change over time (DeAngelis & Waterhouse 1987, Franklin 2010), which may not always be true (Carpenter 2002). For example, evidence is emerging that corals may acclimatize to predicted increases in SST associated with climate change (Baker et al. 2008). “Static” modeling approaches also do not account for species dispersal, migration, and interactions within the seascape (Guisan & Thuiller 2005, Stamoulis & Delevaux 2015) and therefore do not provide information on recovery trajectories of impacted ecosystems (Gurney et al. 2013, Melbourne-Thomas et al. 2011), which can influence management scale and outcomes (Toonen et al. 2011).

In addition, imperfect knowledge of the effects of human drivers and how coral reefs will respond to these drivers means that scenario modeling requires simplifications and assumptions which lead to further uncertainty in model projections (Coreau et al. 2009). By using present condition as the baseline for comparing projected coral reefs, scientists and managers need to recognize that this comparative benchmark represents ecosystems already subject to human impacts (e.g., fishing pressure and land-based source pollution) (Knowlton & Jackson 2008). However, comparing to present conditions still provides an opportunity to identify the trajectory of coral reef communities and fisheries under different human drivers and provide guidance for management (Alagona et al. 2012). In addition, projecting the distribution of species based on assumptions about current habitat suitability, inevitably translates to uncertainty in the associated projections. Therefore, sources of uncertainty in scenario analysis are inevitable. However, predicting the exact future state of coral reefs under each scenario was not our objective and is not necessary to achieve effective management outcomes (Gurney et al. 2013). Instead, we used scenario modeling to illustrate the range of possibilities for the future of coral reefs and identify trends that indicate whether coral reef and biocultural resources may be at risk (Coreau et al. 2009).

In terms of management implications, this research identified three important lessons. First, ridge-to-reef systems differ along a gradient of natural disturbance regimes. Places more exposed to natural disturbances are more resilient to local and global drivers (Hāʻena and Raviravi), compared to places sheltered from natural disturbances (Kaʻūpūlehu and Navatu). Second, ridge-to-reef management can confer resilience to coral reefs. In places exposed to natural disturbances, it is important to protect key habitats such as nurseries and maintain water and habitat quality to promote recovery post-disturbances (Hāʻena and Nakorovou). In places sheltered from natural disturbance, it is important to protect habitat removed from local and global drivers influence, such as deep-water refuges, and protect water quality and key herbivores to promote resistance to disturbances (Kaʻūpūlehu and Navatu). Lastly, size and geological history of oceanic islands influences the ridge-to-reef connections. In larger and geologically diverse oceanic islands, land and sea connections are spatially complex (Hawaiʻi vs Fiji).

This research demonstrated that this novel ridge-to-reef modeling framework is applicable to places driven by very different disturbances regimes while also being easily transferable to geologically different places. By adapting and transferring this framework from non-point source groundwater linkages in Hawaiʻi to point source sediment discharge in Fiji, this study illustrated the flexibility and transferability of this decision support tool. This framework is not a data intensive modeling tool and can also be used to calibrate more complex biophysical models (e.g., MARXAN, CORSET). The application of this tool in Hawaiʻi and Fiji confirmed the utility of fine scale spatial models that can estimate future ecosystem structure under alternative management and climatic scenarios (Guisan & Thuiller 2005, Gurney et al. 2013, Thrush et al. 2009) for islands across the Pacific and Oceania. Given existing resources, time and knowledge limitations, this information can help select management actions, which are relevant to the local context.

This study demonstrated how spatially explicit tools that couple coral reef social and ecological systems at fine spatial resolution, while linking land and sea processes, can support ridge-to reef management and help understand the impact of cumulative human drivers on coral reef resilience. These types of models can help identify drivers of coral reef degradation and consequently provide guidance on appropriate management actions, as well as identify where they could be most effective (Franklin 2010, Stamoulis & Delevaux 2015). Locally developed models, such as those developed here, offer a critical and much needed opportunity for aiding local-scale and place based management of coral reefs in high oceanic island environments.

Finally, this research demonstrated that linkages between people and nature along the ridge-to-reef continuum are critical for informing resilience management. The spectrum of natural disturbances shaping oceanic island environments can interact in various ways with human drivers. When accounting for the geological history, natural disturbance regime, and habitats unique to each place, ridge-to-reef management can promote coral reef resilience in a changing climate.

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